

**TAXONOMY, FISHERY, BIOLOGY AND POPULATION DYNAMICS OF
PLESIONIKA SEMILAEVIS ALONG THE SOUTHWEST COAST OF INDIA**

Thesis submitted to
Cochin University of Science and Technology



in partial fulfilment of the award of the degree of
Doctor of Philosophy
Under the Faculty of Marine Sciences

by
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भारतीय कृषि अनुसंधान परिषद्
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कृषि अनुसंधान एवं शिक्षा विभाग, कृषि मंत्रालय, भारत सरकार।

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This is to certify that the thesis entitled “**Taxonomy, fishery, biology and population dynamics of *Plesionika semilaevis* along the southwest coast of India**” is a bonafide research carried out by Ms. Sreelakshmy S (Reg. No 6128) under my guidance and supervision for the Ph.D. degree in Marine Sciences of the Cochin University of Science and Technology and that no part thereof has been presented for the award of any other degree in any University. Further certified that all relevant corrections and modifications suggested during the presynopsis seminar and recommended by the Doctoral Committee have been incorporated in the thesis.

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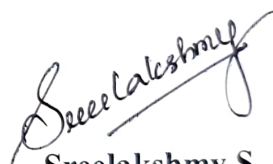
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Declaration

I hereby declare that the thesis entitled “**Taxonomy, fishery, biology and population dynamics of *Plesionika semilaevis* along the southwest coast of India**” is a record of original and bonafide research carried out by me under the supervision and guidance of Dr. Rekha Devi Chakraborty, Principal Scientist, Shellfish Fisheries Division, ICAR-CMFRI and that no part thereof has been presented for the award of any other degree in any University. Wherever the work described is based on the findings of other researchers, due acknowledgement is made in keeping with the general practice of reporting scientific observations.

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13.01.2025


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Abbreviations

μ	:	micron
μg	:	microgram(s)
μl	:	microliter(s)
μM	:	micro molar
AMOVA	:	Analysis of molecular variance analysis
ANOVA	:	Analysis of Variance
AOAC	:	Association of Official Analytical Chemists
BLAST	:	Basic local alignment search tool
bp	:	base pair
°C	:	degree Celsius
CL	:	Carapace Length
CMFRI	:	Central Marine Fisheries Research Institute
COI	:	Cytochrome oxidase I
DNA	:	Deoxyribonucleic acid
EEZ	:	Exclusive Economic Zone
GaSI	:	Gastro-Somatic Index
GSI	:	Gonado-Somatic Index
ICAR	:	Indian Council of Agricultural Research
K2P	:	Kimura-2-parameters
m	:	meters
MEGA	:	Molecular evolutionary genetics
mg	:	milligram(s)
min	:	minute(s)
ML	:	Maximum likelihood
ml	:	millilitre(s)
mM	:	milli molar
MNHN	:	National Museum of Natural History

MPEDA	:	Marine Products Export Development Authority
mtDNA	:	Mitochondrial Deoxyribonucleic Acid
NCBI	:	National Centre for Biotechnology Information
ng	:	nanogram(s)
PCA	:	Principal Component Analysis
PCR	:	Polymerase chain reaction
PERMANOVA	:	Permutational Multivariate Analysis of Variance
pH	:	Hydrogen ion concentration
RNA	:	Ribonucleic Acid
S	:	Svedberg's unit
sec	:	second(s)
TL	:	Total Length
WoRMS	:	World Register of Marine Species

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General introduction and review of literature

<i>Contents</i>	1.1. <i>General Introduction</i>
	1.2. <i>Review of Literature</i>
	1.3. <i>Objectives of the Study</i>

1.1 General Introduction

Fisheries are integral to India's agricultural sector, providing employment, nutritional security, raw materials for industries, and substantial export revenue. The country has a coastline of about 8,129 kilometers along the Arabian Sea and Bay of Bengal and a vast Exclusive Economic Zone (EEZ) covering 2.02 million square kilometers. India's EEZ grants rights and responsibilities for sustainable marine resource management up to 200 nautical miles. Oceanographic differences between coasts influence productivity, with monsoon-driven upwelling on the southwest coast fostering higher primary productivity compared to the southeast coast. The west coast of India contributes approximately 60-65% of the total marine fish landings in the country, as it encompasses highly productive zones like the southwest and northwest coasts. The southwest coast alone accounts for about 31.7%, supported by nutrient-rich upwelling zones (Vivekanandan et al. 2003) highlighting its importance to the fisheries sector.

India's total fish production increased significantly from 0.75 million tonnes in 1950-51 to 14.16 million tonnes in 2019-20, reflecting an average annual growth rate of approximately 8%. Of this total, about 74% originated from inland fisheries, while the remaining 26% was derived from marine capture fisheries (Shyam and Anuja, 2022). The country's estimated fisheries potential is 22.31 million metric tonnes, with marine fisheries accounting for 5.31 million metric tonnes and inland fisheries contributing 17 million metric tonnes (2018

estimates) (Shyam and Anuja, 2022). The Indian marine fishing sub-sector contributes about 1% to the national Gross Domestic Product (GDP). It plays a vital role in the rural coastal economy by supporting income generation, providing job opportunities, and ensuring food security for approximately 3.52 million people. This sector is active along the country's 11000 km coastline, spanning eight maritime coastal states and two union territories.

Crustaceans are highly valued in the global seafood trade, accounting for about 22.8% of the trade's total value (FAO, 2022). In India, shrimps hold significant economic importance due to their high export value. Deep-sea shrimps, in particular, are a major crustacean resource and contribute greatly to India's export market (Mohamed and Suseelan, 1973; Suseelan, 1974; Radhika et al. 2011; Shanis et al. 2014). One distinguishing feature between deep-sea and inshore prawns is their coloration—deep-sea prawns are noted for their bright red color, whereas inshore prawns typically have a muddy hue. These deep-sea prawns are found in the upper continental shelf and slope along the Indian coast, typically at depths of 200 to 800 meters, and represent a potential fishing ground estimated at about 5,000 tonnes (Suseelan, 1996). The history of deep-sea shrimp studies in Indian waters dates back to the 20th century, with records stemming from the surveys conducted by the RIMS Investigator. Government-led exploratory and experimental deep-sea fishing operations were carried out off the Bombay-Saurashtra coast and in the Bay of Bengal by the Government of India and West Bengal, respectively.

Approximately 80% of deep-sea shrimp trawling activities are concentrated along the southwest coast. Deep-sea shrimps chiefly belonging to the Families Pandalidae, Solenoceridae, Crangonidae, Penaeidae, Acantheephyridae, Sergestidae, Aristeidae, Glyphocrangonidae, Hippolytidae, Oplophoridae,

Pasiphaeidae, Sicyoniidae, and Stylodactylidae, have been documented from the southern areas of the west coast (Chakraborty et al. 2023). Trawling on the southwest coast of India occurs all year round, with the exception of the monsoon ban period. There are two primary types of trawling operations based on the target species and fishing depth. The first type focuses on *Aristeus alcocki*, known locally as "red ring," and occurs at depths exceeding 300 meters. The second type targets a diverse range of deep-sea shrimp species, which include both pandalids and other types of penaeid shrimp, within a depth range of 170–300 meters. These operations play an essential role in supporting local fisheries and contributing to the region's seafood industry.

Deep-sea fishing practices in Kerala began at Sakthikulangara, where substantial quantities of deep-sea shrimps, locally referred to as Pullan Konju, were harvested off the Kollam coast. Deep-sea shrimps were also brought ashore at fishing harbors in Kochi, Munambam, and Neendakara. Sakthikulangara harbor has since become the central hub for deep-sea shrimp landings in Kerala, while harbors in Kochi have experienced a notable decline. This shift is attributed to logistical challenges, market dynamics, the concentration of shrimp-exporting companies in Sakthikulangara, and the proximity to productive fishing grounds such as the Quilon Bank.

Crustacean resources made up 7.7% of Kerala's total marine fish landings, with an estimated catch of 48,784 tonnes. Penaeid shrimps accounted for approximately 79% of this total, followed by crabs (13%) and non-penaeid shrimps (8%). Relative to the preceding year, there was an 8.3% increase in penaeid shrimp landings and a remarkable 20-fold rise in non-penaeid shrimp catches in 2023 (CMFRI, 2023). Deep-sea shrimp landings in Kerala were reported at 6,940 tonnes, with penaeids constituting 45% and non-penaeids making up 55% (3,830 tonnes). During 2023, the majority of these deep-sea shrimp landings were recorded in Kollam (97.3%), with Ernakulam contributing

the remaining 2.7% (CMFRI, 2023). Targeted deepsea shrimp fishery includes a few species like *Metapenaeopsis andamanensis*, *M. coniger*, *A. alcocki*, *Heterocarpus chani*, *H. woodmasoni*, *Plesionika quasigrandis*, and *P. semilaevis* (CMFRI, 2008; 2014; 2015; 2016). The annual average landings of deep-sea shrimp in Kerala amounted to approximately 9,186 tonnes during 2013–2020, with MDTN contributing 98% of the total catch, followed by MTN (Chakraborty et al. 2022a). From 2007 to 2020, the species composition was dominated by *M. andamanensis* (27.6%), followed by *A. alcocki* (20%), *P. quasigrandis* (19.9%), *H. chani* (17.6%), *H. woodmasoni* (9.4%), *P. semilaevis* (1.23%), *Penaeopsis jerryi* (0.8%), and *Solenocera hextii* (0.07%) in the deep-sea shrimp catches (Fig. 1.1) (Chakraborty et al. 2022a).

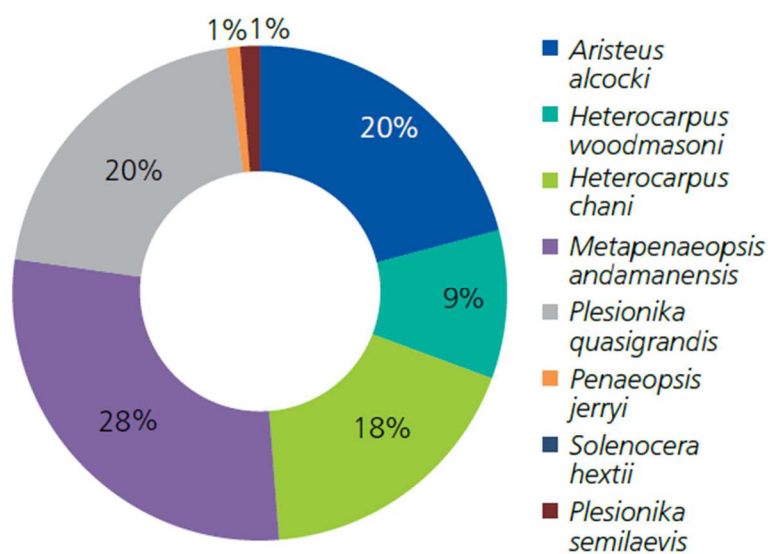


Fig. 1.1. Deep-sea shrimp composition of Kerala during the period 2007-2020 (Source: Chakraborty et al. 2022a)

In 2019-20, marine product exports reached 12.9 lakh metric tons, generating a revenue of ₹46,662.85 crore (USD 6.68 billion). Over the past decade (2010-11 to 2019-20), the sector has demonstrated an average annual growth rate of 6.13% in export quantity and 15.47% in export value

(Shyam and Anuja, 2022). In the fiscal year 2022-23, India's seafood exports reached 17,35,286 tonnes, valued at ₹63,969.14 crore (\$8.09 billion). Frozen shrimp was the leading export item, both in terms of volume and revenue. The United States and China emerged as the primary importers of Indian seafood, with the U.S. being the top buyer by value and China following closely, especially for shrimp products (MPEDA, 2022-23).

Deep-sea shrimps are not only economically significant but also a valuable source of essential nutrients. They are rich in omega-3 polyunsaturated fatty acids, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which contribute to heart health and other benefits. Additionally, deep-sea shrimps provide essential amino acids and carotenoids that offer antioxidant properties, enhancing their nutritional appeal. These attributes boost their demand in both domestic and international markets. The global increase in shrimp consumption, driven by the nutritional advantages and the growing human population, highlights the importance of shrimp fisheries to India's economy (Radhika et al. 2011; Mohamed and Suseelan, 1973).

The genus *Plesionika* Spence Bate, 1888, a member of the deep-sea pandalid shrimp family, is highly diverse, comprising over 100 described species (WoRMS, 2024). Although it is the most diverse group within deep-sea shrimp resources, there is a notable lack of research focusing on *Plesionika* in the Indian Exclusive Economic Zone (EEZ). Misidentification has been an issue with several species in Asian waters. For instance, *P. ocellus* reported by Chace (1985) was later corrected as *P. sindoi* (Chan and Crosnier, 1997). In Indian waters, *P. quasigrandis*, a prominent species of *Plesionika*, was previously identified as “*Parapandalus* (or *Plesionika*) *spinipes*” (Shanis et al. 2012; Chakraborty et al. 2015).

The commercial deep-sea caridean shrimp *P. semilaevis* (previously misidentified as *P. martia*) has long been recorded from India and constitutes an important species of deep-sea shrimp catches on the southern coast of India. Research on this deep-sea caridean shrimp is relatively limited, with no available data on its feeding ecology, reproductive parameters, biochemical composition, or population dynamics in Indian waters. Therefore, this study aims to bridge these knowledge gaps which could contribute significantly to the understanding and management of this species in Indian waters.

1.2 Review of Literature

Integrative taxonomy and diversity

Table 1.1. Temporal taxonomic research on deep-sea shrimp across oceanic regions

Area of Study	Contributions
Atlantic and Pacific Oceans	Dana (1852, 1855), Bate (1881, 1888), Milne-Edwards (1881, 1883), Smith (1882, 1884), Faxon (1896), Alcock and Anderson (1894), Milne-Edwards and Bouvier (1900, 1909), Alcock (1901, 1906), Kemp (1906, 1909), Calman (1909, 1923, 1925), De Man (1911, 1920), and Allen (1966)
Mediterranean waters	Calman (1909,1923,1925), Coutiere (1905), Maurin (1963), Alvarez (1968)
American and Mexican waters.	Faxon (1893, 1895), Rathbun (1906), Bullis (1956), Bullis and Rathjen (1959), Chace (1936), Anderson and Lindner (1971), Chace (1992)
Indian Ocean	Wood-Mason (1873), Wood-Mason and Alcock (1891, 1893), Alcock and Anderson (1894, 1899), Alcock (1901), Lloyd (1907), Kemp (1925), John and Kurien (1959), Kurien (1964, 1965), George (1966), George and Rao (1966), Rao and Suseelan (1967), Mohamed and Suseelan (1973), Suseelan (1974, 1985), Thomas (1979), Suseelan and George (1990), Bhargava et al. (1994), and Ganga et al. (2012).

Table 1.1 describes significant contributions to the taxonomy and research of deep-sea shrimp across different oceanic regions over time. The study of deep-sea crustaceans in Indian waters began in the 20th century, primarily based on specimens collected by the Royal Indian Marine Survey ship (RIMS) Investigator. These surveys led to the description of numerous new species from the Bay of Bengal, Arabian Sea, and Andaman Sea. A significant contribution was made by Alcock (1901), who cataloged 117 species of deep-sea crustaceans, including 85 species of shrimp, from collections made during the period 1885-1900. Following these early studies, the deep-sea crustacean diversity of Indian waters received limited further research and documentation. Later insights into the distribution and abundance of these species were provided through exploratory surveys conducted by institutions such as the Central Marine Fisheries Research Institute, Fishery Survey of India, Centre for Marine Living Resources and Ecology, and the Indo-Norwegian Project.

John and Kurian (1959) and Kurian (1964) documented the deep-sea lobsters and shrimps along the Kerala coast, contributing valuable data on the composition and distribution of species. George (1966) and George and Rao (1966) reported on deep-water decapod crustaceans in the offshore waters of the southwest coast of India. Silas (1969), Mohamed and Suseelan (1973), and Suseelan (1974) described the distribution and abundance of deep-sea prawns using data from exploratory research vessels such as CONCH, KALAVA, VARUNA, KLAUS SUNNANA, TUNA, and VELAMEEN.

Suseelan (1974) investigated the fauna of deep-sea pandalid shrimps off the southwest coast, while Thomas (1979) focused on the deep-sea decapods of the Gulf of Mannar. Oommen (1980) reported on the exploratory survey carried out in the Gulf of Mannar and Quilon Bank regions. Suseelan et al. (1989) provided an account of deep-sea crustaceans off the southwest coast based on data collected by FORV *Sagar Sampada*. James and Pillai (1990) offered insights into

crustaceans and fishes in deep-sea waters from surveys conducted between 1985 and 1988. Bhargava et al. (1994) highlighted the occurrence and range of deep-sea shrimps during the 1990-1994 period, based on foreign fishing vessel operations. Jayaprakash et al. (2006) described the distribution and prevalence patterns of deep-sea fishes and crustaceans from the southwest coast as documented by FORV *Sagar Sampada*. Suseelan and George (1990) and Ganga et al. (2012) reported the distribution and taxonomic details of the deep-sea shrimp, *Aristaeopsis edwardsiana*, off the coast of Trivandrum.

Molecular phylogenetics has become a significant method in modern taxonomy, integrating genetic and molecular data with statistical analysis to infer the evolutionary relationships among organisms (Nezhad et al. 2013). This approach enables researchers to address taxonomic ambiguities and precisely distinguish between individuals, populations, or species based on their genetic makeup. DNA barcoding, in particular, has been instrumental in differentiating species and identifying cryptic ones, leveraging highly conserved regions of mitochondrial DNA such as the Cytochrome c oxidase subunit I (COI) gene and the 16S rRNA gene. These genes are especially valuable in fish phylogenetics due to their conservation across species, which aids in recognizing closely related species and detecting mislabelling in market samples (Santos et al. 2003; Vinson et al. 2004).

The use of COI for DNA barcoding has become a standard practice because of its effectiveness in distinguishing between congeneric species, where COI divergence typically exceeds 2%, compared to intraspecific variation, which remains below 1% (Hebert et al. 2003). While molecular research on deep-sea shrimps within the order Decapoda remains limited, some studies have used mitochondrial and nuclear genes for phylogenetic analysis. Bracken et al. (2009) explored the family-level relationships among deep-sea shrimp species using 16S and 18S rRNA genes.

Integrative studies have further enriched molecular taxonomy, combining genetic data with morphological or ecological information. Notably, Paramasivam et al. (2019) performed a significant study on the deep-sea shrimps off India's southern coast using mitochondrial markers for species identification, contributing to a deeper understanding of species diversity and distribution. Such studies have broadened the molecular knowledge base and refined taxonomic classifications, ultimately aiding in biodiversity monitoring and conservation efforts.

Plesionika species are caridean shrimps, characterized by both sides of the pleura of the second somite of the abdomen extending over the first and third somites. The existence of *Plesionika* spp. has been reported mainly in Japan, Korea, China, Taiwan, Philippines, Indonesia, India, and from few other countries (Chan and Crosnier 1991, 1997; Company and Sarda, 1997; Ahamed and Ohtomi, 2011). Ahamed et al. (2017) provided an important taxonomic key for identifying 45 *Plesionika* species found in Asian waters. This work offered comprehensive insights into the genus *Plesionika*, focusing on their distribution and distinguishing features within the region. The genus *Plesionika* is highly speciose and includes many species groups such as *P. narval*; *P. martia*; *P. rostricrescentis* and *P. ocellus* groups. The genera *Plesionika* is represented by *P. alcocki*, *P. bifurca*, *P. ensis*, *P. martia*, *P. ocellus*, *P. quasigrandis*, *P. unidens*, *P. sindoi*, *P. williamsi*, *P. adensameri* and *P. longicuda*, *P. narval*, *P. reflexa*, *P. semilaevis*, *P. persica* in Indian waters (Shanis et al. 2012; Radhakrishnan et al. 2012; Chakraborty et al. 2015; Chan et al. 2018; Kuberan et al. 2020; Chakraborty and Ganesan 2021). Misidentification of species has been a significant issue in the taxonomy of *Plesionika* species. For example, *Plesionika ocellus*, reported by Chace (1985), was later revised to *Plesionika sindoi* by Chan and Crosnier (1997). In Indian waters, *Plesionika quasigrandis* was previously misidentified as “*Parapandalus* (or *Plesionika*) *spinipes*” (Shanis et al. 2012; Chakraborty et al. 2015). Kuberan et al. (2017) highlighted that earlier records of *P. martia* in the

southwestern region of India were actually misidentifications of *P. semilaevis*, which was further supported by subsequent research (Kuberan et al. 2020; Chan et al. 2020). These examples underscore the critical role of integrative taxonomy, which combines genetic, morphological, and ecological data to achieve accurate species identification. This multifaceted approach is essential for resolving ambiguities within the genus *Plesionika*, aiding in clarifying species boundaries and enhancing our understanding of biodiversity in deep-sea environments.

Fishery

India is home to a diverse range of deep-sea penaeid and caridean shrimp species, encompassing families such as Pandalidae, Solenoceridae, Crangonidae, Penaeidae, Acantheephyridae, Sergestidae, Aristeidae, Glyphocrangonidae, Hippolytidae, Oplophoridae, Pasiphaeidae, Sicyoniidae, and Stylodactylidae. In 2023, the total deep-sea shrimp landings amounted to 6940 tons in Kerala. While these catches contributed a relatively small portion to the overall fisheries sector, there has been a noticeable upward trend in landings in recent years. India exported approximately 17,35,286 tons of seafood in 2022-23, generating a revenue of USD 8.09 billion. The United States and China emerged as the largest importer of Indian shrimp (MPEDA, 2022-23).

Initial research on deep-sea shrimp fisheries in India focused on commercial trawl landings along the Kerala coast, where early studies highlighted a diverse shrimp composition. Dominant species identified included *M. andamanensis*, *A. alcocki*, *S. hextii*, and *P. jerryi*, along with pandalid shrimp such as *H. gibbosus*, *H. woodmasoni*, and *P. quasigrandis* and *P. semilaevis* (Rajan et al. 2001; Nandakumar et al. 2001). The main fishing harbors along the southwest coast are Kalamuku, Sakthikulangara, and Colachel, while the southeast coast operates from harbors in Tuticorin, Nagapattinam, and Chennai.

Trawling operations are categorized into two main types based on target species and fishing depth. The first type targets *A. alcocki* (locally called "red ring") and occurs at depths greater than 300 meters. The second type is more general and involves fishing for a range of deep-sea shrimp species, including pandalids and other penaeids, at depths between 170 and 300 meters (Chakraborty et al. 2022a). The southwest coast predominantly contributes to deep-sea shrimp trawling, accounting for approximately 80% of operations, with fishing activities carried out from September to May, excluding the monsoon ban period. The deep-sea shrimp fishery in India presently targets seven dominant species found in the Arabian Sea and Bay of Bengal: *A. alcocki*, *H. chani*, *H. woodmasoni*, *M. andamanensis*, *P. quasigrandis*, *P. semilaevis*, and *S. hextii*. The genera *Plesionika* is represented by *P. alcocki*, *P. bifurca*, *P. ensis*, *P. martia*, *P. ocellus*, *P. quasigrandis*, *P. unidens*, *P. sindoi*, *P. williamsi*, *P. adensameri* and *P. longicuda*, *P. narval*, *P. reflexa*, *P. semilaevis*, *P. persica* in Indian waters (Shanis et al. 2012; Radhakrishnan et al. 2012; Chakraborty et al. 2015; Chan et al. 2018; Kuberan et al. 2020; Chakraborty and Ganesan 2021).

The Arabian Sea is a particularly significant region for deep-sea shrimp fisheries in India, but it exhibits variability in annual catches. These fluctuations are largely influenced by the presence of highly valued demersal fish and cephalopods. Understanding the current status of deep-sea shrimp fisheries is crucial for devising effective policies that promote sustainable management practices.

Feeding ecology

The feeding ecology of deep-sea organisms plays a critical role in understanding their contributions to ecosystem functioning. Identifying their interactions within the food chain is vital for determining ecological niche width (Bearhop et al. 2004). Examining diet composition and feeding behavior provides insights into growth rates, gonadal maturation, niche partitioning, habitat

preferences, predation, and prey selection. Aquatic organisms allocate a significant amount of their energy to foraging food. Food availability is regarded as a primary limiting factor in deep-sea ecosystems, with trophic interactions being central to the organization of deep-sea faunal communities (Jumars and Gallagher, 1982). Studies by Cartes and Abelló (1992) and Fanelli and Cartes (2004) noted a significant proportion of empty stomachs in deep-sea decapods, with feeding conditions fluctuating based on prey availability more than abiotic factors. Understanding the relationship between animals and their food sources, particularly preferred food items and their seasonal distribution, can assist in identifying potential feeding grounds, offering valuable information for resource prediction and exploitation (Muthiah, 1994).

Comprehensive research has been carried out on the feeding habits of economically significant deep-sea shrimps, like *A. antennatus* and *A. foliacea* (Cartes, 1994; Kapiris, 2004; Chartosia et al. 2005; Kapiris and Thessalou-Legaki, 2011). *Plesionika* species actively prey on benthic invertebrates and have varied diets, with dietary diversity being more pronounced in individuals living in shallower regions (Labropoulou and Kostikas, 1999). They are an essential prey for demersal fishes and cephalopods. Most *Plesionika* species are nektobenthic, feeding on both pelagic and benthic resources (Cartes et al. 1993; Cartes, 1998; Cartes et al. 2002; Fanelli and Cartes, 2004; Vafidis et al. 2005; Fanelli et al. 2007).

In some *Plesionika* species such as *P. ensis*, *P. heterocarpus*, and *P. martia* the major food items observed are detritus, crustacean remains, foraminiferan remains, fish remains, mollusc remains, sediments and sponge parts (Labropoulou and Kostikas, 1999; Fanelli and Cartes, 2004). Omori (1971) examined the feeding habits of *Pandalus kessleri* and *Plesionika izumiae*. Cartes et al. (1993) examined the diurnal and nocturnal feeding patterns and dietary composition of six species of deep-sea shrimp in the Catalan Sea. Labropoulou

and Kostikas (1999) conducted a comparative study on the food and feeding habits of *Plesionika ensis*, *Polycheles typhlops*, *Parapenaeus longirostris*, and *Plesionika heterocarpus*. Cartes (1998) explored the feeding strategies and food resource partitioning of deep-sea decapod crustaceans across various depths.

Fanelli and Cartes (2004) detailed the dietary composition and examined how environmental and biological factors influenced the feeding behaviors of *P. martia*, *P. heterocarpus*, *P. gigliolii*, and *P. edwardsii* in the Alboran Sea. Kitsos et al. (2008) identified the deep-sea shrimp *Plesionika narval* as an active predator and sporadic scavenger, that makes use of a diverse range of benthic resources. Significant variations in the diets of many *Plesionika* species have been observed concerning biological factors, environmental conditions, and geographical regions, particularly in the Mediterranean and West Africa (Fanelli and Cartes, 2004, 2008; Kitsos et al. 2008; Burukovsky, 2017; Bordbar et al. 2019).

In the Indian Ocean, limited studies have addressed the diet composition and feeding habits of deep-sea shrimps, with even less information available on *Plesionika* species. Preliminary data was provided on the feeding behaviors of *H. woodmasoni*, *H. gibbosus*, *Parapandalus spinipes*, *P. martia*, *P. ensis*, *Paniaeopsis philippi* and *P. rectacutus* (Kurian, 1965, Suseelan, 1974). Suseelan (1985) carried out a preliminary investigation of the gut contents of *H. gibbosus* and *H. woodmasoni* collected during exploratory fishery surveys off the southwest coast of India. A study on diet composition and prey selection of the penaeid shrimp *A. alcocki* and *M. andamanensis* in the Arabian Sea was conducted by Paramasivam et al. (2020) and Muralidharan et al. (2023) respectively. Studies on the relationship between feeding intensity and breeding periods of the deep-sea shrimps, *P. quasigrandis*, *H. gibbosus*, and *H. woodmasoni* were studied in the coasts of Kerala (Radhika, 2004; Radhika and Kurup, 2011; Shanis, 2014; Gayathri et al. 2023). There is currently no prior information available on the food and feeding habits of *P. semilaevis* in both Indian and global waters. Despite its widespread distribution, the feeding ecology of this species remains unexplored,

highlighting a significant gap in the understanding of its role in deep-sea ecosystems and trophic interactions.

Reproductive biology

Comprehensive knowledge of the reproductive biology of a species is a crucial step in providing scientific guidance on its resource management. The unique life-history traits of deep-sea organisms, such as longer life spans, slow growth rates, delayed sexual maturity, and low fecundity, make them particularly susceptible to overexploitation, with limited capacity for recovery (Cheung et al. 2005; Morato et al. 2006). The lack of comprehensive life-history data for exploited deep-sea species significantly hampers the creation and implementation of efficient fisheries management plans (Polidoro et al. 2008). Key variables like fecundity, sex ratio, gonadal stages, embryonic development, and reproductive periodicity are crucial for evaluating recruitment, reproductive potential, habitat-specific adaptations, biogeographic distribution, and connectivity of marine organisms (Chemel et al. 2023).

The family Pandalidae, comprising deep-sea shrimps predominantly found in tropical waters, exhibits diverse growth and reproductive patterns. Pandalid species, even within the same genus, display variations in sexual systems (e.g., gonochorism and hermaphroditism) and reproductive modes (e.g., semelparity and iteroparity), leading to significant diversity in their reproductive strategies (Correa and Thiel, 2003; Bauer, 2004). A distinguishing characteristic of many caridean shrimps is their significant energy investment in egg production (Wehrmann and Lardies, 1999). The nutrients and energy stored in eggs play a critical role in embryonic survival and development, influencing the life-history traits of invertebrates (Figueiredo et al. 2008).

While substantial information is available on the reproductive biology of *Plesionika* species in temperate and subtropical regions, significant knowledge

gaps persist in tropical waters. Omori (1971) conducted an extensive study on the reproductive and growth parameters of the caridean shrimp *P. izumiae* in Japanese waters. Thessalou-Legaki (1989) examined the life history parameters of *P. narval* in the central Mediterranean. Ohtomi (1997) investigated the reproductive patterns of *P. semilaevis* in Kagoshima Bay. Santana et al. (1997) examined the life history of *P. edwardsii* in the eastern-central Atlantic. Studies on reproductive parameters of species such as *P. edwardsii*, *P. heterocarpus*, *P. gigliolii*, *P. narval*, *P. martia*, and *P. acanthonotus* have been conducted in the Mediterranean Sea (Company and Sarda, 1997; Maiorano et al. 2002; Anastasopoulou et al. 2017). Chilari et al. (2005) investigated the reproductive parameters and population dynamics of *P. martia* in the eastern Ionian Sea. Possenti et al. (2007) focused on the reproductive biology of female *P. edwardsii* in the northern Tyrrhenian Sea. Ahamed and Ohtomi (2011) further explored the reproductive parameters of *P. izumiae* in Japanese waters. Possenti et al. (2007) studied the reproductive biology of *P. edwardsii* in the Tyrrhenian Sea, while Triay-Portella et al. (2017) provided a detailed study on ovarian maturity and egg development based on microscopic and macroscopic observation for three isolated populations (Madeira, the Canary Islands and Cape Verde Islands) of *P. edwardsii* in the eastern Atlantic.

Preliminary accounts of reproductive characteristics in deep-sea shrimps in Indian waters, including sex ratios, fecundity, and egg size, were given by Rao and Suseelan (1967), Mohamed and Suseelan (1973), Suseelan (1974), Rajan et al. (2001), and Thirumilu and Rajan (2003). Detailed studies on reproductive aspects of deep-sea caridean shrimps from Indian waters are restricted to a few species, *H. gibbosus*, *H. woodmasoni*, *A. alcocki*, and *P. quasigrandis* (Radhika, 2004; Shanis, 2014; Paramasivam et al. 2018; Gayathri and Chakraborty, 2024)

Despite growing economic interest in *Plesionika* species in Indian waters—where *P. semilaevis* and *P. quasigrandis* contribute 21% of the deep-sea

shrimp catch (Chakraborty et al. 2022a) data on their reproductive parameters remain scarce. The only available reproductive study on *P. semilaevis* is by Ohtomi (1997), which described brood size and reproductive periods in Kagoshima Bay. Comprehensive investigations into its gonadal and embryonic development from Indian waters or other regions are lacking. Understanding parameters such as ovarian maturation, embryo development, reproductive periodicity, and brood size is essential for fisheries management. These data facilitate estimating reproductive potential and recruitment, ensuring population stability (Mori et al. 1998; Figueiredo et al. 2008; Kevrekidis and Thessalou-Legaki, 2013).

Biochemical composition

Deep-sea shrimps have surfaced as important sources of essential nutrients, especially long-chain omega-3 polyunsaturated fatty acids (3-PUFAs), along with essential amino acids (Rosa and Nunes, 2004; Tsape et al. 2010). These nutrients contribute significantly to the nutritional profile of these marine organisms, making them important for human consumption. The taste, nutritional value, and health benefits of seafood, including deep-sea shrimps, are significantly influenced by their content of essential amino acids and fatty acids (Chen et al. 2007; Kuley et al. 2008). It is important to recognize that the biochemical composition of marine species is subject to variation due to a range of factors, such as body size, sex, sexual maturity, geographic location, diet, and environmental conditions (Wu et al. 2010; Wang et al. 2021; Muralidharan et al. 2023).

Studies by Karuppasamy et al. (2013) and Bhavan et al. (2010) have highlighted the relatively high protein content found in the edible parts of shrimp. The nutritional value of shrimp extends beyond its quality protein, as it is characterized by a lower lipid (fat) content and a higher proportion of polyunsaturated fatty acids (PUFAs), particularly the essential omega-3 fatty

acids, docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). These PUFAs are known for their significant role in reducing the risk of hypertension, inflammation, diabetes, and cancer (Chakraborty et al. 2016; Ramezani-Fard et al. 2016; Krishnan et al. 2021; Chakraborty et al. 2022b). Research has also shown that while shrimp are relatively high in cholesterol, consuming them as part of a diet rich in PUFAs and low in saturated fatty acids (SFAs) can help reduce cholesterol levels, thus supporting heart health (Sampaio et al. 2006).

Studies by Morais et al. (2002) examined lipid biochemistry changes during embryonic development in temperate caridean species, such as *P. martia*, *Palaemon serratus*, and *P. elegans*, highlighting the dynamic nature of their biochemical composition during growth. Oksuz et al. (2009) further studied the proximate, fatty acid, and elemental compositions of deep-sea shrimp species like *Parapenaeus longirostris* and *P. martia* from the northeastern Mediterranean Sea, emphasizing their varied nutritional properties.

Studies such as those by Banu et al. (2016) analyzed the muscle tissue of penaeid prawns, including *Penaeus monodon*, *P. indicus*, *P. semisulcatus*, *Litopenaeus vannamei*, *Metapenaeus monoceros*, and *M. dobsoni* off the Ramayapatnam coast, revealing important nutritional constituents. Additionally, Rao et al. (2016) analyzed the proximate composition and heavy metal accumulation in the muscles of deep-sea crustaceans like *Acantheephyra armata*, *H. gibbosus*, *P. spinipes*, and *Puerulus sewelli* from the Indian Exclusive Economic Zone (EEZ). Fernandez et al. (2018) conducted a comparative study on the nutritional composition of deep-sea shrimp species, including *A. alcocki*, *H. gibbosus*, *P. spinipes*, and *M. andamanensis*, comparing them to coastal shrimp-like *Fenneropenaeus indicus* and *P. monodon* from the southwest coast of India. Their findings provided further insights into the nutritional variations between deep-sea and coastal species.

The study by Krishnan et al. (2021) analyzed the fatty acid composition of deep-sea shrimp species, emphasizing the presence of essential omega-3 fatty acids like EPA and DHA and their implications for health and diet. This work reinforced the potential benefits of consuming these shrimp species. Chakraborty et al. (2022b) conducted a comparative analysis of the fatty acid profiles of *A. alcocki*, *S. choprai*, *H. chani*, and *P. quasigrandis*, collected from the southwest coast of India in the Arabian Sea. This study highlighted the differences in biochemical makeup across different months, showcasing the influence of seasonal and environmental factors on the nutritional quality of these species.

Global studies have also examined the variability in fatty acid profiles among shrimp species from different regions. For instance, research by Li et al. (2011) and Montaña and Navarro (1996) demonstrated differences in the fatty acid content of wild and cultured *Penaeus vannamei*, with wild populations having higher levels of omega-3 fatty acids. Such findings underscore the impact of environmental conditions, maturity, and seasonal changes on the biochemical composition of shrimp (Ramezani-Fard et al. 2016). Temperature, depth, and diet play significant roles in shaping the biochemical characteristics of deep-sea shrimps globally. For example, studies have indicated that shrimps from colder waters, such as those in the North Atlantic, exhibit elevated levels of omega-3 fatty acids (Henderson et al. 1984; Martin and Ceccaldi, 1977).

Shrimp are a rich source of essential nutrients, including amino acids such as methionine, lysine, cysteine, tryptophan, and threonine (Karuppasamy et al. 2013), as well as a range of vitamins (E, C, B1, B6, B12) and minerals (Heu et al. 2003; AlFaris et al. 2022). Specific minerals, including copper, zinc, manganese, iron, and selenium, are integral to various biological functions and contribute to human health when present in appropriate amounts. For example, selenium acts as an antioxidant, while zinc supports immune function and aids in wound healing (Khansari et al. 2005; Prasad, 2008; Bjørklund et al. 2022). Amino acid profiles in

species such as *Penaeus semisulcatus* and *Metapenaeus monoceros* have shown high levels of essential amino acids, including arginine, leucine, and glutamic acid, contributing to osmoregulation and flavor (Yanar and Celik, 2006; Suryanarayana et al. 1969). Mineral analyses from Indian waters have also indicated significant concentrations of calcium, phosphorus, zinc, and selenium, which are important for dietary intake and influence the textural and nutritional quality of the shrimps (Sikorski et al. 1990).

Despite numerous studies on the biochemical and nutritional properties of deep-sea shrimp, there remains a significant gap in detailed information regarding the biochemical and nutritional characteristics of *P. semilaevis* in Indian waters or in other regions where it is found. This lack of comprehensive data highlights an opportunity for further research to better understand the potential health benefits and nutritional profile of this particular species.

Growth parameters and stock assessment

Deep-sea shrimps play a vital ecological and commercial role in marine ecosystems. The study of population dynamics and growth parameters of deep-sea shrimps is crucial for understanding their ecological roles and ensuring sustainable management of these valuable marine resources. These parameters help assess shrimp populations' health, predict responses to environmental changes, and optimize fisheries strategies. Deep-sea shrimps contribute significantly to global seafood markets and support biodiversity in fragile deep-sea ecosystems. Investigating these aspects also provides insights into the impacts of climate change and human activities on deep-sea species. Such research is essential for conservation and resource sustainability. Studies assessing growth parameters and stock dynamics of various caridean shrimp species globally have been summarized in Table 1.2.

Pauly (1980) developed models linking environmental temperature to shrimp growth rates, demonstrating a direct relationship between habitat

conditions and physiological processes. King and Butler (1985) noted that deep-sea shrimps tend to have longer life spans than their shallow-dwelling counterparts. A distinction in size and depth distribution was observed in the *Plesionika* species (Company and Sarda, 1997; Carbonell et al. 2003). The smaller *Plesionika* species, such as *P. heterocarpus*, *P. gigliolii*, and *P. acanthonotus*, typically have life spans ranging from one to two years. Conversely, larger species like *P. martia* and *P. edwardsii* generally live between two to four years (Company and Sarda, 2000; Maiorano et al. 2002). In the Atlantic, Company et al. (2003) studied *Aristaeomorpha foliacea*, reporting seasonal feeding behaviors and reproductive cycles closely tied to prey abundance and environmental changes. Additionally, studies in the Pacific have utilized length-based stock assessment models to evaluate fishing impacts on species like *Haliporoides sibogae* (Kensley et al. 2000). These models emphasized sustainable harvesting limits based on growth parameters and mortality coefficients.

Table 1.2. Studies on growth parameters and stock assessment of some caridean species

Sl. No.	Species	Area	References
	<i>Plesionika semilaevis</i>	Kagoshima Bay	Ohtomi (1997), Nakahata et al. 2008
	<i>Heterocarpus reedi</i>	Central Chile	Roa and Ernst (1996)
	<i>H. laevigatus</i>	Hawaii	Dailey and Ralston (1986)
	<i>Parapandalus narval</i>	Rhodos Island, Greece	Thessalou-Legaki et al. 1989
	<i>Plesionika edwardsii</i>	eastern central Atlantic	Santana et al. 1997
	<i>Plesionika acanthonotus</i> , <i>P. edwardsii</i> , <i>P. gigliolii</i> , <i>P. heterocarpus</i> , <i>P. martia</i> , <i>P. antigay</i>	Mediterranean and northern Aegean Sea	Company and Sarda, 1997; Vafidis et al. 2008; Campisi et al. 1998; Garcia et al. (2000); Maiorano et al. 2002; Cengiz et al. 2012; Colloca (2002)
	<i>Plesionika martia</i>	eastern Ionian Sea	Chilari et al. 2005;
	<i>Parapandalus narval</i>	Southern Tyrrhenian Sea	Arculeo and Lo, 2011

Studies on growth parameters and stock evaluation of deep-sea shrimp species in Indian waters are summarized in Table 1.3. Research on deep-sea shrimps from Indian waters highlights the influence of the Indian Ocean's unique oceanographic conditions on shrimp populations. Menon et al. (2011) observed

seasonal variations in growth rates, influenced by monsoonal currents and prey availability. Similarly, Radhakrishnan et al. (2018) reported size-at-maturity and fecundity estimates, emphasizing the need for species-specific management strategies. Trawl surveys along the Indian continental shelf have revealed significant variability in shrimp abundance due to overfishing and habitat degradation (Suseelan and Kathirvel, 1985). Population dynamics models have underscored the importance of incorporating life history traits into management policies for sustaining deep-sea shrimp stocks. Studies on deep-sea shrimp in Indian waters are limited to only a few species, with a notable lack of data on *P. semilaevis*. This gap underscores the importance of conducting comprehensive research to understand the growth parameters, population dynamics, and ecological role of this species. Such studies can contribute valuable insights into sustainable management practices and conservation efforts of deep-sea shrimp fisheries in Indian marine ecosystems.

Table 1.3. Studies on growth parameters and stock assessment of deep-sea shrimps from Indian waters

Species	References
In-shore shrimps	
<i>Parapenaeopsis styliifera</i>	Ramamurthy, 1980; Alagaraja et al. 1986; Suseelan and Rajan, 1989
<i>Metapenaeus dobsoni</i>	Alagaraja et al. 1986; George et al. 1988; Pillai and Thirumilu, 2013
<i>Metapenaeus monoceros</i>	Lalitha Devi, 1987; Rao, 1994; Nandakumar, 1997
<i>Exhippolysmata ensirostris</i>	Deshmukh, 1990
<i>Acetes indicus</i>	Deshmukh, 1993
<i>Solenocera crassicornis</i>	Chakraborty et al. 1997
<i>Penaeus</i> species	Banerji and Geroge, 1967; Kurup and Rao, 1974; Lalitha Devi, 1986; Rao et al. 1993; Bhadra and Biradar, 2000
<i>Solenocera choprai</i>	Dineshbabu and Manisseri, 2009
<i>Metapenaeopsis stridulans</i>	Pillai et al. 2012
<i>Melicertus latisulcatus</i>	Sundaramoorthy et al. 2013
Deep-sea shrimps	
<i>H. gibbosus</i> , <i>H. woodmasoni</i>	Radhika, 2004
<i>P. quasigrandis</i>	Shanis, 2014
<i>A. alcocki</i>	Chakraborty et al. 2018

1.3 Objectives of the Study

Based on the existing literature review, the thesis objectives have been defined as follows:

- To collect deep-sea shrimp species from the major landing center along the southwest coast of India and determine the taxonomic identity of *Plesionika semilaevis* through morphological and molecular analyses while also assessing its fishery status
- To investigate the diet composition and feeding activity of *P. semilaevis* across various factors including sex, maturity, seasonal changes, and ontogenic variations.
- To study the reproductive traits, dynamics of oogenesis, and embryonic developments of *P. semilaevis*
- To study the biochemical composition and nutritional profile of *P. semilaevis*
- To analyze the growth parameters and population dynamics of *P. semilaevis*.

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Integrative taxonomy and fishery of *Plesionika semilaevis* from the southwest coast of India

<i>Contents</i>	2.1. <i>Introduction</i>
	2.2. <i>Materials and Methods</i>
	2.3. <i>Results</i>
	2.4. <i>Discussion</i>
	2.5 <i>Conclusion</i>

2.1. Introduction

The Pandalidae family is recognized as the second most commercially important group of shrimps after Penaeidae. Within this family, the genus *Plesionika* includes over 100 species with a global distribution (WoRMS, 2024). Among these, the *Plesionika martia* species group comprises four morphologically similar and often challenging-to-distinguish species: *P. martia* (A. Milne-Edwards, 1883), *P. semilaevis* Spence Bate, 1888, *P. orientalis* Chace, 1985, and *P. parvimartia* Chace, 1985 (Chace, 1985; Hanamura and Takeda, 1987; Hanamura, 1989; Hanamura and Evans, 1996; Chan and Crosnier, 1997; Li and Chan, 2013).

Previously, *P. martia* was reported from India (Alcock, 1901; Suseelan, 1985) and was considered a significant component of India's deep-sea fishery. However, subsequent studies confirmed that morphological records of *P. martia* from the southwest coast of India correspond to *P. semilaevis* (Kubera et al. 2017, 2020). This species, *P. semilaevis*, inhabits depths exceeding 250 meters in the southeastern Arabian Sea and accounts for a significant portion of deep-sea shrimp catches along the southwest coast of India between 2013 and 2020 (Chakraborty et al. 2022a). Its commercial and ecological importance underscores the need for detailed studies on its taxonomy.

Molecular markers have emerged as powerful tools for assessing genetic diversity within and between populations of shrimp species (Maggio et al. 2009; Cannas et al. 2012; Fernández et al. 2011; Lo Brutto et al. 2012). These markers offer insights into the genetic structure, species boundaries, and vulnerability to environmental changes (Buchholz-Sørensen and Vella, 2016). Among molecular tools, mitochondrial genes, such as the large subunit ribosomal DNA (16S rRNA) and Cytochrome oxidase I (COI), are widely employed in taxonomic and phylogenetic studies of marine organisms (Stillman and Reeb, 2001).

The use of molecular markers has been pivotal in species delimitation across various shrimp populations. For instance, molecular studies have clarified relationships in *Aristeus antennatus* (Cannas et al. 2012; Lo Brutto et al. 2012), *Aristaeomorpha foliacea* (Fernández et al. 2011), *Penaeus monodon* (Mandal et al. 2012; Sekar et al. 2014), and *Fenneropenaeus indicus* (Sajeela et al. 2015). These methods provide a robust framework for understanding genetic and phylogenetic relationships in deep-sea shrimp species.

The sequencing of the crustacean collection at the Muséum National d'Histoire Naturelle, MNHN, Paris, has led to the creation of a barcode library for the *Plesionika* genus within the Pandalidae family (Zuccon et al. 2012). Notably, the MNHN collection encompasses specimens from 68% of all *Plesionika* species. The research has yielded crucial genetic insights into *P. semilaevis* within the Mozambique-Madagascar region (Zuccon et al. 2012). The Mozambique Channel exhibits unique characteristics in terms of ocean circulation, regarded as one of the most turbulent areas globally. It's important to acknowledge that the extent of planktonic larval distribution and genetic variations can differ among the deep-sea species and taxa in other regions of the western Indian Ocean, like the Laccadive Archipelago and the southeastern Arabian Sea. Therefore, conducting genetic studies and employing techniques such as DNA sequencing and population genetics is imperative to elucidate specific genetic patterns,

comprehend the factors influencing genetic divergence in both the northern and southern parts of the western Indian Ocean, and delineate the biogeographic regions within the western Indo-Pacific region.

2.2. Materials and Methods

2.2.1 Study area and sample collection

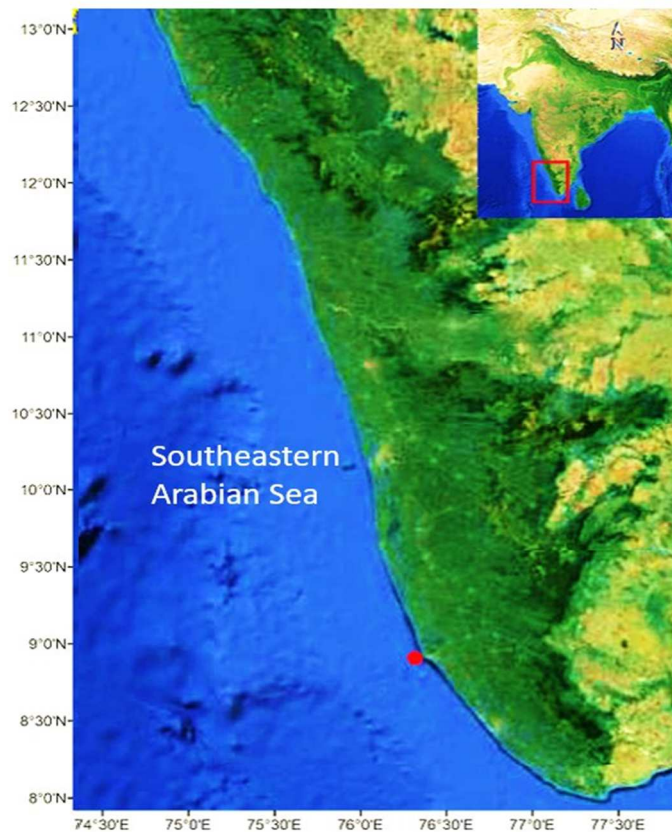


Fig. 2.1. Sampling location: Sakthikulangara Fishing Harbour (red dot)

Sampling was conducted at the commercial deep-sea shrimp trawl landing center in Sakthikulangara, Kerala (Fig. 2.1). This location is a prominent hub for deep-sea shrimp landings along the southwestern coast of India (Fig. 2.2), making it an ideal site for obtaining representative samples. Fortnightly visits were made to the landing center over a three-year period, from August 2019 to May 2022,

excluding the annual monsoon fishing ban. During each visit, samples of freshly caught deep-sea shrimps were obtained from bottom trawlers operating in the southeastern Arabian Sea at depths ranging between 250 and 350 meters. Approximately 20–25 kg of unsorted shrimp samples were collected per visit and transported to the laboratory. An insulated icebox was used to maintain the freshness of the samples during transit.



Fig. 2.2. Heaps of deep-sea shrimp landings at Sakthikulangara fishing harbor

2.2.2. Taxonomic identification and morphometric measurements

Morphological identification of *P. semilaevis* followed the taxonomic keys of Ohtomi and Hayashi (1995), Chan and Crosnier (1997), Ahamed et al. (2017), Kuberan et al. (2020) and Chan et al. (2020). Samples were preserved in 95% ethanol for molecular analysis. Measurements were recorded using a digital caliper with an accuracy of 0.01 mm. Total length (TL) was measured from the tip of the rostrum to the tip of the telson, while carapace length (CL) was measured from the orbital margin to the posterior dorsal edge of the carapace. Sex of an individual was determined by examining the morphology of the endopod of the first pair of pleopods (King and Moffitt, 1984).

2.2.3. Catch trends of *P. semilaevis*

The catch trend of *P. semilaevis* along the southwest coast of India from 2007 to 2022 was analyzed using data from the Fisheries Resources Assessment Division of ICAR-Central Marine Fisheries Research Institute (ICAR-CMFRI), Kochi. The data were estimated employing the Multistage Stratified Random Sampling design (Srinath et al., 2005). This catch and effort data was then utilized to determine the catch per unit effort (CPUE).

2.2.4. DNA extraction and PCR amplification

DNA isolation was done using the preserved tissue utilizing a customized origin marine premium kit (ODP324 02P), following the manufacturer's guidelines. The purity and quantity of extracted DNA were assessed using Nanodrop (Eppendorf Pvt. Ltd). Amplification of a partial sequence of the mitochondrial gene cytochrome oxidase c subunit I (COI) gene was performed with universal primers LCO1490/HCO2198 (Folmer et al. 1994). PCR reactions were performed following the protocol described in Ameri et al. (2022) with slight modifications. Each reaction had a volume of 25 µl and included 40 ng of DNA, 2.5 mM MgCl₂, and 0.3 mM of each primer. The amplification process comprised an initial denaturation phase at 94°C for 5 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 48°C for 35 s with an extension at 72°C for 1 min. The final extension was at 72°C for 5 min.

2.2.5. Phylogenetic analyses

COI sequences from the Mozambique channel-Madagascar specimen (MNHN collections) were retrieved from GenBank, NCBI database and aligned all the sequences using the BIO Edit (Hall, 1999). A maximum likelihood (ML) analysis was carried out for each gene separately using the Kimura 2-parameter (K2P) model in MEGA 7 (Kumar et al. 2016).

2.2.6. Population genetic structure

Haplotype and nucleotide diversity (π) were determined using the software PopART (Leigh and Bryant, 2015). A median-joining haplotype network (Bandelt et al. 1999) was generated to illustrate the inter-relations among haplotypes, employing the default settings of PopART (Leigh and Bryant, 2015) with default settings. An analysis of molecular variance (AMOVA) (Excoffier et al. 1992) was conducted to assess hierarchical population genetic structure among regions with 1000 permutations employed to assess significance.

2.2.7. Bathymetric and ocean current data analysis

Bathymetry plots were generated utilizing Pygmt, a Python library, leveraging the GEBCO dataset accessed through Pygmt from <https://www.generic-mapping-tools.org/remote-datasets/earth-gebco.html>. The process involved acquiring surface current data spanning the period 2010–2020 from the OSCAR surface currents dataset, which is accessible at <https://www.esr.org/research/oscar/oscar-surface-currents/>. Subsequently, we computed the annual average of the surface current data extracted from this dataset.

2.3. Results

2.3.1. Fishery and catch trends of *P. semilaevis*

Along the Kerala coast, two distinct types of deep-sea shrimp trawling operations are conducted, differentiated by their targeted shrimp species. One operation focuses on the "red ring" shrimp, conducted at depths greater than 350 meters, while the other targets deep-sea shrimps, mainly pandalids, at depths ranging from 150 to 350 meters. Fishing trips typically last between 6 to 12 days. Trawlers targeting "red ring" shrimp operate day and night, whereas those targeting other deep-sea shrimps limit their operations to daytime hours. The number of hauls per day ranges from 3 to 5, with each haul lasting 4 to 5 hours. These trawlers use a cod-end mesh size of 25–30 mm to ensure effective harvesting of the shrimp.

The deep-sea shrimp fishery frequently yields a variety of species, with major catches including *Plesionika semilaevis*, *P. quasigrandis*, *Metapenaeopsis andamanensis*, *Heterocarpus woodmasonii*, *H. chanii*, *Aristeus alcocki*, *Penaeopsis jerry*, *Parapenaeus investigatoris*, *Hymenopenaeus equalis*, and *Solenocera hextii*. The catch composition of major deep-sea shrimps during 2019-2022 is shown in Fig. 2.3. Occasionally encountered species include *Plesionika reflexa*, *Metapenaeopsis coniger*, *Glyphocrangon investigatoris*, *Acantheephyra fimbriata*, *Acantheephyra sanguinea* and *Oplophorus gracilirostris*. Rarely observed species include *Plesionika alcocki*, *Pasiphaea alcocki*, *Sicyonia parajaponica*, *Hadropenaeus lucasii*, *Parapontocaris bengalensis*, and *Parastylodactylus sulcatus*.

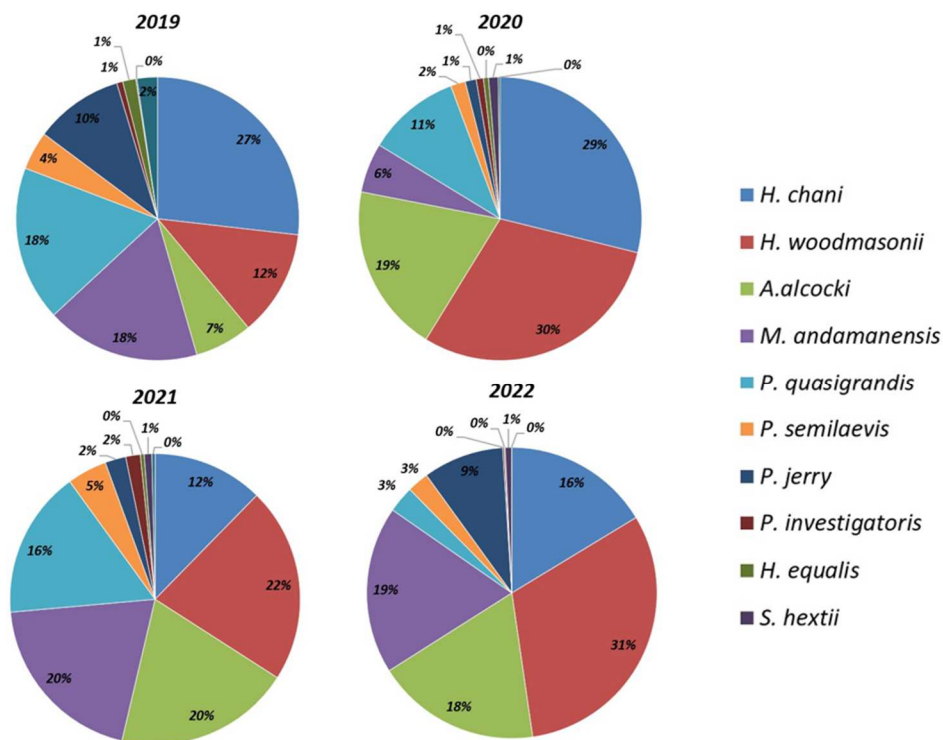


Fig. 2.3. Catch composition of deep-sea shrimps during 2019-2022

The by-catch from these operations includes crabs such as *Charybdis (Goniohellenus) smithii*, and *Homolax megalops*; lobsters like *Nephropsis stewarti*, *Puerulus sewelli*, and *Polycheles typhlops* and squat lobsters such as *Munidopsis scobina*, *Paramunida bineeshi*, and *Eumunida sp.* Additionally, deep-sea fishes are often observed as by-catch, including species such as *Psenopsis cyanea*, *Champsodon vorax*, *Macrorhamphosodes uradoi*, *Chlorophthalmus coniger*, *Neoepinula orientalis*, *Eridacnis radcliffei*, *Aesopia cornuta*, *Beryx splendens*, *Parascolopsis aspinosa*, *Rexa prometheoides*, *Bembrops caudimacula*, and *Arnoglossus sp.*

Analysis of *P. semilaevis* catch data from 2007 to 2022 reveals significant variations in both the total shrimp catch weight (in tons) and the catch per unit effort (CPUE), as depicted in Fig. 2.4. Notable fluctuations were observed in the total catch of *P. semilaevis* throughout the survey period. The highest total catch was recorded in 2019, while the lowest was observed in 2017.

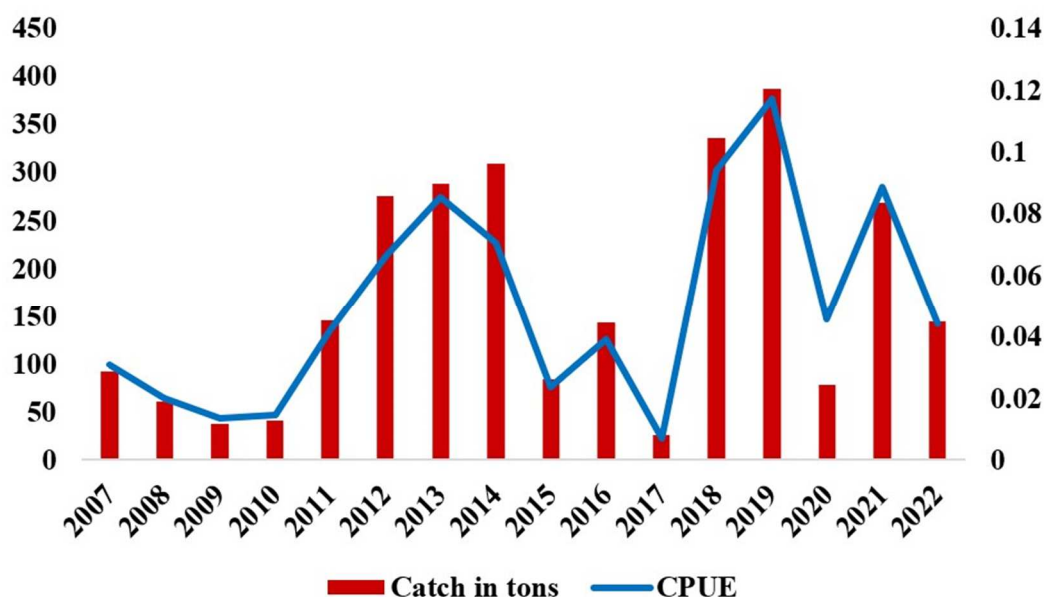


Fig. 2.4. Deep-sea shrimp *P. semilaevis* landings and CPUE along the southwest coast of India during the period 2007-2022

2.3.2. Taxonomic status of *P. semilaevis*

Order: Decapoda

Suborder: Pleocyemata

Infraorder: Caridea

Superfamily: Pandaloidea Haworth, 1825

Family: Pandalidae Haworth, 1825

Genus: *Plesionika* Spence Bate, 1888

Species: *Plesionika semilaevis* Spence Bate, 1888

2.3.3 Sex determination and Morphometric analysis

The endopod of females has a pointed leaf-like structure (Fig. 2.5a), while that of males has a blunt rectangular shape (Fig. 2.5b). The appendix masculina, a specialized structure on the second pleopod of mature male shrimps, was used as a distinguishing feature to sort males from females (Fig. 2.5c). The females were sorted into ovigerous and non-ovigerous states based on the presence of embryos between the pleopods (Fig. 2.6). Males exhibited a CL range 9-25 mm (TL 65-140 mm), while ovigerous females had a CL range of 12-24 mm (TL 72-135 mm), and non-ovigerous females had a CL range of 10-24 mm (TL 70-132 mm). The weight ranged from 0.72-6.25 g in males, 0.85-7.88 g in berried females, and 0.82-6.26 g in non-berried females.

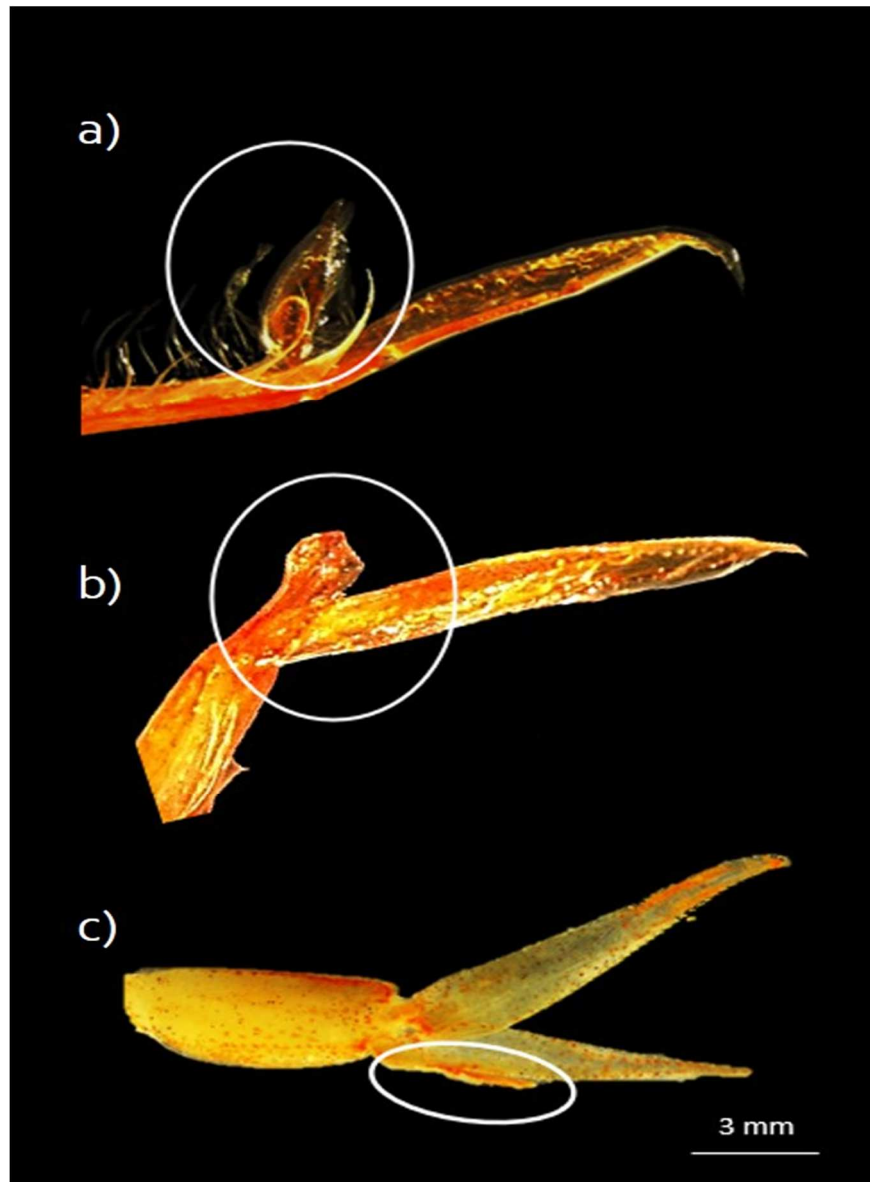


Fig. 2.5. Leaf-shaped endopod of first pleopod in females (a), blunt-shaped endopod of first pleopod in males (b), and appendix masculina in the second pleopod of matured males



Fig. 2.6. *Plesionika semilaevis* Spence Bate, 1888

2.3.4. Taxonomic Description

The rostrum is long and slender, surpassing the antennal scale and significantly extending beyond the scaphocerite. Curved downwards proximally, transitioning to an upward curve and straightening distally beyond the antennular peduncle. Dorsal crest armed with 4–8 teeth, including 2 or 3 teeth on the carapace posterior to the orbital margin, none with barbed tips; ventrally armed with 30–50 teeth (Fig. 2.7a).

Carapace smooth and the lateral surface lacks carinae or grooves but exhibits a slight depression resembling a pit in the hepatic region (Fig. 2.7b). The postrostral ridge extends to about mid-carapace, distinctly elevated and laminate throughout. (Fig. 2.7c). Antennal and pterygostomian spines are moderately large, with the antennal spine longer than the pterygostomian (Fig. 2.7d). The orbital margin features an upper part slightly convex and inclined backward, while the lower part is convex. Eyes kidney-shaped with a distinct ocellus (Fig. 2.7d). The stylocerite is obtuse but tapers to a pointed tip distally, with a strong upward lateral fold, extending to the second segment of the antennular peduncle.

Abdomen smooth, without posteromesial teeth or median dorsal carinae on any somite. Pleuron IV is posteroventrally rounded, while pleuron V is posteroventrally pointed (Fig. 2.7e). The sixth pleuron is approximately twice the length of its maximum height. Tergite III has a rounded posterior margin. Telson as long as the sixth pleuron, equipped with four pairs of dorsolateral spinules, including a lateral pair of spines reaching the posterior telson margin (Fig. 2.7f). The third maxilliped possesses an epipod. The first four pereopods bear epipods. The second pair is subequal, with 19–29 carpal articles. The third pair extends beyond the scaphocerite by the combined lengths of the dactylus, propodus, and carpus. Pereopods are not extremely slender or thread-like (Fig. 2.7g). Coloration: The body predominantly displays a reddish to rose-red hue, with no discernible longitudinal or transverse bands. The ventral carapace and the distal segments of the third maxilliped exhibit a deep red color. Pereiopods I to V feature contrasting patterns, with anterior and posterior segments of the carpus, merus, and propodus appearing whitish, while the dactyls remain distinctly reddish. Pleopods and uropods are pale red, and egg coloration varies from pale green to dark blue, correlating with the maturity stages of the eggs.

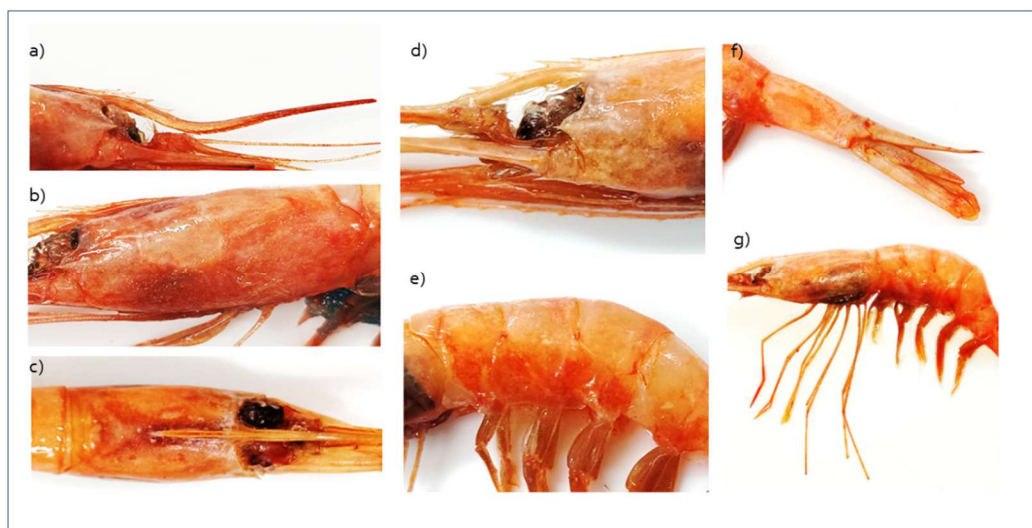


Fig. 2.7. Lateral view of rostrum (a); lateral view of carapace (b); dorsal view of carapace (c); antennal and pterygostomial spines (d); shape of abdominal pleura (e); lateral view of telson with dorsal spines (f); maxillipeds and pereopods (g)

2.3.5. Molecular and Phylogenetic analysis

A Maximum Likelihood (ML) phylogenetic clustering analysis was conducted to investigate the genetic relationships of *P. semilaevis* specimens from different geographical regions. The analysis included sequences from the Mozambique Channel and other *Plesionika* species available in public databases such as NCBI. The study utilized partial mitochondrial cytochrome c oxidase I (COI) sequences, a widely used marker for species identification and phylogenetic studies due to its high resolution in distinguishing closely related taxa. The ML phylogenetic tree revealed significant genotypic variations between *P. semilaevis* specimens from the Arabian Sea and the Mozambique Channel. In addition to *P. semilaevis*, species such as *P. martia* and *P. nesisi* formed separate clades (Fig. 2.8), reflecting potential cryptic species or taxonomic ambiguities within the genus.

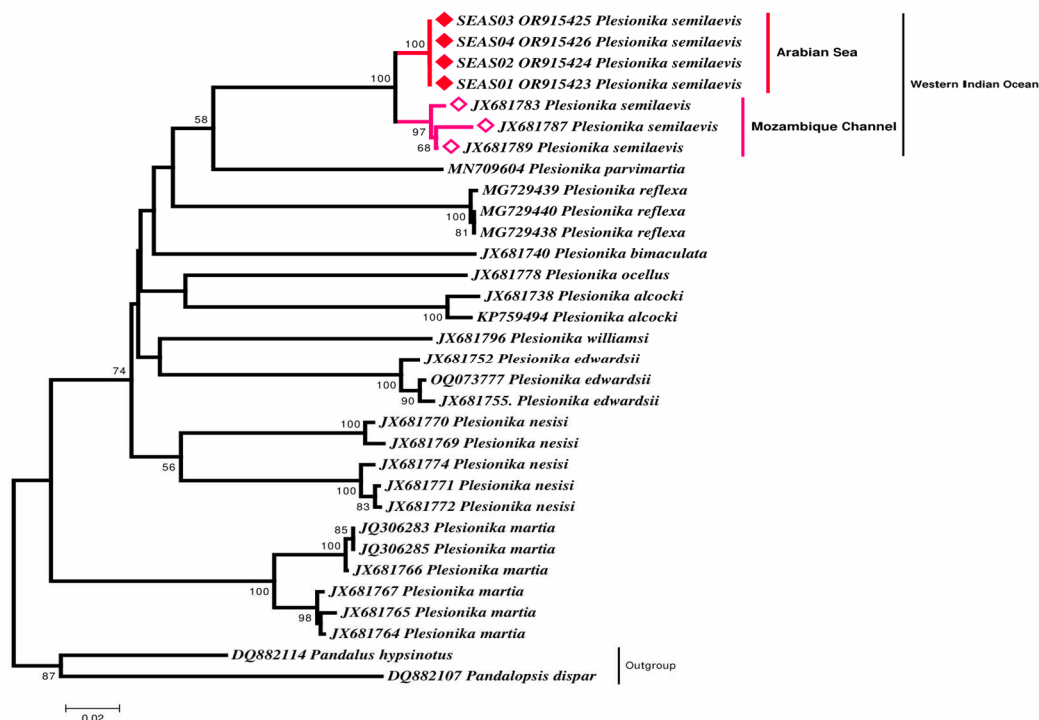


Fig. 2.8. Maximum likelihood (ML) phylogenetic tree of *Plesionika* species based on COI gene

A separate Maximum Likelihood (ML) phylogenetic clustering analysis tree was constructed based on partial mitochondrial cytochrome c oxidizing COI (Fig. 2.9) for specimens collected from the southern (Mozambique channel-Madagascar region) and northern parts (Arabian Sea, Laccadive Sea) of the western Indian Ocean, focusing on the *P. semilaevis* species. The analysis revealed significant genotypic variations between these two distinct geographical regions of the Indian Ocean. Additionally, the Kimura 2-parameter (K2P) pair wise analysis estimated genetic variation in the COI sequence to be between 0.042 and 0.055 (4.2 to 5.5 percent) for the two regions (Table 2.1).

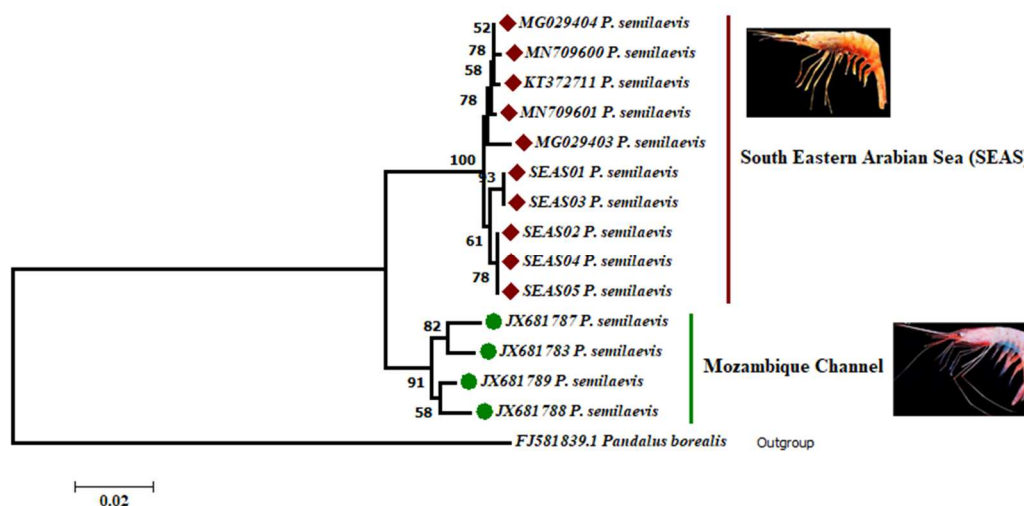


Fig. 2.9. Phylogenetic tree based on COI gene representing a genetic variant of *P. semilaevis* of the Arabian Sea and the Mozambique Channel regions. The image of Mozambique Channel specimen was retrieved from the Muséum National d'Histoire Naturelle, Paris (MNHN-IU-2008-14570)

Table 2.1 Kimura 2 parameter (K2P) genetic distances between the Arabian Sea and the Mozambique Channel specimens based on COI gene

<i>MG029404_P. semilaevis</i>													
<i>MG029403_P. semilaevis</i>	0.007												
<i>MN709601_P. semilaevis</i>	0.002	0.008											
<i>MN709600_P. semilaevis</i>	0.002	0.008	0.003										
<i>KT372711_P. semilaevis</i>	0.002	0.008	0.003	0.003									
<i>SEAS01_P. semilaevis</i>	0.008	0.012	0.007	0.010	0.010								
<i>SEAS02_P. semilaevis</i>	0.007	0.010	0.005	0.008	0.008	0.005							
<i>SEAS03_P. semilaevis</i>	0.008	0.012	0.007	0.010	0.010	0.000	0.005						
<i>SEAS04_P. semilaevis</i>	0.007	0.010	0.005	0.008	0.008	0.005	0.000	0.005					
<i>SEAS05_P. semilaevis</i>	0.007	0.010	0.005	0.008	0.008	0.005	0.000	0.005	0.000				
<i>JX681787_P. semilaevis</i>	0.049	0.054	0.051	0.051	0.051	0.055	0.053	0.055	0.053	0.053			
<i>JX681783_P. semilaevis</i>	0.049	0.055	0.051	0.051	0.051	0.055	0.053	0.055	0.053	0.053	0.015		
<i>JX681789_P. semilaevis</i>	0.042	0.047	0.044	0.044	0.044	0.048	0.046	0.048	0.046	0.046	0.018	0.017	
<i>JX681788_P. semilaevis</i>	0.048	0.053	0.049	0.049	0.049	0.053	0.051	0.053	0.051	0.051	0.023	0.018	0.012

2.3.6. Comparative Morphological Analysis of *P. semilaevis* specimens from the Arabian Sea and Mozambique channel-Madagascar regions

The morphological features of Arabian Sea specimens and those from the Mozambique channel-Madagascar regions (Table 2.2) of *P. semilaevis* were scrutinized, confirming identical morphology without any significant differences (Fig. 2.10). Specifically, the shape of the eye orbital exhibited uniformity across both geographical specimens. The key distinguishing characteristics, the posterior orbital region strongly inclined backward in the upper part with a convex-shaped lower part that differentiates *P. semilaevis* from closely related species, *P. martia*, were consistent across the examined specimens. The carapace is smooth, the rostrum long and slender, curving downward at the basal part but upward and straight distally, extending beyond the antennal scale. Dorsally, it bears 4-6 teeth, including 2 or 3 posterior to the orbital margin. The body is semi-transparent with consistent reddish to rose-red color, lacking longitudinal or transverse bands. Eggs are light bluish in color. The carapace's postrostral ridge is distinctly elevated, extending to about the middle of the carapace. The lateral carapace lacks a carina or groove, showing only a hepatic region that may or may not be depressed as a small pit. Antennal and pterygostomial spines are moderately large, with the former being longer than the latter. None of the abdominal pleura has distinct marginal teeth or denticles.

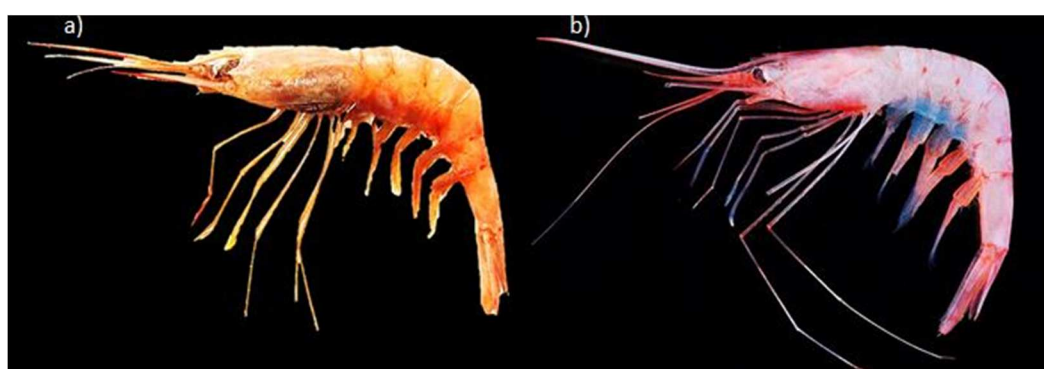


Fig. 2.10. Specimens of *P. semilaevis* from the Arabian Sea (a) and Mozambique channel (b). The image of Mozambique Channel specimen was retrieved from the Muséum National d'Histoire Naturelle, Paris (MNHN-IU-2008-14570)

Table 2.2. Details of *P. semilaevis* specimens used for morphological and phylogenetic analyses

Sl. No	Species	Specimen Voucher	Location	References
1	<i>P. semilaevis</i>	SEAS01	Arabian Sea, Indian Ocean	Present Study
2	<i>P. semilaevis</i>	SEAS02	Arabian Sea, Indian Ocean	Present Study
3	<i>P. semilaevis</i>	SEAS03	Arabian Sea, Indian Ocean	Present Study
4	<i>P. semilaevis</i>	SEAS04	Arabian Sea, Indian Ocean	Present Study
5	<i>P. semilaevis</i>	SEAS05	Arabian Sea, Indian Ocean	Present Study
6	<i>P. semilaevis</i>	SIF-Psp.1	Arabian Sea, Indian Ocean	Unpublished
7	<i>P. semilaevis</i>	-	Arabian Sea, Indian Ocean	Unpublished
8	<i>P. semilaevis</i>	-	Arabian Sea, Indian Ocean	Unpublished
9	<i>P. semilaevis</i>	DABFUK/AR-PLE-26	Arabian Sea, Indian Ocean	Chan et al. 2020
10	<i>P. semilaevis</i>	DABFUK/AR-PLE-27	Arabian Sea, Indian Ocean	Chan et al. 2020
11	<i>P. semilaevis</i>	MNHN:IU-2010-48	Mozambique Channel, Indian Ocean	Zucon et al. 2012
12	<i>P. semilaevis</i>	MNHN:IU-2010-52	Mozambique Channel, Indian Ocean	Zucon et al. 2012
13	<i>P. semilaevis</i>	MNHN:IU-2008-14558	Mozambique Channel, Indian Ocean	Zucon et al. 2012
14	<i>P. semilaevis</i>	MNHN:IU-2008-14570	Mozambique Channel, Indian Ocean	Zucon et al. 2012

2.3.7. Population genetic analyses

Median-joining haplotype networks were constructed to visualize the relationships among haplotypes based on nucleotide polymorphisms in cytochrome oxidase I (Fig. 2.11) partial sequences. An analysis of molecular variance (AMOVA) was used to test for hierarchical population genetic structure among the western Indian Ocean regions using 1000 permutations to test for significance. The analysis revealed that twenty segregating sites differentiating northern and southern populations of the western Indian Ocean which is more than the inter-species level in caridean shrimps and analysis of molecular variance confirms the high genetic diversity ϕ_{ST} 0.99409 ($P < 0.001$) among the cryptic species.

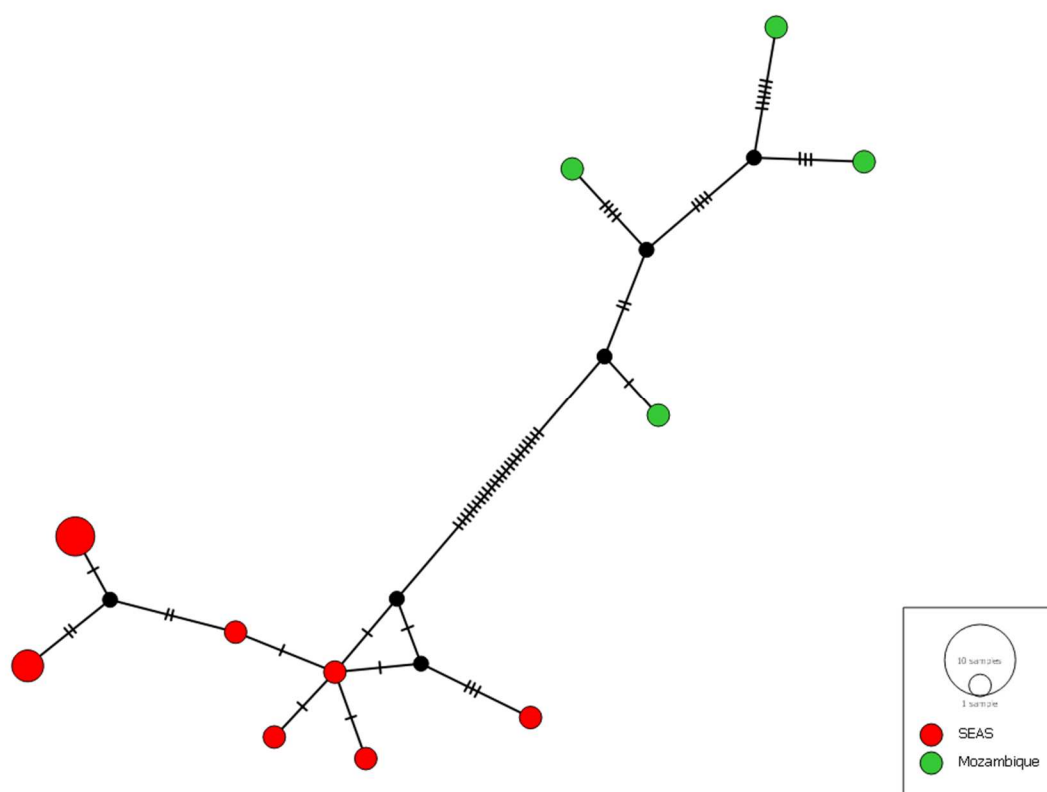


Fig. 2.11. Median-joining networks for representing the inter-species level (cryptic species) genetic divergence among the *P. semilaevis* specimens of the South Eastern Arabian Sea (SEAS), Indian Ocean (Red dots) and Mozambique Channel (Green dots) based on COI sequences. Circle sizes correspond to haplotype frequencies. The dashed line represents one mutational step between the haplotypes (20 segregating sites differentiating the Arabian Sea and Mozambique channel-Madagascar populations)

2.3.8. Bathymetric and ocean current data analysis

The analysis of the bathymetric profile of the Western Indian Ocean provides a comprehensive visual representation of the ocean floor's depth variations along its longitudinal axis (Fig. 2.12). Spanning from the eastern coast of Africa to the western reaches of the Indian subcontinent, the Western Indian Ocean encompasses a diverse array of underwater features, from shallow continental shelves to deep-sea trenches. However, a prominent feature that distinguishes this region is the presence of the Chagos Ridge, a substantial

submarine mountain range that extends across the ocean floor. In the bathymetric profile, the Chagos Ridge emerges as a significant topographic element, prominently dividing the southwestern and northwestern regions of the Western Indian Ocean. This ridge, characterized by its elevated relief and rugged terrain, serves as a geophysical boundary that influences oceanic circulation patterns, marine biodiversity, and geological processes in the surrounding areas. To the southwest of the Chagos Ridge, the bathymetric profile reveals a relatively shallower region, marked by gentle slopes and gradual depth variations.

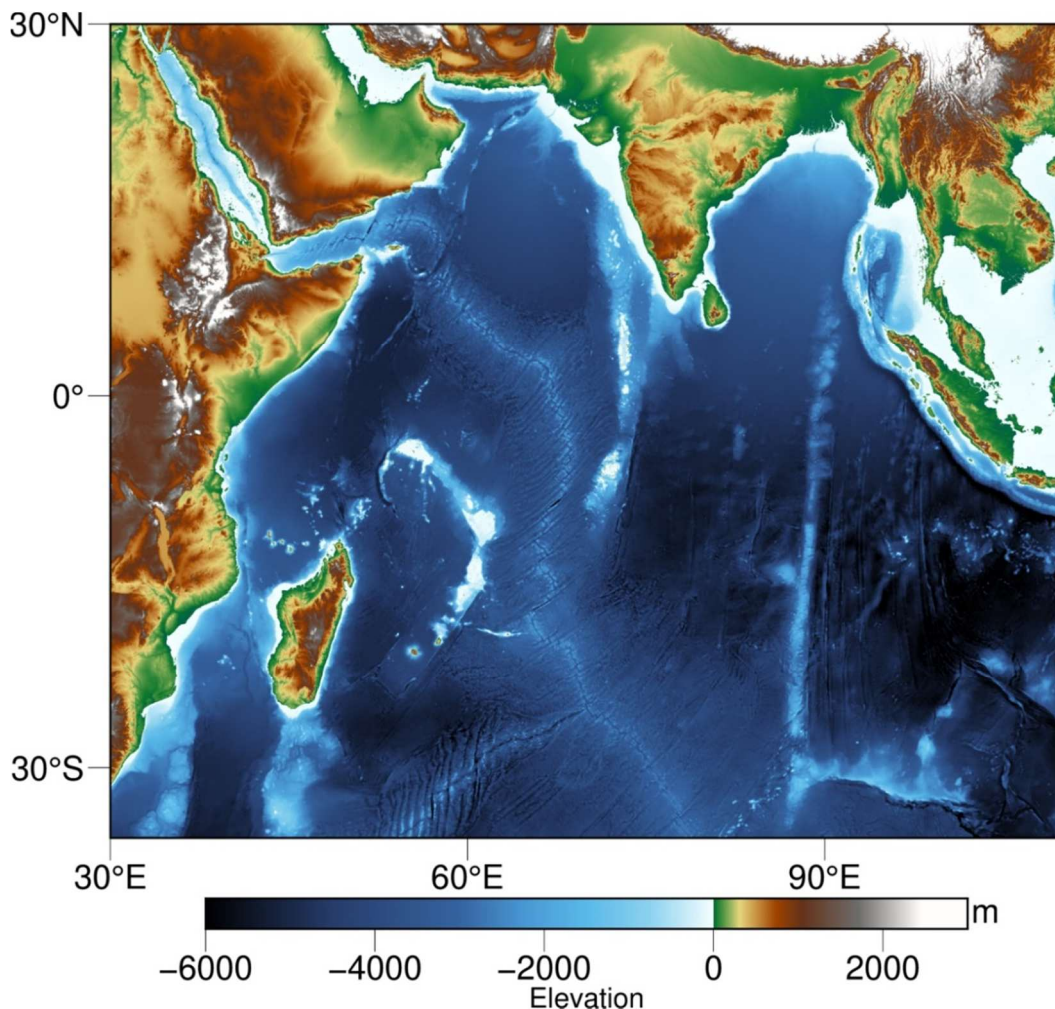


Fig. 2.12. The bathymetric profile of the western Indian Ocean was generated using Pygmt, a Python library, which utilizes the GEBCO dataset

Ocean current profiling of the western Indian Ocean highlights the influence of the Agulhas Current, a warm and swift oceanic current that flows along the eastern coast of Africa on the Mozambique channel-Madagascar region (Fig. 2.13). As the Agulhas Current interacts with the continental shelf of the Mozambique channel-Madagascar region, it creates a complex system of eddies. These eddies play a crucial role in circulating the larvae of deep-sea shrimp species within the region, preventing gene flow among populations. The presence of eddies can also lead to genetic isolation of the shrimp populations, resulting in unique biogeographic patterns.

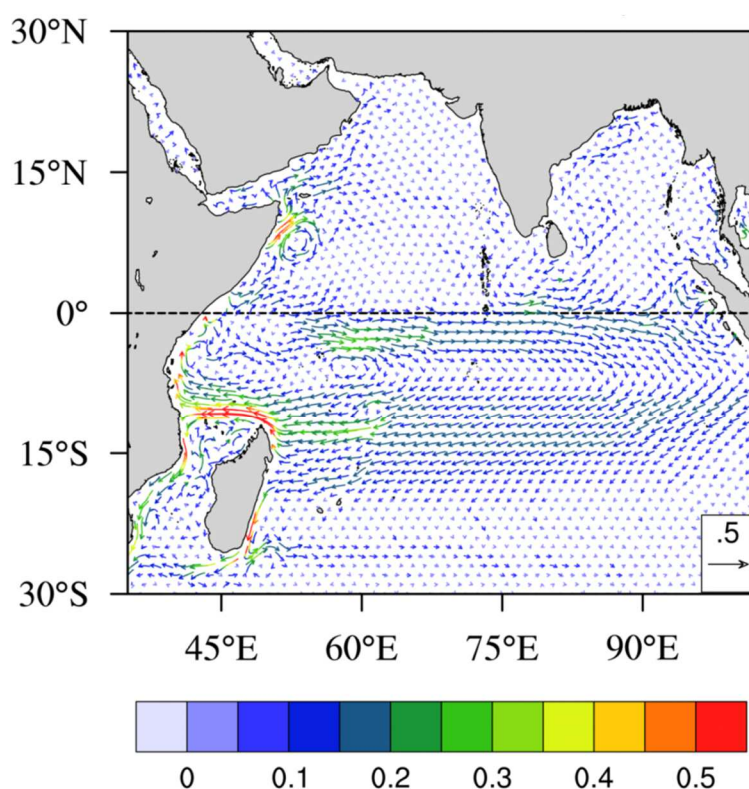


Fig. 2.13. The annual mean of major currents and eddies in the western Indian Ocean (2010-2020) influence the genetic discontinuity observed in deep-sea shrimp populations within the Mozambique channel-Madagascar region and the Arabian Sea. The scale represents the velocity

Conversely, the Arabian Sea depicts the influence of the Arabian Sea Monsoon Current, which undergoes seasonal reversals driven by the Indian monsoon winds. During the southwest monsoon season, the current carries nutrient-rich waters northward along the Arabian peninsula, creating favorable conditions for deep-sea shrimp larvae. As larvae are entrained within the current and transported across the Arabian Sea, they encounter different environmental conditions and oceanic features, leading to genetic differentiation among populations. South Equatorial Current (SEC), as well as eddies in the Mozambique channel-Madagascar region, significantly impacts the distribution and connectivity of *P. semilaevis* populations. The dominance of east-west flow in the central Indian Ocean, along with equatorial counter-currents, contributes to the allopatric cryptic speciation observed in the Arabian Sea.

2.4. Discussion

Deep-sea shrimp landings along the Kerala coast commence towards the end of August or the beginning of September and conclude in May. The fishery remains inactive during June, July, and August due to the monsoon trawling ban and adverse weather conditions that hinder access to deeper waters. December is the peak month for the fishery, contributing approximately 50% of the annual shrimp landings (Paramasivam et al. 2020). The fishery of deep-sea shrimps, particularly *P. semilaevis*, along the southwest coast of India, is of growing economic (Rs. 150-180/kg) significance. Deep-sea shrimp fisheries have gained attention globally due to their high market value, nutritional benefits, and demand in international markets. Among the caridean shrimps, species belonging to the genus *Plesionika* are particularly notable for their contribution to commercial fisheries, especially in tropical and subtropical regions.

The integrative taxonomy and fishery of *P. semilaevis*, from the southwest coast of India, highlight the challenges and opportunities inherent in studying

genus *Plesionika*, a significant group within the diverse family Pandalidae. As one of the most systematically complex families, Pandalidae showcases exceptional diversity in morphology and ecology, particularly in deep-sea or cold-water habitats. Despite repeated morphological analyses, the relationships within this family remain unresolved due to the absence of a comprehensive molecular phylogeny (Liao et al. 2019). This underscores the need for integrative approaches combining morphological, molecular, and ecological data to untangle the evolutionary relationships within the group.

The genus *Plesionika* stands out, encompassing more than 100 described species (WoRMS, 2024). The genus displays notable morphological disparity and ecological adaptations, particularly in deeper or colder waters. However, the systematic classification within *Plesionika* is contentious, with various species groups proposed based on morphology such as *P. narval*; *P. martia*; *P. rostricrescentis* and *P. ocellus* groups (Chan and Crosnier, 1991, 1997). These groupings, while insightful, lack robust phylogenetic validation, leaving their evolutionary relationships unclear. This reflects broader challenges within the genus, where species richness complicates systematic studies, and morphological convergence or divergence due to ecological pressures adds further complexity.

Several species of *Plesionika* have historically been misidentified across Asian waters. For instance, *P. ocellus*, as reported by Chace (1985), was later clarified to represent *P. sindoi* (Chan and Crosnier, 1997). In Indian waters, *P. quasigrandis*, one of the most dominant *Plesionika* species, had previously been misreported as “*Parapandalus* (or *Plesionika*) *spinipes*” (Shanis et al. 2012; Chakraborty et al. 2015). Kuberan et al. (2017) indicated that previous records of *P. martia* in southwestern India were misidentifications of *P. semilaevis*, a closely related species. This assertion received additional support from subsequent studies by Kuberan et al. (2020) and Chan et al. (2020). Notably, the material from southwestern India exhibited a strongly inclined backward upper part of the

orbital margin and a convex lower part. In contrast, *P. martia* is characterized by a nearly vertical orbital margin (Fig. 2.14).

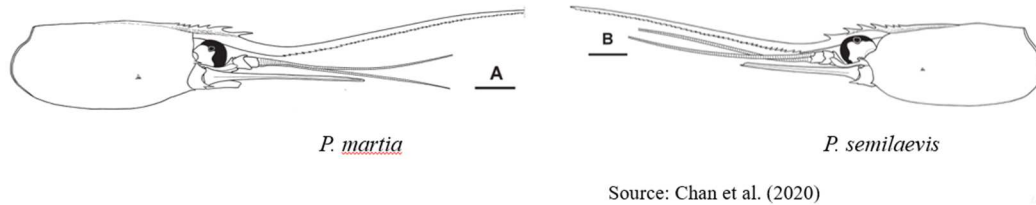


Fig. 2.14. Differences in shape of orbital margin in *P. Martia* and *P. semilaevis*

The economic significance of genus *Plesionika*, particularly in fisheries, underscores the necessity of resolving these taxonomic ambiguities. *P. semilaevis*, a deep-sea shrimp of fishery importance, exemplifies the need for accurate species identification to manage resources sustainably. Integrative taxonomy, employing both traditional morphological methods and modern molecular tools, offers a pathway to address these challenges. Molecular phylogenetic studies, in particular, could provide insights into species boundaries, evolutionary relationships, and the ecological adaptations of *Plesionika* species.

Dispersal of invertebrate larvae in the deep ocean remains poorly understood, especially regarding pelagic traits and time in the water column. While shallow-water species often have short pelagic phases (Zardus and Morse, 1998; Van de Putte et al. 2012), studying larval dispersal in the deep sea is challenging. Population genetics and pairwise genetic distances (P-distances) provide insights into connectivity despite limitations (Bay et al. 2006). Kartavtsev (2011) reported mean COI P-distances of 0.89% for populations and 3.78% for species within the same genus. In *P. semilaevis*, P-distances of 4.2–5.4% in western Indian Ocean populations exceed this threshold, suggesting potential cryptic species despite morphological similarities.

Gene flow discontinuities between Arabian Sea and Mozambique Channel populations may result from larval duration (Riginos and Victor, 2001), dispersal mechanisms, geographical barriers, and ecological factors (Bird et al. 2007). Cryptic species or ecotypes within widespread decapods suggest local adaptation to barriers like upwelling zones, currents, and temperature gradients (Wilson et al. 2013). Bathymetric features, including the Chagos Ridge, significantly influence connectivity by obstructing currents and shaping ecosystems. The ridge separates the western Indian Ocean into distinct regions with varying underwater topographies, limiting gene flow between populations (Dilmahamod et al. 2016).

Ocean currents also shape larval dispersal. The Mozambique Channel, between southeast Africa and Madagascar, acts as a genetic barrier despite species' pelagic larvae (Reddy et al. 2014; Tsang et al. 2012). Currents like the Somali and Agulhas further influence connectivity, contributing to isolation and genetic differentiation in species with extended larval stages (Lavery et al. 2014). This isolation drives mutation accumulation, producing distinct lineages over time. Similar patterns are observed in *Aristaeomorpha foliacea*. Fernández et al. (2013) revealed significant COI-based genetic differences among populations in the Mediterranean, Mozambique Channel, and Australia. These results highlight how ocean currents and eddies shape larval distribution and genetic structuring, even for species with wide dispersal potential.

2.5. Conclusions

The deep-sea caridean shrimp, *Plesionika semilaevis*, is an important species for the fisheries of the southwest coast of India, supporting local economies and contributing to biodiversity in the region's marine ecosystems. While traditional morphological assessments have been used to classify and identify *P. semilaevis*, these methods alone can be insufficient due to the potential for cryptic species and subtle distinctions between populations. The current study

highlights significant genetic differentiation between *P. semilaevis* populations from the Arabian Sea and the Mozambique Channel, marked by P-distances of 4.2–5.4%, which surpass the threshold observed for species within the same genus. These findings indicate that morphological characteristics alone may not accurately reflect genetic diversity and evolutionary history, suggesting the existence of cryptic lineages. Integrating genetic data with morphological and ecological insights allows for a more comprehensive understanding of *P. semilaevis* taxonomy, revealing the complexities of population structure influenced by oceanographic barriers such as the Chagos Ridge and regional currents. Integrative taxonomy combining molecular and morphological data is crucial for clarifying species boundaries and enhancing our ability to manage and protect deep-sea marine resources effectively.

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Feeding ecology of the pandalid shrimp, *Plesionika semilaevis* Spence Bate, 1888 in South Eastern Arabian Sea

<i>Contents</i>	3.1. <i>Introduction</i>
	3.2. <i>Materials and Methods</i>
	3.3. <i>Results</i>
	3.4. <i>Discussion</i>
	3.5. <i>Conclusion</i>

3.1. Introduction

The feeding ecology of deep-sea organisms is crucial in understanding their relative roles in ecosystem functioning. To determine this ecological niche width, it is essential to identify the interaction of the organisms within the food chain (Bearhop et al. 2004). The study of diet composition and feeding behaviour enables the understanding of the rate of growth, gonadal maturation, niche partitioning, habitat preferences, predation and prey selection. Food is considered the major limiting factor in the functioning of deep-sea ecosystems and trophic aspects have been considered the most important factor in deep-sea faunal community organization (Jumars and Gallagher, 1982). An understanding of the relationship between animals and food organisms, especially the favourite food items and their seasonal distribution, may help to locate the potential feeding grounds as they provide clues for the prediction and exploitation of the resources (Muthiah, 1994).

Plesionika Bate, 1888 represents a major group of deep-water shrimps under the family *Pandalidae* Haworth, 1825. They are represented by more than

100 species distributed world-wide mainly in subtropical and tropical waters (WORMS, 2024) along the continental shelf and slope (Cartes et al. 1993; Carbonell and Abelló, 1998; Company et al. 2004; Vafidis et al. 2005). They constitute an important prey of demersal fishes and cephalopods. Most species under the genus are nekto-benthic species that feed on pelagic and benthic resources (Cartes et al. 1993; Cartes, 1998; Cartes et al. 2002; Fanelli and Cartes 2004; Vafidis et al. 2005; Fanelli et al. 2007).

Genera *Plesionika* contributes majorly to the commercial landing of deep-sea shrimps in the southern coasts of India. *Plesionika quasigrandis* and *P. semilaevis* are the major species under the genus contributing about 21% of deep-sea fishery in the south-west coast of India (Chakraborty et al. 2022a). *P. semilaevis* is one of the most widely distributed pandalids in the tropical waters of the Atlantic and Indo-Pacific regions. They are distributed on the shelf edge and upper continental slope, found in the depth range of 260–2263 m along the southwest and southeast coast of India, including the Andaman Sea (Alcock 1901; Suseelan 1985).

Considerable variation in the diet of many *Plesionika* species with respect to biological factors, environmental and geographical variables have been observed in the Mediterranean region and West Africa (Fanelli and Cartes, 2004; Fanelli and Cartes, 2008; Kitsos et al. 2008; Burukovsky, 2017; Bordbar et al. 2019). However, no prior studies have been reported on *Plesionika semilaevis* despite its wide distribution. In the Indian ocean information concerning the diet composition and the feeding habits of some deep-sea shrimps have been published but not much information is available regarding the caridean shrimps. A study on the diet composition and prey selection of penaeid shrimp *Aristeus alcocki* was also observed in this region (Paramasivam et al. 2020). The relationship between

feeding intensity and breeding periods of Pandalidae from the *Heterocarpus* genus was observed by Radhika and Kurup (2011).

The present study aims to understand the diet composition and feeding activity of the deep sea caridean shrimp *P. semilaevis* for different sex, maturity, seasonal and ontogenic variations in the South Eastern Arabian Sea.

3.2. Materials and Methods

3.2.1. Sample collection and processing

Deep sea shrimp samples were collected fortnightly from the fish landing centre in Saktikulangara, Kollam, Kerala, from 2019 to 2022 (except during monsoon ban). Samples were acquired from deep-sea bottom trawlers having cod-end mesh size of 20–25 mm, operated at a depth of 250m in the South Eastern Arabian Sea and transported to the laboratory in fresh condition. *P. semilaevis* species were identified based on the taxonomic literatures of Chace (1985), Ohtomi and Hayashi (1995), Chan and Crosnier (1997), Ahamed et al. (2017) and Chan et al. (2020). Sex was determined macroscopically by the shape of the endopod of the first pleopods (King and Moffitt, 1984) and the presence and absence of the male appendix in the second pair of pleopods.

The excess water on shrimps was removed using a blotting paper. Total length (TL), the distance from the tip of the rostrum to the tip of the telson and carapace length (CL), the shortest distance between the posterior margin of the orbit and the middorsal posterior edge of the carapace, was measured using digital calipers with a precision of 0.01 mm. Body weight (W) was measured using a digital balance with a precision of 0.01 g. Samples were separated as males, berried and non-berried females. Each of these was sorted into small (CL<15 mm), medium (CL 15- 19mm) and large (CL>19mm) sized individuals. Small and large individuals were treated as juveniles and adults respectively.

3.2.2. Feeding analysis

The stomachs of the shrimps were dissected, weighed and stomach fullness was recorded. The feeding intensity (FI) was determined by the degree of distension of the stomach due to the presence of food. Since the amount of food in the stomach of shrimps was very little, the points method (Pillay, 1952) was used for feeding analysis. Stomach fullness was expressed in terms of percentage as 100% full, 75% full, 50% full, 25% full, 10% full and 0% full and each one was assigned, 100, 75, 50, 25, 10 and 0 points respectively. For finding out feeding conditions, stomachs were grouped into full (100% full and 75% full stomachs), partially full (50% full and 25% full) and empty (less than 10% full). Seasonal variations in feeding intensity and feeding condition were analysed. The intensity of feeding in relation to the size of the species was carried out to study the differences in feeding in juveniles and adults.

Gastro-Somatic Index (GaSI) was calculated as per (Bhatnagar and Karamchandani, 1970) method:

$$\text{GaSI} = \frac{\text{Total weight of stomach}}{\text{Total weight of shrimp}} * 100$$

Based on the number of empty stomachs (0%full), the vacuity coefficient index (VI) was calculated with the following formula (Hyslop, 1980):

$$\text{Vacuity Index (VI)}: \frac{\text{ES}}{\text{TS}} * 100$$

where, ES — Number of empty stomachs (0% full), TS — Total number of stomachs examined

3.2.3. Stomach contents determination

The stomach contents were emptied into a petridish and examined under a stereoscopic microscope and identified to the possible taxonomic level. Stomach

contents of shrimps could rarely be identified to species level as they lost their structure due to the nibbling action of mandibles on the food and mastication of food by the gastric mill in the stomach. Therefore, the food items were categorized into crustaceans, fish, foraminifera, molluscs, detritus, sponge parts and sediments. Detritus consisted of decomposing organic matter beyond identification.

To obtain precise information regarding the volume of various items, the Index of Preponderance was worked out for males, berried and non-berried females separately based on the method of Natarajan and Jhingran (1961). The Index of Preponderance was calculated based on sex, maturity, season and size for the species.

$$\text{Index of preponderance } I = \frac{V_i O_i}{\sum V_i O_i} * 100$$

Where V_i and O_i represent the percentage of volume and percentage of occurrence indices of each food item respectively.

To explore the importance of various prey, the frequency of occurrence method described by Hyslop (1980), Williams (1981) and Kelleher et al. (2000) was used.

$$\text{Frequency of occurrence, } F = \frac{n}{N_s} * 100$$

where n = the number of stomachs containing a certain prey; N_s = the total number of stomachs examined. Only actively fed stomachs were used for this analysis.

3.2.4. Statistical Analyses

One-way Analysis of Variance (ANOVA) was carried out with the help of SPSS statistical software (version 23.0) to verify if the diet composition and feeding intensity varied according to sex, maturity stage, size and season. A

permutational multivariate analysis of variance (PERMANOVA) with 999 permutations was undertaken to evaluate possible differences in the diet components of *P. semilaevis* between sexes (male, berried and non-berried female), sizes (small, medium and large) and seasons (pre-monsoon and post-monsoon) and possible interactions between categories.

3.3. Results

3.3.1. Population structure

A total of 842 males, 1016 berried and 355 non-berried female samples were analysed for the present study. Frequency of individuals of different sizes in males, berried and non-berried females have been depicted in (Fig. 3.1). In the pre-monsoon specimens, carapace length (CL) ranged from 10-30 mm in males, 12-22 mm in berried females and 10-22 mm in non-berried females, while in the post-monsoon specimens CL ranged from 9-29 mm, 12-24 mm and 10-24 mm respectively. A considerable increase in size was observed in the berried females during post-monsoon.

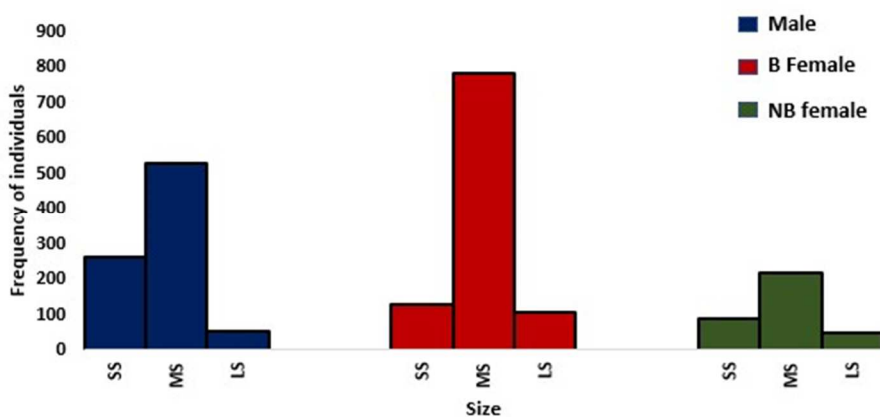


Fig. 3.1. Frequency of individuals of different sizes in males, berried and non-berried females of *P. semilaevis*. B, berried; NB, non-berried; SS, small sized; MS, medium sized; LS, large sized

3.3.2. Seasonal and sex-based feeding



Fig. 3.2. Seasonal variation in feeding intensity of males, berried and non-berried females of *P. semilaevis*. Post-M, Post-Monsoon; Pre-M, Pre-Monsoon

Points method based feeding intensity (FI) calculated showed the highest value for berried females (47.6). Male and non-berried females gave a value of 40.85 and 38.65 respectively. Feeding intensity reduced from pre-monsoon to post-monsoon in all three categories (Fig. 3.2). The highest difference was observed in males, 49.19 in pre-monsoon and 31.51 in post-monsoon. The highest feeding intensity was observed in pre-monsoon samples of berried females (51.41).

One-way ANOVA results revealed significant differences in the percentage of stomach fullness between sex, maturity and season (Table 3.1).

Table 3.1. Summary of the statistical analysis, one-way ANOVA, using percentage of stomach fullness in *Plesionika semilaevis* with sex, size, season and maturity

S.No.	Category	Variable	N	Degrees of freedom	p-value
1.	Sex	Male	842	2212	0.008
		Female	1371		
2.	Maturity	Berried	1016	1370	0.000
		Non- berried	355		
3.	Season	Male			
		Pre-Monsoon	432	842	0.000
		Post-Monsoon	411		
		Berried			
		Pre-Monsoon	708	1016	0.000
		Post-Monsoon	809		
		Non-Berried			
		Pre-Monsoon	145	355	0.045
		Post-Monsoon	211		
4.	Size	Male			
		Small	261	841	0.003
		Medium	529		
		Large	52		
		Berried			
		Small	127	1015	0.000
		Medium	782		
		Large	107		
		Non- berried			
		Small	88	354	0.014
		Medium	218		
		Large	49		

Feeding condition or percentage of stomach fullness in males, berried and non-berried females of *P. semilaevis* and its variation from pre-monsoon to post-monsoon period were observed separately (Fig. 3.3). Berried females showed a higher percentage of full filled stomachs (36.97%) compared to males (29.06%) and non-berried females (28.37%). As a result, the vacuity index (VI) was lowest for the berried females (15.54) than males (21.95) and non-berried females (25.56).

Seasonal variation studies revealed a decrease in values of stomach fullness from pre-monsoon to post-monsoon in *P. semilaevis*. From pre-monsoon to post-monsoon, full stomachs reduced from 35.88% to 21.41% in males, 40.11% to 29.13% in berried females and 33.1% to 24.64% in non-berried females. As a result, the vacuity index value from pre-monsoon to post-monsoon increased in males (12.50 to 32.85), berried females (12.85 to 21.68) and non-berried females (14.48 to 33.18).

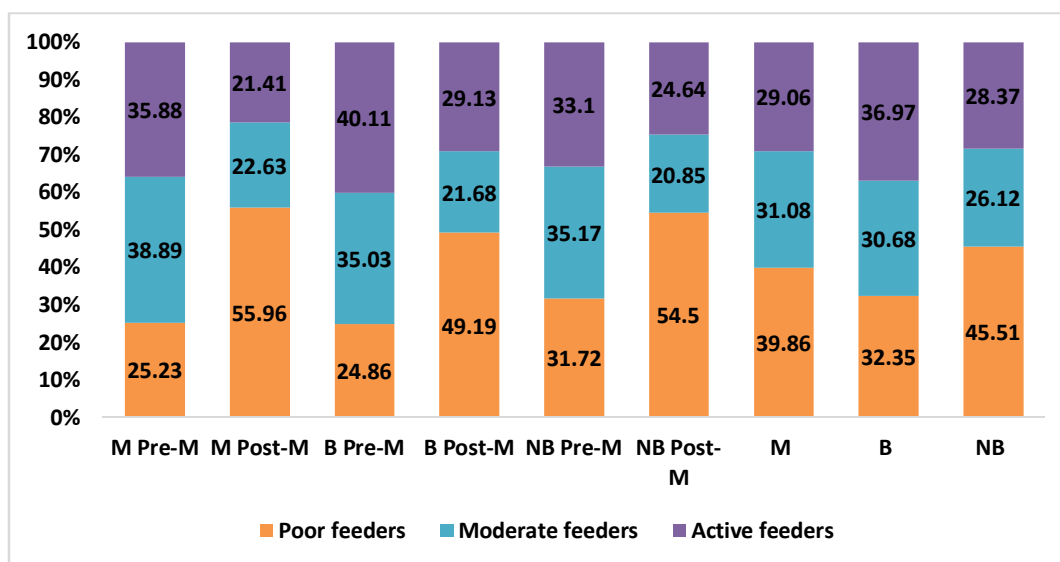


Fig. 3.3. The season-wise differences occurred in the percentage of active feeders, moderate feeders, and poor feeders in male (M), berried (B) and non-berried (NB) females of *P. semilaevis*. Post-M, Post-Monsoon; Pre-M, Pre-Monsoon

3.3.3. Ontogenic variations and feeding behaviour

Feeding intensity in different size groups of individuals of males, berried and non-berried females were analysed (Table 3.2). In males, the higher values of stomach fullness (42.97%) with a FI of 52.5 and VI of 14.06 were recorded for smaller-sized individuals (CL<15mm). The GaSI values ranged from 1.1 to 1.8 in males. Larger-sized males had the highest percentage of empty stomachs (42.3%).

Berried females had higher FI and lower VI values compared to the different size ranges of males and non-berried females. FI ranged from 51.7 in smaller ones to 45.6 in larger ones. GaSI values didn't vary considerably among different size groups of berried females.

Among non-berried females also, smaller ones had higher value of stomach fullness (40.9%) with a FI of 48.1 and VI of 17.1. Larger non-berried ones had higher percentage of empty stomachs (49%). GaSI ranged from 1.8 in smaller individuals to 1.1 in larger individuals.

ANOVA results of males, berried and non-berried females showed a significant variation in the percentage of stomach fullness among different size groups (Table 3.1).

Table 3.2. Ontogenic variation in feeding intensity, vacuity index, feeding condition and gastro-somatic index (GaSI) in males, berried and non-berried females of *P. semilaevis*.

Category	Size	Feeding Intensity (FI)	Vacuity Index (VI)	Empty stomachs (%)	Partially full stomachs (%)	Full stomachs (%)	GaSI
Male	Small	52.5	14.1	27.3	29.7	43.0	1.8
	Medium	43.0	22.2	37.8	29.9	32.3	1.6
	Large	36.0	28.9	42.3	34.6	23.1	1.1
Berried Female	Small	51.7	13.4	28.4	29.9	41.7	1.4
	Medium	47.2	15.8	31.8	31.8	36.4	1.4
	Large	45.6	15.9	42.1	21.5	36.5	1.7
Non-berried Female	Small	48.1	17.1	35.2	23.9	40.9	1.8
	Medium	36.2	27.4	48.0	26.5	25.6	1.5
	Large	35.5	30.6	49.0	26.5	24.5	1.1

3.3.4. Diet composition

Stomach contents recovered from the foregut of shrimps were thoroughly masticated and thus identification of food items was mainly based on broken body parts and skeletal remains. Various components in the stomach content were identified and categorized into the following groups: crustacean remains, fish remains, mollusc remains, detritus, foraminifera and sponge parts (Fig. 3.4). Unidentifiable mass consisting of decomposed plant and animal matter were categorized as 'detritus', and were dominant in the gut contents of both males and females. This was followed by crustacean remains (small crabs, shrimps, amphipods, copepods and euphausiids) and foraminifera. Major foraminifera identified to belong to the families Planulinidae (*Hyalinea* spp, *Planulina* spp), Nonionidae (*Pseudononion* spp), Epistomariidae (*Pseudoeponides* spp), Amphisteginidae (*Amphistegina* spp), Ammoniididae (*Ammonia* spp.), Bolivinidae (*Bolivina* spp), Buliminidae (*Bulimina* spp.) and Uvigerinidae (*Uvigerina* spp.). Foraminifera were identified at the genus level because of their smaller intact size and the presence of tough shells or tests. Fish remains (Fish bones, spines, scales

and fish eggs) constituted a minor portion of the diet while sediments, molluscs (bivalves, gastropods, etc.) and sponges were consumed in lower abundance throughout the study period. Some incidental preys observed were polychaetes and phytoplanktons.

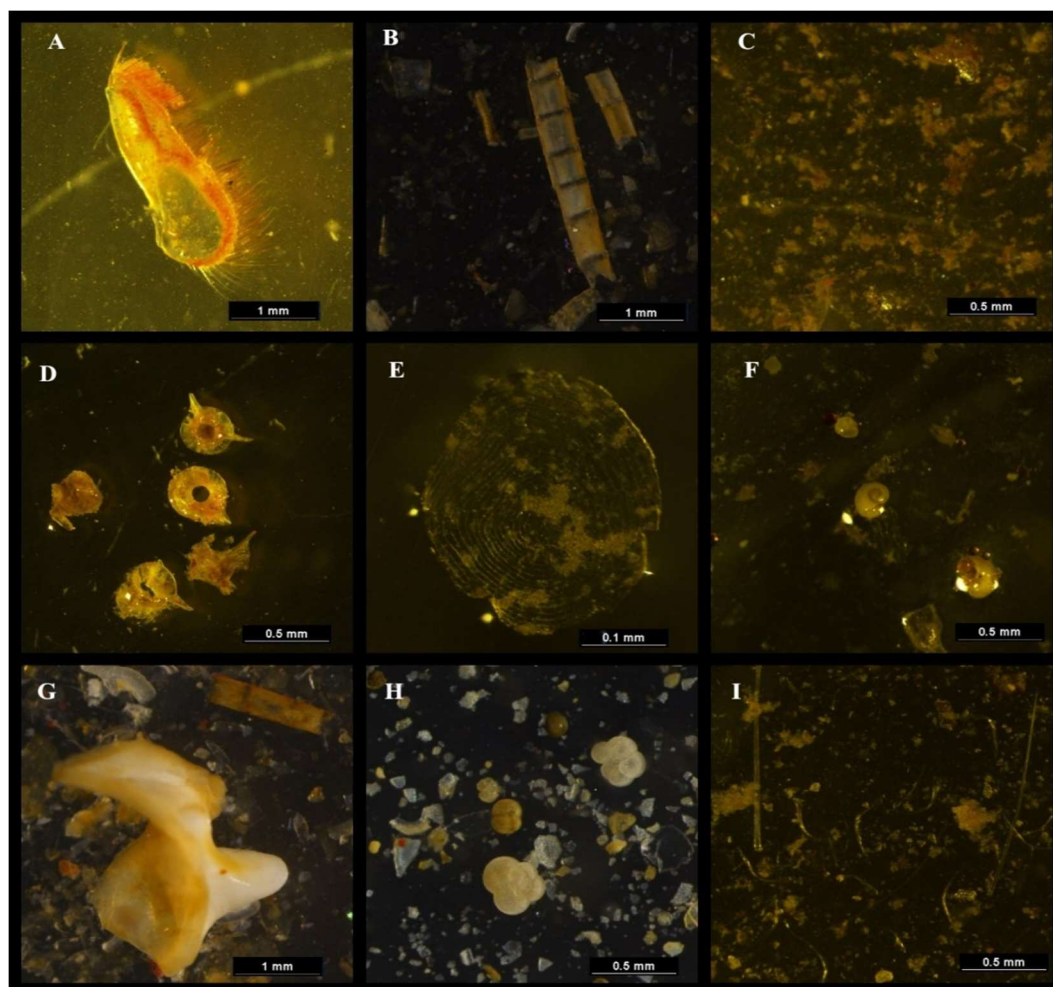


Fig. 3.4. Diet compositions of *Plesionika semilaevis* A, B: crustacean remains; C: detritus; D, E: fish remains; F, G: mollusc remains; H: foraminifera; I: sponge spicules

Index of preponderance values (Fig. 3.5) indicates that detritus contributed the major part of stomach contents of males (43.52), berried females (40.48) and non-berried females (47.31). Crustacean remains formed a higher proportion in berried females (35.21) than in males (34.10) and non-berried females (26.24). Foraminifera was found invariably in all the stomachs and ranked third with an index of 17.59, 17.42 and 18.02 in males, berried females and non-berried females respectively. However, fish remains were present in a few larger specimens of male and female. Sponge parts and sediments were present in the male, berried and non-berried females in meagre quantity. Mollusc remains were present in the lowest proportion in all categories with the least index values. Frequency of occurrence analysis revealed that crustaceans, foraminifera and detritus were the most preferred diet in almost all individuals (>92%) while fish remains were present in about 35% of individuals. Sediment, mollusc and sponges were present in <30% of individuals. Analysis of variance (ANOVA) of diet composition among males and females revealed no significant differences (Table 3.3). However, significant variation ($p < 0.05$) was exhibited between berried and non-berried females for all food contents except foraminifera (0.911) and detritus (0.104).

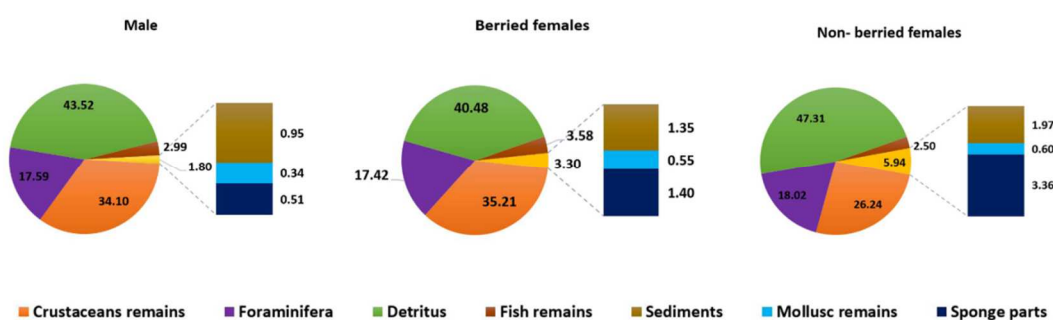


Fig. 3.5. Relative importance of major groups of food items found in the stomach of male, berried and non-berried females of *P. semilaevis*

Table 3.3. Summary of the statistical analysis, one-way ANOVA, using diet components in *P. semilaevis* with sex, maturity, season and size. B, Berried females; NB, Non-berried females, Pre-M, Pre-Monsoon; Post-M, Post-Monsoon; DF, degrees of freedom

Category	Variable	N	DF	p-value						
				Crustaceans	Foraminifera	Detritus	Fish remains	Sediments	Mollusc remains	Sponge parts
Sex	Male	204								
	Female	295	498	0.414	0.855	0.084	0.601	0.146	0.243	0.000
Maturity	B	217								
	NB	78	294	0.000	0.911	0.104	0.010	0.000	0.040	0.000
Season	Male									
	Pre-M	121								
	Post-M	75	195	0.000	0.418	0.000	0.003	0.551	0.332	0.104
	B									
	Pre-M	155								
	Post-M	80	234	0.000	0.837	0.008	0.574	0.117	0.022	0.000
Size	NB									
	Pre-M	35								
	Post-M	42	76	0.000	0.147	0.000	0.017	0.079	0.422	0.146
	Male									
	Small	54								
	Medium	134	199	0.006	0.005	0.041	0.000	0.018	0.030	0.188
Size	Large	12								
	B									
	Small	32								
	Medium	156	214	0.007	0.001	0.112	0.003	0.000	0.000	0.174
	Large	27								
	NB									
Size	Small	19								
	Medium	44	75	0.020	0.005	0.000	0.001	0.000	0.001	0.970
	Large	13								

3.3.5. Seasonal variation in diet composition

The detritus found in the stomach was more for males, berried and non-berried females during the post-monsoon period (57.66, 50.36 and 55.24)

compared to the pre-monsoon period (36.31, 37.38 and 31.49). On the contrary, the index values for other major components like crustacean remains, foraminifera and fish remains decreased from pre-monsoon to post-monsoon in all three categories (Fig. 3.6). Minor constituents of the gut like sediments, mollusc remains and sponge parts didn't follow a particular trend in seasonal analysis. Crustaceans, foraminifera and fish remains were present more in the gut of individuals examined in pre-monsoon. Mollusc remains, sponge parts and sediments were present in less quantity in the guts of shrimps during both seasons. Analysis of variance revealed significant variation in diet composition of males, berried and non-berried females from pre-monsoon to post-monsoon. In berried females $p < 0.05$ was observed for all components except foraminifera, fishes and sediments (Table 3.3). In males and non-berried females $p < 0.05$ was observed for crustaceans, detritus and fish remains.

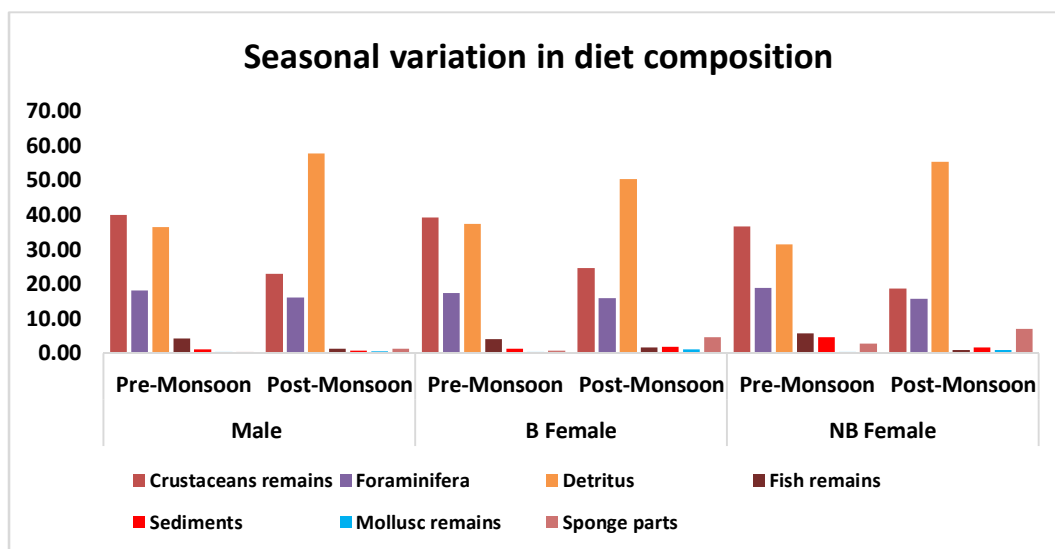


Fig. 3.6. Pre-monsoon and post-monsoon variation in the index of preponderance values of various diet components of *P. semilaevis*.

3.3.6. Ontogenic variations in diet composition

In males, berried and non-berried females, diet composition varied considerably with an increase in size (Fig. 3.7). The percentage of crustaceans, fish and mollusc remains increased with an increase in the size of the individuals, while the percentage of foraminifera and sediments decreased with an increase in size. Amphipods, copepods and euphausiids were present more in smaller sized individuals while broken parts of shrimps and crabs were present more in larger sized individuals. Detritus and sponge parts were present in similar portions in all the size groups. Detritus constituted the major content of diet among all size groups of individuals.

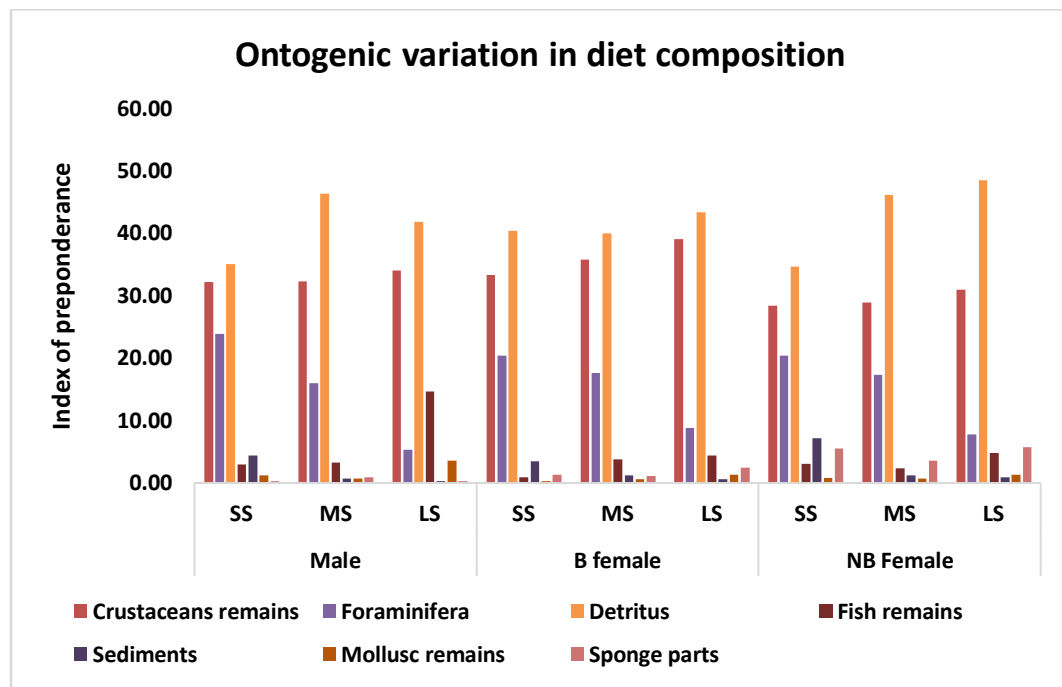


Fig. 3.7. Ontogenic variations in the index of preponderance values of various diet components of male, berried and non-berried females of *P. semilaevis*. SS, small sized; MS, medium sized; LS, large sized

With an increase in size in the individuals of *P. semilaevis* the frequency of occurrence of larger prey like crustaceans (96% to 100%), fish (15% to 46%) and mollusc (12% to 33%) increased in the diet (Fig. 3.8). Similarly, the presence of foraminifera (100%) and sediment (63%) was more frequent in the young ones compared to larger ones.

In males and non-berried females, ANOVA revealed a significant variation in diet composition for different size groups ($p < 0.05$) for all the components except for sponges (Table 3.3). While in the case of berried females diet components showed a significant difference of $p < 0.007$ except for detritus and sponge parts.

The PERMANOVA test showed that there were significant differences in the diet between the seasons, sex and size (Table 3.4). Also, there were significant differences in the interaction between sex and size and between sex and season.

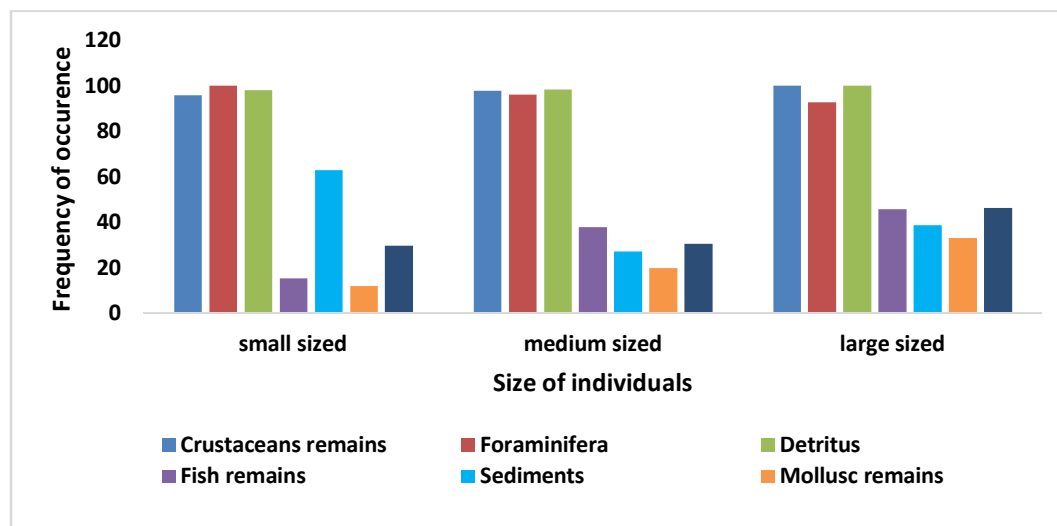


Fig. 3.8. Frequency of occurrence of various diet components in different-sized individuals of *P. semilaevis*

Table 3.4. Results of the PERMANOVA (Permutational multivariate analysis of variance) analysis of the diet components of *P. semilaevis* between sexes (male, berried and non-berried female), sizes (small, medium and large) and seasons (pre-monsoon and post-monsoon). F, Fisher's F statistic; r, similarity among groups; P, probability values.

Factor	F	r	P(>F)
Sex	11.819	0.04260	0.001
Season	27.205	0.04903	0.001
Size	9.0214	0.03485	0.001
Sex: Season	11.911	0.04115	0.001
Sex: Size	4.1886	0.01618	0.003

3.4. Discussion

The feeding ecology of *P. semilaevis* reveals the influence of both environmental (seasonal) and biological (sex, maturity, size) factors on the diet composition and feeding intensity. The overall percentage of empty stomachs is high in this species, similar to other deep-sea pandalid shrimp (Fanelli and Cartes, 2004; Radhika and Kurup, 2011). Deep-sea trawling is done during the morning hours and these deep-sea shrimps are reported to be nocturnal feeders (Kapiris, 2012), which can be attributed to the higher percentage of empty stomachs in the studied groups. Moreover, a high percentage of empty stomachs is an indication of high metabolic rates or low feeding rates (Kapiris, 2004). The low feeding condition in deep-sea caridean shrimps may be an adaptation to the deep-sea environment, where food act as a limiting factor (Jumars and Gallagher, 1982).

Female shows higher feeding intensity than males because of sexual dimorphism and increased growth rates. *Plesionika* spp. is reported to have a continuous reproduction pattern with seasonal peaks (Company and Sarda, 1997; Colloca, 2002; Maiorano et al. 2002; Vafidis et al. 2005). Berried females of *P.*

semilaevis were present during both pre-monsoon and post-monsoon and were having higher values of stomach fullness compared to males and non-berried females. For caridean deep-sea shrimps, many authors describe higher feeding activity (higher values of stomach fullness) for berried females, because of the increased metabolic demands after spawning (Maynou and Cartes 1998; Cartes et al. 2008, Kapiris et al. 2010). This could be because of the lesser feeding activity observed in caridean shrimps during gonadal development when the space in the cephalic cavity for the stomach is compromised due to fully developed ovaries affecting their food intake directly (Weinberg, 1980; Radhika and Kurup, 2011).

The decreasing feeding intensity from pre-monsoon to post-monsoon season detected in both sexes and maturity stages could be associated with environmental processes. The seasonal rhythms in feeding behaviour of *P. semilaevis* and monsoon related variation in feeding intensity can be ascribed to the upwelling, an oceanographic phenomenon occurring in the eastern Arabian Sea that replaces the warmer nutrient deplete surface water with dense cooler nutrient rich bottom water (Johannessen et al. 1987; Smitha et al. 2014).

Ontogenetic shifts in feeding behaviour were also apparent in males, berried and non-berried females of *P. semilaevis*. Juveniles showed an increased feeding intensity compared to adult ones as they have faster growth rates and higher energy requirements (Kapiris and Thessalou-Legaki, 2011).

Plesionika species are distributed mainly in subtropical and tropical waters (Chace 1985), and a majority of these species feed on both pelagic and benthic resources (Cartes, 1998; Cartes et al. 2002). The species grind their food and ingest only small fragments, hence from the state of the gut contents most prey could only be identified at a higher taxonomic level. The diet component mostly consists of endobenthic (foraminifera, bivalves, sediments etc.), epibenthic (amphipods, euphausiids, gastropods, etc.) and bathypelagic organisms (small

decapods and fishes) (Fig. 3.6) similar to the diet of other deep-water shrimps found in Indian waters (Karuppasamy and Menon, 2004; Radhika and Kurup, 2011; Paramasivam et al. 2020). This may be because of the resemblance in the faunal assemblages of the macro-benthic communities persisting on the continental slopes of the region. Based on the results of the present study, *P. semilaevis* can be considered as having a diversified diet because of their wide trophic niche.

Decapod crustaceans are generally considered scavengers or detritivores (Gage and Tyler, 1991). Scavenging is an important facultative foraging mode for deep-sea shrimps. The results of the present study indicate that detritus formed the major percentage of gut contents similar to those reported for other deep-sea shrimp species (Burukovskij, 1992; Karuppasamy and Menon, 2004; Radhika and Kurup, 2011). The protein-energy ratio is highest in the detritus than in any other factor in the biota (Julian *et al.* 2003). The other food items observed are crustacean remains, foraminifera, fish remains, mollusc remains, sediments and sponge parts similar to those reported in other *Plesionika* species such as *P. edwardsi*, *P. narval*, *P. heterocarpus*, *P. ensis*, and *P. martia* (Labropoulou and Kostikas, 1999; Fanelli and Cartes, 2004; Kitsos et al. 2008). The presence of detritus, foraminifera and sediment in the gut indicated a possible benthic feeding activity and scavenging nature while the presence of broken parts of shrimps and fishes suggests its good swimming ability evidencing that it also feeds on benthopelagic forms.

Ontogenetic shifts in diet were apparent in *P. semilaevis* among small, medium and large-sized individuals. Among males, berried and non-berried females, larger prey like fishes, molluscs and crustaceans were preferred more by medium and large-sized individuals, forming effective predators due to their good swimming capability and larger size mandibles. Foraminifera, sediments and

smaller crustaceans were more consumed by smaller sized individuals. With an increase in size, individuals cease to consume sediment and smaller prey and switch their diet to larger and energetic prey, such as fishes. This broad ecological niche width indicates that *P. semilaevis* play a critical role in deep-sea food webs as an intermediate trophic level organism.

3.5. Conclusion

This study provides the first examination of the diet composition of deep-sea shrimp *Plesionika semilaevis* in the South Eastern Arabian Sea and the influence of environmental and biological parameters on its feeding behaviour. These species have a diversified diet ranging from smaller foraminifera to larger fishes and crustaceans and can be considered generalist feeders. Scavenging is an important facultative foraging mode observed in this species. Berried females have more feeding intensity than non-berried females and males. Juveniles have more energy requirements hence increased feeding was observed in them compared to adults. The larger individuals consumed more energetic prey like crustaceans, fishes and molluscs as compared to the smaller ones that had a more sedentary diet like detritus and foraminifera. *P. semilaevis* have higher feeding intensity during the pre-monsoon period. The monsoon dependent variation in feeding intensity may be the response of benthopelagic organisms like crustaceans to seasonal oceanographic phenomena such as upwelling and vertical mixing.

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Reproductive traits, dynamics of oogenesis and embryonic developments in the deep-sea shrimp *Plesionika semilaevis* from the southeastern Arabian Sea

<i>Contents</i>	4.1. <i>Introduction</i>
	4.2. <i>Materials and Methods</i>
	4.3. <i>Results</i>
	4.4. <i>Discussion</i>
	4.5. <i>Conclusion</i>

4.1. Introduction

Commercial fisheries are expanding into deeper waters, and the paucity of information on the life histories of the deepwater species being fished is considered a significant barrier to developing and implementing effective management strategies. The specific life-history characteristics of many deep-sea organisms like longer life span, slow growth, late sexual maturity and low fecundity make them especially vulnerable to depletion with a limited potential to rebound from overexploitation (Cheung et al. 2005; Morato et al. 2006). The dearth of life history information for the exploited deep-sea species poses a significant obstacle to the development and use of effective management strategies (Polidoro et al. 2008).

The fecundity, sex ratio, gonadal and embryonic development and periodicity are essential variables to consider when evaluating the recruitment, reproductive potential, biogeographic dispersion, adaptations to specific habitats and connectivity of marine species (Chemel et al. 2023). A species' life strategy is

directly linked to its reproductive behavior. Inadequate environmental conditions in deep-sea environments, such as lack of seasonality in temperature, photoperiod, and food availability, result in low reproductive success (Bauer, 2004).

Pandalidae, a family of tropical-water dwelling deep-sea shrimps, have distinctive growth and reproduction habits. Even within the same genus, pandalid species exhibit a diversity of sexual systems (gonochorism and hermaphroditism) and kinds of reproduction (semelparity and iteroparity). As a result, reproductive strategies vary greatly among pandalid species (Correa and Thiel, 2003; Bauer, 2004). Genus *Plesionika*, under the family Pandalidae represents a significant group of deep-sea caridean shrimps represented by more than 100 species distributed worldwide. A characteristic feature of many pandalid shrimps is the energy they allocate for egg production (Corey and Reid, 1991; Wehrtmann and Lardies, 1999). The energy and nutrients found in the egg help the embryos survive and develop, thus having a significant impact on the life-history characteristics of invertebrates (Begon et al. 1996; Figueiredo et al. 2008). A fair amount of information is available regarding the reproductive biology of *Plesionika* species found in various temperate and subtropical climates, however, there exists a knowledge gap when it comes to tropical waters. Significant reproductive studies of *Plesionika* species are of *P. heterocarpus*, *P. edwardsii*, *P. narval*, *P. gigliolii*, *P. martia* and *P. acanthonotus* from the Mediterranean Sea (Company and Sarda, 1997; Colloca, 2002; Maiorano et al. 2002; Anastasopoulou et al. 2017), *P. izumiae* from the Japanese waters (Omori, 1971; Ahamed and Ohtomi, 2011), *P. martia* from Ionian Sea (Chilari et al. 2005) and *P. edwardsii* from the Tyrrhenian Sea and North Atlantic (Possenti et al. 2007; Triay-Portella et al. 2017). Despite the increasing commercial interest in *Plesionika* species in Indian waters, contributing to 21% (*P. semilaevis* and *P. quasigrandis*) of the deep-sea shrimp catches (Chakraborty et al. 2022a), aspects of the reproductive biology of these species remain almost unknown.

Plesionika semilaevis Spence Bate, 1888 is one of the commercially and ecologically important deep-sea shrimp species found at a depth of 250 meters and above in the southeastern Arabian Sea, contributing 1.23% of the deep-sea shrimp catches in the south-west coast of India (Chakraborty et al. 2022a). It plays a critical role in deep-sea food webs as an intermediate trophic-level organism (Sreelakshmy et al. 2023). A study done by Ohtomi (1997) described the reproductive parameters like brood size and reproductive period of *P. semilaevis* from Kagoshima Bay and is the only report available on the reproductive aspects of this species. Detailed studies on the reproductive biology of *P. semilaevis* including ovarian and embryonic development from Indian waters and any other geographical area with its distribution are lacking.

Information on ovarian maturation, embryo development, reproductive period, and brood size is beneficial from a fisheries perspective for understanding the reproductive biology of the species, estimating reproductive potential, and recruitment for maintaining the species' population stability (Mori et al. 1998; Figueiredo et al. 2008; Kevrekidis and Thessalou-Legaki, 2013). Against this background, this study aims to investigate the detailed aspects of the reproductive biology of *P. semilaevis* along with the developmental stages of the ovaries and embryos by macroscopic and microscopic analysis. The study also sought to determine the species' spawning season, which will give the essential prerequisite for stock assessment and stock sustainability and establish successful fishery management.

4.2. Materials and methods

4.2.1. Sampling

Samples of deep-sea shrimps were collected fortnightly between August 2019 and May 2022, except during the monsoon ban period (June to August) from about 5-6 deep-sea bottom trawlers during each sampling. The trawlers have an overall length of 15-40 m and are powered with high horse power engine (350 - 500 hp). They were operated at a depth of 150–250 m in the southwest coast of India, with a 25–26 mm mesh size in its cod-end. The samples were transported in fresh condition in an insulated ice box to the laboratory for further analysis. Morphological identification of *P. semilaevis* followed the taxonomic keys of Chace (1985), Ohtomi and Hayashi (1995), Chan and Crosnier (1997), Ahamed et al. (2017), Kuberan et al. (2020) and Chan et al. (2020). By examining the morphology of the endopod of the first pair of pleopods, the sex of an individual was determined (King and Moffitt, 1984). The females were sorted into ovigerous and non-ovigerous states based on the presence of embryos between the pleopods. Carapace length (CL) and total length (TL) were measured to the nearest 0.01 mm using calipers. An electronic digital balance with a 0.001 g precision was used to measure the body weight (BW).

4.2.2. Gametogenesis and stages of ovarian development

Macroscopic and microscopic examination was used to establish the stages of female gonadal development. For macroscopic analysis, all individual shrimps were dissected and their ovaries were examined under a stereoscope and categorized into five developmental stages based on location in the cephalothoracic cavity, shape, size, and relative intensity of the color of ovary (Maiorano et al. 2002; Anastasopoulou et al. 2017; Triay-Portella et al. 2017). The mature ovary occupied most of the cephalothoracic cavity's dorsal region, extending anteriorly to the orbital margin visible over the carapace as blue head roe.

Microscopic analysis of each development stage of ovaries was carried out by selecting 10 specimens from each stage. The ovary was removed and fixed in 5% formalin for 24 hours for additional histological examination. The fixed tissues were dehydrated in ethanol solutions, cleared in xylene, embedded in paraffin and sliced into 5-6 µm sections. The sections were stained with hematoxylin followed by eosin (Triay-Portella et al. 2014) and mounted for further microscopic analysis. The developmental changes in the ovary were observed using a compound microscope (Leica DM 750) at a magnification of 4x-100x. The oocytes were classified into different developmental stages based on the size of cells, cytoplasmic appearance and presence of lipid globules and yolk granules.

4.2.3. Stages of embryo development, brood size and embryo size

All females were examined for the presence of different stages of embryos attached to the pleopods. The embryos were carefully separated from the pleopods and categorized into four stages based on the color of the embryos. These embryos were then observed under a stereoscopic microscope (Nikon SMZ1270, Japan) to observe the different changes in embryos with development.

The total weight of embryos was weighed to the nearest 0.001 g, a subsample was weighed, and the number of embryos was counted under a binocular microscope. The brood size was estimated for ovigerous females with embryos in different stages of development as follows:

Brood size

$$= \frac{\text{Number of embryos in the subsample} * \text{Total weight of the embryos}}{\text{Weight of the subsample}}$$

The variations in brood size relative to the body size (CL) of females carrying embryos at different developmental stages was also determined. For each

stage of embryo development, the sizes of the embryos were calculated using a total of 100 ovigerous females of each stage. The major (length) and minor (width) axes of 10–20 randomly chosen embryos of each individual were measured under a stereomicroscope with an ocular micrometer to the nearest 0.01 mm. Each individual's mean embryo length and width were calculated and finally, mean embryo sizes (length and width) for each embryonic stage were computed. Embryo volume (v) was estimated for each embryonic stage using the formula given by Turner and Lawrence (1979):

$$\text{Embryo volume (v)} = \pi d_1^2 d_2 / 6$$

where d_1 is the minor axis (mm) and d_2 is the major axis (mm).

One-way analysis of variance (ANOVA) was carried out with the help of SPSS statistical software in order to determine the variation in developmental stages with embryo size (length, width and volume) and female body size (CL).

4.2.4. Reproductive period, sex ratio, GSI and size at sexual maturity

The reproductive period was investigated by considering the percentage of ovigerous females and their maturity stages of ovaries and embryos. The frequency of females with various stages of embryo development was noted month-wise to estimate the spawning and hatching periods. Monthly variation in the sex ratio (females / males) was also calculated and their deviation from the expected 1:1 were tested using the chi-square analysis.

Gonad weight (GW), of females were taken to the nearest 0.001 g, and the gonadosomatic Index (GSI) was calculated as the percentage weight of the gonad to the total body weight (Grant and Tyler, 1983).

Size at sexual maturity (CL₅₀) was determined based on two factors, i.e., the CL length at which 50% of females are ovigerous (CL_{50em}) and the CL at which 50% of the females have mature ovary (CL_{50ov}) (Triay-Portella et al. 2017).

This was estimated by a logistic equation as described by King (1995): $P = 1/1 + \exp(a + b * CL)$, (R Studio, version 4.1.1.).

where P is the predicted proportion of ovigerous females / females with matured ovaries, a and b are the estimated coefficients of the logistic equation, and CL is the carapace length.

4.3. Results

4.3.1. Size structure

Males and females are sorted out based on the morphological sexual differences between them. Sex was determined based on the shape of the endopod of the first pleopods. The endopod of females has a pointed leaf-like structure, while that of males has a blunt rectangular shape. A total of 997 males and 1802 females consisting of 1233 ovigerous and 569 non-ovigerous individuals were examined for this study. Ovigerous females had a CL range of 12-24mm (TL 72-135mm) and non-ovigerous females had a CL range of 10-24mm (TL 70-132mm).

4.3.2. Gametogenesis and ovarian development

Ovaries are paired organs with a tubular structure and bilateral symmetry located dorsally in the cephalothoracic cavity overlying the digestive gland. Significant macroscopic variations were observed in the ovaries and categorized into five stages based on the relative intensity of color, size and position of the ovaries (Fig. 4.1). The GSI values ranged between 0.093 to 4.33. Histologically ovary consists of several layers of developing oocytes encased by a thin gonadal wall. Oogonia, early previtellogenic oocyte, late previtellogenic oocyte, early vitellogenic oocyte, late vitellogenic oocyte and atretic oocyte are the different stages of oocyte development. These phases could be distinguished by their differences in cell size, shape, cytoplasmic appearance, accumulation of yolk granules, and presence of lipid globules in the cytoplasm.

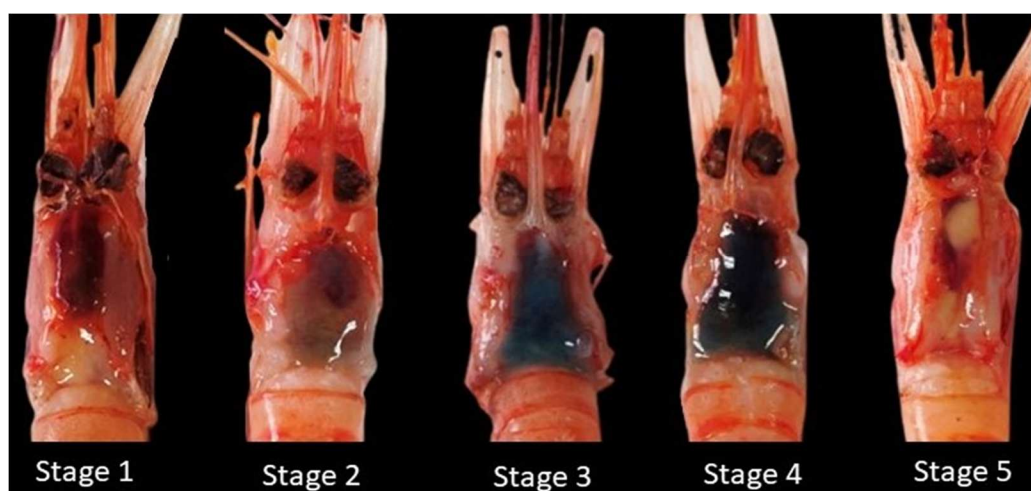


Fig. 4.1. Macroscopic variation in different stages of ovarian development

Stage 1 refers to immature females with thin translucent cream-colored gonads that are not visible through the carapace and weigh between 0.002 g to 0.01 g. The GSI values ranged between 0.093-0.25. Ovaries at stage 1 present a predominance of oogonia and early previtellogenic oocytes. Oogonia were spherical cells found in clusters in the center of ovaries known as germinal zone (Fig. 4.2a) and had a diameter of 0.004-0.005 mm, possessed a large and well-defined nucleus, non-evident nucleolus, homogenous thin rim of basophilic cytoplasm without granulation and strongly reactive to hematoxylin (Fig. 4.2b). Early previtellogenic oocytes are spherical with a diameter of 0.02-0.03 mm were round to elliptical with thin granulation in the cytoplasm (Fig. 4.2c). They have a smaller nucleus, visible nucleoli and are less basophilic than oogonia. Although follicular cells are present, they aren't associated with the oocytes (Fig. 4.2d).

Stage 2 refers to developing females with pale creamy blue gonads visible through the carapace weighing 0.009 g to 0.06 g. The GSI values ranged between 0.66-1.38. The ovaries appear more turgid and histologically disorganized, with abundant connective tissues. Oogonia, early previtellogenic oocytes, late previtellogenic oocytes and follicle cells were observed. Follicle cells do not appear to be associated with the oocytes. Late previtellogenic oocytes are basophilic, semi-spherical, and a little larger, with a diameter of 0.045-0.055 mm. The nucleus is large, with nucleoli visible in the interior (Fig. 4.2e).

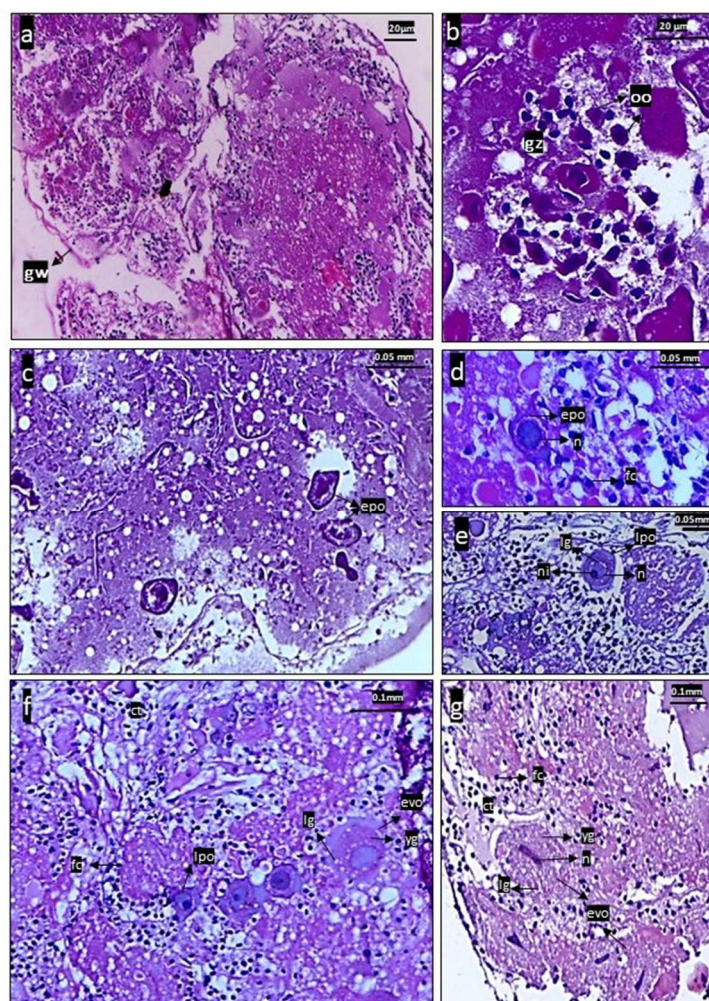


Fig. 4.2. Histological sections of different stages of ovary of *P. semilaevis*: Stage 1 (a,b), Stage 2 (c,d,e), Stage 3 (f,g); gz, germinal zone; oo, oögonium; epo, early previtellogenic oocyte; n, nucleus; ni, nucleoli; fc, follicular cells; lpo, late previtellogenic oocyte; evo, early vitellogenic oocyte; lg, lipid globules; ct, connective tissue; yg, yolk granules

Stage 3 refers to early mature females with light blue ovaries weighing between 0.029 g to 0.12 g, clearly visible through the exoskeleton. The GSI values ranged between 1.67-2.43. At stage 3, the ovaries had two distinct zones: the central germinal zone, which contained oögonia, early and late previtellogenic oocytes, and the peripheral growth zone, which included late previtellogenic

oocytes, early and late vitellogenic oocytes associated with the follicle cells. During vitellogenesis, the ooplasm becomes acidophilic due to the accumulation of yolk granules, which results in a pink stain. Early vitellogenic oocytes had a diameter of 0.1-0.2 mm and were marked by vitellogenic granulations, lipid globules and a thick chorion (Fig. 4.2f). Lipid globules have a transparent appearance and are primarily observed in the central part of the cell, while yolk granules have an opaque appearance and are distributed evenly (Fig. 4.2g). Late vitellogenic oocytes are the largest cells with a diameter of 0.3-0.5 mm and a granular appearance due to an abundance of yolk granules and lipid globules.

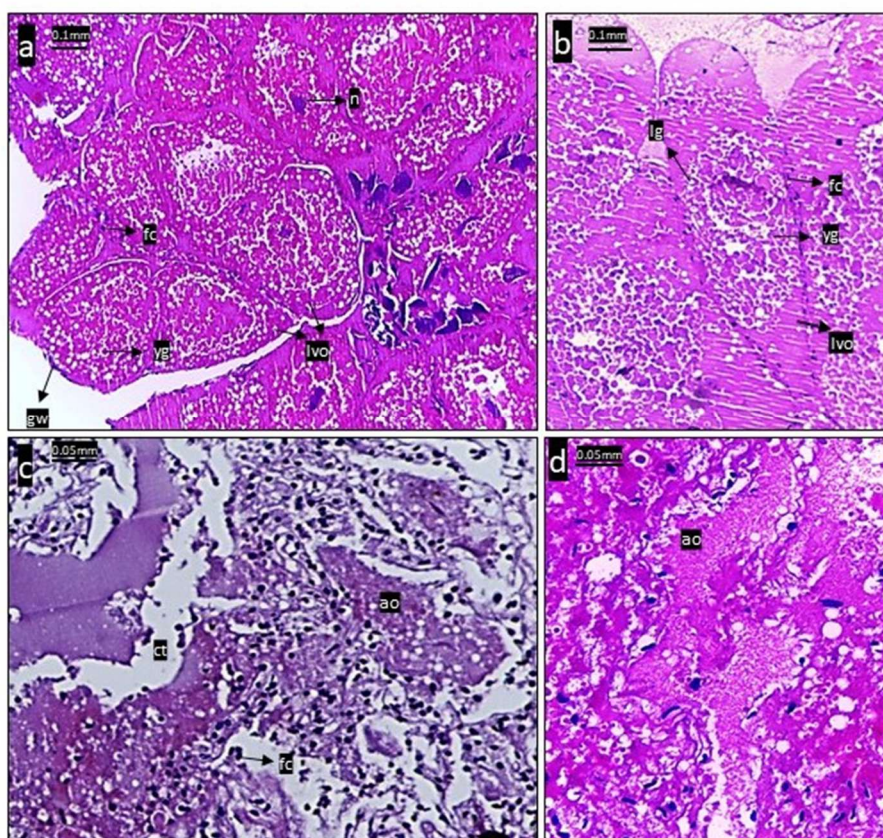


Fig. 4.3. Histological sections of different stages of ovary of *P. semilaevis*: Stage 4 (a,b), Stage 5 (c,d); fc, follicular cells; gw, gonadal wall; lvo, late vitellogenic oocyte; lg, lipid globules; ct, connective tissue; yg, yolk granules; n, nucleus; ao, atretic oocytes

Stage 4 refers to fully mature females with dark blue head roe. The ovaries are dark bluish-black in color, turgid and occupying the entire space in the cephalothoracic cavity extending up to the abdomen, weighing between 0.08 g to 0.22g. The GSI values ranged between 3.0 to 4.33. At stage 4, ovaries revealed a confined germinal zone enveloped by advanced late vitellogenic oocytes. Late vitellogenic oocytes are large and irregularly shaped, with cytoplasm wholly filled with dense yolk granules and lipid globules, hindering the visualization of the nucleus (Fig. 4.3a, b). At this point, oocytes have grown to their entire size and are encircled by a layer of flattened follicle cells.

Stage 5 refers to spent females with cream-colored flaccid ovaries. These ovaries have an unorganized appearance and are distinguished by the abundance of connective tissue, follicular cells, and atretic oocytes that are undergoing reabsorption (Fig. 4.3c). Atretic oocytes in the reabsorption process can be easily identified by vacuolated cytoplasm (Fig. 4.3d). Even though the immature and spawned stage ovaries have similar coloration, the presence of atretic oocytes is the primary feature that allows for microscopical differentiation between the two stages. The proportion of oogonium also increases in this stage.

4.3.3. Stages of embryo development, brood size and embryo size

Four different stages of eggs with distinct color variations were observed by morphological examination (Fig. 4.4). In stage I, the embryos are bright blue in color, lacking eye pigmentation. Yolk filled 80-100% of the embryo volume. In stage II, the embryos have a bluish-green appearance. Minute eye pigmentations are visible under the microscope but not to the naked eye. Ventral cleft starts to appear with the visible demarcation of cephalothorax and abdomen. In stage III, embryos are pale olive-green colored with eye pigmentation clearly visible. Embryos have large cephalothoraces, extended abdomen, visible segmentation, rudimentary appendages and distinctly clear ventral cleft. In stage IV, embryos brown-colored appearance because of the mucous-like substance holding the embryos together. The embryos are ready to hatch, with their segmentations completed and eye spots fully pigmented.

The overall mean brood size ($\pm$ SD) was 6413 ± 2457 (ranging from 2093 to 12887). The brood size also varied based on the different stages of the development of embryos. The females with stage I and stage II embryos (non-eyed stages) had the highest brood sizes 8324 ± 2076 (4166-12887 embryos) and 6981 ± 1866 (4068-11291) embryos respectively. The embryos were more compact and clustered together tightly. Significant embryo loss was observed during the development of the embryos. In stage III and stage IV (eyed stages), the brood size was reduced to 5179 ± 1265 (3004-8411) and 3449 ± 970 (2093-6048) embryos respectively. Embryo loss was estimated to be 59.6% from stage I to stage IV embryos.

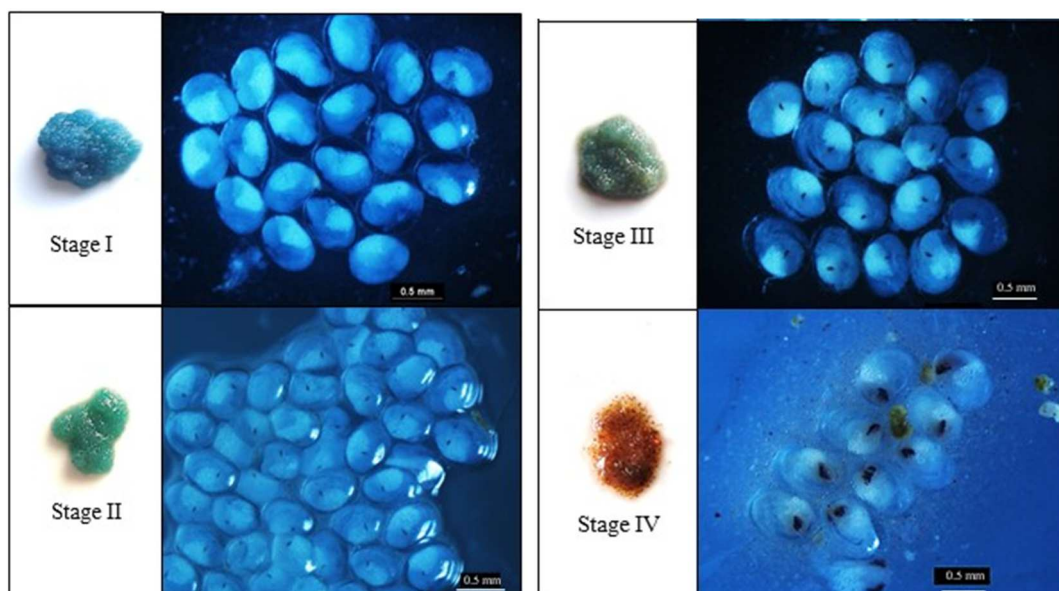


Fig. 4.4. Macroscopic (left column) and microscopic (right column) variation in different stages (I-IV) of embryo development in *P. semilaevis*

The brood size increased significantly with the female sizes for all the stages of embryo development. The maximum brood size was 7502 for smaller individuals (CL 12-15 mm), 10813 for medium-sized individuals (CL 16-19 mm) and 12887 for larger individuals (CL 20-24mm). A significant positive correlation was observed between the brood size of embryos at different developmental stages and carapace length (Fig. 4.5).

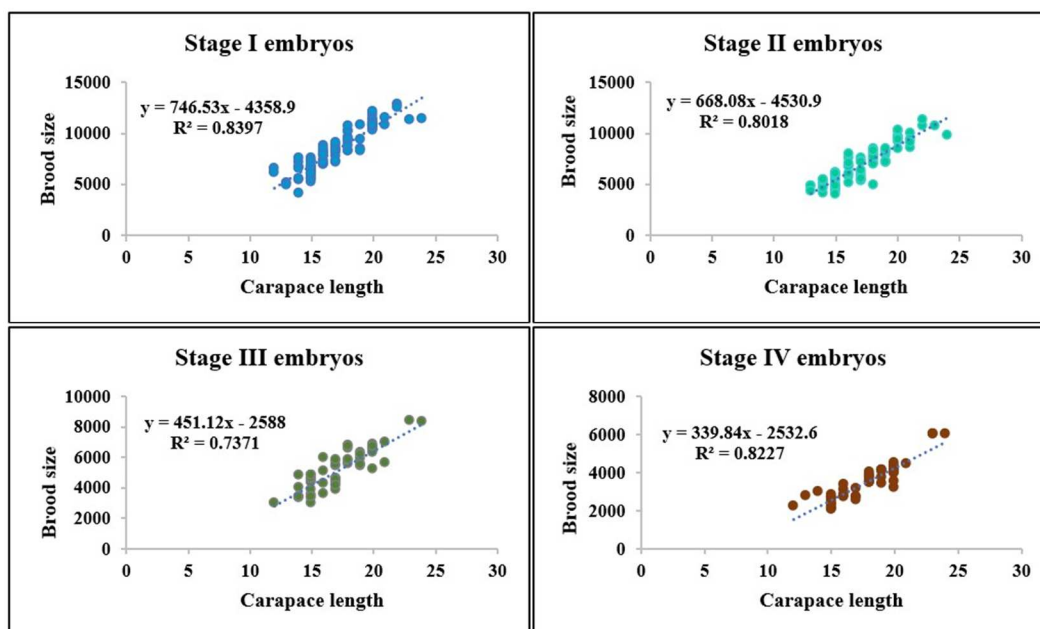
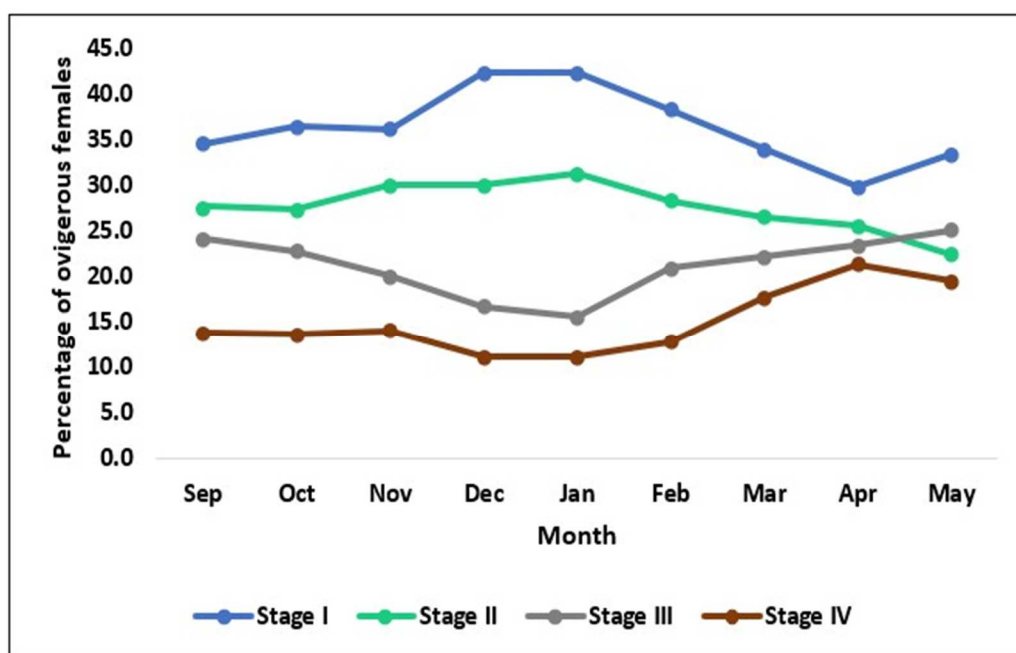


Fig. 4.5. Relationships between carapace length (mm) and brood size for different stages (I-IV) of embryo development

Table 4.1 displays the mean length and width of the embryos and the mean volume of the embryos at each developmental stage. The embryo length increased gradually with each developmental stage. Such a gradual change was not observed for embryo width, but a sharp increase in width was observed from stage II to stage III. The embryo volume remained in the range of 0.043-0.051 mm³ during the first two stages but started to increase significantly to 0.091 mm³ in the later stages. The embryo's volume increased by 109 % from stage I to stage IV. Analysis of variance showed a significant variation in embryo length ($p=0$; $F=928$), width ($p=0$; $F=1725.5$) and volume ($p=0$; $F=2584$) with each developmental stage, however, the embryo developmental stages did not differ much with the size of the female ($p<0.05$; $F=2.918$).

Table 4.1. Mean length, width and volume of embryos of *P. semilaevis* at each developmental stage

Stage	Embryo length $\pm$ SD (mm)	Embryo width $\pm$ SD (mm)	Embryo volume $\pm$ SD (mm ³)	CL range (mm)	No. of shrimps observed
I	0.511 $\pm$ 0.028	0.401 $\pm$ 0.024	0.043 $\pm$ 0.006	10-23	100
II	0.568 $\pm$ 0.019	0.412 $\pm$ 0.007	0.051 $\pm$ 0.003	12-25	100
III	0.616 $\pm$ 0.02	0.513 $\pm$ 0.009	0.085 $\pm$ 0.003	13-25	100
IV	0.657 $\pm$ 0.01	0.51 $\pm$ 0.013	0.091 $\pm$ 0.005	13-25	100

**Fig. 4.6.** Monthly changes in percentage occurrence of different developmental stages of embryos in ovigerous females of *P. semilaevis*

4.3.4. Reproductive Period, sex ratio, GSI and size at sexual maturity

Fig. 4.6 illustrates the monthly variations in the proportion of *P. semilaevis* ovigerous females carrying embryos at various developmental stages. Although ovigerous females were present in every month's sample, their frequency changed on a monthly basis. The percentage of ovigerous females increased from November to February (66.4% to 84%) and decreased from March to October (67.7% to 45.2%), with the least number of ovigerous females present in September (35.7%). The percentage of ovigerous females incubating stage I embryos peaked in December and January. Ovigerous females with stage II embryos showed a similar peak from November to February. The proportion of embryos with eyed stages i.e., stages III and IV, increased steadily from January to May and April, respectively. The stage IV embryos, just before hatching, were highest from March to May, suggesting a significant hatching period. All ovigerous females with stage I bright blue embryos had cream-colored ovaries, either immature stage 1 ovaries preparing for the next brood or atretic ovaries with released oocytes. Over half of the females with stage II embryos had pale cream-colored developing ovaries. All mature females with stage IV eggs and more than half of the females with stage III eggs had blue-colored ripe ovaries, indicating upcoming spawning and new brood.

The overall sex ratio (males: females) was 1:1.8, which is significantly different from the expected sex ratio (1:1). Females outnumbered males in all the months studied. The highest percentage of females was observed during February (73.8%) and the least during October (52.7%). Monthly variation in sex ratio and results of chi-square analyses are provided in Table 4.2. The monthly sex-ratio showed significant variation from the hypothetical ratio 1:1 for all the months except October.

Table 4.2. Month-wise sex ratio in *P. semilaevis*

Sl. No	Month	Sex Ratio (Male: Female)	Chi-square value (X^2)	Level of significance
1.	January	1:2.02(100,202)	34.45	P<0.01*
2.	February	1:2.82 (142,401)	123.53	P<0.01*
3.	March	1:1.44 (178,257)	14.35	P<0.01*
4.	April	1:2.16 (45,97)	19.04	P<0.01*
5.	May	1:1.81 (37,67)	8.65	P<0.01*
6.	September	1:1.55 (74,115)	8.89	P<0.01*
7.	October	1:1.11 (123,137)	0.75	p>0.05
8.	November	1:1.61 (146,235)	20.79	P<0.01*
9.	December	1:1.91 (152,291)	43.61	P<0.01*
10.	Overall	1:1.81 (997,1802)	274.08	P<0.01*

*Significant

Size at first maturity, determined by the presence of embryos between pleopods (CL_{50em}), was found to be 15.07 mm CL (Fig. 4.7a). Size at first maturity determined from pooled early mature (Stage 3) and fully mature (Stage 4) ovarian stages (CL_{50ov}) was estimated at 15.51mm CL (Fig. 4.7b).

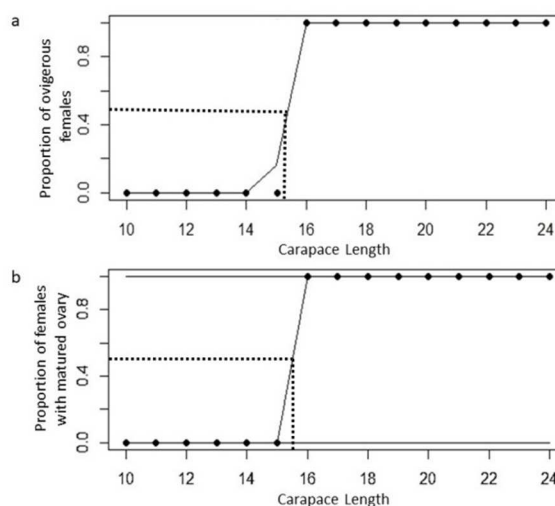


Fig. 4.7. Graphs for estimating size at first maturity based on the proportion of ovigerous females (a) and matured ovaries (b) of females of *P. semilaevis*

4.4. Discussion

Several aspects, including reproductive period, ovarian and embryonic stages of development, embryo size, brood size, size at maturity and sex ratio, were studied for *P. semilaevis* from the southeastern Arabian Sea.

Based on the color and position of the ovary in the cephalothoracic cavity, five ovarian maturation stages were recognized in the females of *P. semilaevis*. The classification of ovarian development in detailed stages is essential to gather comprehensive data for future reproductive and population dynamics studies. Mature ovaries are bright dark bluish-black, visible through the carapace as a head roe. Ohtomi and Hayashi (1995) and Ohtomi (1997) described the mature ovary as blue for *P. semilaevis*, Maiorano et al. (2002) as greenish blue for *P. martia*, Colloca (2002) and Possenti et al. (2007), Triay-Portella et al. (2017) as dark blue for *P. edwardsii* and Ahamed and Ohtomi (2011) as dark yellow for *P. izumiae*. Decapod crustacean ovaries change color during the reproductive cycle due to variations in the amount of carotenoids present during oogenesis (Liñán-Cabello et al. 2002; Gregati et al. 2010), accumulation of yolk granules and the decrease of cytoplasmic organelles during vitellogenic stages.

The histological analysis supported the maturity scale based on the morphology of ovaries. The histology of ovarian tissues and the findings of the GSI analysis indicates that changes in the color and form of the ovaries closely correspond to the development of oocytes. The average GSI value increased from 0.093 in females with stage 1 ovary to 4.33 in females with stage 4 ovary. The central region of the ovary showed the presence of oogonia and previtellogenic oocytes. In contrast, more developed vitellogenic oocytes were present towards the periphery of the ovary, corroborating Braga et al. (2009). As observed, the oogonia proliferating in the germinal epithelium develops into previtellogenic oocytes, moving to the growth zone between the large vitellogenic oocytes to

form small germinative islets. The high number of nucleoli inside the nucleus of previtellogenic oocytes suggests that they have become quite active. The enlargement of the growing vitellogenic oocytes mainly results from the expansion of the cytoplasm, which has become acidophilic due to the presence of yolk granules and lipid droplets. Follicle cells form a layer around the vitellogenic oocytes. Follicular cells either synthesize vitellogenin and secrete it into the hemolymph, which is later collected by the oocytes (Yano and Chinzei, 1987), or may take part in the collection of yolk proteins into the oocytes. The identification and differentiation of the immature and spawned stages primarily rely on the atretic oocytes observed. Since the ovaries at the immature and spawned stages have the same coloration and the same germinative cells (oogonia and early previtellogenic oocytes) are primarily found in these stages, atretic oocytes were considered to be the key trait in their histological differentiation.

The brood size ranged from 2093 to 12887 embryos. For all four embryonic stages, there was a positive link between shrimp size (CL) and brood size. Ohtomi (1997) observed a smaller brood size (1048 to 8702 embryos) in *P. semilaevis* from the subtropical waters of Kagoshima Bay, Japan. The physical space between the pleopods available for the attachment of the embryos is the cause of this correlation. A significant decrease in brood size during incubation was observed in the ovigerous females of *P. semilaevis*. Similar observations were reported for the other *Plesionika* species (Ohtomi, 1997; Maiorano et al. 2002; Ahamed and Ohtomi, 2011; Triay-Portella et al. 2017) and other caridean shrimps (Penha-Lopes et al. 2007; Echeverría-Sáenz and Wehrtmann, 2011; deMoraes et al. 2017). In caridean shrimps, embryo loss during incubation is a common observation that can be attributed to a number of biological (parasites, micro predators, etc.) and physical (mechanical stress, increase in embryo size, etc.) factors (Balasundaram and Pandian, 1982; Kuris, 1991; Oh and Hartnoll, 1999; Hernáez et al. 2010). Since no parasites and micro predators were observed in the

present study, the embryo loss could be due to the restricted space to carry the embryos beneath the pleon due to increased embryo volume (Suh et al. 2003). Fishing methods can also contribute to embryo loss in all stages.

The mean embryo sizes following spawning and prior to hatching were 0.51×0.40 mm and 0.66×0.50 mm, respectively. Ohtomi (1997) also reported a similar pattern of increasing embryo size with each development stage in *P. semilaevis* from Kagoshima Bay. He observed a mean embryo size of 0.60×0.56 mm just after spawning and 0.78×0.53 mm prior to hatching, which is higher than our results. The volume of the embryos also increased with each development stage. The increase was very distinct from stage II to stage III (0.05 mm^3 to 0.085 mm^3) with the development of rudimentary appendages, ventral cleft, and large cephalothoraces. However, this increase in embryo volume during incubation is common in crustaceans due to the rise in water content and biochemical changes in the embryo during development (Lardies and Wehrtmann, 1997; Wehrtmann and Kattner, 1998).

Ovigerous females were present in all the sampling months, with a peak from November to February, indicating this to be the main reproductive period. Ohtomi (1997) reported the occurrence of ovigerous females of *P. semilaevis* in Kagoshima Bay, Japan, from May to December and suggested the influence of photoperiod on species reproduction. According to Omori (1971), *P. izumiae* breeding in Suruga Bay was frequent as the water warmed in the late spring and summer. Studies on the reproduction of caridean shrimps have shown that water temperature significantly influences spawning (Kikuchi, 1962; Allen, 1966; Maiorano et al. 2002; Vafidis et al. 2005). According to Bauer (1992), neritic species of caridean shrimp in temperate waters will have shorter breeding periods than those in subtropical and tropical areas. Due to generally constant and high temperatures, the reproductive cycle is prolonged and year-round in tropical

waters (Orton, 1920). The tropical climate prevailing in the southeastern Arabian Sea could be the reason for its continuous reproductive activity.

Stage I and stage IV embryos occurred all months, suggesting that this species is iteroparous. However, the prevalence of ovigerous females carrying stage I embryos rose from November to February, with peaks in December and January indicating their primary spawning season. Stage IV embryos had a higher occurrence from March to May, suggesting this to be their significant hatching period. Ovigerous females carrying stage I embryos lacked mature ovaries, whereas ovigerous females carrying embryos in stage IV, which were close to hatching, had mature ovaries. Additionally, all maturity stages were visible in the ovaries of non-ovigerous females who were larger than the size at sexual maturity, suggesting that once *P. semilaevis* achieves sexual maturity, it spawns multiple times during a year. This reproductive pattern has been described for various tropical and temperate deep-sea shrimps (Bauer, 1989; Company and Sarda, 1997; Ohtomi, 1997; Maiorano et al. 2002; Anastasopoulou et al. 2017; Paramasivam et al. 2018; Kuberan et al. 2021).

The maximum CLs observed by Ohtomi (1997) was 19.25 mm in females, while in this study, the maximum CL observed was 24mm. With higher latitudes, shrimps tend to have smaller sizes. Geographical differences in the maximum body size may have resulted from differences in longevity, growth rate, and food availability among the populations, or they may have been caused by physiological growth mechanisms (Ohtomi, 1997). Triay-Portella (2017) preferred the calculation of size at maturity based on ovarian maturation rather than ovigerous condition in the case of *P. edwardsii*, as a significant fraction of non-ovigerous females were mature, leading to an overestimation of size at maturity. In the present study, the size at sexual maturity estimated based on ovarian maturation and ovigerous condition showed similar values since the occurrence of ovigerous females was relatively higher than non-ovigerous females.

In fisheries management, the size at which shrimps of a given population become sexually mature for the first time is an important management parameter used to monitor whether enough juveniles in an exploited stock mature and spawn (Beverton and Holt, 1959; Jennings et al. 1998). The size during sexual maturity is especially significant and is frequently used as a criterion for the minimum permissible capture size (Lucifora et al. 1999). Information on the reproductive parameters of deep-sea resources forms the basis for developing and implementing resource management strategies for the sustainable harvest of the deep-sea fishery. The data gathered in this study can be applied to research on the recruitment dynamics of the species, which will help manage resources more effectively and act as a prerequisite for stock assessment and stock sustainability and establish successful fishery management.

4.5. Conclusions

This is the first comprehensive study on reproductive parameters, including the ovarian and embryonic development of *P. semilaevis* in Indian waters and other locations where this species is distributed. Females reproduce multiple times a year as evidenced by the presence of ovigerous females in all the sampling months. The major spawning and hatching periods were estimated to be December to February and March to May, respectively. They are sequential breeders i.e., after reaching sexual maturity, they are able to produce subsequent broods, as indicated by their ovarian maturation with embryonic development. The data gathered in this study can be applied to research on reproductive dynamics, which will help manage resources more effectively and advance the ability of the species to reproduce in captivity. These studies are notable for their significance in identifying the different stages of ovarian maturation and embryonic development in detail which helps to obtain accurate information about the length at maturity and the hatching and spawning seasons, which is essential when establishing management measures. They are also significant in determining whether the current closed season is appropriate for the species.

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Biochemical analysis and nutritional profile of *Plesionika semilaevis*

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	5.2. <i>Materials and Methods</i>
	5.3. <i>Results</i>
	5.4. <i>Discussion</i>
	5.5. <i>Conclusion</i>

5.1. Introduction

Crustaceans hold significant commercial appeal and represent approximately 22.8 % of the global seafood trade's value (FAO, 2022). Deep-sea shrimps, in particular, stand out as a high-priced group of invertebrates in the global fishery sector, with widespread distribution throughout tropical regions. They hold significant economic importance in the Southeast Asian area, primarily due to their high export value (Shanis, 2014).

Nutrient-rich foods are increasingly being introduced to sustain the human body and satisfy culinary preferences. Assessing the nutritional quality of these foods involves a comprehensive analysis of their complex nutrient compositions, including proximate composition, amino acids, minerals, and fatty acids. The taste, nutritional value, and health advantages of seafood products, such as deep-sea shrimps, are closely linked to their levels of essential amino acids and fatty acids (Chen et al. 2007; Kuley et al. 2008). It is necessary to acknowledge that the biochemical composition of marine organisms can be influenced by various factors, including size, sex, sexual maturity, geographical location, dietary sources, and environmental conditions (Wu et al. 2010; Wang et al. 2021; Muralidharan et al. 2023).

Studies reported by Karuppasamy et al. (2013) and Bhavan et al. (2010) highlighted the relatively higher protein content present in the edible parts of shrimps. The nutritional qualities of shrimp are not solely attributed to their high-quality protein content but also to their relatively lower lipid (fat) content, along with a higher proportion of polyunsaturated fatty acids (PUFAs). These species are rich in essential omega-3 fatty acids docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). These PUFAs can play crucial roles in preventing conditions such as hypertension, inflammation, diabetes, and cancer (Chakraborty et al. 2016; Ramezani-Fard et al. 2016; Krishnan et al. 2021; Chakraborty et al. 2022b). Studies have shown that despite shrimp's high cholesterol content, incorporating shrimp into a diet with a balance of PUFAs, alongside reduced saturated fatty acid (SFA) intake, can contribute to lowering cholesterol levels, making it a heart-healthy option (Sampaio et al. 2006).

Additionally, shrimp are rich in essential nutrients, including essential amino acids such as methionine, lysine, cysteine, tryptophan, and threonine (Karuppasamy et al. 2013), minerals and vitamins (Vitamin E, C, B1, B6, B12, etc.) (Heu et al. 2003; Chakraborty et al. 2022d; AlFaris et al. 2022). Certain elements, namely copper, zinc, manganese, iron, and selenium, play crucial biological roles and are highly beneficial for human health when present in shrimp at acceptable levels (Khansari et al. 2005). Selenium, for instance, is a vital antioxidant mineral, while zinc is crucial for immune function and wound healing (Prasad, 2008; Bjørklund et al. 2022). Furthermore, they are low in calories and fats, making them a healthy dietary choice. The chemical and nutritional composition of shrimp can be notably affected by different preparation methods such as salting, frying, grilling, and boiling (AlFaris et al. 2022).

In the southwest coast of India, *Plesionika semilaevis* (Spence Bate, 1888) is a deep-sea shrimp species of significant commercial and ecological importance. It is typically found at 250 meters and beyond depths in the southeastern Arabian Sea. While there have been previous reports on the biochemical composition of some deep-sea shrimps from the southeastern Arabian Sea (Fernandez et al. 2018;

Chakraborty et al. 2021; Chakraborty et al. 2022b, 2022d), there is a notable absence of information regarding the biochemical and nutritional characteristics of the deep-sea shrimp *P. semilaevis* from Indian waters or any other geographical region where it is found.

Thus, this current study aims to bridge the existing information gap by assessing the essential biochemical components in the muscle tissue of *P. semilaevis* specimens obtained from the southwest coast of India. The analysis encompasses crucial parameters such as moisture, ash, protein, amino acids, carbohydrates, lipids, fatty acids, cholesterol and minerals.

5.2. Materials and methods

5.2.1. Collection and preparation of sample

Deep-sea shrimp samples were collected fortnightly from the deep-sea landing center in Sakthikulangara, Kollam, Kerala. These shrimps were captured at depths ranging between 200 to 400 meters. The monthly data was categorized into pre-monsoon (January-March) and post-monsoon (September-November) periods to gather information on seasonal variations. Approximately 20-25 kg of shrimp samples were collected and immediately preserved in an insulated icebox with crushed ice before being transported to the laboratory. In the laboratory, samples of *P. semilaevis* were identified using taxonomic keys provided by Ohtomi and Hayashi (1995), Ahamed et al. (2017), Kuberan et al. (2020), and Chan et al. (2020). The sex of each individual was determined by examining the morphology of the endopod of the first pair of pleopods (King and Moffitt, 1984). Subsequently, female shrimps were further categorized into ovigerous and non-ovigerous states based on the presence of embryos between their pleopods. Precise measurements of carapace length (CL) and total length (TL) were conducted using calipers, with a precision of 0.01 mm, while an electronic digital balance with a precision of 0.001 g was utilized to determine the body weight (BW) of the specimens. After initial processing, including cleaning and shell removal, the edible meat portion of the shrimp was isolated. The meat yield,

represented as a percentage of the wet weight, was calculated by dividing the weight of the meat by the total weight of the specimen and then multiplying by 100. For further biochemical analyses, homogenous samples were prepared by grinding the tissues, and these samples were securely stored at -80°C.

5.2.2. Proximate composition

To assess the moisture content and crude ash of the samples, established methods (AOAC, 1990; AOAC, 2005) were employed. The determination of total protein, carbohydrate and lipid was performed according to the methods described by Lowry et al. (1951), Anthrone method (Ludwig and Goldberg, 1956) and Folch et al. (1957) respectively. The spectrophotometric analysis of total cholesterol was carried out following the procedure outlined by Krishnan et al. (2019) using *o*-phthalaldehyde (50 mg dL⁻¹ in glacial acetic acid) (Merck Specialities Pvt. Ltd., Mumbai, India). A standard curve was prepared and the cholesterol levels of the samples were quantified in milligrams per 100 grams of wet sample.

5.2.3. Fatty acid analysis and nutritional indices

The fatty acid composition of the edible portion of shrimp samples during pre-monsoon and post-monsoon was analyzed using a method previously described by Chakraborty et al. (2014a). The process involved saponifying and trans-esterifying the extracted lipids to produce fatty acid methyl esters (FAMES). These FAMES were then extracted using a mixture of *n*-hexane (Merck) and water (1:2, v/v). After separation in a separating funnel, the aqueous layer was discarded, and the *n*-hexane layer was collected. Next, the *n*-hexane layer underwent a drying process using anhydrous sodium sulfate (Merck) before being concentrated for further analysis.

Esterified fatty acid analysis was conducted using a gas chromatograph (Nexis GC-2030, Shimadzu, Japan) connected with SH-Rxi-5Sil MS capillary column (30 m × 0.25 mm, 250 nm, Shimadzu, USA) along with a flame ionization detector (FID). A split-less injection mode was set at a split ratio of 100 and an oven temperature gradient method was employed (starting at 60°C, increasing to

150°C with a 5-minute hold time at a rate of 15°C min⁻¹). Subsequently, the temperature was raised to 280°C and maintained for 15 minutes (at a rate of 25°C per minute) to ensure the detection of all peaks. The injector and ion source temperatures were held at 260°C and 230°C, respectively. Ultra-high purity (> 99.99%) helium was served as carrier gas at a flow rate of 1.22 mL min⁻¹, while the pressure was maintained at 74.4 kPa. The quantification of FAMES was achieved by comparing their retention times with established standards (SupelcoTM 37 FAME Mix). Results were expressed as % CFA (percent cumulative fatty acids).

Ultimately, the average values of specific fatty acids were employed to calculate the levels of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA). The study evaluated the nutritional standards of the shrimps, represented by different ratios of fatty acids, such as *n*-3/*n*-6 and PUFA/SFA. To shed light on the potential thrombogenic and atherogenic impacts of the consumable portions of the shrimps, the thrombogenicity index (TI) and atherogenicity index (AI) were assessed using a previously established methodology by Ulbricht and Southgate (1991).

$$TI = (14:0 + 16:0 + 18:0) / [(0.5 \times \Sigma MUFA) + (0.5 \times \Sigma n-6PUFA) + (3 \times \Sigma n-3PUFA) + (\Sigma n-3PUFA / \Sigma n-6PUFA)]$$

$$AI = (12:0 + 4 \times 14:0 + 16:0) / (\Sigma MUFA + \Sigma n-3PUFA + \Sigma n-6PUFA)$$

5.2.4. Minerals analysis

A 0.1g sample was subjected to digestion using a 4:1 ratio of suprapur nitric acid (HNO₃) (Merck) and suprapur sulfuric acid (H₂SO₄) (Merck) within a microwave digester (Microwave Mini, Anton Paar). Following digestion, the samples were adjusted to a 25 mL volume using ultrapure water. Subsequently, the samples were further diluted before being analyzed using ICP-MS (iCAP Q, Thermo Fisher). The calibration of the analysis was performed using a multielement standard (Merck) containing known concentrations of various elements.

5.2.5. Amino acid analysis and nutritional indices

The amino acid composition was analyzed using a Shimadzu LC-10 AT High-Performance Liquid Chromatography (HPLC) Amino Acid Analyzer system. The system was equipped with a cation exchange column, specifically a sulfonated polyvinyl styrene column, and a fluorescence detector (Lakshmanan et al. 2013).

The following parameters and ratios were computed: total essential amino acids (Σ EAA), total non-essential amino acids (Σ NEAA), total amino acids (Σ AA), total aromatic amino acids (Σ ArAA), total sulfur-containing amino acids (Σ SAA), and the ratios of Σ EAA to Σ NEAA, Σ EAA to Σ AA, Σ NEAA to Σ AA, cysteine to Σ SAA (Cys/ Σ SAA), arginine to lysine (Arg/Lys) and leucine to isoleucine (Leu/Ile).

5.2.6. Statistical analysis

Statistical analysis was conducted using the Statistical Program for Social Sciences 13.0 (SPSS Inc, Chicago, USA, v.13.0). All analyses were performed in triplicate, and the means of all parameters were assessed for significance using analysis of variance (ANOVA), followed by Duncan's multiple range tests. The level of significance for all analyses was set at $p < 0.05$. To examine the variation in fatty acid and amino acid contents in muscle tissues, Principal Component Analysis (PCA) was carried out using R Studio (version 4.1.1.). PCA was performed based on the correlation matrix, and factors with eigenvalues greater than 1 were extracted.

5.3. Results

5.3.1. Sample measurements and proximate composition

The range of measurements for total length (TL), carapace length (CL) and total weight is mentioned in Table 5.1. The shrimp meat's yield was determined to be $53.44 \pm 4\%$ in non-berried females, $48.4 \pm 2.88\%$ in berried females and $52.16 \pm 3.7\%$ in males. The proximate composition of *P. semilaevis* specimens, categorized as males, berried females, and non-berried females, is outlined in Table 5.1. There were negligible differences in moisture and protein levels

between male, berried female, and non-berried female specimens. Males and females exhibited comparable levels of ash content in their tissues. Also, notable distinctions emerged in carbohydrate, lipid, and fat levels, with female samples exhibiting markedly higher amounts compared to males.

Table 5.1. Morphometric data and proximate composition in the muscle tissues of *P. semilaevis*

	NB	B	Male
TL (mm)	67-132	72-136	70-133
CL (mm)	10-24	12-24	10-24
Weight (g)	0.85-6.26	1.13-7.5	0.72-6.01
Meat yield (%)	53.44±4.00 ^a	48.4±2.88 ^a	52.16±3.7 ^a
Moisture (%)	81.55±0.56 ^a	81.62±0.48 ^a	82.42±0.16 ^a
Ash (%)	3.52±0.08 ^a	3.51±0.03 ^a	3.21±0.07 ^a
Carbohydrate (%)	0.79±0.01 ^b	0.82±0.05 ^b	0.60±0.03 ^a
Fat (%)	0.82±0.03 ^b	0.85±0.03 ^b	0.77±0.02 ^a
Proteins (%)	13.73±0.81 ^a	12.56±0.51 ^a	13.1±0.41 ^a
Lipids (%)	1.47±0.14 ^b	1.46±0.22 ^b	1.14±0.13 ^a
Cholesterol (mg 100g ⁻¹)	61.3±0.24 ^c	58.88±0.63 ^b	64.08±0.59 ^a

TL, CL and weight are presented as a range, while other parameters are presented as means±standard deviation (SD).

Values in the same row with different superscripts are significantly different ($p<0.05$).

Abbreviations: NB, non-berried females; B, berried females; TL, Total length; CL, carapace length.

Carbohydrate content was notably lower in the male sample at 0.60±0.03%, while the non-berried and berried samples contained 0.79±0.01 % and 0.82±0.05%, respectively. Similarly, lipid content was slightly lower in the male sample at 1.14±0.13%, compared to 1.47±0.14% and 1.46±0.22% in the non-berried and berried samples, respectively. The female samples demonstrated comparatively higher fat content, with the non-berried and berried samples

containing $0.82 \pm 0.03\%$ and $0.85 \pm 0.03\%$, respectively, while the male sample exhibited the lowest fat content at $0.77 \pm 0.02\%$. Additionally, berried females demonstrated reduced cholesterol content in comparison to both non-berried females and males.

5.3.2. Fatty acid analysis and nutritional indices

The presence of a total of 15 fatty acids was observed in the samples of *P. semilaevis* (Table 5.2), encompassing both essential and non-essential fatty acids. Fig. 5.1 & 5.2 represent the seasonal variation in fatty acid composition in muscle tissues of *P. semilaevis*. Among SFA, palmitic acid (16:0) was the most prominent among male, berried and non-berried females, accounting for a substantial portion (22-27%). Furthermore, palmitic acid showed a significant increase from pre-monsoon to post-monsoon for males and non-berried females. The highest value for C16:0 was observed in the case of males in post-monsoon (27.04%). Lauric acid (12:0) was observed only during the post-monsoon period in the tissues of *P. semilaevis*.

Similarly, pentadecanoic acid (15:0) and margaric acid (17:0) displayed a significant increase from pre-monsoon to post-monsoon for males, berried and non-berried females. On the other hand, there was a noticeable decrease in stearic acid (18:0) levels observed among males, berried females, and non-berried females, spanning from the pre-monsoon period to the post-monsoon period.

The MUFA identified in this species included oleic acid (18:1 n -9) and palmitoleic acid (16:1 n -7). The combined levels of MUFA were more pronounced during the pre-monsoon than post-monsoon. Oleic acid accounted for a noteworthy proportion of the overall fatty acids in both males and females (14-21%). Among females, the concentration of oleic acid surpassed that of males, reaching its peak during the pre-monsoon period (21%). The aggregate MUFA content exhibited a decline across all instances from the pre-monsoon to the post-monsoon phase.

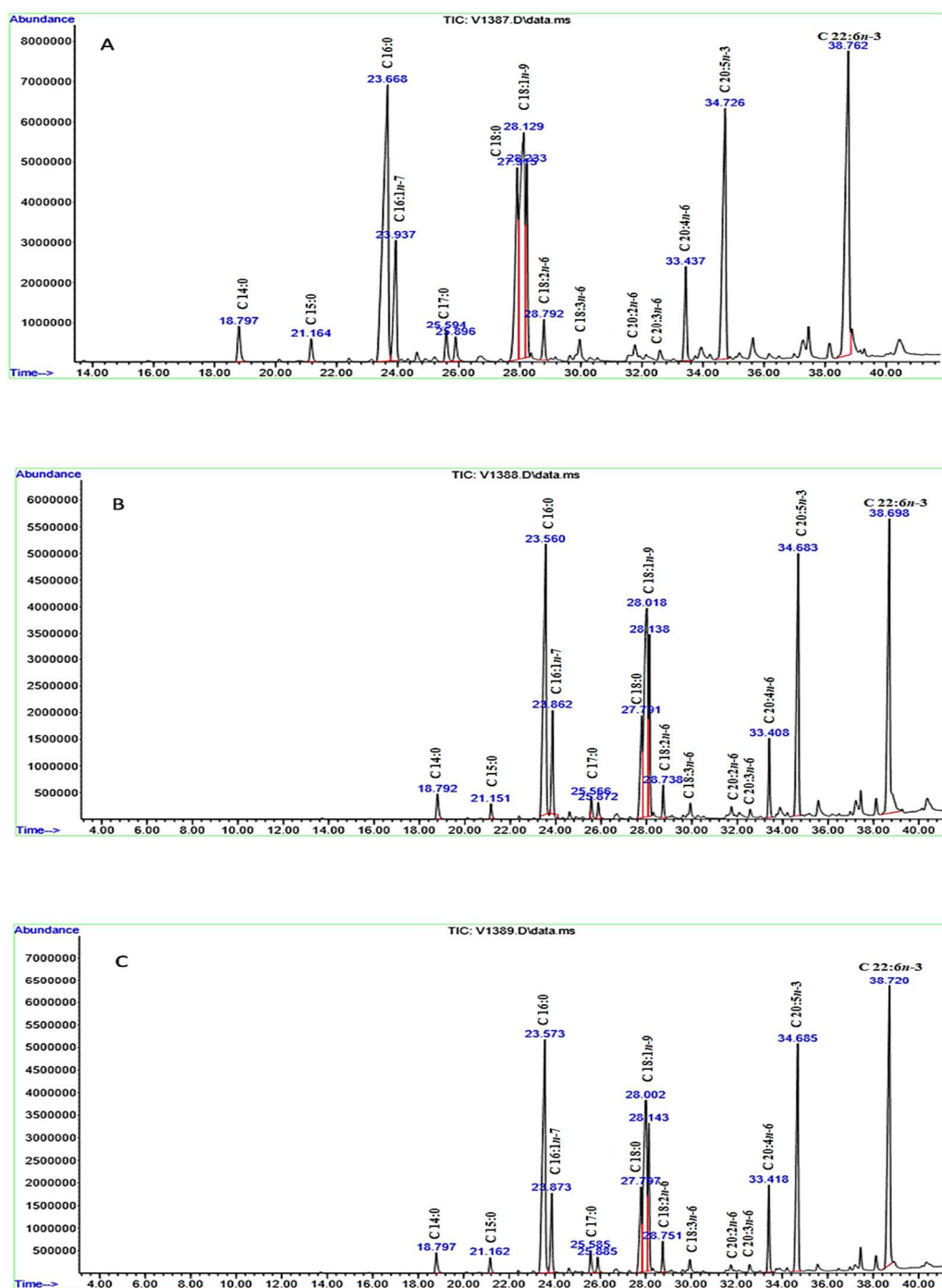


Fig. 5.1. Fatty acid composition in muscle tissues of *P. semilaevis* during pre-monsoon period. A, non-berried females; B, berried females; C, males

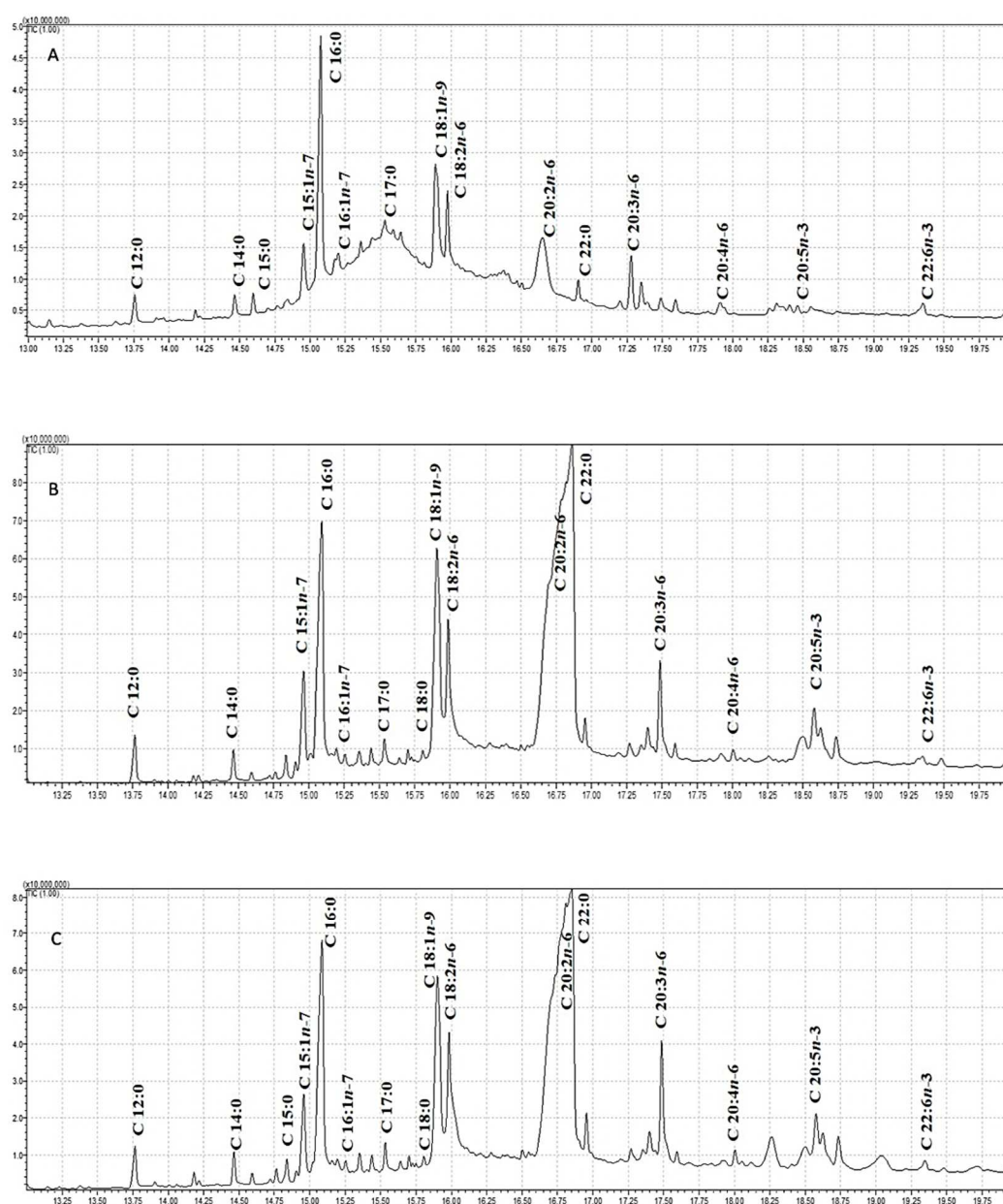


Fig. 5.2. Fatty acid composition in muscle tissues of *P. semilaevis* during post-monsoon period. A, non-berried females; B, berried females; C, males

Table 5.2. The fatty acid composition in muscle tissues of *P. semilaevis* (% of total fatty acids)

Fatty acid	NB		B		Male	
	Pre-monsoon	Post-monsoon	Pre-monsoon	Post-monsoon	Pre-monsoon	Post-monsoon
Saturated fatty acids (SFA)						
12:00	nd	3.61±0.22	nd	2.98±0.71	nd	3.32±0.77
14:00	1.52±0.09	1.28±0.43	1.48±0.07	0.69±0.13	1.25±0.09	1.36±0.29
15:00	0.97±0.08	2.06±0.34	0.76±0.05	0.9±0.24	0.92±0.01	2.05±0.05
16:00	24.6±1.82	26.42±3.22	23.30±1.53	22.69±7.8	21.9±0.18	27.04±0.98
17:00	1.29±0.01	1.67±0.43	1.03±0.10	1.67±0.11	1.17±0.08	1.60±0.13
18:00	7.98±1.95	0.73±0.04	6.44±0.05	0.48±0.02	5.57±0.43	0.46±0.07
ΣSFA	36.36±0.18	35.77±2.6	33.02±1.67	29.41±6.95	30.80±0.67	35.84±1.13
Monounsaturated fatty acids (MUFA)						
16:1n-7	5.51±0.29	1.83±1.43	5.35±0.37	1±0.10	4.38±0.24	2.12±1.05
18:1n-9	18.68±1.62	19.24±1.08	20.97±1.17	16.74±6.38	16.88±0.96	14.41±6.14
ΣMUFA	24.19±1.33	21.07±0.35	26.32±1.53	17.74±6.33	21.23±1.20	16.53±5.09
Polyunsaturated fatty acids (PUFA)						
18:2n-6	1.35±0.07	6.69±0.5	1.28±0.08	14.66±6.53	1.21±0.25	6.84±3.82
18:3n-6	0.88±0.03	0.70±0.01	0.86±0.07	nd	0.62±0.05	0.48±0.41
20:2n-6	0.62±0.19	2.68±2.35	0.65±0.2	0.39±0.05	0.57±0.13	1.49±0.01
20:3n-6	0.5±0.12	6.24±1.27	0.49±0.14	4.51±1.88	1.21±0.87	10.51±1.33
20:4n-6 (ARA)	3.3±0.13	2.90±0.53	3.3±0.23	2.08±1.55	6.18±1.77	4.46±3.37
20:5n-3 (EPA)	12.87±0.64	7.02±2.93	14.3±1.27	17.50±7.29	13.25±2.19	6.11±0.26
22:6n-3 (DHA)	18.23±0.08	3.76±1.1	18.64±2.43	2.15±1.08	23.66±2.13	6.67±5.84
ΣPUFA	37.75±0.65	29.99±2.68	39.52±3.61	41.28±14.6	46.70±2.40	36.56±6.81
Fatty acid indices						
Σn-3	31.1±0.72	10.78±2.61	32.94±3.7	19.65±8.37	36.91±0.06	12.78±5.58
Σn-6	6.65±0.08	19.21±1.11	6.57±0.09	21.64±6.25	9.79±2.46	23.78±1.25
EPA/ARA	3.9±0.05	2.55±1.45	4.33±0.08	11.61±6.99	2.35±1.08	2.65±2.78
DHA/ARA	5.53±0.19	1.28±0.15	5.63±0.34	1.31±0.60	3.99±0.84	1.29±0.45
Σn-3/Σn-6	4.68±0.16	0.56±0.15	5.02±0.63	0.88±0.14	3.94±1.04	0.53±0.21
ΣPUFA/ΣSFA	1.04±0.01	0.85±0.15	1.20±0.17	1.60±1.04	1.52±0.11	1.03±0.23
UFA/SFA	1.7±0.03	1.44±0.20	2.00±0.16	2.20±1.0	2.21±0.09	1.48±0.10
AI	0.50±0.02	0.69±0.09	0.48±0.07	0.49±0.2	0.40±0.02	0.69±0.01
TI	0.3±0.0	0.42±0.08	0.25±0.04	0.32±0.1	0.22±0.1	0.34±0.08

Data are presented as means±standard deviation (SD).

Abbreviations: NB, non-berried females; B, berried females; ARA, arachidonic acid; nd, not detected; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; UFA, unsaturated fatty acids; AI, atherogenicity index; TI, thrombogenicity index.

In the edible portion of the shrimps, total PUFA were higher in comparison to SFA and MUFA. *n*-3 fatty acids comprised the dominant share of PUFA in *P. semilaevis*, regardless of sex and seasons. The principal components among these were the C20-22*n*-3 PUFA derivatives, namely eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which constituted a substantial portion of the fatty acid profile. This was followed by the proportion of arachidonic acid (20:4*n*-6) and linoleic acid (18:2*n*-6). Linoleic acid and dihomog- γ -linolenic acid (20:3*n*-6) showed a significant increase in concentration from pre-monsoon to post-monsoon.

Arachidonic acid (ARA), EPA and DHA showed a significant decrease from pre-monsoon to post-monsoon, with an exception in the case of berried females, where a slight increase was observed in the concentration of EPA from pre-monsoon to post-monsoon. Males, berried females, and non-berried females displayed a greater proportion of *n*-3 fatty acids (31-37%) in the pre-monsoon phase, while a higher percentage of *n*-6 fatty acids (19-24%) were observed in the post-monsoon period. Male specimens of *P. semilaevis* exhibited a higher proportion of ARA compared to their female counterparts. During the pre-monsoon period, DHA content exceeded that of EPA in all observed samples. Conversely, in the post-monsoon period, EPA content surpassed DHA in female *P. semilaevis* specimens, with similar values seen in males.

The fatty acid composition differed significantly with sex and season, as evident in the PCA plot (Fig. 5.3). The first two principal components (Dim 1 and Dim 2) accounted for 44.2% and 28.7% of the fatty acid variation, respectively.

An elevated $n-3/n-6$ ratio, serving as a significant biomedical indicator, was noted within the range of 4-5 across all samples during the pre-monsoon period, while a range of 0.5-1 was observed in the post-monsoon season. *P. semilaevis* exhibited a higher concentration of $n-3$ fatty acids, including DHA and EPA, accompanied by an optimal $n-3/n-6$ polyunsaturated fatty acid ratio. Notably, there was no evident variation in the $n-3/n-6$ ratio between male and female samples. This species displayed an increased PUFA/SFA ratio (0.85-1.6) across all analyzed samples, with the highest value of 1.6 observed in post-monsoon berried females. The indices of atherogenicity (AI) were within the range of 0.40-0.50 and 0.49-0.69 for pre-monsoon and post-monsoon samples, respectively. Similarly, the indices of thrombogenicity (TI) were recorded between 0.22-0.3 for pre-monsoon and 0.32-0.42 for post-monsoon samples. Notably, AI and TI values showed no noticeable disparity between males and females.

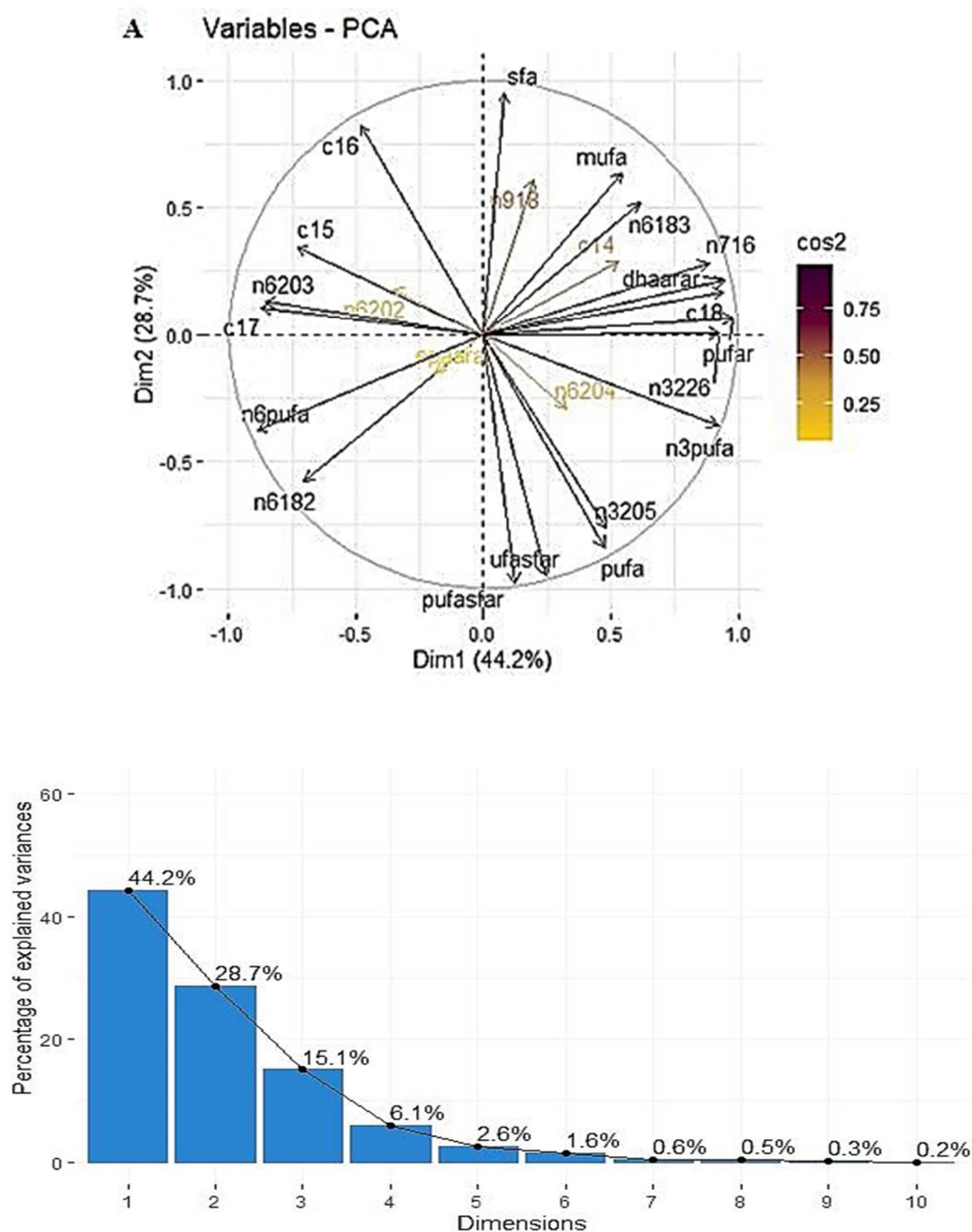


Fig. 5.3. (A): Principal component analysis of the fatty acids found in muscle tissue of *P. semilaevis* (B) Scree plot of 10 variables: Six variables with eigenvalues >1 (1): pufar, *n*-3/*n*-6 ratio; (2): dhaara, DHA/ARA ratio; (3): c18; (18:00) (4): n3226; DHA (5): n6pufa; *n*-6 PUFA (6): n3pufa, *n*-3 PUFA

5.3.3 Minerals analysis

Among the macro-minerals identified, sodium (Na), phosphorus (P) and magnesium (Mg) levels showed minimal divergence, with females showing slightly higher levels (Table 5.3). Similarly, potassium (K) and calcium (Ca) demonstrated comparable levels with males having marginally higher values. In the context of micro-minerals, females and males displayed compelling differences. Notably, the female sample exhibited significantly greater iron (Fe) content at $44.20 \pm 0.94 \text{ mg kg}^{-1}$, whereas the male sample had a lower concentration of $33.7 \pm 1.54 \text{ mg kg}^{-1}$. Similar trends were observed for copper (Cu) and zinc (Zn), where the female samples exhibited elevated levels compared to their male counterparts, with copper at $5.20 \pm 0.29 \text{ mg kg}^{-1}$ for females and $4.6 \pm 0.41 \text{ mg kg}^{-1}$ for males and zinc at $16.83 \pm 0.28 \text{ mg kg}^{-1}$ for females and $15.36 \pm 0.71 \text{ mg kg}^{-1}$ for males. Conversely, selenium (Se) and manganese (Mn) levels remained consistent between genders. One-way ANOVA results revealed significant differences in the composition of Zn, Fe and P ($p < 0.05$) between sex.

Table 5.3. The mineral composition in muscle tissues of *P. semilaevis*

Minerals	Male (mg kg ⁻¹)	Female (mg kg ⁻¹)
Na	9195.2±140.72	9256.8±90.5
Mg	378.7±25.8	382.3±30.01
Ca	2920.7±58.5	2903.6±81.9
Mn	1.57±0.17	1.52±0.07
Fe	33.7±1.54	44.20±0.94
Cu	4.6±0.41	5.20±0.0.29
Zn	15.36±0.71	16.83±0.28
Se	0.85±0.05	0.82±0.10
P	10294.5±68.6	10419.8±33.1
K	10645.1±188.6	10607.4±168.8

Data are presented as means±standard deviation (SD).

5.3.4. Amino acid analysis and nutritional indices

In the muscle tissue of *P. semilaevis*, a total of seventeen amino acids were detected, encompassing both essential and non-essential amino acids (Table 5.4). The Σ EAA and Σ NEAA values were higher in berried females compared to non-berried females and males. Among the non-essential amino acids, glutamic acid predominated, with a significantly greater content of $3.65 \pm 0.20 \text{ g } 100\text{g}^{-1}$ in non-berried females, $3.67 \pm 0.08 \text{ g } 100\text{g}^{-1}$ in berried females, and $3.57 \pm 0.01 \text{ g } 100\text{g}^{-1}$ in males. Aspartic acid and arginine followed in abundance. In terms of essential amino acids, lysine was the most abundant, with levels of $2.49 \pm 0.24 \text{ g } 100\text{g}^{-1}$ in non-berried females, $2.73 \pm 0.10 \text{ g } 100\text{g}^{-1}$ in berried females, and $2.17 \pm 0.08 \text{ g } 100\text{g}^{-1}$ in males. Leucine and valine were the subsequent essential amino acids in higher quantities.

Nutritional indices, including various amino acid ratios, are presented in the Table 5.4. The Σ EAA/ Σ NEAA ratio was 0.71 ± 0.00 for berried females and 0.70 ± 0.01 for males and non-berried females. Males exhibited the highest values for Σ ArAA and the Arg/Lys ratio ($1.46 \pm 0.01 \text{ g } 100\text{g}^{-1}$ and 0.77 ± 0.01 , respectively), while berried females had the highest values for Σ SAA and the Cys/ Σ SAA ratio ($0.49 \pm 0.01 \text{ g } 100\text{g}^{-1}$ and 0.24 ± 0.01 , respectively). The Leu/Ile ratio was slightly higher in non-berried females. Σ EAA/ Σ EAA and Σ NEAA/ Σ EAA showed similar values across all categories.

Table 5.4. The amino acid composition in muscle tissues of *P. semilaevis*

Amino acids	NB (g 100g ⁻¹)	B (g 100g ⁻¹)	Male(g 100g ⁻¹)
Essential amino acid (EAA)			
Histidine	0.52±0.04	0.51±0.03	0.50±0.01
Isoleucine	0.97±0.02	1.03±0.03	0.98±0.02
Leucine	1.65±0.05	1.73±0.04	1.65±0.07
Lysine	2.49±0.24	2.73±0.10	2.17±0.08
Methionine	0.36±0.01	0.38±0.01	0.36±0.04
Phenylalanine	0.76±0.04	0.7±0.03	0.80±0.01
Threonine	0.55±0.01	0.56±0.01	0.64±0.01
Valine	1.02±0.04	0.92±0.02	0.98±0.03
ΣEAA	8.31±0.31	8.55±0.11	8.08±0.03
Non-essential amino acid (NEAA)			
Alanine	1.25±0.11	1.29±0.05	1.24±0.01
Aspartic acid	2.11±0.04	2.16±0.17	2.14±0.00
Glutamic acid	3.65±0.20	3.67±0.08	3.57±0.01
Serine	0.8±0.01	0.82±0.01	0.86±0.01
Glycine	1.27±0.11	1.24±0.03	1.18±0.03
Tyrosine	0.63±0.02	0.71±0.02	0.66±0.01
Cysteine	0.09±0.01	0.12±0.01	0.10±0.02
Proline	0.25±0.01	0.29±0.01	0.29±0.02
Arginine	1.75±0.17	1.72±0.01	1.66±0.04
ΣNEAA	11.8±0.61	12.01±0.19	11.48±0.05
Amino acid indices			
ΣAA	20.12±0.91	20.56±0.3	19.56±0.02
ΣEAA/ΣNEAA	0.70±0.01	0.71±0.00	0.70±0.01
Σ ArAA	1.39±0.02	1.4±0.05	1.46±0.01
Σ SAA	0.44±0.02	0.49±0.01	0.43±0.03
Leu/Ile	1.71±0.09	1.68±0.08	1.69±0.05
Cys/ΣSAA	0.2±0.01	0.24±0.01	0.15±0.02
Arg/Lys	0.7±0.00	0.63±0.02	0.77±0.01
ΣEAA/ΣAA	0.41±0.00	0.42±0.00	0.41±0.00
ΣNEAA/ΣAA	0.59±0.00	0.58±0.00	0.58±0.00

Data are presented as means±standard deviation (SD).

Abbreviations: NB, non-berried females; B, berried females; AA, amino acids; ArAA, aromatic amino acids; SAA, sulfur containing amino acids; Leu, leucine; Ile, Isoleucine; Cys, cysteine; Arg; arginine; Lys, lysine.

The amino acid composition differed significantly with sex, as evident in the PCA plot (Fig. 5.4). The first two principal components (Dim 1 and Dim 2) accounted for 42.6% and 29.1% of the amino acid variation, respectively.

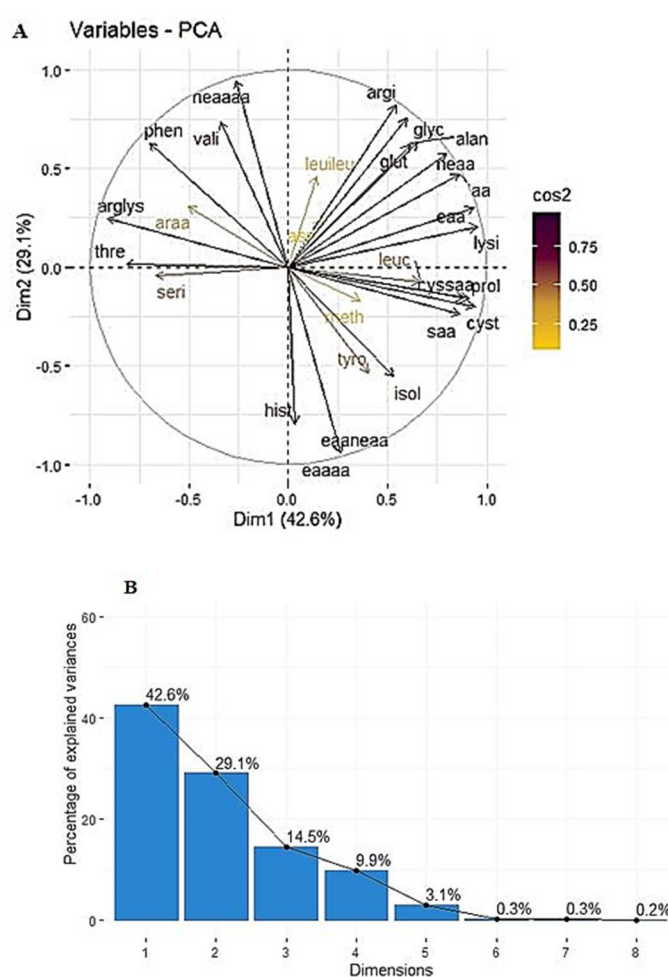


Fig. 5.4. (A): Principal component analysis of the amino acids found in muscle tissue of *P. semilaevis* (B) Scree plot of 10 variables. Five amino acids with eigenvalues >1 (1): lysi, lysine; (2): eaa; essential amino acids (EAA) (3): cyst, cysteine; (4): prol, proline; (5): arglys, Arg/Lys ratio

5.4. Discussion

5.4.1. Proximate composition

Evaluating the proximate profiles, which encompass parameters such as protein, lipid, carbohydrate, fat, ash, and moisture content, is often imperative to ensure compliance with food and commercial regulations. Shrimps are known for their high perishability due to their elevated moisture and amino acid levels (Shamasunder and Prakash, 1994). In the current investigation, moisture content exceeding 81% was observed, indicating the freshness of deep-sea shrimps, aligning with previous studies where water content exceeding 70% signified freshness (Sriket et al. 2007; Chakraborty et al. 2022d).

The ash content provides insights into the shrimp's mineral composition richness (Wang et al. 2021). In this study, the ash content was similar in female and male shrimps indicating a lack of variation in mineral constituents. In a study carried out by Rosa and Nunes (2004) in the Atlantic Ocean, ash levels varied between 1.9% and 2.1% in *Aristeus antennatus* and *Parapenaeus longirostris*. Previous research by Fernandez et al. (2018) reported ash content ranging from 0.7% to 1.96% for deep-sea shrimps from the Arabian Sea, while Chakraborty et al. (2022d) indicated a range of 3% to 6% for shrimps from the same region. Remarkably, these earlier findings closely align with the results of the current study.

Among the organic nutrients, carbohydrates are typically the first to be utilized to generate the necessary energy. In this study, males exhibited lower carbohydrate levels than females, and among the female group, berried females displayed higher carbohydrate content.

When comparing the fat content in *P. semilaevis* (ranging from 0.77% to 0.85%) with that of other deep-sea shrimps from the same region, Chakraborty et al. (2022d) documented notably higher fat levels, such as 1.63% in *Aristeus*

alcocki, 1.95% in *Heterocarpus chani*, 0.92% in *Plesionika quasigrandis*, 1.53% in *Solenocera choprai* and 0.84% in *Metapenaeopsis andamanensis*.

From a nutritional perspective, protein is an important component in seafood, playing a critical role in supporting regular bodily functions and ensuring the growth and maintenance of body tissues. Notably, berried females exhibited lower protein levels in the tissue compared to males and non-berried females. This distinction can be attributed primarily to the greater allocation of protein for the development of eggs in berried females (Dinakaran et al. 2009; Rosa and Nunes, 2003). Fernandez et al. (2018) reported a protein range of 18.81% to 22.33% in select deep-sea shrimps off the southwestern coast of India. In a recent study by Chakraborty et al. (2022d), deep-sea shrimps from the Arabian Sea, displayed protein content ranging from 9.8% to 12.7%. Notably, the protein content observed in *P. semilaevis* was greater than that of these shrimps. Rao et al. (2016) reported a protein content of 14.92% in *Heterocarpus gibbosus* specimens collected from the west coast and 17.42% in samples gathered from the east coast. Discrepancies in protein content could arise from variations in growth stages, dietary factors, geographic location, and seasonal influences (Sikorski et al. 1990).

Lipids play a critical role in preserving the structural and physiological integrity of cellular and sub-cellular membranes. Typically, shrimp muscle contains lower lipid content, making it preferable for consumers (Bhavan et al. 2008). The lipid content in shellfish generally falls within the range of 0.3% to 3.2% (Oksuz et al. 2009). Chakraborty et al. (2022d) noted a lipid content range of 1.89% to 2.64% in other deep-sea shrimps from the Arabian Sea. In our study, the lipid content in the edible tissue of *P. semilaevis* was even lower, ranging from 1.14% to 1.47%. Furthermore, the total lipid level was found to be higher in female shrimps compared to male shrimps, aligning with the findings of Bhavan et al. (2010). The increased total lipid content observed in adult female shrimps may be attributed to the demands of specific physiological activities associated with reproduction (Bhavan et al. 2010).

The cholesterol levels in deep-sea shrimp are lower than those in shallow-water shrimps, as documented by Krzynowek and Panunzio (1989) and Chakraborty et al. (2022d). The findings regarding cholesterol content in *P. semilaevis* align with values observed in other deep-sea shrimps from the Arabian Sea reported by Chakraborty et al. (2022d). These comparisons illustrate variations in proximate content among different shrimp species in the same geographical area.

5.4.2. Fatty acid analysis and nutritional indices

The primary source of energy for the growth of marine fishes and crustaceans is SFA, with a particular emphasis on palmitic acid (16:0) due to its higher caloric content (Chakraborty et al. 2022c). In *P. semilaevis*, the predominant SFA present is palmitic acid. In studies of deep-sea shrimps like *Parapenaeus longirostris* and *Plesionika martia* from the North Eastern Mediterranean Sea, palmitic acid emerged as the dominant saturated fatty acid in muscle tissue (Oksuz et al. 2009). The primary feeding period varies among species, as evident in observations of various shrimp species from the Arabian Sea (Paramasivam et al. 2020; Gayathri et al. 2023; Sreelakshmy et al. 2023; Muralidharan et al. 2023). Interestingly, the concentration of SFA has been observed to rise during periods of increased feeding activity (Shirai et al. 2002). In the case of *P. semilaevis*, the pre-monsoon period stands out as a major feeding activity period (Sreelakshmy et al. 2023), during which higher levels of SFA are evident in males, berried, and non-berried females.

Palmitic acid is recognized as a significant source of metabolic energy during the egg formation process in females (Ramezani-Fard et al. 2016). Studies on ovarian maturation have indicated that deep-sea shrimps exhibit year-round spawning, with a peak occurring from January to April (Paramasivam et al. 2018; Sreelakshmy and Chakraborty, 2023). During the pre-monsoon period, which is the major reproductive period for *P. semilaevis* (Sreelakshmy and Chakraborty,

2023), females exhibited a higher percentage of palmitic acid in their fatty acid composition when compared to males. However, this trend of higher palmitic acid content in females was not observed during the post-monsoon period. This finding aligns with previous reports of spawning-associated variations in fatty acids, specifically palmitic acid (16:0), in female marine fish (Huynh et al. 2007). These findings suggest that the reproductive activities of female *P. semilaevis* during the pre-monsoon period may influence their fatty acid composition, specifically an increase in palmitic acid, to support their energy needs for egg formation and reproduction.

Moving on to MUFA, *P. semilaevis* was found to have oleic acid as the predominant MUFA, aligning with prior research indicating that the principal MUFA in marine lipids usually consists of 18 carbon atoms (Yanar & Celik, 2005; Chakraborty et al. 2022d). Oleic acid has been identified as important for energy metabolism during gonadal development (Huynh et al. 2007). Notably, in the present study, female shrimps exhibited higher levels of oleic acid than males. In humans, *n*-9 fatty acids play a role in reducing the risk of arteriosclerosis, cardiovascular disease, and stroke.

ARA plays a crucial role in the female reproductive cycle as a precursor to prostaglandin hormones essential for reproduction and vitellogenesis (Bell and Sargent, 2003). In the present study, the higher levels of ARA in females, especially in berried stages during the pre-monsoon period, indicate their reproductive maturity, coinciding with their spawning and hatching period from December to May (Sreelakshmy and Chakraborty, 2023).

Regarding *n*-3 PUFA, particularly EPA and DHA, their presence suggests better growth and survival of *P. semilaevis* in the wild. Elevated levels of EPA and DHA are associated with enhanced stress tolerance and increased membrane permeability (Farias et al. 2014). Oksuz et al. (2009) reported that the total PUFA

in the edible portions of *P. longirostris* and *P. martia* were found in higher quantities when compared to the total SFA and MUFA. The current study aligns with these earlier findings, confirming the prevalence of PUFA in shrimps over other classes of fatty acids (Braganolo and Rodriuez-Amaya, 2001; Maia et al. 2022). *n*-3 fatty acids are renowned for their multifaceted health benefits in humans, encompassing anti-inflammatory and anti-coagulant properties while also playing a vital role in bone formation and metabolism. DHA is particularly vital for pregnant and nursing mothers and young children, while EPA serves as a precursor to anti-inflammatory compounds necessary for efficient brain and cellular functioning (Chakraborty et al. 2014a). Given that *P. semilaevis* contains substantial amounts of PUFA, it can indeed serve as a healthy dietary option, potentially contributing to overall well-being and mental health.

Chakraborty et al. (2022b) conducted a comparative analysis of the fatty acid profiles of *Aristeus alcocki*, *Solenocera choprai*, *Heterocarpus chani*, and *Plesionika quasigrandis*, captured along the southwest coast of India in the Arabian Sea, over different months. Their findings showed that *n*-3 fatty acids were most abundant during the period from December to February in the studied year, with a notable decrease in concentrations during March and April. In the present study, it was observed that the concentration of *n*-3 fatty acids was highest in the pre-monsoon samples (January to March) in comparison to the post-monsoon samples (September to November). Conversely, the concentration of *n*-6 fatty acids displayed an opposite trend, with higher levels observed during the post-monsoon period. This information underscores the significance of considering temporal factors when evaluating the nutritional profiles of these marine organisms, revealing seasonal variations in their fatty acid composition.

The ratio of *n*-3 to *n*-6 fatty acids is recognized as a critical biomedical marker for assessing the nutritional value of marine-derived lipids. An increased *n*-3/*n*-6 ratio is associated with a reduced risk of coronary heart disease and cancer

(Chakraborty et al. 2014a; Chakraborty et al. 2021). Notably, *P. semilaevis* exhibited a higher $n-3/n-6$ fatty acid ratio during the pre-monsoon period, which is indicative of a nutritious diet. Maintaining a proper balance and interaction between $n-3$, $n-6$, and $n-9$ fatty acids is vital for overall health (Christensen et al. 2001). A healthy diet is expected to have a PUFA/SFA ratio exceeding 0.45 (HMSO, 2001) to reduce the risk of cardiovascular diseases. *P. semilaevis* exceeded this recommended limit in males, berried, and non-berried females during both pre-monsoon and post-monsoon periods, making it a potential source of beneficial PUFAs. Foods with a lower PUFA/SFA ratio are generally considered unsuitable for consumption due to their potential to raise blood cholesterol levels. Thrombogenicity index (TI) and atherogenicity index (AI) are important parameters reflecting the metabolic effects of different fatty acids. Lower TI and AI levels are associated with a highly nutritious diet, which can potentially reduce the risk of cardiovascular diseases (Tonial et al. 2014). In the case of *P. semilaevis*, the observed AI and TI values ranging from 0.40 to 0.69 and 0.22 to 0.42, respectively, suggest that this deep-water shrimp could be considered a healthy seafood choice.

5.4.3. Minerals

In *P. semilaevis*, the most prevalent macro-mineral is potassium (K), followed by phosphorus (P), sodium (Na), calcium (Ca), and magnesium (Mg), as indicated. These findings align with those reported by Oksuz et al. (2009) in their study on deep-sea shrimps, specifically *Parapenaeus longirostris*. Potassium plays a crucial role in the body, functioning in conjunction with Mg, Na and Cl as electrolytes to regulate intracellular osmotic pressure and maintain acid-base balance. In *Penaeus* species, K ranks as the second most abundant mineral, following Ca (Truong et al. 2023). In comparison to coastal shrimp, deep-sea shrimp have higher concentrations of Ca and Na while displaying lower levels of K (Fernandez et al. 2018).

P in conjunction with Ca, plays a significant role in vertebrates and comprises a substantial portion of the exoskeleton in crustaceans (Hynd, 2019). In a study focused on *Parapenaeus longirostris* from the Marmara Sea, Özden (2010) noted P concentrations ranging from 2685.9 to 3657.7 mg kg⁻¹, which is notably lower compared to the phosphorus levels found in *P. semilaevis* (10294.5±68.6 mg kg⁻¹ in males and 10419.8±33.1 mg kg⁻¹ in females).

P. semilaevis exhibited similar Na and K levels to those observed in other deep-sea shrimps studied off the southwest coast of India by Fernandez et al. (2018). However, it displayed lower Ca quantities in comparison. Mg serves various functions, including maintaining membrane integrity, modulating neuromuscular transmission, and acting as a catalyst for a wide range of enzymes. In the case of *P. semilaevis*, the levels of Mg were found to be 378.7±25.8 mg kg⁻¹ in males and 382.3±30.01 mg kg⁻¹ in females, which were lower than the values reported in *Parapenaeus longirostris* and *Plesionika matia* (Özden, 2010; Oksuz et al. 2009).

Among micro-minerals, iron (Fe) emerged as the most prevalent element, followed by zinc (Zn), copper (Cu), manganese (Mn), and selenium (Se). Notably, in *P. longirostris*, the microelement concentrations were highest for iron, zinc, and copper, with values of 18, 6.1, and 2.2 mg/kg, respectively (Özden, 2010). Seafood serves as a reasonably good source of Fe and plays several critical roles in the body (Cámara et al. 2005). In *P. semilaevis*, the concentration of Fe in the tissues was 33.7±1.54 in males and 44.2±0.94 in females, while Fernandez et al. (2018) reported a range of 41.7 to 76.17 mg kg⁻¹ in other deep-sea shrimps from the same locality, with the lowest and highest values observed in *M. andamanensis* and *A. alcocki* respectively. The higher concentration of iron (Fe) observed in females compared to males implies a potential role for this element in the process of oogenesis (Méndez et al. 2001).

Cu and Zn are vital elements that play essential roles in the growth, cellular metabolism, and overall survival of most animals, including crustaceans (Candra et al. 2019). Notably, in crustaceans, such as shrimp, hemocyanin serves as the oxygen carrier and accounts for approximately 40% of the copper (Cu) stores (NRC, 2011). The levels of Cu ($4.6 \pm 0.41 \text{ mg kg}^{-1}$ in males and $5.20 \pm 0.29 \text{ mg kg}^{-1}$ in females) and Zn ($15.36 \pm 0.71 \text{ mg kg}^{-1}$ in males and $16.83 \pm 0.28 \text{ mg kg}^{-1}$ in females) observed in *P. semilaevis* are lesser than the Cu and Zn levels observed by Fernandez et al. (2018) in other deep-sea shrimps from Arabian Sea. In contrast, Rao et al. (2016) found similar values for Cu at $4.11 \pm 0.79 \text{ mg kg}^{-1}$ but notably higher values for Zn at $36.54 \pm 1.06 \text{ mg kg}^{-1}$ in *P. spinipes* (later identified as *P. quasigrandis*) from the west coast. The elevation in Zn concentration within female shrimps further underscores its significance in the reproductive process. Regarding Mn concentrations, *P. semilaevis* exhibited levels akin to those reported in other deep-sea shrimps (Oksuz et al. 2009; Özden, 2010; Fernandez et al. 2018).

Selenium is a trace element that serves as a cofactor for the reduction of antioxidant enzymes such as glutathione peroxidase, playing a critical role in protecting cells, tissues, and membranes against oxidative damage. In the case of *P. semilaevis*, Se concentrations were found to be 0.85 ± 0.05 in males and 0.82 ± 0.10 in females. These levels fall within the range observed by Özden (2010) for *P. longirostris* from the Marmara Sea. Notably, the Se values in the present study are higher than those reported by Plessi et al. (2001), Sirichakwal et al. (2005) and Burger and Gochfeld (2006) for other shrimp species.

The concentrations of the analyzed metals were found to be well within the regulatory limits, suggesting that the samples collected from deep-sea do not pose any threat to consumers (Food and Agriculture Organisation, 1983; World Health Organisation 1989; Food and Agriculture Organisation/World Health Organisation, 1999; European Union, 2008).

5.4.4. Amino acid composition and nutritional indices

Amino acids serve as the fundamental building blocks of proteins, playing crucial roles in the construction of cell structures and serving as energy sources. Research conducted by Sikorski et al. (1990) on the amino acid composition of prawns unveiled that glycine, alanine, serine, and threonine contribute to the sweet taste of prawns, while arginine, leucine, valine, methionine, phenylalanine, histidine, and isoleucine contribute to a bitter taste. Yanar and Celik (2006) observed that the most prevalent NEAA in *Penaeus semisulcatus* and *Metapenaeus monoceros* from the eastern Mediterranean were glutamic acid, aspartic acid, and arginine, aligning with our findings. Additionally, the major EAA noted in both studies are lysine, leucine, and valine.

Banu et al. (2016) analyzed amino acid content in the muscle of penaeid shrimps and reported higher quantities of EAA in comparison to NEAA in the muscle tissues. However, our present study indicates a significant increase in NEAA compared to EAA, consistent with the findings of Chakraborty et al. (2022d) in other deep-sea shrimps from the same locality.

The EAA/NEAA ratio in *P. semilaevis* falls within a balanced range of 0.70-0.71, underscoring the shrimps' status as excellent sources of protein (Chakraborty et al. 2022d). In comparison to other deep-sea shrimps found off the southwest coast of India, these shrimps also contain higher levels of aromatic amino acids (Chakraborty et al. 2022d). These amino acids are known initiators for catecholamine production and thyroid hormone synthesis. Additionally, they possess significant quantities of sulfur-containing amino acids, ranging from 0.43 to 0.49 g 100g⁻¹. These amino acids play a pivotal role in lipid metabolism and have beneficial effects against atherosclerosis and metabolic disorders (Oda, 2006). The presence of sulfur-containing amino acids in muscle tissues of *P. semilaevis* suggests that protein derived from these deep-water shrimps can effectively complement dietary amino acid deficiencies. Leucine, a branched-

chain amino acid, is known to stimulate protein synthesis in biological systems (Tipton, 2017). Notably, the leucine-isoleucine ratio in these shrimps falls within the limits prescribed by FAO/WHO (1999), ranging from 1.68 to 1.71. However, it's worth mentioning that excessive leucine intake may impact the biochemical pathways of tryptophan and niacin, potentially leading to pellagra (Krishnaswamy and Gopalan, 1971).

In the current study, *P. semilaevis* exhibits a Cys: Σ SAA ratio similar to that of other deep-sea species in the same locality. The cholesterolemic effects of proteins are closely tied to their amino acid composition and the Arg/Lys proportion (Rajamohan and Kurup, 1997). In the current study, the arginine-lysine ratio falls within the range of 0.70–1.68, aligning with the ratios found in meat and vegetables (Nurhan, 2007). This highlights the significance of these shrimps in maintaining a favorable cholesterolemic index. Notably, the EAA/AA ratio in *P. semilaevis* ranges from 0.41 to 0.42, above the threshold of 0.39, suggesting that *P. semilaevis* can be considered an ideal protein-rich food source (Chakraborty et al. 2022d).

5.5. Conclusions

The present study is the first to comprehensively analyze the nutritional composition of deep-sea shrimp *P. semilaevis*. The proximate composition, mineral analysis, fatty acid and amino acid profiling collectively reveal the presence of high-value nutrients in the edible tissues of shrimp. It presents a notably lower fat and lipid content in its edible tissue compared to several other deep-sea shrimp species from the same region. A higher PUFA content with lower thrombogenicity and atherogenicity indices indicates its potential to promote cardiovascular health. Significant quantities of aromatic and sulfur-containing amino acids, along with a favorable arginine-lysine ratio, underscores the potential of these deep-sea shrimps as an ideal protein-rich food source, capable of

addressing amino acid deficiencies and promoting a favourable cholesterolemic index in the diet. The differences observed in muscle constituents between male, berried and non-berried female shrimps signify variances in sexual development and the associated energy demands for sustaining body physiology. This implies that gender has an impact on both the rate of growth and the quality of meat in *P. semilaevis*. When comparing this study to other shrimp species, it's clear that different species offer varying nutrient benefits. This highlights the importance of biodiversity in shrimp consumption to meet diverse nutritional needs.

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Growth parameters and population dynamics of *Plesionika semilaevis* on the southwest coast of India

Contents

- 6.1. *Introduction*
- 6.2. *Materials and Methods*
- 6.3. *Results*
- 6.4. *Discussion*
- 6.5. *Conclusion*

6.1. Introduction

The primary goal of fishery stock assessment is to evaluate the well-being of a given stock and offer scientific guidance for its sustainable management within fisheries. While fishery resources possess the capacity for renewal, their status hinges on various influences. Factors such as exploitation rate, fishing season, and the size of catches depend on fishing activities and can be regulated to safeguard the stock's health. Having comprehensive insights into the stock's condition empowers researchers and fisheries managers to anticipate potential yields and determine the necessary effort for the sustainable utilization of these resources (Beverton and Holt, 1957).

Growth in crustaceans is irregular and influenced by several biotic factors (maturity, age, the quality and amount of the food, presence of predators, moult frequency, increment etc.) and abiotic parameters (salinity, dissolved oxygen, photoperiod, temperature, etc.) (Dall et al. 1990; Lizarraga et al. 2008). Short-lived species like shrimps often rely significantly on environmental fluctuations in their population dynamics, with regional variations in population structure often

attributed to environmental diversity rather than intrinsic genetic factors (Miazaki et al. 2021). Obtaining age data directly or estimating age frequency poses challenges as they do not possess durable hard structures (King, 2013; Punt et al. 2013). As a result, population parameters are typically derived from length-frequency data instead. The length-weight relationship is a fundamental method that provides reliable biological data and holds significant importance in fishery assessments. It serves as a tool for determining the "condition factor," which serves as an indicator for both growth and feeding intensity (Fagade, 1979) and also it exerts an influence on the reproductive cycle in species (Welcome, 1979).

Deep-sea shrimps are caught in the trawls operated at a depth of 200-500 m and are distinguished by their bright red color. The genus *Plesionika* is the most abundant in the family, comprising over 100 species (WoRMS, 2024) worldwide. *Plesionika semilaevis* and *P. quasigrandis* recorded at a depth of 250-400 m emerge as the predominant species among the *Plesionika* genus, contributing significantly to 21% of deep-sea shrimp fishery along the Kerala coast (Chakraborty et al. 2022a). *P. semilaevis*, widely distributed among tropical waters of the Indo-Pacific and Atlantic regions, inhabits shelf edges and upper continental slopes at depths ranging from 260 to 2263 meters along the southeast and southwest coasts of India (Alcock, 1901; Suseelan, 1985). Given their considerable commercial and ecological importance, there is a pressing need to thoroughly evaluate the stock status of these species to develop more effective management strategies capable of addressing the substantial harvesting activities along the southwest coast of India.

Detailed information regarding its feeding (Sreelakshmy et al. 2023), reproductive parameters (Sreelakshmy and Chakraborty, 2023) and biochemical parameters (Sreelakshmy et al. 2024) from the southeastern Arabian Sea are available. However, no information regarding its population parameters is available from the Indian waters. The only information available globally is on the

length-weight parameters of *P. semilaevis* from Kagoshima Bay, Japan by Ohtomi (1997). Available information on growth parameters and population dynamics of other deep-sea shrimps from the southwest coast is on *Heterocarpus woodmasoni*, *H. gibbosus* (Radhika, 2004), *P. quasigransis* (Shanis, 2014; Chakraborty et al. 2014b) and *Aristeus alcocki* (Chakraborty et al. 2018). The present study is the first effort to comprehend the population characteristics of the deep-sea pandalid shrimp, *P. semilaevis* from the southwest coast of India. An attempt has been made to provide details on the population structure, growth parameters, mortality, exploitation and longevity of this species and evaluate the status of this resource along the south-west coast of India.

6.2. Materials and Methods

6.2.1. Length-weight relationship

Length-weight relationship was analysed for the samples collected bimonthly during the period between 2016 to 2022 from Saktikulangara landing centre, Kollam, Kerala. Males and females were separated and total length (TL) and body weight (W) were measured with precision to the nearest 0.1 mm and 0.01 g, respectively.

The length-weight relationships were determined using the formula $W = aL^b$ (Le Cren, 1951), which is logarithmically expressed as

$$\text{Log } W = \log a + b \log L$$

Where W is the wet body weight in g, L is the total length of the shrimp in cm and a and b are the length-weight parameters.

The coefficient 'b' offers insights into the condition of shrimp and aids in discerning whether somatic growth is isometric ($b=3$) or allometric ($b<3$; negative allometric and $b>3$; positive allometric) (Ricker, 1973; Spiegel, 1991).

Analysis of covariance (ANCOVA) was employed to test the homogeneity (equality) of regression slopes between male and female individuals.

The Fulton's condition factor (K) of the shrimps was determined from the relationship:

$$K = 100 W/L^3 \text{ (Fulton, 1902)}$$

6.2.2. Growth parameters

Using the von Bertalanffy growth function (VBGF), growth parameters such as asymptotic length (L_∞), growth rate (K) and the theoretical age of a shrimp at which length is zero (t_0), were calculated for male, female and pooled data employing the electronic length frequency analysis (ELEFAN) using TropFishR package (von Bertalanffy, 1938; Mildenerger et al. 2017). L_∞ and K values calculated for the pooled data were used as inputs for further stock assessment studies.

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \text{ (Pauly, 1984)}$$

where L_t represents the length of the shrimp at age t , L_∞ stands for the asymptotic length measured in cm, K represents the growth rate coefficient in year⁻¹, and t_0 denotes the theoretical age of the shrimp at which its length is zero.

An initial seed value for L_∞ was established by utilizing $L_{\max}$, derived from the mean of the 1% largest individual in the sample and computed using Pauly (1984) formula:

$$L_\infty = L_{\max}/0.95$$

The estimation of species longevity ($T_{\max}$) was conducted utilizing the method:

$$T_{\max} = 3/K \text{ (Pauly, 1979)}$$

The growth performance index (Φ') was determined employing the formula:

$$\Phi' = 2\log L_{\infty} + \log K \text{ (Pauly and Munro, 1984)}$$

6.2.3. Mortality parameters and exploitation rate

Total mortality (Z) for the pooled data was calculated utilizing a linearized length-converted catch curve method (Pauly and David, 1981; Sparre and Venema, 1992)

The natural mortality rate (M) was determined using the equation:

$$M = 4.118 \times K^{0.73} \times L_{\infty}^{-0.333} \text{ (Then et al. 2015)}$$

Fishing mortality (F) was computed using the following formula:

$$Z - M \text{ (Qamar et al. 2016)}$$

The exploitation rate (E) was calculated using the equation:

$$F/Z \text{ (Georgiev and Kolarov, 1962)}$$

6.2.4. Length at first capture (L_{c50}) and size at sexual maturity (TL_{50})

The lengths of capture at 50%, 75% and 95% were acquired from the ascending data points of the selectivity curve, obtained through linear regression analysis (Pauly, 1979; Gayanilo et al. 2005). The length at first capture was taken as L_{c50} . The optimum length of exploitation (L_{opt}) was computed utilizing the equation:

$$L_{opt} = (3 / (3 + M/K)) * L_{\infty} \text{ (Froese and Binohlan, 2000)}$$

Size at sexual maturity (TL_{50}) was determined based on the TL at which 50% of females are berried (TL_{50}), estimated via a logistic equation as described by King (1995):

$$P = 1 / (1 + \exp(a + b * CL))$$

6.2.5. Virtual population analysis (VPA)

VPA is a technique enabling the reconstruction of population dynamics using total catch data categorized by age or length (Sparre and Venema, 1998). The inputs required for length-based VPA estimation encompass the exploitation rate, length-weight parameters (pooled data), mortality parameters, and catches.

6.2.6. Data analysis

The length-frequency data were aggregated into intervals of 1 cm in length. Subsequently, the data were analyzed utilizing the TropFish R package within the R statistical tool to evaluate the population parameters.

6.3. Results

6.3.1. Length frequency distribution

The length frequency composition indicates that male specimens ranged from a minimum of 65 mm to a maximum of 140 mm, while female specimens ranged from 70 mm to 135 mm. The size distribution demonstrates that the average length of the sampled specimens is 102.1 ± 13.44 mm for males and 101.9 ± 11.31 mm for females (Fig. 6.1)

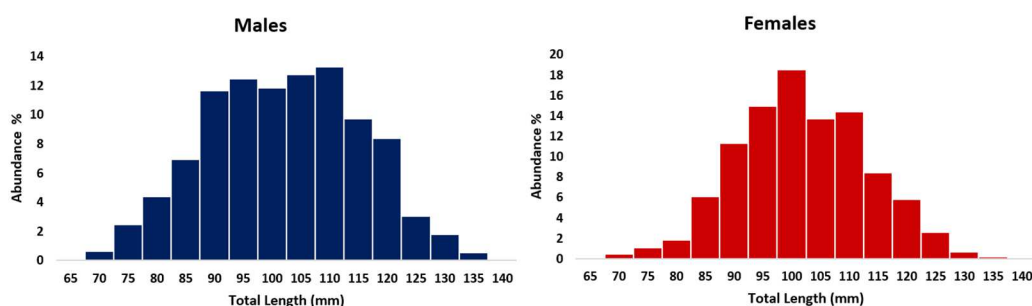


Fig. 6.1. Length frequency distribution in males and females of *P. semilaevis*

6.3.2. Length-weight relationship

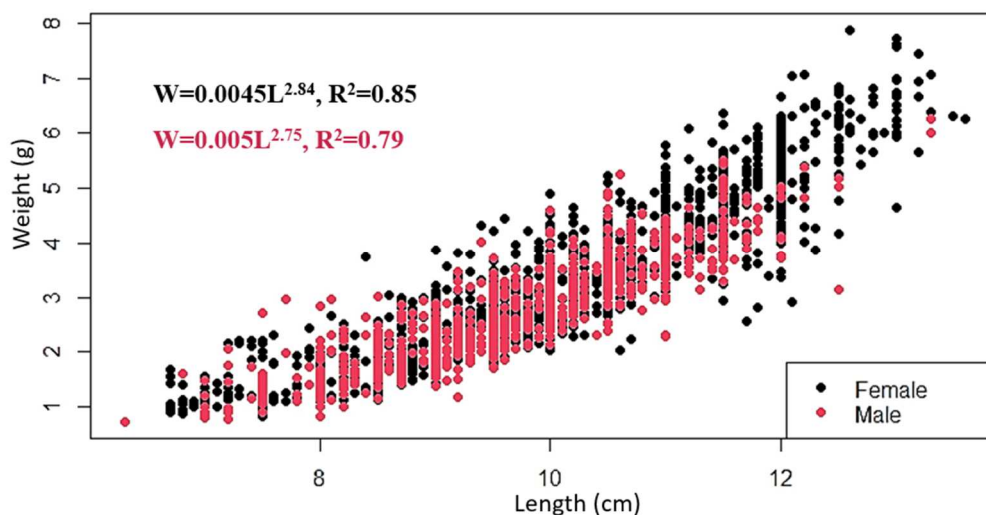


Fig. 6.2. Length-weight relationship of *P. semilaevis* in southeastern Arabian Sea

The relationship between weight (W) and length (L) was expressed by the formula $W=0.005L^{2.75}$ ($R^2=0.79$) in males and $W=0.0045L^{2.84}$ ($R^2=0.85$) in females (Fig. 6.2). This indicates a negative allometric relationship between total length and body wet weight for both males ($b=2.75$) and females ($b=2.84$). The a and b parameters for pooled data were 0.0042 and 2.86 and were used as input parameters in estimating yield per recruit analysis using TropFishR. ANCOVA for length and weight variables indicated a high significant difference ($p < 0.001$) between sexes in *P. semilaevis* indicating variations in length and weight between males and females. Fulton's condition factor (K) ranged from 0.16 to 0.75 in females with an average of 0.32 ± 0.05 . While in males the value of K ranged from 0.2 to 0.68 with an average of 0.30 ± 0.05 .

6.3.3. Growth parameters

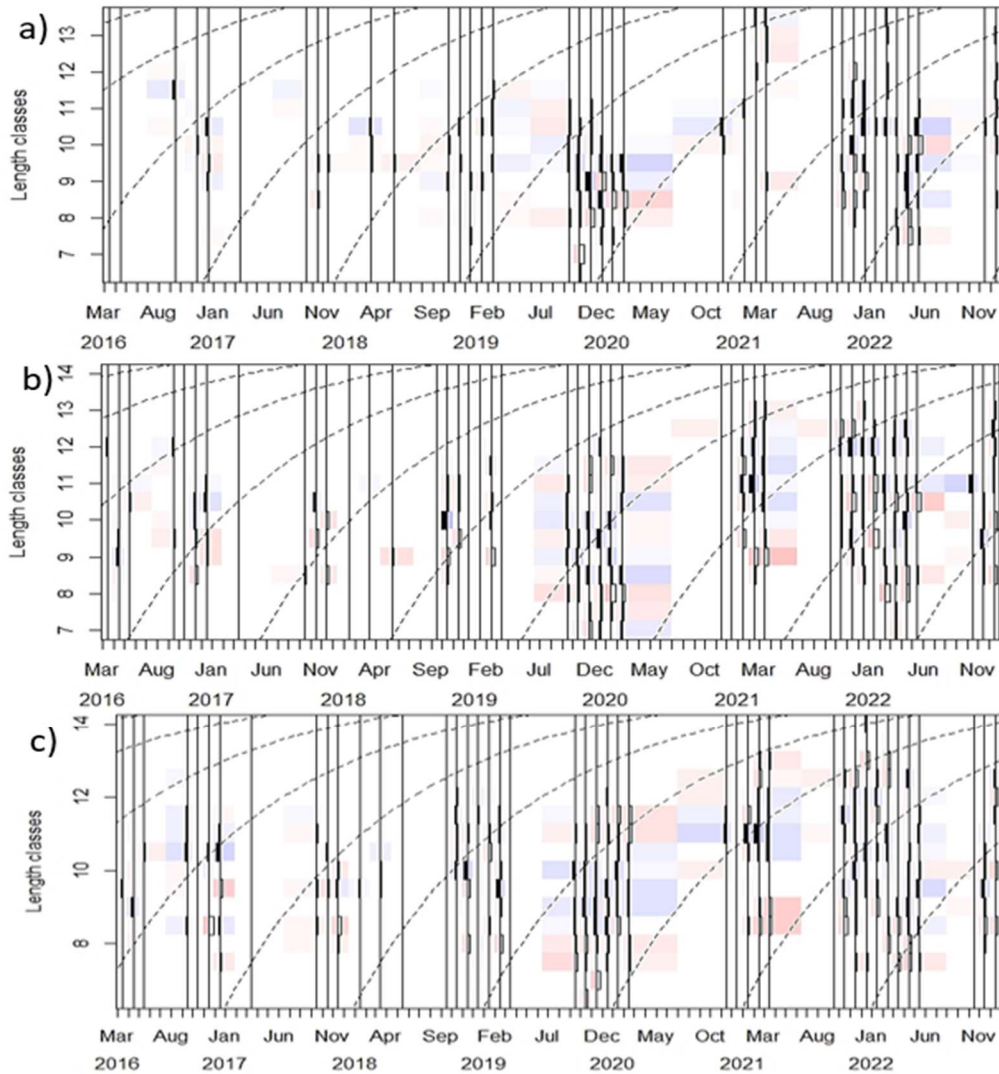


Fig. 6.3. Length-frequency histograms displaying growth curves (dashed lines) obtained through bootstrapped ELEFAN with GA analysis superimposed for male (a), female (b) and pooled (c) specimens of *P. semilaevis*. Black bars signify positive peaks and white bars indicate negative peaks. This method aims to maximize the occurrence of positive peaks. Faint red and blue colors highlight positive and negative peaks, respectively

The growth parameters were established utilizing the von Bertalanffy growth equation employing Electronic Length Frequency Analysis (ELEFAN)

within the TropFishR package (Fig. 6.3). For males, the estimated values of growth parameters were 14.0 cm for L_{∞} and 0.74 year⁻¹ for the growth coefficient K , while for females, the values were 14.3 cm for L_{∞} and 0.73 year⁻¹ for K . Theoretical age (t_0) at length zero was determined as -0.0032 for both sexes and longevity ($T_{\max}$) was estimated as 4.07 years for males and 4.12 years for females. The growth performance index (Φ') was 2.16 for males and 2.17 for females. L_{∞} and K values calculated for the pooled data were 14.3 cm and 0.73 year⁻¹ (Table 6.1) and were used as inputs for further stock assessment studies.

6.3.4. Exploitation rate and mortality parameters

Table 6.1. Growth parameters, mortality, and exploitation rates of *P. semilaevis* (pooled data) assessed by TropFishR

Parameters	Values
Growth parameters	
Asymptotic length (L_{∞})	14.3 cm
Growth coefficient (K)	0.73 year ⁻¹
Tanchor	0.8
t_0	0.003
$T_{\max}$	4.11 years
Growth performance index (Φ')	2.21
Rn value	0.13
Mortality and exploitation	
Natural mortality (M)	1.12 years ⁻¹
Total mortality (Z)	3.18 year ⁻¹
Fishing mortality (F_{current})	2.06 year ⁻¹
$F_{\max}$	2.2 year ⁻¹
$F_{0.1}$	1.8 year ⁻¹
$F_{0.5}$	0.4 year ⁻¹
Current exploitation (E_{current})	0.65
$E_{\max}$	0.66
$E_{0.1}$	0.62
$E_{0.5}$	0.26

From the linearized length-converted catch curve, total mortality (Z) was estimated to be $3.18 \pm 0.1 \text{ year}^{-1}$ for *P. semilaevis* (Fig. 6.4a). The natural mortality (M) was estimated to be 1.12 years^{-1} and fishing mortality (F) was calculated as 2.06 year^{-1} . The current fishing mortality ($F_{\text{current}} = 2.06 \text{ year}^{-1}$) is higher than the estimated F_{msy} , fishing pressure that gives the maximum sustainable yield ($F_{0.1} = 1.8 \text{ year}^{-1}$) and lesser than the maximum reference fishing mortality ($F_{\text{max}} = 2.2 \text{ year}^{-1}$) (Fig. 6.4c) (Table 6.1). The estimated current exploitation rate (E_{current}) was 0.65, near that of E_{msy} , exploitation that gives the maximum sustainable yield ($E_{0.1} = 0.62$) and lesser than the maximum exploitation rate ($E_{\text{max}} = 0.66$).

6.3.5. Length at First Capture (L_{c50}) and size at sexual maturity (TL_{50})

Fig. 6.4b shows the age at probability of capture (t_{50}) for *P. semilaevis*. The age at t_{50} was 1.37 years and the age at 75% and 95% probability of capture was $t_{75} = 1.48$ years and $t_{95} = 1.67$ years, respectively. Concurrently, the lengths associated with these ages were found to be $L_{c50} = 9.46 \text{ cm}$, $L_{c75} = 9.9 \text{ cm}$, and $L_{c95} = 10.56 \text{ cm}$. The L_{opt} was estimated as 9.46 cm. The length at first maturity (TL_{50}) for females was calculated as 8.73 cm (Fig. 6.5).

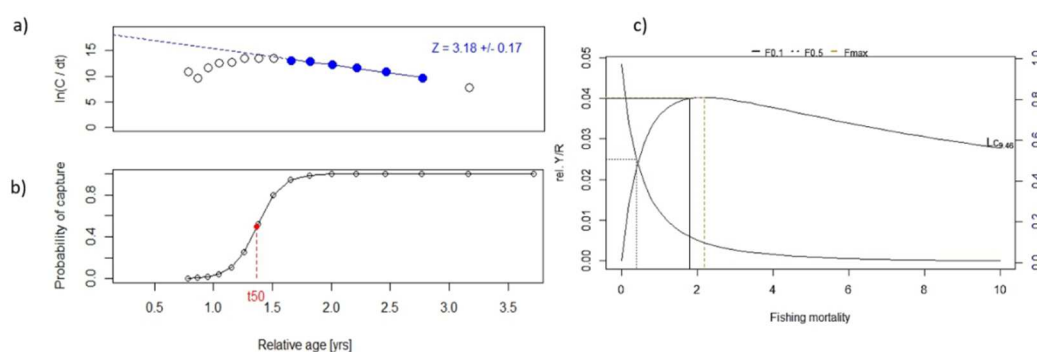


Fig. 6.4. Linearized length-converted catch curve of *P. semilaevis* (a), the selectivity function of the catch curve estimated a length at first capture (L_{c50}) at 9.46 cm (b), and yield and biomass per recruit analysis with $F_{0.1} = 1.8 \text{ year}^{-1}$, $F_{\text{max}} = 2.2 \text{ year}^{-1}$, $F_{0.5} = 0.4 \text{ year}^{-1}$

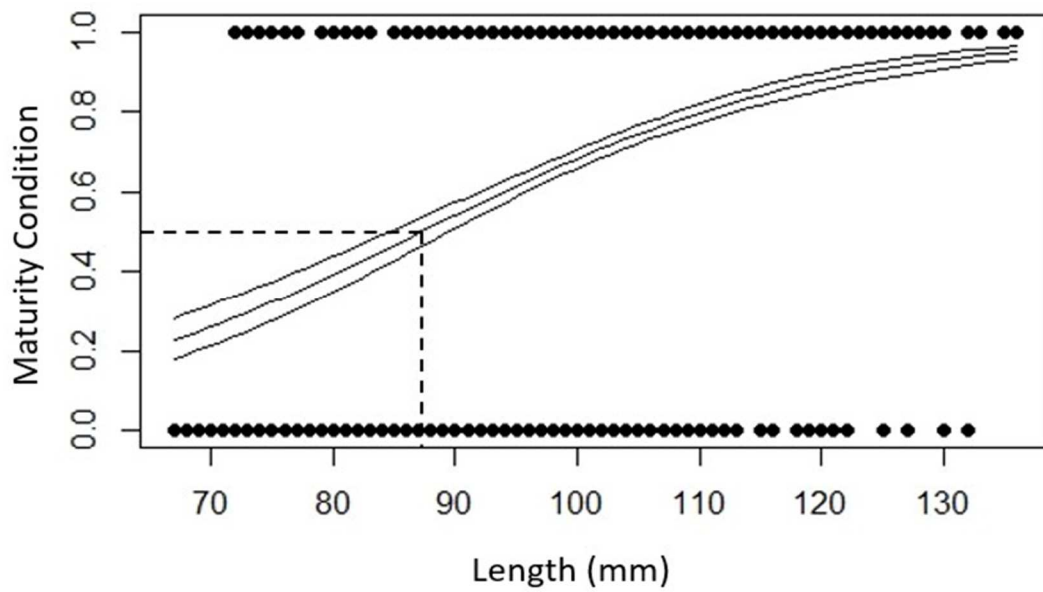


Fig. 6.5. The size at first maturity (TL_{50}) calculated for *P. semilaevis*

6.3.6. Virtual population analysis

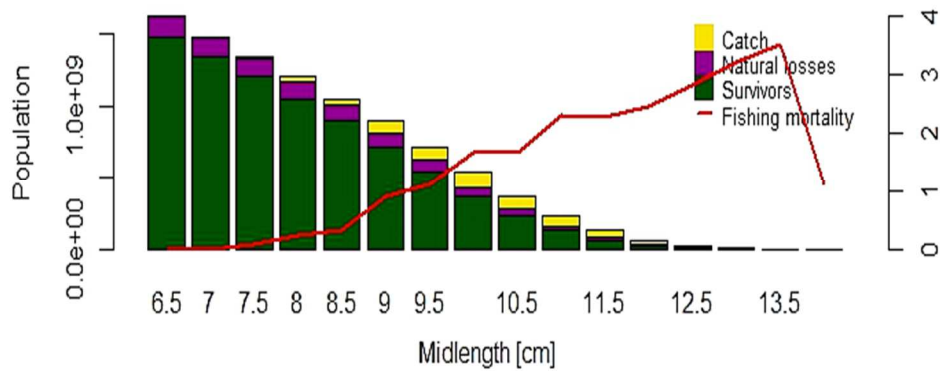


Fig. 6.6. Length structured virtual population analysis of *P. semilaevis*

The virtual population analysis of *P. semilaevis* is illustrated in Fig. 6.6, depicting a sequential decline in the number of survivors with increasing individual length. Fishing mortality was highest among individuals in the mid-length range of 13.5 cm. The results indicate that individuals up to the mid-length group of 9.5 cm succumbed mainly to natural causes and there onwards became more vulnerable to the gears leading to a steady increase in fishing mortality. Specimens at mid-length groups of 9-11 cm were more exposed to the fishing gears.

6.4. Discussion

The length frequency composition indicates that male specimens ranged from 63 mm to 133 mm, while female specimens ranged from 67 mm to 136 mm with an average length of 102.1 ± 13.44 mm for males and 101.9 ± 11.31 mm for females. The size distribution reveals that among males about 50% of samples fall below this average length class, whereas in females, about 54 % of samples fall below this length class. This indicates an almost equal proportion of young and adult shrimps in the catch for both sexes.

The growth pattern for males and females in the current study indicates a negative allometric growth, implying that the increase in shrimp body length was faster than the shrimp body weight. Table 6.2 displays a noteworthy variation in length-weight parameters across various *Plesionika* species in diverse water bodies worldwide.

Table 6.2. Estimates of population parameters of *Plesionika* species in different water bodies of the world

Species	Location	a	b	L_{∞}	$K \text{ year}^{-1}$	Φ'	Reference
<i>P. semilaevis</i>	Southeastern Arabian Sea						Current study
Male		0.005	2.75	14 cm (TL)	0.74	2.16	
Female		0.0045	2.84	14.3 cm (TL)	0.73	2.17	
<i>P. semilaevis</i>	Kagoshima Bay, Japan						Ohtomi, 1997
Male		nd	nd	15.5 mm (CL)	0.103	nd	
Female		nd	nd	17.8 mm (CL)	0.091	nd	
<i>P. heterocarpus</i>	Mediterranean Sea						Company and Sarda, 2000
Male		0.0006	3.08	22.4 mm (CL)	1	0.62	
Female		0.0008	2.98	23 mm (CL)	0.9	0.62	
<i>P. giglioli</i>	Mediterranean Sea						Company and Sarda, 2000
Male		0.001	2.92	21 mm (CL)	0.55	0.26	
Female		0.002	2.6	20.5 mm (CL)	0.75	0.44	
<i>P. martia</i>	Ionian Sea, Mediterranean						Maiorano et al., 2002
Male		0.001	2.84	28 mm (CL)	0.5	2.59	
Female		0.001	2.85	30.5 mm (CL)	0.44	2.61	
<i>P. martia</i>	Aegean Sea, editerranean						Kocak et al., 2012
Male		0.008	2.17	23.4 mm (CL)	0.49	2.44	
Female		0.007	2.25	26.3 mm (CL)	0.38	2.42	
<i>P. canthonotus</i>	Mediterranean Sea						Company and Sarda, 2000
Male		0.0008	2.96	18.4 mm (CL)	0.5	0.13	
Female		0.002	2.55	19 mm (CL)	0.55	0.23	
<i>P. quasigrandis</i>	Kerala coast, Arabian Sea						Shanis, 2014
Male		0.0000	3.28	13.9 cm (TL)	0.68	2.72	
Female		0.0000	3.46	14.5 cm (TL)	0.52	2.66	
<i>P. quasigrandis</i>	Kerala coast, Arabian Sea						Chakraborty et al., 2014b
Male		0.003	3.11	12.4 cm (TL)	0.7	4.03	
Female		0.004	3.01	13.0 cm (TL)	0.8	4.13	
<i>P. narval</i>	Ustica, Tyrrhenian Sea						Arculeo and Lo, 2011
Male		nd	nd	17.8 mm (CL)	0.71	2.28	
Female		nd	nd	27.4 mm (CL)	0.65	2.62	
<i>P. edwardsi</i>	Madeira, Atlantic						González et al., 2016
Male		0.005	2.36	33.1 mm (CL)	0.54	2.77	
Female		0.003	2.52	36.2 mm (CL)	0.59	2.88	

The variation in the length-weight relationship can be attributed to factors such as habitat, seasonal, maturity stage, sex, health and abundance of food items (Tesch, 1971; Sossoukpe et al. 2016; de Carvalho-Souza et al. 2023).

The condition factor, K serves as a crucial indicator of shrimp wellbeing or fatness. Typically falling within the range of 0 to 2, with a mean value around 1 for fish, it reflects the nutritional status and overall health of the organism (Hanif, 2022). A low K , (females, 0.32 ± 0.05 and males, 0.30 ± 0.05) as observed in this study (Hanif, 2022), suggests a thin and elongated shrimp. K values are influenced by various factors such as size, sex, season, and gonad development, with females typically exhibiting higher values due to larger and heavier gonads (Froese, 2006). Factors like feeding rate and environmental conditions also contribute to variations in K (Heincke, 1908). In the case of *P. semilaevis*, a lower K might be attributed to factors such as feeding patterns, environmental influences, or the inherent lean nature of the species.

To effectively manage fisheries, it is advised to have a comprehensive knowledge of the life history parameters of species (Hilborn and Walters, 1992). In cases where age-structured data are lacking, length-composition data are commonly employed to assess the dynamics of species populations (Sparre and Venema, 1998). The only available previous study on the growth parameters of *P. semilaevis* is a work done by Ohtomi (1997) in Kagoshima Bay, Japan. He calculated the L_{∞} for males and females as 15.47 and 17.83 mm carapace length and the K value calculated were 0.103 for males and 0.091 for females. The estimated longevity of *P. semilaevis* was approximately 3 years (males 34 months and females 38 months). The maximum theoretical length, $L_{\infty} = 14$ cm (TL) for males and 14.3 cm TL for females in the current study. The growth coefficient K , of the shrimp was 0.74 year^{-1} and 0.73 year^{-1} for males and females respectively which is higher than the estimate for *P. semilaevis* in Japanese waters by Ohtomi (1997) (Table 6.2). This suggests that *P. semilaevis* from tropical waters is a fast-

growing shrimp species compared to temperate waters. This is also evident in other *Plesionika* species from temperate and tropical regions (Table 6.2).

The growth performance index is regarded as a valuable tool for comparing growth curves among populations of the same species or different species within the same family (Park et al., 2013). The growth performance index (Φ') was 2.16 for males and 2.17 for females. From the study, the growth performance index was similar to estimates from Shanis (2014) for *P. quasigrandis* from the same region. K , L_∞ and Φ' values indicated differences in these parameters among various *Plesionika* species and geographic regions (Table 6.2). The potential factors contributing to variations in growth parameters like K , L_∞ and Φ' may include geographical locations, environmental conditions, stock, population size, feeding habits, diet composition and the data analysis method used (Tesch, 2003; Sequeira et al. 2009; Sossoukpe et al. 2016; Hirota et al. 2022; Barua et al. 2023; Sreelakshmy et al. 2023).

In the study on populations, two categories of mortality are considered: natural mortality (M) and fishing mortality (F), adding up to total mortality (Z). In the present study, natural mortality was determined utilizing the formula proposed by Then et al. (2015). For *P. semilaevis*, Z was determined to be 3.18 year^{-1} , M as 1.12 years^{-1} and F as 2.06 year^{-1} . In this instance, the F value was higher than that of M , indicating that fishing is the primary cause of the decline in individuals within the southeastern Arabian Sea. The F value is higher than the F_{msy} ($F_{0.1} = 1.8 \text{ year}^{-1}$) and lesser than the maximum fishing mortality rate ($F_{\text{max}} = 2.2 \text{ year}^{-1}$), suggesting that the shrimp species is not experiencing high fishing pressure in the study area. Additionally, another key parameter is exploitation E_{current} , which is 0.65 for *P. semilaevis* which is near to that of E_{msy} ($E_{0.1} = 0.62$) suggesting that there exists an optimal level of exploitation for *P. semilaevis* in the southeastern Arabian Sea ensuring the maintenance of its maximum sustainable yield. Additionally, the E_{current} is less than the maximum exploitation rate ($E_{\text{max}} = 0.66$)

indicating that the resource from the southeastern Arabian Sea is not over-exploited.

The length at first capture (L_{c50}) was 9.46 cm while the age at first capture (t_{50}) was 1.37 years. Shanis (2014) documented the L_{c50} for *P. quasigrandis* from the same locality to be 8.63 cm, while Chakraborty et al. (2014b) observed a L_{c50} value of 8.48 cm in males and 9.34 cm in females. Variations in the mesh size of fishing gears employed in fishing activities may contribute to differences in the length at first capture. It is conceivable that fishing gears with larger mesh sizes are more likely to capture larger shrimps, whereas those with smaller mesh sizes may capture smaller ones. A similar value of the optimum length of exploitation and L_{c50} suggests that the shrimps are being harvested at a safe size and that a sufficient number of juvenile shrimps are allowed to mature from the stock. Also, the size at first maturity (TL_{50}) calculated for the females was 8.73 cm, which is much smaller than the L_{c50} value, hence allowing the spawning of females.

The results from the Virtual Population Analysis (VPA) indicate that individuals with mid lengths from 9.5 cm and higher are significantly susceptible to fishing pressure, possibly because larger-sized individuals hold greater economic value. Additionally, smaller-sized individuals exhibit higher natural mortality rates compared to fishing mortality rates. The increased number of survivors within the population suggests that recruitment overfishing is unlikely in the stock of this species located in the southeastern Arabian Sea. This observation could be attributed to the stock of this species not being harvested before reaching the first maturity stage.

In recent times, monitoring the status of fishery resources, including the collection of biological data, has become crucial due to the growing demand for these resources. Biomass and CPUE estimates are commonly used to determine stock indices, which are essential for the effective management of fishery

resources. The variation in landings of *P. semilaevis* species from 2007 to 2022 can result from various factors, including shifts in abundance, technological advancements, variations in the effort exerted by different fishing gear, changes in fishing grounds, or market-driven demands that lead to the targeted harvesting of specific resources.

6.5. Conclusion

The study aimed to assess the stock status of *P. semilaevis* from the southeastern Arabian Sea based on growth and population parameters. The length-weight parameters reveal a negative allometric growth pattern for both sexes, suggesting that shrimp body length increased at a faster rate than shrimp body weight. The assessed shrimp species was found to be a fast-growing species. The species appears to be in a sustainable condition since the current fishing mortality rate was below the $F_{\max}$. The size at first maturity ($TL_{50} = 8.73$) is much smaller than the length at capture ($L_{c50} = 9.46$ cm) value, thus indicating the potential for female spawning and growth of juveniles. The value of E_{current} was near that of E_{msy} indicating an optimal exploitation level for *P. semilaevis* in the Southeastern Arabian Sea to sustain its maximum yield.

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Summary and Conclusion

This thesis presents the first comprehensive study on the taxonomy, fishery biology, and population dynamics of *Plesionika semilaevis* from the southwest coast of India. Integrating molecular, ecological, and biological approaches, the research provides pioneering insights into the species, contributing significantly to marine biodiversity, fisheries management, and conservation efforts.

P. semilaevis, a key species in the deep-sea fishery along the southwest coast of India, plays a vital role in supporting local economies and maintaining the biodiversity of the region's marine ecosystems. As a commercially significant species, its sustainable management relies on an in-depth understanding of its biology, population structure, and connectivity. While morphological assessments have traditionally served as the primary method for species identification, these methods may overlook genetic diversity and the existence of cryptic lineages.

Morphological measurements and mitochondrial cytochrome oxidase I (COI) gene sequences were analyzed for samples of *P. semilaevis* collected from the southeastern Arabian Sea and the Mozambique Channel. Phylogenetic analysis using maximum likelihood revealed two distinct clades, separating the populations of the Arabian Sea and the Mozambique Channel-Madagascar regions. The genetic divergence observed, with intra-species differences for the COI gene ranging from 4.2% to 5.4%, exceeded the inter-species threshold typically observed in the genus. This significant differentiation indicates the existence of cryptic species within *P. semilaevis*.

Haplotype network analysis further supported this genetic divergence, revealing 20 segregating sites in the COI gene between the two regions. The analysis of molecular variance (AMOVA) confirmed high genetic diversity ($\phi_{ST} = 0.99409$, $P < 0.001$), underscoring the genetic isolation between these populations. Oceanographic features such as the South Equatorial Current (SEC), eddies in the Mozambique Channel, the east-west flow of the SEC, and equatorial counter-currents, along with geographic barriers like the Chagos Ridge, were identified as major drivers of this isolation. These factors limit gene flow and contribute to the formation of allopatric cryptic species in the Arabian Sea and Mozambique Channel.

The findings of this study emphasize the complex population structure of *P. semilaevis* within the Indian Ocean and highlight the limitations of relying solely on morphological characteristics for species identification. Integrative taxonomy, which combines molecular and morphological data, proves essential in delineating species boundaries, identifying cryptic lineages, and understanding the evolutionary relationships within the genus *Plesionika*. Such an approach is particularly critical for species like *P. semilaevis*, where cryptic diversity may have significant implications for fisheries management and conservation.

The feeding ecology of deep-sea shrimp like *Plesionika semilaevis* plays a pivotal role in understanding their contribution to marine food webs as intermediate trophic organisms. This study, conducted over a span of three years in the southeastern Arabian Sea, is the first to comprehensively analyze the feeding behavior and dietary preferences of this species, integrating environmental and biological variables. The analysis revealed that *P. semilaevis* exhibits a highly diversified diet, establishing it as a generalist feeder with a broad trophic niche. The prey spectrum ranged from smaller organisms like foraminifera to larger crustaceans and fishes. Crustaceans, detritus, and foraminifera emerged as the dominant dietary components, while fishes, mollusks, and sponges

constituted secondary prey items. The dietary variation observed among the shrimp was influenced significantly by factors such as size, sex, reproductive state, and season. Berried females displayed the highest feeding intensity compared to males and non-berried females, underscoring their increased energy demands during reproduction. Similarly, juveniles exhibited more active feeding behavior than adults, likely driven by their heightened metabolic and growth requirements.

Seasonal variations played a crucial role in the feeding intensity of *P. semilaevis*. The pre-monsoon period marked the highest feeding activity across all groups, with a noticeable decline in post-monsoon samples. This seasonal trend may be attributed to oceanographic processes such as upwelling and vertical mixing, which enhance food availability in the benthic zone during pre-monsoon months. The analysis of feeding intensity relative to shrimp size highlighted that smaller individuals predominantly consumed less mobile prey like detritus and foraminifera, while larger individuals targeted more energy-rich prey such as crustaceans, mollusks, and fishes. This study emphasizes the facultative scavenging behavior of *P. semilaevis*, showcasing its ability to adapt feeding strategies to the availability of food resources in its deep-sea habitat.

The results underline the importance of seasonal oceanographic phenomena, such as upwelling, in shaping the feeding ecology of benthic and benthopelagic organisms. The insights gained from this research provide a foundational understanding of the trophic role of *P. semilaevis* in deep-sea ecosystems and highlight its ecological adaptability, which is critical for the sustainable management of its populations and the broader marine biodiversity of the southeastern Arabian Sea.

Reproductive traits are vital indicators of a population's resilience to environmental and anthropogenic pressures, especially in commercial species like *P. semilaevis*. Despite extensive studies on reproductive biology in temperate and

sub-tropical waters, limited information exists about the species in tropical waters such as the Indian Ocean. This study investigates the reproductive biology of *P. semilaevis* from the southeastern Arabian Sea, encompassing reproductive periods, ovarian and embryonic development, embryo size, brood size, and size at sexual maturity. Histological analysis of ovarian samples revealed asynchronous oocyte development, with multiple stages of oocytes co-occurring in the ovary but in varying proportions. Females demonstrated the ability to spawn multiple times within a single reproductive cycle, as evidenced by ovarian maturation during the embryo incubation phase.

Females were classified into ovigerous and non-ovigerous stages, and embryonic development was categorized into four distinct stages. Ovigerous females were present throughout the year, indicating continuous reproduction, though the primary reproductive season spanned November to February. Spawning and hatching were concentrated from December to February and March to May, respectively, as deduced from the proportion of embryos in various developmental stages.

Embryo size increased significantly with developmental progression ($p=0$), but it was not correlated with female body size ($p>0.05$). Brood size showed a positive correlation with female body size across all stages of embryo development. However, a marked decrease in brood size occurred as embryos matured, reflecting natural attrition during development. The size at sexual maturity was determined based on the carapace length at which 50% of females were ovigerous ($CL_{50em} = 15.07$ mm) or had mature ovaries ($CL_{50ov} = 15.51$ mm). Brood size varied significantly, ranging from 2,093 to 12,887 embryos, with average embryo sizes increasing from 0.51×0.40 mm post-spawning to 0.66×0.50 mm prior to hatching. These insights are critical for managing *P. semilaevis* populations, especially in light of its commercial significance. The detailed characterization of ovarian and embryonic development stages, brood size, and

size at maturity provides essential data for establishing sustainable management measures. Understanding the primary reproductive season helps determine whether current closed seasons align with peak reproductive activity, ensuring the protection of spawning females.

This study also explored the nutritional profile of *P. semilaevis*, providing detailed insights into its potential as a nutritious food source. The research assessed gender-specific differences in proximate composition, mineral content, amino acid profiles, and fatty acid composition. Females exhibited significantly higher levels of carbohydrates, lipids, and fats compared to males, reflecting the energy demands associated with reproduction and physiological processes. The fatty acid profile of *P. semilaevis* highlighted palmitic acid as the predominant saturated fatty acid, oleic acid as the primary monounsaturated fatty acid, and C20-22 *n*-3 fatty acid analogues as the dominant polyunsaturated fatty acids (PUFAs). Notably, the PUFA content, particularly the C20-22 *n*-3 analogues, varied significantly by sex and season, peaking during the pre-monsoon period in males, berried females, and non-berried females.

The shrimp's fatty acid composition underscores its health benefits, with lower thrombogenicity and atherogenicity indices suggesting its potential to support cardiovascular health. This, combined with its favorable PUFA profile, positions *P. semilaevis* as a heart-healthy dietary choice. The macro-mineral analysis revealed potassium as the most abundant mineral, followed by phosphorus, while iron and zinc dominated among micro-minerals. These elements are crucial for various physiological functions, adding to the species' nutritional value. Additionally, the amino acid profile demonstrated an ideal balance between essential and non-essential amino acids, marking *P. semilaevis* as a protein-rich food source. The presence of significant quantities of aromatic and sulfur-containing amino acids, along with a favorable arginine-to-lysine ratio,

highlights its potential to address amino acid deficiencies and contribute to a balanced diet.

The study also revealed gender-specific differences in the nutritional composition of the shrimp. For instance, berried females exhibited distinct muscle constituents compared to non-berried females and males, a reflection of the physiological energy demands associated with reproduction. These differences not only influence the quality of meat but also point to variations in growth rates and energy allocation strategies among sexes. Such findings highlight the interplay between biological and nutritional factors, emphasizing the need for targeted management of deep-sea shrimp populations based on their reproductive biology and nutritional attributes. When compared to other shrimp species, *P. semilaevis* demonstrates a lower fat and lipid content in its edible tissues while offering a high PUFA concentration. These characteristics distinguish it from other deep-sea shrimp species in the region and affirm its nutritional uniqueness. The study underscores the importance of biodiversity in shrimp consumption, as different species provide varied nutritional benefits that cater to diverse dietary requirements.

The study assessed length-weight relationships and found a negative allometric growth pattern for both sexes, indicating that shrimp body length increased faster than body weight. This growth pattern reflects the biological characteristics of *P. semilaevis* and provides insights into its life strategies. Growth parameters derived from the von Bertalanffy Growth Function (VBGF) revealed an asymptotic length (L_{∞}) of 14 cm total length (TL) for males and 14.3 cm TL for females, with growth rates (K) of 0.74 year⁻¹ for males and 0.73 year⁻¹ for females. The growth performance index (Φ') was 2.16 for males and 2.17 for females, indicating a fast-growing species with relatively short longevity.

The size at first maturity (TL₅₀) was estimated at 8.73 cm TL, smaller than the length at first capture (Lc₅₀), which was 9.46 cm TL. This difference

highlights the opportunity for females to spawn and juveniles to grow before being harvested, supporting the sustainability of the fishery. Mortality rates were also analyzed, with natural mortality (M) at 1.12 year^{-1} , fishing mortality (F) at 2.06 year^{-1} , and total mortality (Z) at 3.18 year^{-1} . The exploitation rate (E) was calculated at 0.65, close to the maximum sustainable yield exploitation rate ($E_{\text{msy}} = 0.62$), indicating that the current exploitation level is sustainable.

The findings suggest that *P. semilaevis* is a fast-growing species with stable population parameters over the study period. The current fishing practices maintain the species in a sustainable state, with fishing mortality below the F_{max} , ensuring that the population is not overexploited. The estimated size at maturity relative to the size at capture supports the potential for reproductive success, allowing the population to replenish naturally. The results indicate that the fishery for *P. semilaevis* in the southeastern Arabian Sea is currently sustainable, with an optimal exploitation rate that balances economic benefits with ecological conservation. Future management practices should continue to focus on maintaining this balance to ensure the long-term viability of this commercially important species.

Future research should address unresolved taxonomic ambiguities in other *Plesionika* species, as this study focused exclusively on resolving those of *P. semilaevis*. Additionally, while this species is dominant along the southern coast of India, its absence from the northwest and northeast coasts raises questions. Detailed studies are needed to explore whether it is truly absent in these areas or if ecological factors, such as currents, temperature, or habitat conditions, are limiting its distribution. Understanding the environmental variables favoring its dominance in the southern coast will provide crucial insights into its ecological adaptations and distribution dynamics.

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List of Publications

Peer-reviewed articles

1. **Sreelakshmy, S.**, Chakraborty, R. D., Chakraborty, K. & Dhara, S. (2024). Biochemical analysis and nutritional profile of *Plesionika semilaevis*, a deep-sea shrimp from the Arabian Sea. Journal of Food Composition and Analysis, 128, 106034. doi: <https://doi.org/10.1016/j.jfca.2024.106034>
2. **Sreelakshmy S.** & Chakraborty, R. D. (2023). Reproductive traits, dynamics of oogenesis and embryonic developments in the deep-sea shrimp *Plesionika semilaevis* from the southeastern Arabian Sea. Deep Sea Research Part I: Oceanographic Research Papers, 199, 104133. doi: <https://doi.org/10.1016/j.dsr.2023.104133>
3. **Sreelakshmy S.**, Chakraborty, R. D. & Sreesanth L. (2023). Feeding ecology of the pandalid shrimp, *Plesionika semilaevis* Spence Bate 1888) in South Eastern Arabian Sea, Regional Studies in Marine Science, Volume 61, 102866, ISSN 2352-4855. doi: <https://doi.org/10.1016/j.rsma.2023.102866>
4. Chakraborty, R. D., Sreelakshmy S., Sarada, P.T., Sreesanth L. (2024). Feeding habits of the deep-sea shrimp *Plesionika quasigrandis* Chace, 1985 (Decapoda: Caridea: Pandalidae) in the southeastern Arabian Sea. Journal of Crustacean Biology, 44 (3). doi: <https://doi.org/10.1093/jcbiol/ruae041>
5. Chakraborty, R.D., **Sreelakshmy, S.**, Aghana, M., Gayathri, A. P. & Sreesanth, L. (2023). Occurrence of Deep-sea shrimp, *Hadropenaeus lucasii* (Spence Bate, 1881) from the southwest coast of India. Zootaxa, 5254 (1), 127-132. ISSN 1175 5334. doi: [10.11646/zootaxa.5254.1.7](https://doi.org/10.11646/zootaxa.5254.1.7)

Papers presented in International/National conferences

1. Sreelakshmy S and Rekha Devi Chakraborty. “New insights into the vitellogenesis process and early development of deep-sea shrimp *Plesionika semilaevis* Spence Bate, 1888”, International Conference on Responsible Aquaculture and Sustainable Fisheries Interact (RASHI), 13th-16th December, 2022, College of Fisheries, Tripura, India. (Mode of presentation - Oral)
2. Sreelakshmy S and Rekha Devi Chakraborty. “Growth parameters and niche breadth analysis of caridean shrimp provide new insights for sustainable deep-sea shrimp fisheries and ecosystem management of the southwest coast of India”, International Conference-Natural Science and Green Technologies for Sustainable Development (NTSD-2022), 30th Nov-2nd Dec 2022, Goa University, Goa, India. (Mode of presentation - Oral)
3. Sreelakshmy S and Rekha Devi Chakraborty. Conference Proceedings “Feeding habits of the deep-sea pandalid shrimp, *Plesionika semilaevis*, Spence Bate, 1888 from the southwest coast of India”, 34th Kerala Science Congress, 10-12th Feb 2022, Trivandrum, Pg 323-324. Received best paper award. (Mode of presentation – Poster)

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journal homepage: www.elsevier.com/locate/rsmaFeeding ecology of the pandalid shrimp, *Plesionika semilaevis* (Spence Bate 1888) in South Eastern Arabian SeaSreelakshmy S.^{a,b}, Rekha Devi Chakraborty^{a,*}, Sreesanth L.^a^a Shellfish Fisheries Division, Central Marine Fisheries Research Institute, Ernakulam North P.O., P.B. No. 1603, Cochin 682018, Kerala, India^b Cochin University of Science and Technology, South Kalamassery, Kochi, Kerala, 682022, India

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ABSTRACT

The feeding ecology of deep-sea crustaceans is crucial in understanding the ecological roles and interactions of deep-sea organisms as they play a critical role in deep-sea food webs as intermediate trophic level organisms. This study provides the first examination of the feeding ecology of deep-sea shrimp *Plesionika semilaevis* (Spence Bate 1888) and provides new insights into deep-sea community structure. An aggregate number of 2213 individuals (842 males, 1016 berried and 355 non-berried females) were collected from the South Eastern Arabian Sea from 2019 to 2022 and their feeding ecology was studied in relation to the environmental (season) and biological (maturity, sex and size) factors. The index of preponderance values indicates the species has a diversified diet with a wide trophic niche ranging from smaller foraminifera to larger crustaceans and fishes. Frequency of occurrence (FOC) reveals that crustaceans, detritus and foraminifera forms the main prey while fishes, molluscs and sponges form the secondary prey. Berried females had the highest feeding intensity compared to males and non-berried females. Among the studied groups, the percentage of full stomachs was higher during the pre-monsoon period than post-monsoon. Feeding intensity was highest for smaller individuals and decreased gradually with an increase in size. Statistical analyses (ANOVA) also confirmed the significant differences ($p < 0.05$) in the diet composition and feeding intensity of berried and non-berried females, pre-monsoon and post-monsoon samples and, juveniles and adults. The PERMANOVA test showed that there were significant differences in diet in the interaction between sex and size ($p = 0.003$) and between sex and season ($p = 0.001$). The present study also suggests that the seasonal variation in feeding intensity could be attributed to oceanographic phenomena like upwelling prevailing in the South Eastern Arabian Sea.

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1. Introduction

The feeding ecology of deep-sea organisms is crucial in understanding their relative roles in ecosystem functioning. To determine this ecological niche width, it is essential to identify the interaction of the organisms within the food chain (Bearhop et al., 2004). The study of diet composition and feeding behaviour enables the understanding of the rate of growth, gonadal maturation, niche partitioning, habitat preferences, predation, and prey selection. Food is considered the major limiting factor in the functioning of deep-sea ecosystems and trophic aspects have been considered the most important factor in deep-sea faunal community organization (Jumars and Gallagher, 1982). An understanding of the relationship between animals and food organisms, especially the favourite food items and their seasonal distribution, may help to locate the potential feeding grounds as they

provide clues for the prediction and exploitation of the resources (Muthiah, 1994).

Plesionika (Bate, 1888) represents a major group of deep-water shrimps under the family *Pandalidae* (Haworth, 1825). They are represented by more than 100 species distributed world-wide mainly in subtropical and tropical waters (WoRMS (2022) along the continental shelf and slope (Cartes et al., 1993; Carbonell and Abelló, 1998; Company et al., 2004; Vafidis et al., 2005). They constitute an important prey of demersal fishes and cephalopods. Most species under the genus are nektonic species that feed on pelagic and benthic resources (Cartes et al., 1993; Cartes, 1998; Cartes et al., 2002; Fanelli and Cartes, 2004; Vafidis et al., 2005; Fanelli et al., 2007).

Genera *Plesionika* contributes majorly to the commercial landing of deep-sea shrimps in the southern coasts of India. *Plesionika quasigrandis* and *P. semilaevis* are the major species under the genus contributing about 21% of deep-sea fishery in the south-west coast of India (Chakraborty et al., 2022). *P. semilaevis* is one of the most widely distributed pandalids in the tropical waters of

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the Atlantic and Indo-Pacific regions. They are distributed on the shelf edge and upper continental slope, found in the depth range of 260–2263 m along the southwest and southeast coast of India, including the Andaman Sea (Alcock, 1901; Suseelan, 1985).

Considerable variation in the diet of many *Plesionika* species with respect to biological factors, environmental and geographical variables have been observed in the Mediterranean region and West Africa (Fanelli and Cartes, 2004, 2008; Kitsos et al., 2008; Burukovsky, 2017; Bordbar et al., 2019). However, no prior studies have been reported on *Plesionika semilaevis* despite its wide distribution. In the Indian ocean information concerning the diet composition and the feeding habits of some deep-sea shrimps have been published but not much information is available regarding the caridean shrimps. A study on the diet composition and prey selection of penaeid shrimp *Aristeus alcocki* was also observed in this region (Paramasivam et al., 2020). The relationship between feeding intensity and breeding periods of Pandalidae from the *Heterocarpus* genus was observed by Radhika and Kurup (2011).

The present study aims to understand the diet composition and feeding activity of the deep sea caridean shrimp *P. semilaevis* for different sex, maturity, seasonal and ontogenic variations in the South Eastern Arabian Sea.

2. Materials and methods

2.1. Sample collection and processing

Deep sea shrimp samples were collected fortnightly from the fish landing centre in Saktikulangara, Kollam, Kerala (Fig. 1), from 2019 to 2022 (except during monsoon ban). Samples were acquired from deep-sea bottom trawlers having cod-end mesh size of 20–25 mm, operated at a depth of 250 m in the South Eastern Arabian Sea and transported to the laboratory in fresh condition. *P. semilaevis* species were identified based on the taxonomic literatures of Chace (1985), Ohtomi and Hayashi (1995), Chan and Crosnier (1997), Ahamed et al. (2017) and Chan et al. (2020). Sex was determined macroscopically by the shape of the endopod of the first pleopods (King and Moffitt, 1984) (Fig. 2) and the presence and absence of the male appendix in the second pair of pleopods.

The excess water on shrimps was removed using a blotting paper. Total length (TL), the distance from the tip of the rostrum to the tip of the telson and carapace length (CL), the shortest distance between the posterior margin of the orbit and the mid-dorsal posterior edge of the carapace, was measured using digital callipers with a precision of 0.01 mm. Body weight (W) was measured using a digital balance with a precision of 0.01 g. Samples were separated as males, berried and non-berried females (Fig. 2). Each of these was sorted into small (CL < 15 mm), medium (CL 15–19 mm) and large (CL > 19 mm) sized individuals. Small and large individuals were treated as juveniles and adults respectively.

2.2. Feeding analysis

The stomachs of the shrimps were dissected, weighed and stomach fullness was recorded. The feeding intensity (FI) was determined by the degree of distension of the stomach due to the presence of food. Since the amount of food in the stomach of shrimps was very little, the points method (Pillay, 1952) was used for feeding analysis. Stomach fullness was expressed in terms of percentage as 100% full, 75% full, 50% full, 25% full, 10% full and 0% full and each one was assigned, 100, 75, 50, 25, 10 and 0 points respectively. For finding out feeding conditions, stomachs were grouped into full (100% full and 75% full stomachs), partially full

(50% full and 25% full) and empty (less than 10% full). Seasonal variations in feeding intensity and feeding condition were analysed. The intensity of feeding in relation to the size of the species was carried out to study the differences in feeding in juveniles and adults.

Gastro-Somatic Index (GaSI) was calculated as per (Bhatnagar and Karamchandani, 1970) method:

$$\text{GaSI} = \frac{\text{Total weight of stomach}}{\text{Total weight of shrimp}} * 100$$

Based on the number of empty stomachs (0% full), the vacuity coefficient index (VI) was calculated with the following formula (Hyslop, 1980):

$$\text{Vacuity Index (VI)} : \frac{\text{ES}}{\text{TS}} * 100$$

where, ES = Number of empty stomachs (0% full), TS = Total number of stomachs examined

2.3. Stomach contents determination

The stomach contents were emptied into a petridish and examined under a stereoscopic microscope and identified to the possible taxonomic level. Stomach contents of shrimps could rarely be identified to species level as they lost their structure due to the nibbling action of mandibles on the food and mastication of food by the gastric mill in the stomach. Therefore, the food items were categorized into crustaceans, fish, foraminifera, molluscs, detritus, sponge parts and sediments. Detritus consisted of decomposing organic matter beyond identification.

To obtain precise information regarding the volume of various items, the Index of Preponderance was worked out for males, berried and non-berried females separately based on the method of Natarajan and Jhingran (1961). The Index of Preponderance was calculated based on sex, maturity, season and size for the species.

$$\text{Index of preponderance } I = \frac{\sum Vi Oi}{\sum Vi} * 100$$

where Vi and Oi represent the percentage of volume and percentage of occurrence indices of each food item respectively.

To explore the importance of various prey, the frequency of occurrence method described by Hyslop (1980), Williams (1981) and Kelleher et al. (2000) was used.

$$\text{Frequency of occurrence, } F = \frac{n}{Ns} * 100$$

where n = the number of stomachs containing a certain prey; Ns = the total number of stomachs examined. Only actively fed stomachs were used for this analysis.

2.4. Statistical analyses

One-way Analysis of Variance (ANOVA) was carried out with the help of SPSS statistical software (version 23.0) to verify if the diet composition and feeding intensity varied according to sex, maturity stage, size and season. A permutational multivariate analysis of variance (PERMANOVA) with 999 permutations was undertaken to evaluate possible differences in the diet components of *P. semilaevis* between sexes (male, berried and non-berried female), sizes (small, medium and large) and seasons (pre-monsoon and post-monsoon) and possible interactions between categories.



Fig. 1. The geographical location of the fishing area in south eastern Arabian sea (red dot indicating deep-sea landing centre, Saktikulangara). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Population structure

A total of 842 males, 1016 berried and 355 non-berried female samples were analysed for the present study (Fig. 2). Frequency of individuals of different sizes in males, berried and non-berried females have been depicted in (Fig. 3). In the pre-monsoon specimens, carapace length (CL) ranged from 10–30 mm in males, 10–22 mm in berried females and 10–22 mm in non-berried females, while in the post-monsoon specimens CL ranged from 9–29 mm, 12–29 mm and 10–26 mm respectively. A considerable increase in size was observed in the berried females during post-monsoon.

3.2. Seasonal and sex-based feeding

Points method based feeding intensity (FI) calculated showed the highest value for berried females (47.6). Male and non-berried females gave a value of 40.85 and 38.65 respectively. Feeding intensity reduced from pre-monsoon to post-monsoon in all three categories (Fig. 4). The highest difference was observed in males,

49.19 in pre-monsoon and 31.51 in post-monsoon. The highest feeding intensity was observed in pre-monsoon samples of berried females (51.41).

One-way ANOVA results revealed significant differences in the percentage of stomach fullness between sex, maturity and season (Table 1).

Feeding condition or percentage of stomach fullness in males, berried and non-berried females of *P. semilaevis* and its variation from pre-monsoon to post-monsoon period were observed separately (Fig. 5). Berried females showed a higher percentage of full filled stomachs (36.97%) compared to males (29.06%) and non-berried females (28.37%). As a result, the vacuity index (VI) was lowest for the berried females (15.54) than males (21.95) and non-berried females (25.56).

Seasonal variation studies revealed a decrease in values of stomach fullness from pre-monsoon to post-monsoon in *P. semilaevis* (Fig. 5). From pre-monsoon to post-monsoon, full stomachs reduced from 35.88% to 21.41% in males, 40.11% to 29.13% in berried females and 33.1% to 24.64% in non-berried females. As a result, the vacuity index value from pre-monsoon to post-monsoon increased in males (12.50 to 32.85), berried females (12.85 to 21.68) and non-berried females (14.48 to 33.18).

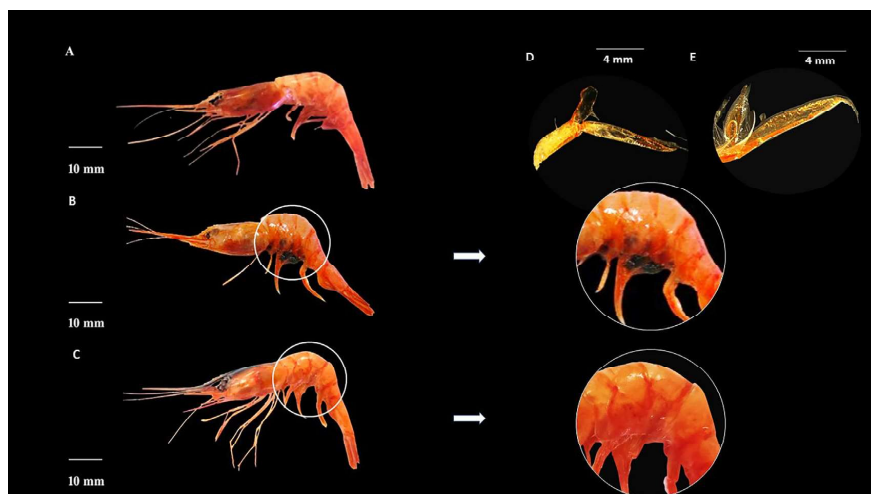


Fig. 2. Representative images of *Plesionika semilaevis* (A) male, (B) berried female, (C) non-berried female, (D) blunt-shaped endopod of first pleopod in males and (E) leafy-pointed endopod of first pleopod in females.

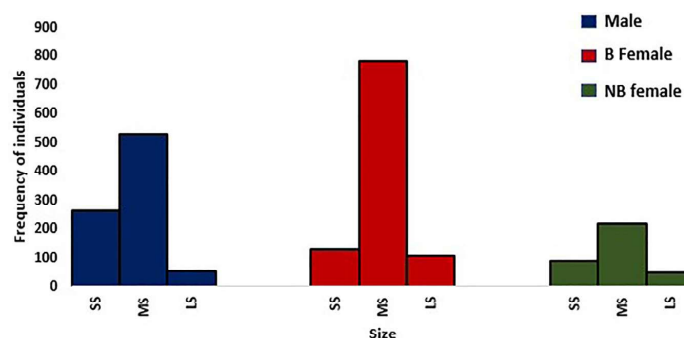


Fig. 3. Frequency of individuals of different sizes in males, berried and non-berried females of *P.semilaevis*. B, berried; NB, non-berried; SS, small sized; MS, medium sized; LS, large sized.

3.3. Ontogenic variations and feeding behaviour

Feeding intensity in different size groups of individuals of males, berried and non-berried females were analysed (Table 2). In males, the higher values of stomach fullness (42.97%) with a FI of 52.5 and VI of 14.06 were recorded for smaller-sized individuals (CL < 15 mm). The GaSI values ranged from 1.1 to 1.8 in males. Larger-sized males had the highest percentage of empty stomachs (42.3%).

Berried females had higher FI and lower VI values compared to the different size ranges of males and non-berried females. FI ranged from 51.7 in smaller ones to 45.6 in larger ones. GaSI values did not vary considerably among different size groups of berried females.

Among non-berried females also, smaller ones had higher value of stomach fullness (40.9%) with a FI of 48.1 and VI of 17.1. Larger non-berried ones had higher percentage of empty stomachs (49%). GaSI ranged from 1.8 in smaller individuals to 1.1 in larger individuals.

ANOVA results of males, berried and non-berried females showed a significant variation in the percentage of stomach fullness among different size groups (Table 1).

3.4. Diet composition

Stomach contents recovered from the foregut of shrimps were thoroughly masticated and thus identification of food items was mainly based on broken body parts and skeletal remains. Various components in the stomach content were identified and categorized into the following groups: crustacean remains, fish remains, mollusc remains, detritus, foraminifera and sponge parts (Fig. 6). Unidentifiable mass consisting of decomposed plant and animal matter were categorized as 'detritus', and were dominant in the gut contents of both males and females. This was followed by crustacean remains (small crabs, shrimps, amphipods, copepods and euphausiids) and foraminifera. Major foraminifera identified to belong to the families Planulinidae (Hyalinea spp, Planulina spp), Nonionidae (Pseudononion spp), Epistomariidae (Pseudoeponides spp), Amphisteginidae (Amphistegina spp), Ammonitidae (Ammonia spp.), Boliviniidae (Bolivina spp), Buliminidae (Bulimina spp.) and Uvigerinidae (Uvigerina spp.). Foraminifera were identified at the genus level because of their smaller intact size and the presence of tough shells or tests. Fish remains (Fish bones, spines, scales and fish eggs) constituted a minor portion

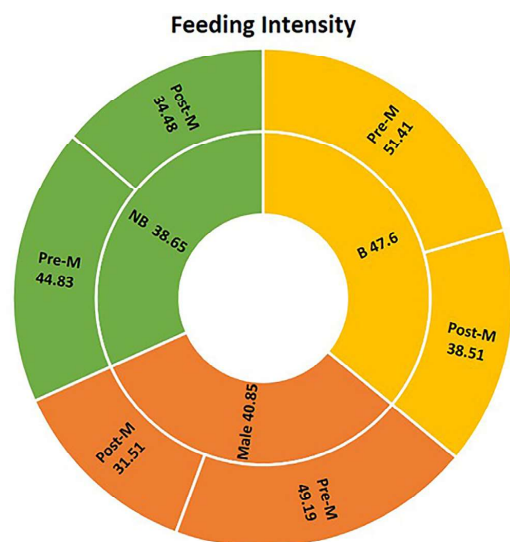


Fig. 4. Seasonal variation in feeding intensity of males, berried and non-berried females of *P. semilaevis*. Post-M, Post-Monsoon; Pre-M, Pre-Monsoon.

Table 1

Summary of the statistical analysis, one-way ANOVA, using percentage of stomach fullness in *Plesionika semilaevis* with sex, size, season and maturity.

S. No.	Category	Variable	N	Degrees of freedom	p-value
1.	Sex	Male	842	2212	0.008
		Female	1371		
2.	Maturity	Berried	1016	1370	0.000
		Non-berried	355		
3.	Season	Male			
		Pre-Monsoon	432	842	0.000
		Post-Monsoon	411		
		Berried			
		Pre-Monsoon	708	1016	0.000
		Post-Monsoon	809		
		Non-Berried			
		Pre-Monsoon	145	355	0.045
		Post-Monsoon	211		
4.	Size	Male			
		Small	261	841	0.003
		Medium	529		
		Large	52		
		Berried			
		Small	127	1015	0.000
		Medium	782		
		Large	107		
		Non-berried			
		Small	88	354	0.014
		Medium	218		
		Large	49		

of the diet while sediments, molluscs (bivalves, gastropods, etc.) and sponges were consumed in lower abundance throughout the study period. Some incidental preys observed were polychaetes and phytoplanktons.

Index of preponderance values (Fig. 7) indicates that detritus contributed the major part of stomach contents of males (43.52), berried females (40.48) and non-berried females (47.31). Crustacean remains formed a higher proportion in berried females

(35.21) than in males (34.10) and non-berried females (26.24). Foraminifera was found invariably in all the stomachs and ranked third with an index of 17.59, 17.42 and 18.02 in males, berried females and non-berried females respectively. However, fish remains were present in a few larger specimens of male and female. Sponge parts and sediments were present in the male, berried and non-berried females in meagre quantity. Mollusc remains were present in the lowest proportion in all categories with the least index values. Frequency of occurrence analysis revealed that crustaceans, foraminifera and detritus were the most preferred diet in almost all individuals (>92%) while fish remains were present in about 35% of individuals. Sediment, mollusc and sponges were present in <30% of individuals. Analysis of variance (ANOVA) of diet composition among males and females revealed no significant differences (Table 3). However, significant variation ($p < 0.05$) was exhibited between berried and non-berried females for all food contents except foraminifera (0.911) and detritus (0.104).

3.5. Seasonal variation in diet composition

The detritus found in the stomach was more for males, berried and non-berried females during the post-monsoon period (57.66, 50.36 and 55.24) compared to the pre-monsoon period (36.31, 37.38 and 31.49). On the contrary, the index values for other major components like crustacean remains, foraminifera and fish remains decreased from pre-monsoon to post-monsoon in all three categories (Fig. 8). Minor constituents of the gut like sediments, mollusc remains and sponge parts did not follow a particular trend in seasonal analysis. Crustaceans, foraminifera and fish remains were present more in the gut of individuals examined in pre-monsoon. Mollusc remains, sponge parts and sediments were present in less quantity in the guts of shrimps during both seasons. Analysis of variance revealed significant variation in diet composition of males, berried and non-berried females from pre-monsoon to post-monsoon. In berried females $p < 0.05$ was observed for all components except foraminifera, fishes and sediments (Table 3). In males and non-berried females $p < 0.05$ was observed for crustaceans, detritus and fish remains.

3.6. Ontogenic variations in diet composition

In males, berried and non-berried females, diet composition varied considerably with an increase in size (Fig. 9). The percentage of crustaceans, fish and mollusc remains increased with an increase in the size of the individuals, while the percentage of foraminifera and sediments decreased with an increase in size. Amphipods, copepods and euphausiids were present more in smaller sized individuals while broken parts of shrimps and crabs were present more in larger sized individuals. Detritus and sponge parts were present in similar portions in all the size groups. Detritus constituted the major content of diet among all size groups of individuals.

With an increase in size in the individuals of *P. semilaevis* the frequency of occurrence of larger prey like crustaceans (96% to 100%), fish (15% to 46%) and mollusc (12% to 33%) increased in the diet (Fig. 10). Similarly, the presence of foraminifera (100%) and sediment (63%) was more frequent in the young ones compared to larger ones.

In males and non-berried females, ANOVA revealed a significant variation in diet composition for different size groups ($p < 0.05$) for all the components except for sponges (Table 3). While in the case of berried females diet components showed a significant difference of $p < 0.007$ except for detritus and sponge parts.

The PERMANOVA test showed that there were significant differences in the diet between the seasons, sex and size (Table 4). Also, there were significant differences in the interaction between sex and size and between sex and season.

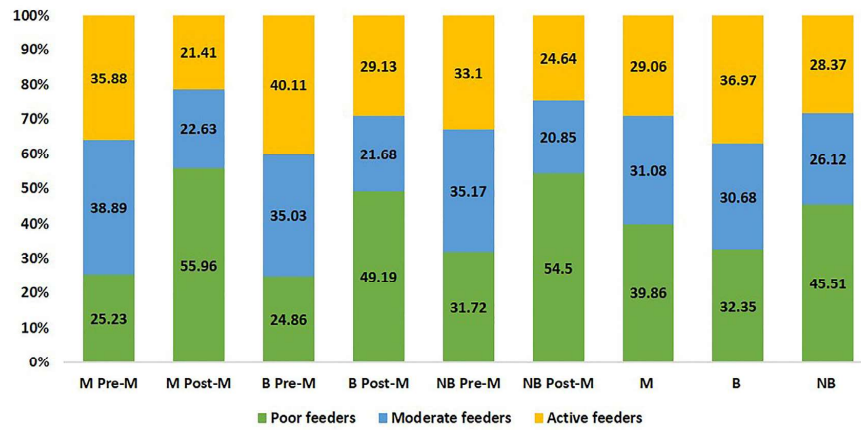


Fig. 5. The season-wise differences occurred in the percentage of empty, partially full and full stomachs in male (M), berried (B) and non-berried (NB) females of *P. semilaevis*. Post-M, Post-Monsoon; Pre-M, Pre-Monsoon.

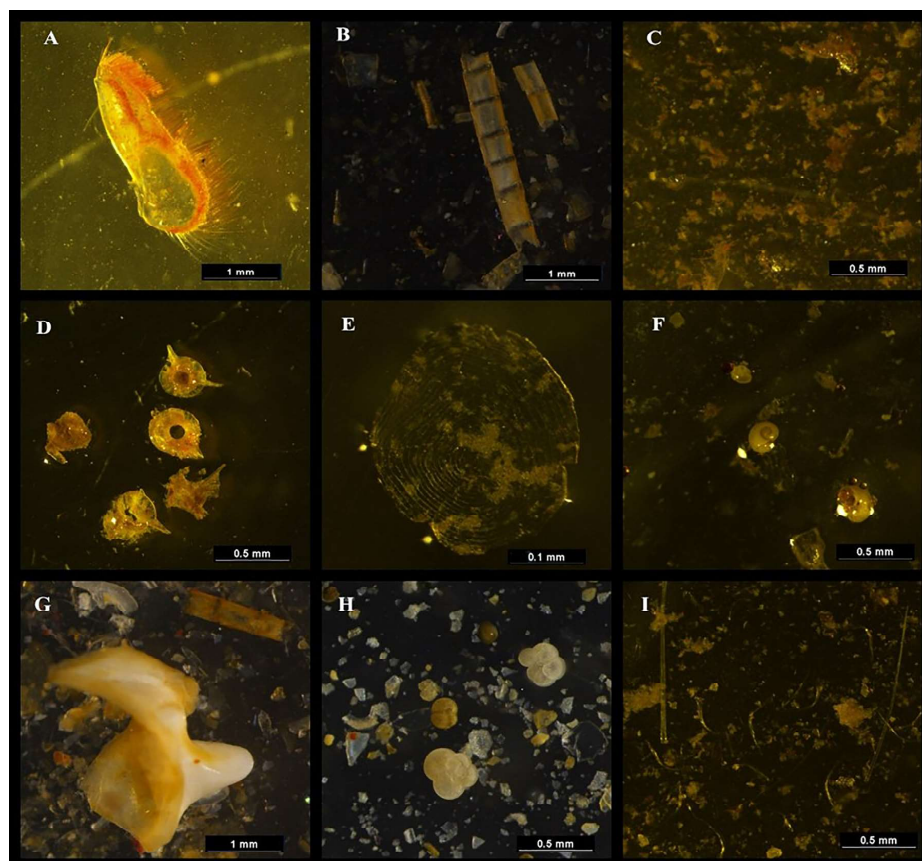
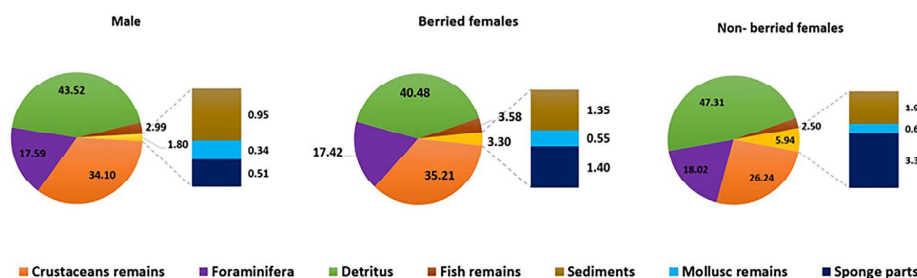
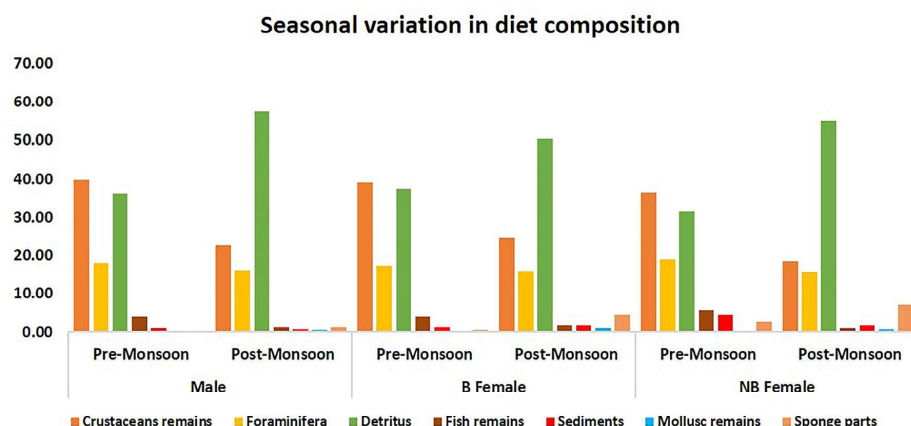


Fig. 6. Diet compositions of *Plesionika semilaevis*. A, B: crustacean remains; C: detritus; D, E: fish remains; F, G: mollusc remains; H: foraminifera; I: sponge spicules.

Table 2Ontogenic variation in feeding intensity, vacuity index, feeding condition and gastro-somatic index (GaSI) in males, berried and non-berried females of *P. semilaevis*.

Category	Size	Feeding Intensity (FI)	Vacuity Index (VI)	Empty stomachs (%)	Partially full stomachs (%)	Full stomachs (%)	GaSI
Male	Small	52.5	14.1	27.3	29.7	43.0	1.8
	Medium	43.0	22.2	37.8	29.9	32.3	1.6
	Large	36.0	28.9	42.3	34.6	23.1	1.1
Berried female	Small	51.7	13.4	28.4	29.9	41.7	1.4
	Medium	47.2	15.8	31.8	31.8	36.4	1.4
	Large	45.6	15.9	42.1	21.5	36.5	1.7
Non-berried female	Small	48.1	17.1	35.2	23.9	40.9	1.8
	Medium	36.2	27.4	48.0	26.5	25.6	1.5
	Large	35.5	30.6	49.0	26.5	24.5	1.1

**Fig. 7.** Relative importance of major groups of food items found in the stomach of male, berried and non-berried females of *P. semilaevis*.**Fig. 8.** Pre-monsoon and post-monsoon variation in the index of preponderance values of various diet components of *P. semilaevis*.

4. Discussion

The feeding ecology of *P. semilaevis* reveals the influence of both environmental (seasonal) and biological (sex, maturity, size) factors on the diet composition and feeding intensity. The overall percentage of empty stomachs is high in this species, similar to other deep-sea pandalid shrimp (Fanelli and Cartes, 2004; Radhika and Kurup, 2011). Deep-sea trawling is done during the morning hours and these deep-sea shrimps are reported to be nocturnal feeders (Kapiris, 2012), which can be attributed to the higher percentage of empty stomachs in the studied groups. Moreover, a high percentage of empty stomachs is an indication of high metabolic rates or low feeding rates (Kapiris, 2004). The low feeding condition in deep-sea caridean shrimps may be an adaptation to the deep-sea environment, where food act as a limiting factor (Jumars and Gallagher, 1982).

Female shows higher feeding intensity than males because of sexual dimorphism and increased growth rates. *Plesionika* spp. is reported to have a continuous reproduction pattern with seasonal peaks (Company and Sarda, 1997; Colloca, 2002; Maiorano et al., 2002; Vafidis et al., 2005). Berried females of *P. semilaevis* were present during both pre-monsoon and post-monsoon and were having higher values of stomach fullness compared to males and non-berried females. For caridean deep-sea shrimps, many authors describe higher feeding activity (higher values of stomach fullness) for berried females, because of the increased metabolic demands after spawning (Maynou and Cartes, 1998; Cartes et al., 2008; Kapiris et al., 2010). This could be because of the lesser feeding activity observed in caridean shrimps during gonadal development when the space in the cephalic cavity for the stomach is compromised due to fully developed ovaries affecting their food intake directly (Weinberg, 1980; Radhika and Kurup, 2011).

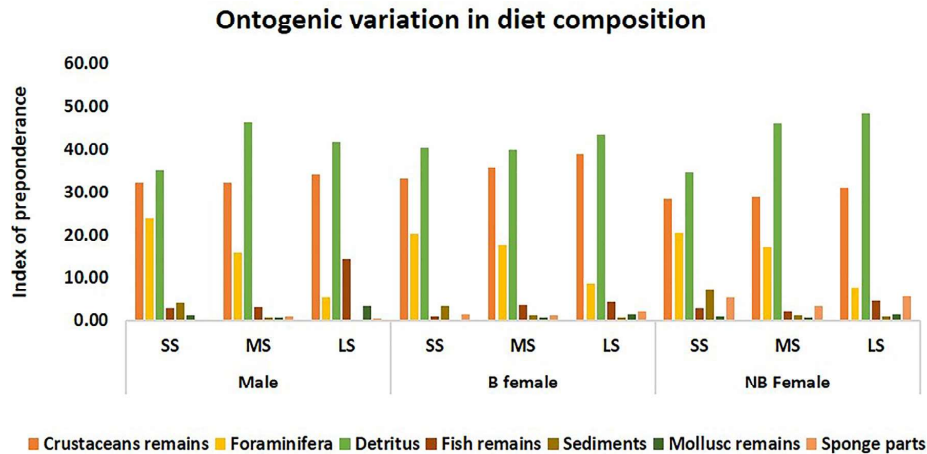


Fig. 9. Ontogenic variations in the index of preponderance values of various diet components of male, berried and non-berried females of *P. semilaevis*. SS, small sized; MS, medium sized; LS, large sized.

Table 3

Summary of the statistical analysis, one-way ANOVA, using diet components in *P. semilaevis* with sex, maturity, season and size. B, Berried females; NB, Non-berried females, Pre-M, Pre-Monsoon; Post-M, Post-Monsoon; DF, degrees of freedom.

Category	Variable	N	DF	p-value						
				Crustaceans	Foraminifera	Detritus	Fish remains	Sediments	Mollusc remains	Sponge parts
Sex	Male	204								
	Female	295	498	0.414	0.855	0.084	0.601	0.146	0.243	0.000
Maturity	B	217	294	0.000	0.911	0.104	0.010	0.000	0.040	0.000
	NB	78								
Season	Male									
	Pre-M	121	195	0.000	0.418	0.000	0.003	0.551	0.332	0.104
	Post-M	75								
	B									
	Pre-M	155	234	0.000	0.837	0.008	0.574	0.117	0.022	0.000
	Post-M	80								
Size	NB									
	Pre-M	35	76	0.000	0.147	0.000	0.017	0.079	0.422	0.146
	Post-M	42								
	Male									
	Small	54	199	0.006	0.005	0.041	0.000	0.018	0.030	0.188
	Medium	134								
Size	B									
	Small	32	214	0.007	0.001	0.112	0.003	0.000	0.000	0.174
	Medium	156								
	Large	27								
	NB									
	Small	19	75	0.020	0.005	0.000	0.001	0.000	0.001	0.970
	Medium	44								
	Large	13								

The decreasing feeding intensity from pre-monsoon to post-monsoon season detected in both sexes and maturity stages could be associated with environmental processes. The seasonal rhythms in feeding behaviour of *P. semilaevis* and monsoon related variation in feeding intensity can be ascribed to the upwelling, an oceanographic phenomenon occurring in the eastern Arabian Sea that replaces the warmer nutrient deplete surface water with dense cooler nutrient rich bottom water (Johannessen et al., 1987; Smitha et al., 2014).

Ontogenetic shifts in feeding behaviour were also apparent in males, berried and non-berried females of *P. semilaevis*. Juveniles showed an increased feeding intensity compared to adult ones

as they have faster growth rates and higher energy requirements (Kapiris and Thessalou-Legaki, 2011).

Plesionika species are distributed mainly in subtropical and tropical waters (Chace, 1985), and a majority of these species feed on both pelagic and benthic resources (Cartes, 1998; Cartes et al., 2002). The species grind their food and ingest only small fragments, hence from the state of the gut contents most prey could only be identified at a higher taxonomic level. The diet component mostly consists of endobenthic (foraminifera, bivalves, sediments etc.), epibenthic (amphipods, euphausiids, gastropods, etc.) and bathypelagic organisms (small decapods and fishes) (Fig. 6) similar to the diet of other deep-water shrimps found

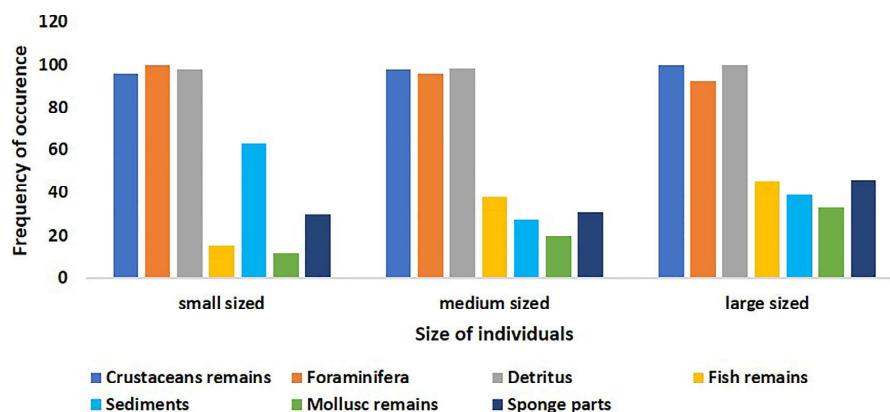


Fig. 10. Frequency of occurrence of various diet components in different-sized individuals of *P. semilaevis*.

Table 4

Results of the PERMANOVA (Permutational multivariate analysis of variance) analysis of the diet components of *P. semilaevis* between sexes (male, berried and non-berried female), sizes (small, medium and large) and seasons (pre-monsoon and post-monsoon). F, Fisher's F statistic; r, similarity among groups; P, probability values.

Factor	F	r	P(>F)
Sex	11.819	0.04260	0.001
Season	27.205	0.04903	0.001
Size	9.0214	0.03485	0.001
Sex: Season	11.911	0.04115	0.001
Sex: Size	4.1886	0.01618	0.003

in Indian waters (Karuppasamy and Menon, 2004; Radhika and Kurup, 2011; Paramasivam et al., 2020). This may be because of the resemblance in the faunal assemblages of the macro-benthic communities persisting on the continental slopes of the region. Based on the results of the present study, *P. semilaevis* can be considered as having a diversified diet because of their wide trophic niche.

Decapod crustaceans are generally considered scavengers or detritivores (Gage and Tyler, 1991). Scavenging is an important facultative foraging mode for deep-sea shrimps. The results of the present study indicate that detritus formed the major percentage of gut contents similar to those reported for other deep-sea shrimp species (Burukovskij, 1992; Karuppasamy and Menon, 2004; Radhika and Kurup, 2011). The protein-energy ratio is highest in the detritus than in any other factor in the biota (Julian et al., 2003). The other food items observed are crustacean remains, foraminifera, fish remains, mollusc remains, sediments and sponge parts similar to those reported in other *Plesionika* species such as *P. edwardsi*, *P. narval*, *P. heterocarpus*, *P. ensis*, and *P. martia* (Labropoulou and Ioannis, 1999; Fanelli and Cartes, 2004; Kitsos et al., 2008). The presence of detritus, foraminifera and sediment in the gut indicated a possible benthic feeding activity and scavenging nature while the presence of broken parts of shrimps and fishes suggests its good swimming ability evidencing that it also feeds on benthopelagic forms.

Ontogenetic shifts in diet were apparent in *P. semilaevis* among small, medium and large-sized individuals. Among males, berried and non-berried females, larger prey like fishes, molluscs and crustaceans were preferred more by medium and large-sized individuals, forming effective predators due to their good swimming capability and larger size mandibles. Foraminifera, sediments and smaller crustaceans were more consumed by smaller

sized individuals. With an increase in size, individuals cease to consume sediment and smaller prey and switch their diet to larger and energetic prey, such as fishes. This broad ecological niche width indicates that *P. semilaevis* play a critical role in deep-sea food webs as an intermediate trophic level organism.

5. Conclusion

This study provides the first examination of the diet composition of deep-sea shrimp *Plesionika semilaevis* in the South Eastern Arabian Sea and the influence of environmental and biological parameters on its feeding behaviour. These species have a diversified diet ranging from smaller foraminifera to larger fishes and crustaceans and can be considered generalist feeders. Scavenging is an important facultative foraging mode observed in this species. Berried females have more feeding intensity than non-berried females and males. Juveniles have more energy requirements hence increased feeding was observed in them compared to adults. The larger individuals consumed more energetic prey like crustaceans, fishes and molluscs as compared to the smaller ones that had a more sedentary diet like detritus and foraminifera. *P. semilaevis* have higher feeding intensity during the pre-monsoon period. The monsoon dependent variation in feeding intensity may be the response of benthopelagic organisms like crustaceans to seasonal oceanographic phenomena such as upwelling and vertical mixing.

CRedit authorship contribution statement

Sreelakshmy S.: Collection of sample, Identification, Formal analysis, Methodology, Writing – original draft. **Rekha Devi Chakraborty:** Conceptualization, Fund acquisition, Collection of sample, Identification, Methodology, Formal analysis, Investigation, Project administration, Resources, Supervision, Validation, Writing and editing – original draft. **Sreesanth L.:** Collection of sample, Identification.

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.

Data availability

Data will be made available on request.

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Ethical approval

All necessary permits for sampling have been obtained by the authors from the competent authorities and are mentioned in the acknowledgement.

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Reproductive traits, dynamics of oogenesis and embryonic developments in the deep-sea shrimp *Plesionika semilaevis* from the southeastern Arabian sea

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ABSTRACT

Reproductive traits are a crucial biological indicator of a population's resistance to anthropogenic and environmental pressures. The reproductive biology of *Plesionika* species from temperate and sub-tropical regions is relatively well known. However, a knowledge gap exists regarding the species' reproduction and life strategies in tropical waters like the Indian Ocean. This paper covers the reproductive period, ovarian and embryonic development, embryo size, brood size and size at sexual maturity of *Plesionika semilaevis*, a commercially important species from the tropical waters of the southeastern Arabian Sea. Histological analysis revealed asynchronous oocyte development with multiple oocyte stages present in each ovary sample, although with varying proportions. Maturation of the ovary was seen during the embryo incubation phase, which indicates that females are able to spawn several times during a reproductive cycle. A total of 1802 females of *P. semilaevis* were examined and sorted into ovigerous and non-ovigerous stages, and the embryos were divided into four stages of development. Although ovigerous females were present in every month's samples, the main reproductive season is from November to February, as evidenced by the larger percentage of ovigerous females during this time. Based on the percentage of embryos in various stages, the spawning and hatching periods were estimated to be December to February and March to May, respectively. Embryo size increased with the developmental stage ($p = 0$) but was independent of body size ($p > 0.05$). A positive correlation was observed between brood size and female body size in all four stages of embryo development but, as the embryos developed a significant decrease in brood size was noticed. Based on the size at which 50% of the females had matured ovaries and 50% were ovigerous, the size at sexual maturity, CL_{50ov} and CL_{50em} , was calculated to be 15.51 mm and 15.07 mm in carapace length, respectively. The brood size ranged from 2093 to 12887 embryos with a mean size of 0.51×0.40 mm following spawning and 0.66×0.50 mm prior to hatching.

1. Introduction

Commercial fisheries are expanding into deeper waters, and the paucity of information on the life histories of the deepwater species being fished is considered a significant barrier to developing and implementing effective management strategies. The specific life-history characteristics of many deep-sea organisms like longer life span, slow growth, late sexual maturity and low fecundity make them especially vulnerable to depletion with a limited potential to rebound from over-exploitation (Cheung et al., 2005; Morato et al., 2006). The dearth of life history information for the exploited deep-sea species poses a significant obstacle to the development and use of effective management strategies (Polidoro et al., 2008).

The fecundity, sex ratio, gonadal and embryonic development and periodicity are essential variables to consider when evaluating the recruitment, reproductive potential, biogeographic dispersion, adaptations to specific habitats and connectivity of marine species (Chemel et al., 2023). A species' life strategy is directly linked to its reproductive behavior. Inadequate environmental conditions in deep-sea environments, such as lack of seasonality in temperature, photoperiod, and food availability, result in low reproductive success (Bauer, 2004).

Pandalidae, a family of tropical-water dwelling deep-sea shrimps, have distinctive growth and reproduction habits. Even within the same genus, pandalid species exhibit a diversity of sexual systems (gonochorism and hermaphroditism) and kinds of reproduction (semelparity and iteroparity). As a result, reproductive strategies vary greatly among

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pandalid species (Correa and Thiel, 2003; Bauer, 2004). Genus *Plesionika*, under the family Pandalidae represents a significant group of deep-sea caridean shrimps represented by more than 100 species distributed worldwide. A characteristic feature of many pandalid shrimps is the energy they allocate for egg production (Corey and Reid, 1991; Wehrtmann and Lardies, 1999). The energy and nutrients found in the egg help the embryos survive and develop, thus having a significant impact on the life-history characteristics of invertebrates (Begon et al., 1996; Figueiredo et al., 2008). A fair amount of information is available regarding the reproductive biology of *Plesionika* species found in various temperate and subtropical climates, however, there exists a knowledge gap when it comes to tropical waters. Significant reproductive studies of *Plesionika* species are of *P. heterocarpus*, *P. edwardsii*, *P. narval*, *P. giglioli*, *P. martia* and *P. acanthonotus* from the Mediterranean Sea (Company and Sarda, 1997; Colloca, 2002; Maiorano et al., 2002; Anastasopoulou et al., 2017), *P. izumiae* from the Japanese waters (Omori, 1971; Ahamed and Ohtomi, 2011), *P. martia* from Ionian Sea (Chilari et al., 2005) and *P. edwardsii* from the Tyrrhenian Sea and North Atlantic (Possenti et al., 2007; Triay-Portella et al., 2017). Despite the increasing commercial interest in *Plesionika* species in Indian waters, contributing to 21% (*P. semilaevis* and *P. quasigrandis*) of the deep-sea shrimp catches (Chakraborty et al., 2022), aspects of the reproductive biology of these species remain almost unknown.

Plesionika semilaevis (Bate, 1888) is one of the commercially and ecologically important deep-sea shrimp species found at a depth of 250 m and above in the southeastern Arabian Sea, contributing 1.23% of the deep-sea shrimp catches in the south-west coast of India (Chakraborty et al., 2022). It plays a critical role in deep-sea food webs as an intermediate trophic-level organism (Sreelakshmy et al., 2023). A study done by Ohtomi (1997) described the reproductive parameters like brood size and reproductive period of *Plesionika semilaevis* from Kagoshima Bay and is the only report available on the reproductive aspects of this species. Detailed studies on the reproductive biology of *Plesionika semilaevis* including ovarian and embryonic development from Indian waters and any other geographical area with its distribution are lacking.

Information on ovarian maturation, embryo development, reproductive period, and brood size is beneficial from a fisheries perspective for understanding the reproductive biology of the species, estimating reproductive potential, and recruitment for maintaining the species' population stability (Mori et al., 1998; Figueiredo et al., 2008; Kevrekidis and Thessalou-Legaki, 2013). Against this background, this study aims to investigate the detailed aspects of the reproductive biology of *Plesionika semilaevis* along with the developmental stages of the ovaries and embryos by macroscopic and microscopic analysis. The study also sought to determine the species' spawning season, which will give the essential prerequisite for stock assessment and stock sustainability and establish successful fishery management.

2. Materials and methods

2.1. Sampling

Samples of deep-sea shrimps were collected fortnightly between August 2019 and May 2022, except during the monsoon ban period (June to August) from about 5 to 6 deep-sea bottom trawlers during each sampling. The trawlers have an overall length of 15–40 m and are powered with high horse power engine (350–500 hp). They were operated at a depth of 150–250 m in the southwest coast of India, with a 25–26 mm mesh size in its cod-end. The samples were transported in fresh condition in an insulated ice box to the laboratory for further analysis. Morphological identification of *P. semilaevis* followed the taxonomic keys of Chace (1985), Ohtomi and Hayashi (1995), Chan and Crosnier (1997), Ahamed et al. (2017), Kuberan et al. (2020) and Chan et al. (2020). By examining the morphology of the endopod of the first pair of pleopods, the sex of an individual was determined (King and Moffitt, 1984). The females were sorted into ovigerous and

non-ovigerous states based on the presence of embryos between the pleopods. Carapace length (CL) and total length (TL) were measured to the nearest 0.01 mm using calipers. An electronic digital balance with a 0.001 g precision was used to measure the body weight (BW).

2.2. Gametogenesis and stages of ovarian development

Macroscopic and microscopic examination was used to establish the stages of female gonadal development. For macroscopic analysis, all individual shrimps were dissected and their ovaries were examined under a stereoscope and categorized into five developmental stages based on location in the cephalothoracic cavity, shape, size, and relative intensity of the color of ovary (Maiorano et al., 2002; Anastasopoulou et al., 2017; Triay-Portella et al., 2017). The mature ovary occupied most of the cephalothoracic cavity's dorsal region, extending anteriorly to the orbital margin visible over the carapace as blue head roe.

Microscopic analysis of each development stage of ovaries was carried out by selecting 10 specimens from each stage. The ovary was removed and fixed in 5% formalin for 24 h for additional histological examination. The fixed tissues were dehydrated in ethanol solutions, cleared in xylene, embedded in paraffin and sliced into 5–6 µm sections. The sections were stained with hematoxylin followed by eosin (Triay-Portella et al., 2014) and mounted for further microscopic analysis. The developmental changes in the ovary were observed using a compound microscope (Leica DM 750) at a magnification of 4x–100x. The oocytes were classified into different developmental stages based on the size of cells, cytoplasmic appearance and presence of lipid globules and yolk granules.

2.3. Stages of embryo development, brood size and embryo size

All females were examined for the presence of different stages of embryos attached to the pleopods. The embryos were carefully separated from the pleopods and categorized into four stages based on the color of the embryos. These embryos were then observed under a stereoscopic microscope (Nikon SMZ1270, Japan) to observe the different changes in embryos with development.

The total weight of embryos was weighed to the nearest 0.001 gm, a subsample was weighed, and the number of embryos was counted under a binocular microscope. The brood size was estimated for ovigerous females with embryos in different stages of development as follows:

$$\text{Brood size} = \frac{\text{Number of embryos in the subsample} \times \text{Total weight of the embryos}}{\text{Weight of the subsample}}$$

The variations in brood size relative to the body size (CL) of females carrying embryos at different developmental stages was also determined. For each stage of embryo development, the sizes of the embryos were calculated using a total of 100 ovigerous females of each stage. The major (length) and minor (width) axes of 10–20 randomly chosen embryos of each individual were measured under a stereomicroscope with an ocular micrometer to the nearest 0.01 mm. Each individual's mean embryo length and width were calculated and finally, mean embryo sizes (length and width) for each embryonic stage were computed. Embryo volume (v) was estimated for each embryonic stage using the formula given by Turner and Lawrence (1979):

$$\text{Embryo volume (v)} = \pi d_1^2 d_2 / 6$$

where d_1 is the minor axis (mm) and d_2 is the major axis (mm).

One-way analysis of variance (ANOVA) was carried out with the help of SPSS statistical software in order to determine the variation in developmental stages with embryo size (length, width and volume) and female body size (CL).

2.4. Reproductive period, sex ratio, GSI and size at sexual maturity

The reproductive period was investigated by considering the

percentage of ovigerous females and their maturity stages of ovaries and embryos. The frequency of females with various stages of embryo development was noted month-wise to estimate the spawning and hatching periods. Monthly variation in the sex ratio (females/males) was also calculated and their deviation from the expected 1:1 were tested using the chi-square analysis.

Gonad weight (GW), of females were taken to the nearest 0.001 g, and the gonadosomatic Index (GSI) was calculated as the percentage weight of the gonad to the total body weight (Grant and Tyler, 1983).

Size at sexual maturity (CL_{50}) was determined based on two factors, i.e., the CL length at which 50% of females are ovigerous (CL_{50em}) and the CL at which 50% of the females have mature ovary (CL_{50ov}) (Triay-Portella et al., 2017). This was estimated by a logistic equation as described by King (1995): $P = 1 / (1 + \exp(a + b * CL))$, (R Studio, version 4.1.1.).

where P is the predicted proportion of ovigerous females/females with matured ovaries, a and b are the estimated coefficients of the logistic equation, and CL is the carapace length.

3. Results

3.1. Size structure

Males and females are sorted out based on the morphological sexual differences between them. Sex was determined based on the shape of the endopod of the first pleopods. The endopod of females has a pointed leaf-like structure, while that of males has a blunt rectangular shape (Fig. 1). A total of 997 males and 1802 females consisting of 1233 ovigerous and 569 non-ovigerous individuals were examined for this study. Ovigerous females had a CL range of 12–24 mm (TL 72–136 mm) and non-ovigerous females had a CL range of 10–24 mm (TL 67–132 mm).

3.2. Gametogenesis and ovarian development

Ovaries are paired organs with a tubular structure and bilateral symmetry located dorsally in the cephalothoracic cavity overlying the digestive gland. Significant macroscopic variations were observed in the ovaries and categorized into five stages based on the relative intensity of

color, size and position of the ovaries (Fig. 2). The GSI values ranged between 0.093 and 4.33. Histologically ovary consists of several layers of developing oocytes encased by a thin gonadal wall. Oogonia, early previtellogenic oocyte, late previtellogenic oocyte, early vitellogenic oocyte, late vitellogenic oocyte and atretic oocyte are the different stages of oocyte development. These phases could be distinguished by their differences in cell size, shape, cytoplasmic appearance, accumulation of yolk granules, and presence of lipid globules in the cytoplasm.

Stage 1 refers to immature females with thin translucent cream-colored gonads that are not visible through the carapace and weigh between 0.002 g and 0.01 g. The GSI values ranged between 0.093 and 0.25. Ovaries at stage 1 present a predominance of oogonia and early previtellogenic oocytes. Oogonia were spherical cells found in clusters in the center of ovaries known as germinal zone (Fig. 3a) and had a diameter of 0.004–0.005 mm, possessed a large and well-defined nucleus, non-evident nucleolus, homogenous thin rim of basophilic cytoplasm without granulation and strongly reactive to hematoxylin (Fig. 3b). Early previtellogenic oocytes are spherical with a diameter of 0.02–0.03 mm were round to elliptical with thin granulation in the cytoplasm (Fig. 3c). They have a smaller nucleus, visible nucleoli and are less basophilic than oogonia. Although follicular cells are present, they aren't associated with the oocytes (Fig. 3d).

Stage 2 refers to developing females with pale creamy blue gonads visible through the carapace weighing 0.009 g–0.06 g. The GSI values ranged between 0.66 and 1.38. The ovaries appear more turgid and histologically disorganized, with abundant connective tissues. Oogonia, early previtellogenic oocytes, late previtellogenic oocytes and follicle cells were observed. Follicle cells do not appear to be associated with the oocytes. Late previtellogenic oocytes are basophilic, semi-spherical, and a little larger, with a diameter of 0.045–0.055 mm. The nucleus is large, with nucleoli visible in the interior (Fig. 3e).

Stage 3 refers to early mature females with light blue ovaries weighing between 0.029 g and 0.12 g, clearly visible through the exoskeleton. The GSI values ranged between 1.67 and 2.43. At stage 3, the ovaries had two distinct zones: the central germinal zone, which contained oogonia, early and late previtellogenic oocytes, and the peripheral growth zone, which included late previtellogenic oocytes, early and late vitellogenic oocytes associated with the follicle cells. During vitellogenesis, the ooplasm becomes acidophilic due to the

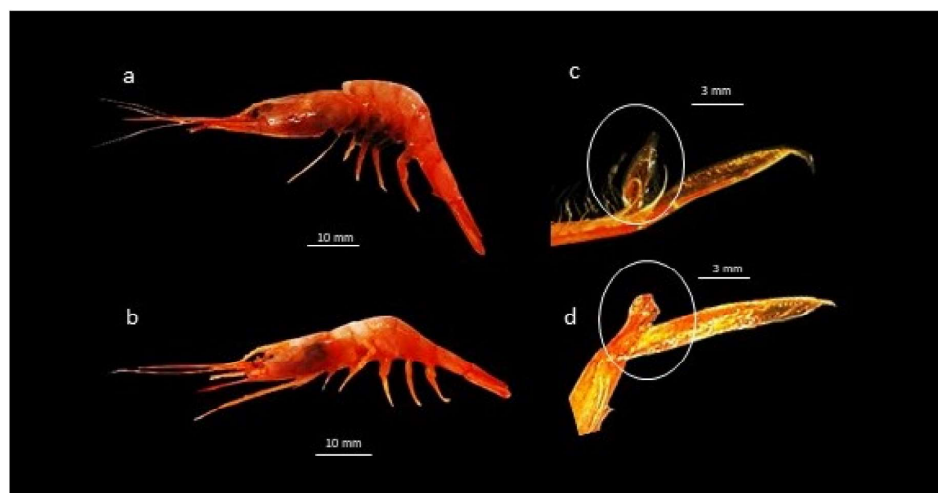


Fig. 1. Ovigerous (a) and non-ovigerous (b) females of *P. semilaevis*, (c) leaf-shaped endopod of first pleopod in females (c) and blunt-shaped endopod of first pleopod in males (d).

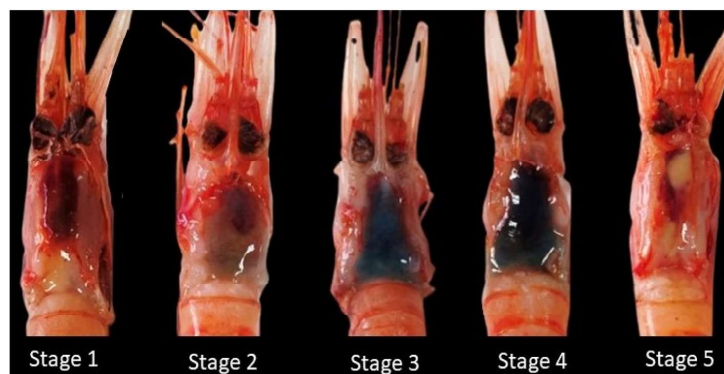


Fig. 2. Macroscopic variation in different stages of ovarian development.

accumulation of yolk granules, which results in a pink stain. Early vitellogenic oocytes had a diameter of 0.1–0.2 mm and were marked by vitellogenic granulations, lipid globules and a thick chorion (Fig. 3f). Lipid globules have a transparent appearance and are primarily observed in the central part of the cell, while yolk granules have an opaque appearance and are distributed evenly (Fig. 3g). Late vitellogenic oocytes are the largest cells with a diameter of 0.3–0.5 mm and a granular appearance due to an abundance of yolk granules and lipid globules.

Stage 4 refers to fully mature females with dark blue head roe. The ovaries are dark bluish-black in color, turgid and occupying the entire space in the cephalothoracic cavity extending up to the abdomen, weighing between 0.08 g and 0.22g. The GSI values ranged between 3.0 and 4.33. At stage 4, ovaries revealed a confined germinal zone enveloped by advanced late vitellogenic oocytes. Late vitellogenic oocytes are large and irregularly shaped, with cytoplasm wholly filled with dense yolk granules and lipid globules, hindering the visualization of the nucleus (Fig. 4a and b). At this point, oocytes have grown to their entire size and are encircled by a layer of flattened follicle cells.

Stage 5 refers to spent females with cream-colored flaccid ovaries. These ovaries have an unorganized appearance and are distinguished by the abundance of connective tissue, follicular cells, and atretic oocytes that are undergoing reabsorption (Fig. 4c). Atretic oocytes in the reabsorption process can be easily identified by vacuolated cytoplasm (Fig. 4d). Even though the immature and spawned stage ovaries have similar coloration, the presence of atretic oocytes is the primary feature that allows for microscopical differentiation between the two stages. The proportion of oögonium also increases in this stage.

3.3. Stages of embryo development, brood size and embryo size

Four different stages of eggs with distinct color variations were observed by morphological examination (Fig. 5). In stage I, the embryos are bright blue in color, lacking eye pigmentation. Yolk filled 80–100% of the embryo volume. In stage II, the embryos have a bluish-green appearance. Minute eye pigmentations are visible under the microscope but not to the naked eye. Ventral cleft starts to appear with the visible demarcation of cephalothorax and abdomen. In stage III, embryos are pale olive-green colored with eye pigmentation clearly visible. Embryos have large cephalothoraces, extended abdomen, visible segmentation, rudimentary appendages and distinctly clear ventral cleft. In stage IV, embryos brown-colored appearance because of the mucous-like substance holding the embryos together. The embryos are ready to hatch, with their segmentations completed and eye spots fully pigmented.

The overall mean brood size ($\pm$ SD) was 6413 ± 2457 (ranging from 2093 to 12887). The brood size also varied based on the different stages of the development of embryos. The females with stage I and stage II embryos (non-eyed stages) had the highest brood sizes 8324 ± 2076 (4166–12887 embryos) and 6981 ± 1866 (4068–11291) embryos respectively. The embryos were more compact and clustered together tightly. Significant embryo loss was observed during the development of the embryos. In stage III and stage IV (eyed stages), the brood size was reduced to 5179 ± 1265 (3004–8411) and 3449 ± 970 (2093–6048) embryos respectively. Embryo loss was estimated to be 59.6% from stage I to stage IV embryos.

The brood size increased significantly with the female sizes for all the stages of embryo development. The maximum brood size was 7502 for smaller individuals (CL 12–15 mm), 10813 for medium-sized individuals (CL 16–19 mm) and 12887 for larger individuals (CL 20–24 mm). A significant positive correlation was observed between the brood size of embryos at different developmental stages and carapace length (Fig. 6).

Table 1 displays the mean length and width of the embryos and the mean volume of the embryos at each developmental stage. The embryo length increased gradually with each developmental stage. Such a gradual change was not observed for embryo width, but a sharp increase in width was observed from stage II to stage III. The embryo volume remained in the range of 0.043–0.051 mm³ during the first two stages but started to increase significantly to 0.091 mm³ in the later stages. The embryo's volume increased by 109% from stage I to stage IV. Analysis of variance showed a significant variation in embryo length ($p = 0$; $F = 928$), width ($p = 0$; $F = 1725.5$) and volume ($p = 0$; $F = 2584$) with each developmental stage, however, the embryo developmental stages did not differ much with the size of the female ($p < 0.05$; $F = 2.918$).

3.4. Reproductive period, sex ratio, GSI and size at sexual maturity

Fig. 7 illustrates the monthly variations in the proportion of *P. semilaevis* ovigerous females carrying embryos at various developmental stages. Although ovigerous females were present in every month's sample, their frequency changed on a monthly basis. The percentage of ovigerous females increased from November to February (66.4%–84%) and decreased from March to October (67.7%–45.2%), with the least number of ovigerous females present in September (35.7%). The percentage of ovigerous females incubating stage I embryos peaked in December and January. Ovigerous females with stage II embryos showed a similar peak from November to February. The proportion of embryos with eyed stages i.e., stages III and IV, increased steadily from January to May and April, respectively. The stage IV

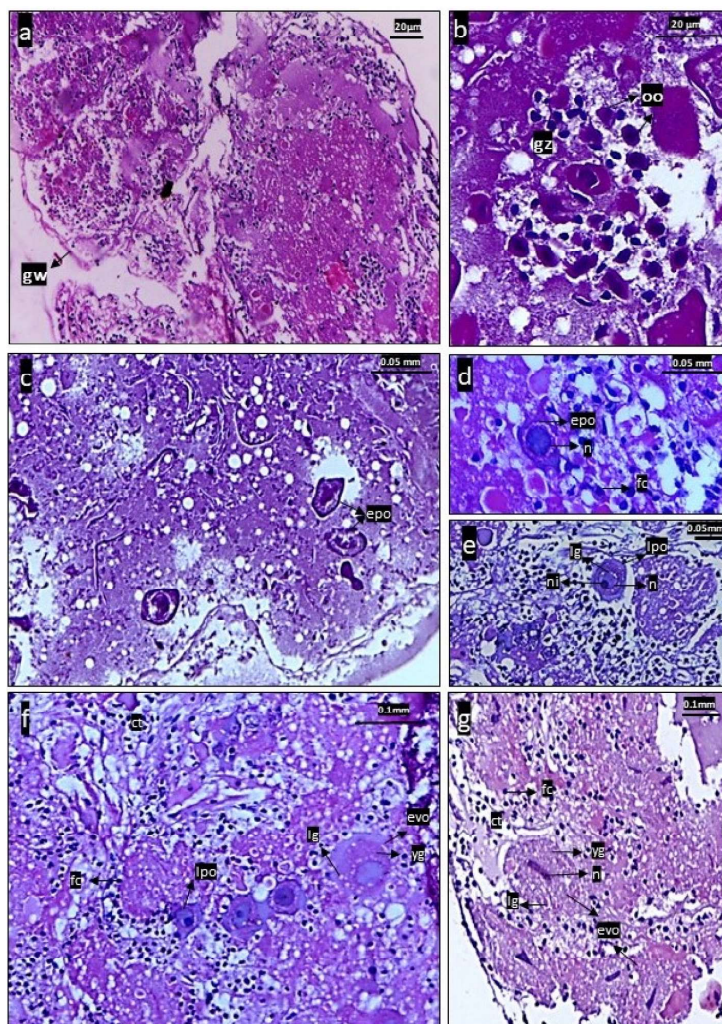


Fig. 3. Histological sections of different stages of ovary of *P. semilaevis*: Stage 1 (a,b), Stage 2 (c,d,e), Stage 3 (f,g); gz, germinal zone; oo, oogonium; epo, early previtellogenic oocyte; n, nucleus; ni, nucleoli; fc, follicular cells; lpo, late previtellogenic oocyte; evo, early vitellogenic oocyte; lg, lipid globules; ct, connective tissue; yg, yolk granules.

embryos, just before hatching, were highest from March to May, suggesting a significant hatching period. All ovigerous females with stage I bright blue embryos had cream-colored ovaries, either immature stage I ovaries preparing for the next brood or atretic ovaries with released oocytes. Over half of the females with stage II embryos had pale cream-colored developing ovaries. All mature females with stage IV eggs and more than half of the females with stage III eggs had blue-colored ripe ovaries, indicating upcoming spawning and new brood.

The overall sex ratio (males: females) was 1:1.8, which is significantly different from the expected sex ratio (1:1). Females outnumbered males in all the months studied. The highest percentage of females was observed during February (73.8%) and the least during October (52.7%). Monthly variation in sex ratio and results of chi-square analyses are provided in Table 2. The monthly sex-ratio showed significant

variation from the hypothetical ratio 1:1 for all the months except October.

Size at first maturity, determined by the presence of embryos between pleopods (CL_{50em}), was found to be 15.07 mm CL (Fig. 8a). Size at first maturity determined from pooled early mature (Stage 3) and fully mature (Stage 4) ovarian stages (CL_{50ov}) was estimated at 15.51 mm CL (Fig. 8b).

4. Discussion

Several aspects, including reproductive period, ovarian and embryonic stages of development, embryo size, brood size, size at maturity and sex ratio, were studied for *P. semilaevis* from the southeastern Arabian Sea.

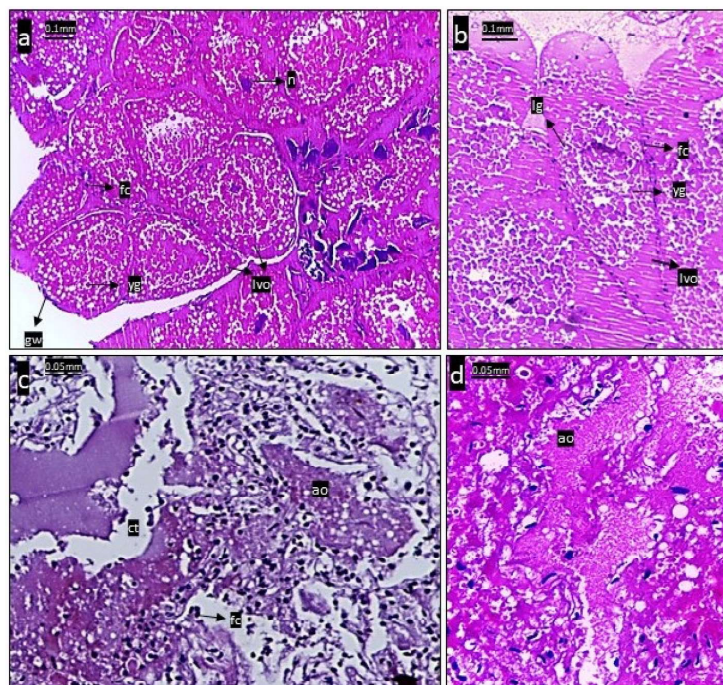


Fig. 4. Histological sections of different stages of ovary of *P. semilaevis*: Stage 4 (a,b), Stage 5 (c,d); fc, follicular cells; gw, gonadal wall; lvo, late vitellogenic oocyte; lg, lipid globules; ct, connective tissue; yg, yolk granules; n, nucleus; ao, atretic oocytes.

Based on the color and position of the ovary in the cephalothoracic cavity, five ovarian maturation stages were recognized in the females of *Plesionika semilaevis*. The classification of ovarian development in detailed stages is essential to gather comprehensive data for future reproductive and population dynamics studies. Mature ovaries are bright dark bluish-black, visible through the carapace as a head roe. Ohtomi and Hayashi (1995) and Ohtomi (1997) described the mature ovary as blue for *P. semilaevis*, Maiorano et al. (2002) as greenish blue for *P. martia*, Colloca (2002) and Possenti et al. (2007), Triay-Portella et al. (2017) as dark blue for *P. edwardsii* and Ahamed and Ohtomi (2011) as dark yellow for *P. izumiae*. Decapod crustacean ovaries change color during the reproductive cycle due to variations in the amount of carotenoids present during oogenesis (Liñán-Cabello et al., 2002; Gregati et al., 2010), accumulation of yolk granules and the decrease of cytoplasmic organelles during vitellogenic stages.

The histological analysis supported the maturity scale based on the morphology of ovaries. The histology of ovarian tissues and the findings of the GSI analysis indicates that changes in the color and form of the ovaries closely correspond to the development of oocytes. The average GSI value increased from 0.093 in females with stage 1 ovary to 4.33 in females with stage 4 ovary. The central region of the ovary showed the presence of oogonia and previtellogenic oocytes. In contrast, more developed vitellogenic oocytes were present towards the periphery of the ovary, corroborating Braga et al. (2009). As observed, the oogonia proliferating in the germinal epithelium develops into previtellogenic oocytes, moving to the growth zone between the large vitellogenic oocytes to form small germinative islets. The high number of nucleoli inside the nucleus of previtellogenic oocytes suggests that they have become quite active. The enlargement of the growing vitellogenic oocytes mainly results from the expansion of the cytoplasm, which has

become acidophilic due to the presence of yolk granules and lipid droplets. Follicle cells form a layer around the vitellogenic oocytes. Follicular cells either synthesize vitellogenin and secrete it into the hemolymph, which is later collected by the oocytes (Yano and Chinzei, 1987), or may take part in the collection of yolk proteins into the oocytes. The identification and differentiation of the immature and spawned stages primarily rely on the atretic oocytes observed. Since the ovaries at the immature and spawned stages have the same coloration and the same germinative cells (oogonia and early previtellogenic oocytes) are primarily found in these stages, atretic oocytes were considered to be the key trait in their histological differentiation.

The brood size ranged from 2093 to 12887 embryos. For all four embryonic stages, there was a positive link between shrimp size (CL) and brood size. Ohtomi (1997) observed a smaller brood size (1048–8702 embryos) in *P. semilaevis* from the subtropical waters of Kagoshima Bay, Japan. The physical space between the pleopods available for the attachment of the embryos is the cause of this correlation. A significant decrease in brood size during incubation was observed in the ovigerous females of *P. semilaevis*. Similar observations were reported for the other *Plesionika* species (Ohtomi, 1997; Maiorano et al., 2002; Ahamed and Ohtomi, 2011; Triay-Portella et al., 2017) and other caridean shrimps (Penha-Lopes et al., 2007; Echeverría-Sáenz and Wehrmann, 2011; deMoraes et al., 2017). In caridean shrimps, embryo loss during incubation is a common observation that can be attributed to a number of biological (parasites, micro predators, etc.) and physical (mechanical stress, increase in embryo size, etc.) factors (Balasundaram and Pandian, 1982; Kuris, 1991; Oh and Hartnoll, 1999; Hernández et al., 2010). Since no parasites and micro predators were observed in the present study, the embryo loss could be due to the restricted space to carry the embryos beneath the pleon due to increased embryo volume (Suh et al., 2003).

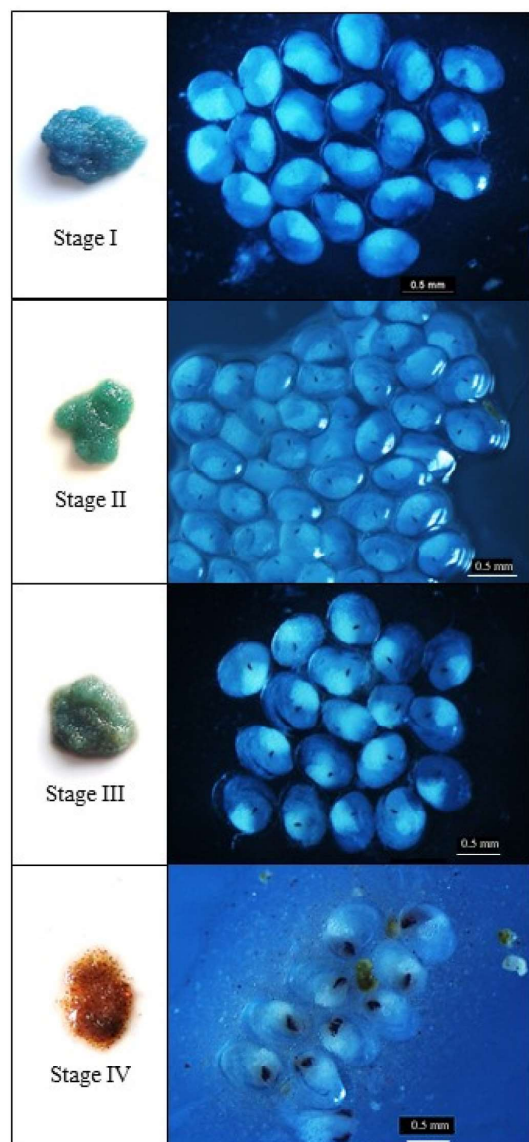


Fig. 5. Macroscopic (left column) and microscopic (right column) variation in different stages (I-IV) of embryo development in *P. semilaevis*.

Fishing methods can also contribute to embryo loss in all stages.

The mean embryo sizes following spawning and prior to hatching were 0.51×0.40 mm and 0.66×0.50 mm, respectively. Ohtomi (1997) also reported a similar pattern of increasing embryo size with each development stage in *P. semilaevis* from Kagoshima Bay. He observed a mean embryo size of 0.60×0.56 mm just after spawning and 0.78×0.53 mm prior to hatching, which is higher than our results. The volume of the embryos also increased with each development stage. The increase was very distinct from stage II to stage III (0.05 mm^3 – 0.085 mm^3)

with the development of rudimentary appendages, ventral cleft, and large cephalothoraces. However, this increase in embryo volume during incubation is common in crustaceans due to the rise in water content and biochemical changes in the embryo during development (Lardies and Wehrtmann, 1997; Wehrtmann and Kattner, 1998).

Ovigerous females were present in all the sampling months, with a peak from November to February, indicating this to be the main reproductive period. Ohtomi (1997) reported the occurrence of ovigerous females of *P. semilaevis* in Kagoshima Bay, Japan, from May to December and suggested the influence of photoperiod on species reproduction. According to Omori (1971), *P. izumiae* breeding in Suruga Bay was frequent as the water warmed in the late spring and summer. Studies on the reproduction of caridean shrimps have shown that water temperature significantly influences spawning (Kikuchi, 1962; Allen, 1966; Maiorano et al., 2002; Vafidis et al., 2005). According to Bauer (1992), neritic species of caridean shrimp in temperate waters will have shorter breeding periods than those in subtropical and tropical areas. Due to generally constant and high temperatures, the reproductive cycle is prolonged and year-round in tropical waters (Orton, 1920). The tropical climate prevailing in the southeastern Arabian Sea could be the reason for its continuous reproductive activity.

Stage I and stage IV embryos occurred all months, suggesting that this species is iteroparous. However, the prevalence of ovigerous females carrying stage I embryos rose from November to February, with peaks in December and January indicating their primary spawning season. Stage IV embryos had a higher occurrence from March to May, suggesting this to be their significant hatching period. Ovigerous females carrying stage I embryos lacked mature ovaries, whereas ovigerous females carrying embryos in stage IV, which were close to hatching, had mature ovaries. Additionally, all maturity stages were visible in the ovaries of non-ovigerous females who were larger than the size at sexual maturity, suggesting that once *P. semilaevis* achieves sexual maturity, it spawns multiple times during a year. This reproductive pattern has been described for various tropical and temperate deep-sea shrimps (Bauer, 1989; Company and Sarda, 1997; Ohtomi, 1997; Maiorano et al., 2002; Anastasopoulou et al., 2017; Paramasivam et al., 2018; Kuberan et al., 2021).

The maximum CLs observed by Ohtomi (1997) was 19.25 mm in females, while in this study, the maximum CL observed was 24 mm. With higher latitudes, shrimps tend to have smaller sizes. Geographical differences in the maximum body size may have resulted from differences in longevity, growth rate, and food availability among the populations, or they may have been caused by physiological growth mechanisms (Ohtomi, 1997). Triay-Portella et al. (2017) preferred the calculation of size at maturity based on ovarian maturation rather than ovigerous condition in the case of *P. edwardsii*, as a significant fraction of non-ovigerous females were mature, leading to an overestimation of size at maturity. In the present study, the size at sexual maturity estimated based on ovarian maturation and ovigerous condition showed similar values since the occurrence of ovigerous females was relatively higher than non-ovigerous females.

In fisheries management, the size at which shrimps of a given population become sexually mature for the first time is an important management parameter used to monitor whether enough juveniles in an exploited stock mature and spawn (Beverton and Holt, 1959; Jennings et al., 1998). The size during sexual maturity is especially significant and is frequently used as a criterion for the minimum permissible capture size (Lucifora et al., 1999). Information on the reproductive parameters of deep-sea resources forms the basis for developing and implementing resource management strategies for the sustainable harvest of the deep-sea fishery. The data gathered in this study can be applied to research on the recruitment dynamics of the species, which will help manage resources more effectively and act as a prerequisite for stock assessment and stock sustainability and establish successful fishery management.

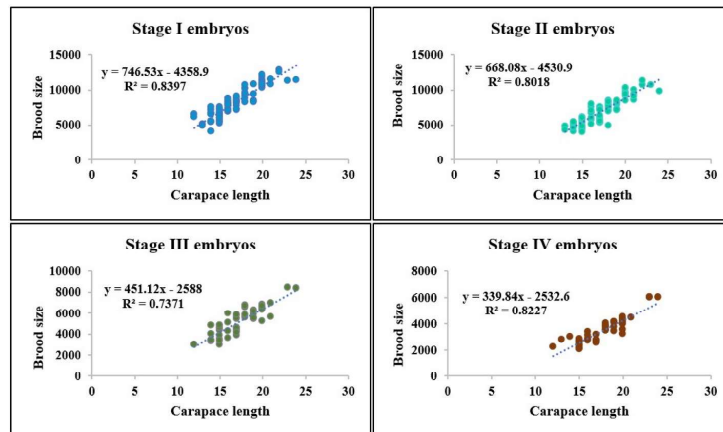


Fig. 6. Relationships between carapace length (mm) and brood size for different stages (I-IV) of embryo development.

Table 1
Mean length, width and volume of embryos of *P. semilaevis* at each developmental stage.

Stage	Embryo length $\pm$ SD (mm)	Embryo width $\pm$ SD (mm)	Embryo volume $\pm$ SD (mm ³)	CL range (mm)	No. of shrimps observed
I	0.511 $\pm$ 0.028	0.401 $\pm$ 0.024	0.043 $\pm$ 0.006	10–23	100
II	0.568 $\pm$ 0.019	0.412 $\pm$ 0.007	0.051 $\pm$ 0.003	12–25	100
III	0.616 $\pm$ 0.02	0.513 $\pm$ 0.009	0.085 $\pm$ 0.003	13–25	100
IV	0.657 $\pm$ 0.01	0.51 $\pm$ 0.013	0.091 $\pm$ 0.005	13–25	100

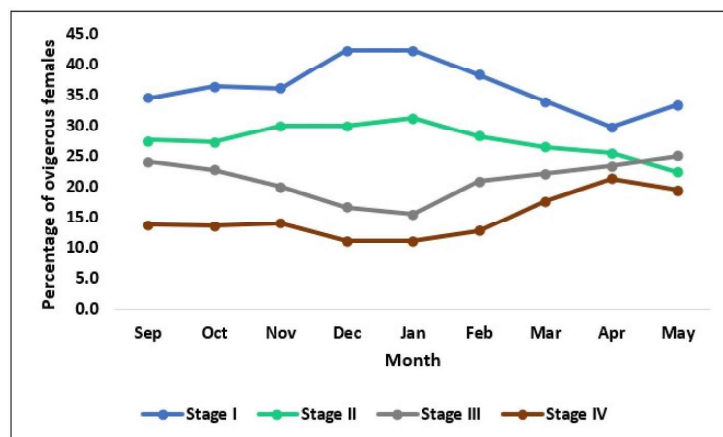


Fig. 7. Monthly changes in percentage occurrence of different developmental stages of embryos in ovigerous females of *P. semilaevis*.

5. Conclusions

This is the first comprehensive study on reproductive parameters, including the ovarian and embryonic development of *P. semilaevis* in Indian waters and other locations where this species is distributed. Females reproduce multiple times a year as evidenced by the presence of ovigerous females in all the sampling months. The major spawning and hatching periods were estimated to be December to February and March to May, respectively. They are sequential breeders i.e., after reaching sexual maturity, they are able to produce subsequent broods, as

indicated by their ovarian maturation with embryonic development. The data gathered in this study can be applied to research on reproductive dynamics, which will help manage resources more effectively and advance the ability of the species to reproduce in captivity. These studies are notable for their significance in identifying the different stages of ovarian maturation and embryonic development in detail which helps to obtain accurate information about the length at maturity and the hatching and spawning seasons, which is essential when establishing management measures. They are also significant in determining whether the current closed season is appropriate for the species.

Table 2
Month-wise sex ratio in *P. semilaevis*.

Sl. No	Month	Sex Ratio (Male: Female)	Chi-square value (X^2)	Level of significance
1.	January	1:2.02(100,202)	34.45	$P < 0.01^a$
2.	February	1:2.82 (142,401)	123.53	$P < 0.01^a$
3.	March	1:1.44 (178,257)	14.35	$P < 0.01^a$
4.	April	1:2.16 (45,97)	19.04	$P < 0.01^a$
5.	May	1:1.81 (37,67)	8.65	$P < 0.01^a$
6.	September	1:1.55 (74,115)	8.89	$P < 0.01^a$
7.	October	1:1.11 (123,137)	0.75	$P > 0.05$
8.	November	1:1.61 (146,235)	20.79	$P < 0.01^a$
9.	December	1:1.91 (152,291)	43.61	$P < 0.01^a$
10.	Overall	1:1.81 (997,1802)	274.08	$P < 0.01^a$

^a Significant.

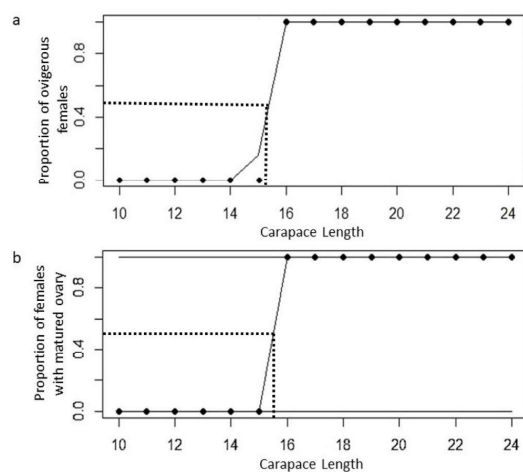


Fig. 8. Graphs for estimating size at first maturity based on the proportion of ovigerous females (a) and matured ovaries (b) of females of *P. semilaevis*.

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Authors' contribution

All the authors participated sufficiently in the work. All authors read and approved the final manuscript.

Sreelakshmy S: Conceptualization, methodology, formal analysis, investigation, writing-original draft.

Rekha Devi Chakraborty: Conceptualization, methodology, resources, supervision, writing-review and editing.

Declaration of competing interest

"The authors declare that they have no conflicts of interest".

Data availability

Data will be made available on request.

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Biochemical analysis and nutritional profile of *Plesionika semilaevis*, a deep-sea shrimp from the Arabian Sea

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ABSTRACT

This study presents the first comprehensive examination of the nutritional profile of the deep-sea shrimp, *Plesionika semilaevis* from the Arabian Sea. The research compared the gender-related differences in proximate composition, mineral content, amino acids, and fatty acids composition. Notable distinctions were observed in carbohydrate, lipid, and fat levels, with females displaying significantly higher quantities than males. Palmitic, oleic acids and C20–22 *n*-3 fatty acid analogues, were the principal saturated, monounsaturated, and polyunsaturated fatty acids, respectively. Fatty acid profile exhibited substantial variations by sex and season with C20–22 *n*-3 fatty acid analogues being prominent during the pre-monsoon period in males, berried females, and non-berried females. Lower thrombogenicity and atherogenicity indices indicate that this shrimp species holds promise as a healthful dietary choice. Potassium is the most prevalent macro-mineral in *P. semilaevis*, followed by phosphorus while among micro-minerals, iron predominates, followed by zinc. The amino acid profile indicates the shrimps as an ideal protein-rich food with a well-balanced ratio of essential to non-essential amino acids. These findings offer valuable insights into the nutritional value of this deep-sea shrimp species, aiding in its utilization as a source of nutritious food.

1. Introduction

Crustaceans hold significant commercial appeal and represent approximately 22.8% of the global seafood trade's value (FAO, 2022). Deep-sea shrimps, in particular, stand out as a high-priced group of invertebrates in the global fishery sector, with widespread distribution throughout tropical regions. They hold significant economic importance in the Southeast Asian area, primarily due to their high export value (Shanis, 2014).

Nutrient-rich foods are increasingly being introduced to sustain the human body and satisfy culinary preferences. Assessing the nutritional quality of these foods involves a comprehensive analysis of their complex nutrient compositions, including proximate composition, amino acids, minerals, and fatty acids. The taste, nutritional value, and health advantages of seafood products, such as deep-sea shrimps, are closely linked to their levels of essential amino acids and fatty acids (Chen et al., 2007; Kuley et al., 2008). It is necessary to acknowledge that the biochemical composition of marine organisms can be influenced by

various factors, including size, sex, sexual maturity, geographical location, dietary sources, and environmental conditions (Wu et al., 2010; Wang et al., 2021; Muralidharan et al., 2023).

Studies reported by Karuppasamy et al. (2013) and Bhavan et al. (2010) highlighted the relatively higher protein content present in the edible parts of shrimps. The nutritional qualities of shrimp are not solely attributed to their high-quality protein content but also to their relatively lower lipid (fat) content, along with a higher proportion of polyunsaturated fatty acids (PUFAs). These species are rich in essential omega-3 fatty acids docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). These PUFAs can play crucial roles in preventing conditions such as hypertension, inflammation, diabetes, and cancer (Chakraborty et al., 2016; Ramezani-Fard et al., 2016; Krishnan et al., 2021; Chakraborty et al., 2022a). Studies have shown that despite shrimp's high cholesterol content, incorporating shrimp into a diet with a balance of PUFAs, alongside reduced saturated fatty acid (SFA) intake, can contribute to lowering cholesterol levels, making it a heart-healthy option (Sampaio et al., 2006).

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Additionally, shrimp are rich in essential nutrients, including essential amino acids such as methionine, lysine, cysteine, tryptophan, and threonine (Karuppasamy et al., 2013), minerals and vitamins (Vitamin E, C, B1, B6, B12, etc.) (Heu et al., 2003; Chakraborty et al., 2022c; AlFaris et al., 2022). Certain elements, namely copper, zinc, manganese, iron, and selenium, play crucial biological roles and are

highly beneficial for human health when present in shrimp at acceptable levels (Khansari et al., 2005). Selenium, for instance, is a vital antioxidant mineral, while zinc is crucial for immune function and wound healing (Prasad, 2008; Bjørklund et al., 2022). Furthermore, they are low in calories and fats, making them a healthy dietary choice. The chemical and nutritional composition of shrimp can be notably affected

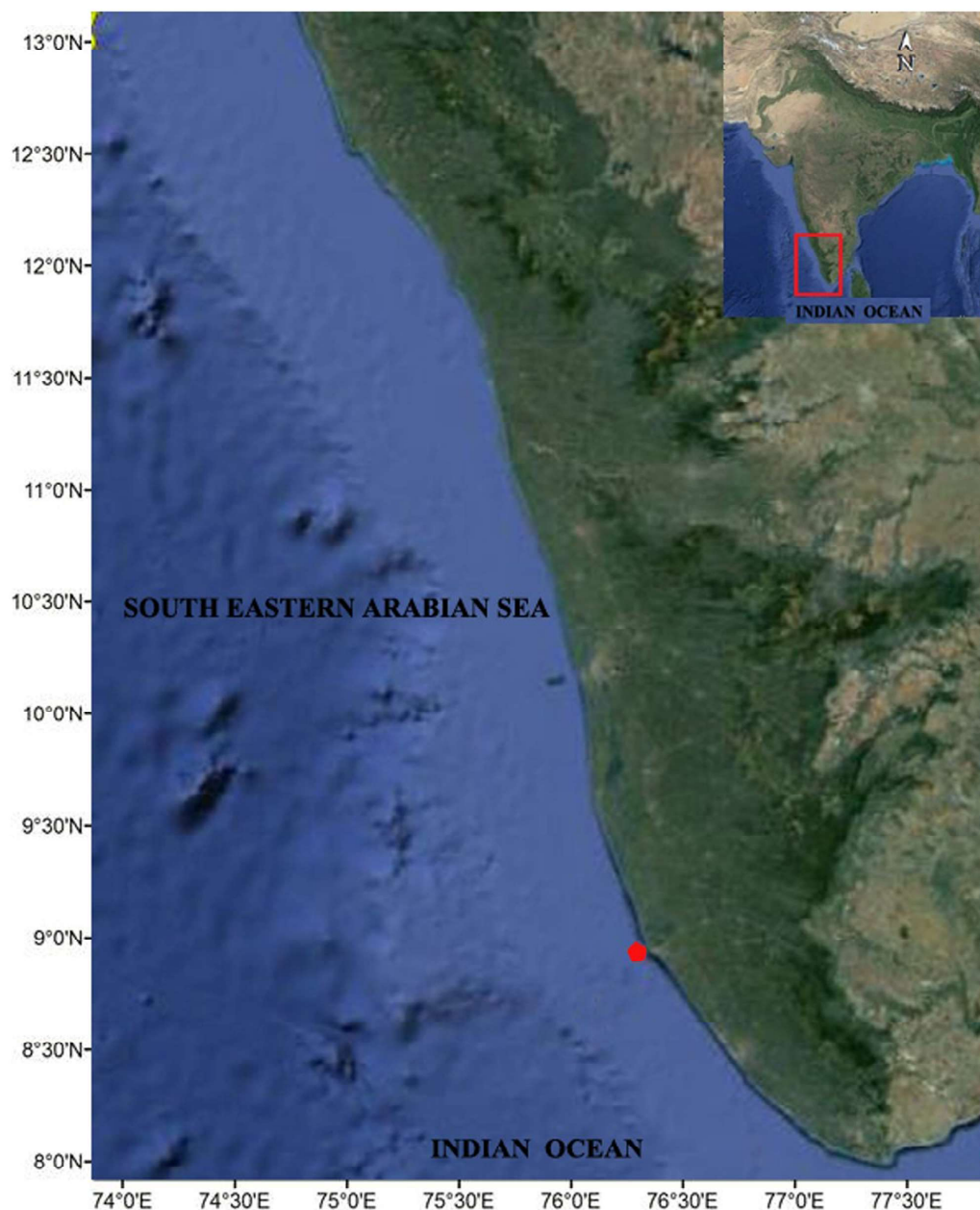


Fig. 1. The geographical location of the fishing area in south eastern Arabian Sea (red dot indicating deep-sea landing centre, Saktikulangara).

by different preparation methods such as salting, frying, grilling, and boiling (AlFaris et al., 2022).

In the southwest coast of India, *Plesionika semilaevis* (Spence Bate, 1888) is a deep-sea shrimp species of significant commercial and ecological importance. It is typically found at 250 m and beyond depths in the southeastern Arabian Sea. While there have been previous reports on the biochemical composition of some deep-sea shrimps from the southeastern Arabian Sea (Fernandez et al., 2018; Chakraborty et al., 2021; Chakraborty et al., 2022a, 2022c), there is a notable absence of information regarding the biochemical and nutritional characteristics of the deep-sea shrimp *P. semilaevis* from Indian waters or any other geographical region where it is found.

Thus, this current study aims to bridge the existing information gap by assessing the essential biochemical components in the muscle tissue of *P. semilaevis* specimens obtained from the southwest coast of India. The analysis encompasses crucial parameters such as moisture, ash, protein, amino acids, carbohydrates, lipids, fatty acids, cholesterol and minerals.

2. Materials and methods

2.1. Collection and preparation of sample

Deep-sea shrimp samples were collected fortnightly from the deep-sea landing center in Sakthikulangara, Kollam, Kerala (Fig. 1). These shrimps were captured at depths ranging between 200 to 400 m. The monthly data was categorized into pre-monsoon (January–March) and post-monsoon (September–November) periods to gather information on seasonal variations. Approximately 20–25 kg of shrimp samples were collected and immediately preserved in an insulated icebox with crushed ice before being transported to the laboratory. In the laboratory, samples of *P. semilaevis* were identified using taxonomic keys provided by Ohtomi and Hayashi (1995), Ahamed et al. (2017), Kuberan et al. (2020), and Chan et al. (2020). The sex of each individual was determined by examining the morphology of the endopod of the first pair of pleopods (King and Moffitt, 1984). Subsequently, female shrimps were further categorized into ovigerous and non-ovigerous states based on the presence of embryos between their pleopods. Precise measurements of carapace length (CL) and total length (TL) were conducted using calipers, with a precision of 0.01 mm, while an electronic digital balance with a precision of 0.001 g was utilized to determine the body weight (BW) of the specimens. After initial processing, including cleaning and shell removal, the edible meat portion of the shrimp was isolated. The meat yield, represented as a percentage of the wet weight, was calculated by dividing the weight of the meat by the total weight of the specimen and then multiplying by 100. For further biochemical analyses, homogenous samples were prepared by grinding the tissues, and these samples were securely stored at -80°C .

2.2. Proximate composition

To assess the moisture content and crude ash of the samples, established methods (AOAC, 1990; AOAC, 2005) were employed. The determination of total protein, carbohydrate and lipid was performed according to the methods described by Lowry et al. (1951), anthrone method (Ludwig and Goldberg, 1956) and Folch et al. (1957), respectively. The spectrophotometric analysis of total cholesterol was carried out following the procedure outlined by Krishnan et al., (2019) using *o*-phthalaldehyde (50 mg dL^{-1} in glacial acetic acid) (Merck Specialities Pvt. Ltd., Mumbai, India). A standard curve was prepared and the cholesterol levels of the samples were quantified in milligrams per 100 g of wet sample.

2.3. Fatty acid analysis and nutritional indices

The fatty acid composition of the edible portion of shrimp samples

during pre-monsoon and post-monsoon was analyzed using a method previously described by Chakraborty et al. (2014). The process involved saponifying and trans-esterifying the extracted lipids to produce fatty acid methyl esters (FAMES). These FAMES were then extracted using a mixture of *n*-hexane (Merck) and water (1:2, v/v). After separation in a separating funnel, the aqueous layer was discarded, and the *n*-hexane layer was collected. Next, the *n*-hexane layer underwent a drying process using anhydrous sodium sulphate (Merck) before being concentrated for further analysis.

Esterified fatty acid analysis was conducted using a gas chromatograph (Nexis GC-2030, Shimadzu, Japan) connected with SH-Rxi-5Sil MS capillary column (30 m $\times$ 0.25 mm, 250 nm, Shimadzu, USA) along with a flame ionization detector (FID). A split-less injection mode was set at a split ratio of 100 and an oven temperature gradient method was employed (starting at 60°C , increasing to 150°C with a 5-minute hold time at a rate of $15^{\circ}\text{C min}^{-1}$). Subsequently, the temperature was raised to 280°C and maintained for 15 min (at a rate of $25^{\circ}\text{C per minute}$) to ensure the detection of all peaks. The injector and ion source temperatures were held at 260°C and 230°C , respectively. Ultra-high purity ($> 99.99\%$) helium was served as carrier gas at a flow rate of 1.22 mL min^{-1} , while the pressure was maintained at 74.4 kPa. The quantification of FAMES was achieved by comparing their retention times with established standards (SupelcoTM 37 FAME Mix). Results were expressed as % CFA (percent cumulative fatty acids).

Ultimately, the average values of specific fatty acids were employed to calculate the levels of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA). The study evaluated the nutritional standards of the shrimps, represented by different ratios of fatty acids, such as *n*-3/*n*-6 and PUFA/SFA. To shed light on the potential thrombogenic and atherogenic impacts of the consumable portions of the shrimps, the thrombogenicity index (TI) and atherogenicity index (AI) were assessed using a previously established methodology by Ulbricht and Southgate (1991).

$$\text{TI} = (14:0 + 16:0 + 18:0)/[(0.5 \times \Sigma \text{MUFA}) + (0.5 \times \Sigma \text{n-6 PUFA}) + (3 \times \Sigma \text{n-3 PUFA}) + (\Sigma \text{n-3 PUFA} / \Sigma \text{n-6 PUFA})]$$

$$\text{AI} = (4 \times 14:0 + 18:0 + 16:0)/(\Sigma \text{MUFA} + \Sigma \text{n-3 PUFA} + \Sigma \text{n-6 PUFA})$$

2.4. Minerals analysis

A 0.1 g sample was subjected to digestion using a 4:1 ratio of suprapur nitric acid (HNO_3) (Merck) and suprapur sulfuric acid (H_2SO_4) (Merck) within a microwave digester (Microwave Mini, Anton Paar). Following digestion, the samples were adjusted to a 25 mL volume using ultrapure water. Subsequently, the samples were further diluted before being analyzed using ICP-MS (iCAP Q, Thermo Fisher). The calibration of the analysis was performed using a multielement standard (Merck) containing known concentrations of various elements.

2.5. Amino acid analysis and nutritional indices

The amino acid composition was analyzed using a Shimadzu LC-10 AT High-Performance Liquid Chromatography (HPLC) amino acid analyzer system. The system was equipped with a cation exchange column, specifically a sulfonated polyvinyl styrene column, and a fluorescence detector (Lakshmanan et al., 2013).

The following parameters and ratios were computed: total essential amino acids (ΣEAA), total non-essential amino acids (ΣNEAA), total amino acids (ΣAA), total aromatic amino acids (ΣArAA), total sulfur-containing amino acids (ΣSAA), and the ratios of ΣEAA to ΣNEAA , ΣEAA to ΣAA , ΣNEAA to ΣAA , cysteine to ΣSAA ($\text{Cys}/\Sigma \text{SAA}$), arginine to lysine (Arg/Lys) and leucine to isoleucine (Leu/Ile).

2.6. Statistical analysis

Statistical analysis was conducted using the Statistical Program for Social Sciences 13.0 (SPSS Inc, Chicago, USA, v.13.0). All analyses were performed in triplicate, and the means of all parameters were assessed for significance using analysis of variance (ANOVA), followed by Duncan's multiple range tests. The level of significance for all analyses was set at $p < 0.05$. To examine the variation in fatty acid and amino acid contents in muscle tissues, Principal Component Analysis (PCA) was carried out using R Studio (version 4.1.1.). PCA was performed based on the correlation matrix, and factors with eigenvalues greater than 1 were extracted.

3. Results

3.1. Sample measurements and proximate composition

The range of measurements for total length (TL), carapace length (CL) and total weight is mentioned in Table 1. The shrimp meat's yield was determined to be $53.44 \pm 4\%$ in non-berried females, $48.4 \pm 2.88\%$ in berried females and $52.16 \pm 3.7\%$ in males. The proximate composition of *P. semilaervis* specimens, categorized as males, berried females, and non-berried females, is outlined in Table 1. There were negligible differences in moisture and protein levels between male, berried female, and non-berried female specimens. Males and females exhibited comparable levels of ash content in their tissues. Also, notable distinctions emerged in carbohydrate, lipid, and fat levels, with female samples exhibiting markedly higher amounts compared to males. Carbohydrate content was notably lower in the male sample at $0.60 \pm 0.03\%$, while the non-berried and berried samples contained $0.79 \pm 0.01\%$ and $0.82 \pm 0.05\%$, respectively. Similarly, lipid content was slightly lower in the male sample at $1.14 \pm 0.13\%$, compared to $1.47 \pm 0.14\%$ and $1.46 \pm 0.22\%$ in the non-berried and berried samples, respectively. The female samples demonstrated comparatively higher fat content, with the non-berried and berried samples containing $0.82 \pm 0.03\%$ and $0.85 \pm 0.03\%$, respectively, while the male sample exhibited the lowest fat content at $0.77 \pm 0.02\%$. Additionally, berried females demonstrated reduced cholesterol content in comparison to both non-berried females and males.

3.2. Fatty acid, nutritional indices, and mineral composition

The presence of a total of 14 fatty acids was observed in the samples of *P. semilaervis* (Table 2), encompassing both essential and non-essential fatty acids. Figs. 2 and 3 represent the seasonal variation in fatty acid

composition in muscle tissues of *P. semilaervis*. Among SFA, palmitic acid (16:0) was the most prominent among male, berried and non-berried females, accounting for a substantial portion (22–27%). Furthermore, palmitic acid showed a significant increase from pre-monsoon to post-monsoon for males and non-berried females. The highest value for C16:0 was observed in the case of males in post-monsoon (27.04%). Similarly, pentadecanoic acid (15:0) and margaric acid (17:0) displayed a significant increase from pre-monsoon to post-monsoon for males, berried and non-berried females. On the other hand, there was a noticeable decrease in stearic acid (18:0) levels observed among males, berried females, and non-berried females, spanning from the pre-monsoon period to the post-monsoon period.

The MUFA identified in this species included oleic acid (18:1n-9) and palmitoleic acid (16:1n-7). The combined levels of MUFA were more pronounced during the pre-monsoon than post-monsoon. Oleic acid accounted for a noteworthy proportion of the overall fatty acids in both males and females (14–21%). Among females, the concentration of oleic acid surpassed that of males, reaching its peak during the pre-monsoon period (21%). The aggregate MUFA content exhibited a decline across all instances from the pre-monsoon to the post-monsoon phase.

In the edible portion of the shrimps, total PUFA were higher in comparison to SFA and MUFA. The n-3 fatty acids comprised the dominant share of PUFA in *P. semilaervis*, regardless of sex and seasons. The principal components among these were the C20–22n-3 PUFA derivatives, namely eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which constituted a substantial portion of the fatty acid profile. This was followed by the proportion of arachidonic acid (20:4n-6) and linoleic acid (18:2n-6). Linoleic acid and dihomo- γ -linolenic acid (20:3n-6) showed a significant increase in concentration from pre-monsoon to post-monsoon.

Arachidonic acid (ARA), EPA and DHA showed a significant decrease from pre-monsoon to post-monsoon, with an exception in the case of berried females, where a slight increase was observed in the concentration of EPA from pre-monsoon to post-monsoon. Males, berried females, and non-berried females displayed a greater proportion of n-3 fatty acids (31–37%) in the pre-monsoon phase, while a higher percentage of n-6 fatty acids (19–24%) were observed in the post-monsoon period. Male specimens of *P. semilaervis* exhibited a higher proportion of ARA compared to their female counterparts. During the pre-monsoon period, DHA content exceeded that of EPA in all observed samples. Conversely, in the post-monsoon period, EPA content surpassed DHA in female *P. semilaervis* specimens, with similar values seen in males.

The fatty acid composition differed significantly with sex and season, as evident in the PCA plot (Fig. 4). The first two principal components (Dim 1 and Dim 2) accounted for 44.2% and 28.7% of the fatty acid variation, respectively.

An elevated n-3/n-6 ratio, serving as a significant biomedical indicator, was noted within the range of 4–5 across all samples during the pre-monsoon period, while a range of 0.5–1 was observed in the post-monsoon season. *P. semilaervis* exhibited a higher concentration of n-3 fatty acids, including DHA and EPA, accompanied by an optimal n-3/n-6 polyunsaturated fatty acid ratio. Notably, there was no evident variation in the n-3/n-6 ratio between male and female samples. This species displayed an increased PUFA/SFA ratio (1–1.8) across all analyzed samples, with the highest value of 1.8 observed in post-monsoon berried females. The indices of atherogenicity (AI) were within the range of 0.48–0.62 and 0.46–0.63 for pre-monsoon and post-monsoon samples, respectively. Similarly, the indices of thrombogenicity (TI) were recorded between 0.22–0.3 for pre-monsoon and 0.32–0.42 for post-monsoon samples. Notably, AI and TI values showed no noticeable disparity between males and females.

Among the macro-minerals identified, sodium (Na), phosphorus (P) and magnesium (Mg) levels showed minimal divergence, with females showing slightly higher levels (Table 3). Similarly, potassium (K) and calcium (Ca) demonstrated comparable levels with males having marginally higher values. In the context of micro-minerals, females and

Table 1
Morphometric data and proximate composition in the muscle tissues of *P. semilaervis*.

	NB	B	Male
TL (mm)	67–132	72–136	70–133
CL (mm)	10–24	12–24	10–24
Weight (g)	0.85–6.26	1.13–7.5	0.72–6.01
Meat yield (%)	53.44 $\pm$ 4.00 ^a	48.4 $\pm$ 2.88 ^a	52.16 $\pm$ 3.7 ^a
Moisture (%)	81.55 $\pm$ 0.56 ^a	81.62 $\pm$ 0.48 ^a	82.42 $\pm$ 0.16 ^a
Ash (%)	3.52 $\pm$ 0.08 ^a	3.51 $\pm$ 0.03 ^a	3.21 $\pm$ 0.07 ^a
Carbohydrate (%)	0.79 $\pm$ 0.01 ^b	0.82 $\pm$ 0.05 ^b	0.60 $\pm$ 0.03 ^a
Fat (%)	0.82 $\pm$ 0.03 ^b	0.85 $\pm$ 0.03 ^b	0.77 $\pm$ 0.02 ^a
Proteins (%)	13.73 $\pm$ 0.81 ^a	12.56 $\pm$ 0.51 ^a	13.1 $\pm$ 0.41 ^a
Lipids (%)	1.47 $\pm$ 0.14 ^b	1.46 $\pm$ 0.22 ^b	1.14 $\pm$ 0.13 ^a
Cholesterol (mg 100 g ⁻¹)	61.3 $\pm$ 0.24 ^c	58.88 $\pm$ 0.63 ^b	64.08 $\pm$ 0.59 ^a

TL, CL and weight are presented as a range, while other parameters are presented as means $\pm$ standard deviation (SD).

Values in the same row with different superscripts are significantly different ($p < 0.05$).

Abbreviations: NB, non-berried females; B, berried females; TL, Total length; CL, carapace length.

Table 2

The fatty acid composition in muscle tissues of *P. semilaevis* (% of total fatty acids).

Fatty acid	NB Pre-monsoon	Post-monsoon	B Pre-monsoon	Post-monsoon	Male Pre-monsoon	Post-monsoon
Saturated fatty acids (SFA)						
14:0	1.52±0.09	1.28±0.43	1.48±0.07	0.69±0.13	1.25±0.09	1.36±0.29
15:0	0.97±0.08	2.06±0.34	0.76±0.05	0.9±0.24	0.92±0.01	2.05±0.05
16:0	24.6±1.82	26.42±3.22	23.30±1.53	22.69±7.8	21.9±0.18	27.04±0.98
17:0	1.29±0.01	1.67±0.43	1.03±0.10	1.67±0.11	1.17±0.08	1.60±0.13
18:0	7.98±1.95	0.73±0.04	6.44±0.05	0.48±0.02	5.57±0.43	0.46±0.07
ΣSFA	36.36±0.18	32.16±3.41	33.02±1.67	25.42±7.62	30.80±0.67	32.52±0.84
Monounsaturated fatty acids (MUFA)						
16:1n-7	5.51±0.29	1.83±1.43	5.35±0.37	1±0.10	4.38±0.24	2.12±1.05
18:1n-9	18.68±1.62	19.24±1.08	20.97±1.17	16.74±6.38	16.88±0.96	14.41±6.14
ΣMUFA	24.19±1.33	21.07±0.35	26.32±1.53	17.74±6.33	21.23±1.20	16.53±5.09
Polyunsaturated fatty acids (PUFA)						
18:2n-6	1.35±0.07	6.69±0.5	1.28±0.08	14.66±6.53	1.21±0.25	6.84±3.82
18:3n-6	0.88±0.03	0.70±0.01	0.86±0.07	nd	0.62±0.05	0.48±0.41
20:2n-6	0.62±0.19	2.68±2.35	0.65±0.2	0.39±0.05	0.57±0.13	1.49±0.01
20:3n-6	0.5±0.12	6.24±1.27	0.49±0.14	4.51±1.88	1.21±0.87	10.51±1.33
20:4n-6 (ARA)	3.3±0.13	2.90±0.53	3.3±0.23	2.08±1.55	6.18±1.77	4.46±3.37
20:5n-3 (EPA)	12.87±0.64	7.02±2.93	14.3±1.27	17.50±7.29	13.25±2.19	6.11±0.26
22:6n-3 (DHA)	18.23±0.08	3.76±1.1	18.64±2.43	2.15±1.08	23.66±2.13	6.67±5.84
ΣPUFA	37.75±0.65	29.99±2.68	39.52±3.61	41.28±14.6	46.70±2.40	36.56±6.81
Fatty acid indices						
Σn-3	31.1±0.72	10.78±2.61	32.94±3.7	19.65±8.37	36.91±0.06	12.78±5.58
Σn-6	6.65±0.08	19.21±1.11	6.57±0.09	21.64±6.25	9.79±2.46	23.78±1.25
EPA/ARA	3.9±0.05	2.55±1.45	4.33±0.08	11.61±6.99	2.35±1.08	2.65±2.78
DHA/ARA	5.53±0.19	1.28±0.15	5.63±0.34	1.31±0.60	3.99±0.84	1.29±0.45
Σn-3/Σn-6	4.68±0.16	0.56±0.15	5.02±0.63	0.88±0.14	3.94±1.04	0.53±0.21
ΣPUFA/ΣSFA	1.04±0.01	0.95±0.18	1.20±0.17	1.77±1.09	1.52±0.11	1.13±0.24
UFA/SFA	1.7±0.03	1.61±0.24	2.00±0.16	2.43±1.04	2.21±0.09	1.63±0.10
AI	0.62±0.02	0.63±0.09	0.54±0.04	0.46±0.1	0.48±0.02	0.62±0.02
TI	0.3±0.0	0.42±0.08	0.25±0.04	0.32±0.1	0.22±0.1	0.34±0.08

Data are presented as means±standard deviation (SD).

Abbreviations: NB, non-berried females; B, berried females; ARA, arachidonic acid; nd, not detected; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; UFA, unsaturated fatty acids; AI, atherogenicity index; TI, thrombogenicity index.

males displayed compelling differences. Notably, the female sample exhibited significantly greater iron (Fe) content at $44.20 \pm 0.94 \text{ mg kg}^{-1}$, whereas the male sample had a lower concentration of $33.7 \pm 1.54 \text{ mg kg}^{-1}$. Similar trends were observed for copper (Cu) and zinc (Zn), where the female samples exhibited elevated levels compared to their male counterparts, with copper at $5.20 \pm 0.29 \text{ mg kg}^{-1}$ for females and $4.6 \pm 0.41 \text{ mg kg}^{-1}$ for males and zinc at $16.83 \pm 0.28 \text{ mg kg}^{-1}$ for females and $15.36 \pm 0.71 \text{ mg kg}^{-1}$ for males. Conversely, selenium (Se) and manganese (Mn) levels remained consistent between genders. One-way ANOVA results revealed significant differences in the composition of Zn, Fe and P ($p < 0.05$) between sex.

3.3. Amino acid composition and nutritional indices

In the muscle tissue of *P. semilaevis*, a total of eighteen amino acids were detected, encompassing both essential and non-essential amino acids (Table 4). The ΣEAA and ΣNEAA values were higher in berried females compared to non-berried females and males. Among the non-essential amino acids, glutamic acid predominated, with a significantly greater content of $3.65 \pm 0.20 \text{ g } 100 \text{ g}^{-1}$ in non-berried females, $3.67 \pm 0.08 \text{ g } 100 \text{ g}^{-1}$ in berried females, and $3.57 \pm 0.01 \text{ g } 100 \text{ g}^{-1}$ in males. Aspartic acid and arginine followed in abundance. In terms of essential amino acids, lysine was the most abundant, with levels of $2.49 \pm 0.24 \text{ g } 100 \text{ g}^{-1}$ in non-berried females, $2.73 \pm 0.10 \text{ g } 100 \text{ g}^{-1}$ in berried females, and $2.17 \pm 0.08 \text{ g } 100 \text{ g}^{-1}$ in males. Leucine and valine were the subsequent essential amino acids in higher quantities.

Nutritional indices, including various amino acid ratios, are presented in the Table 4. The ΣEAA/ΣNEAA ratio was 0.71 ± 0.00 for berried females and 0.70 ± 0.01 for males and non-berried females. Males exhibited the highest values for ΣArAA and the Arg/Lys ratio ($1.46 \pm 0.01 \text{ g } 100 \text{ g}^{-1}$ and 0.77 ± 0.01 , respectively), while berried

females had the highest values for ΣSAA and the Cys/ΣSAA ratio ($0.49 \pm 0.01 \text{ g } 100 \text{ g}^{-1}$ and 0.24 ± 0.01 , respectively). The Leu/Ile ratio was slightly higher in non-berried females. ΣEAA/ΣAA and ΣNEAA/ΣAA showed similar values across all categories.

The amino acid composition differed significantly with sex, as evident in the PCA plot (Fig. 5). The first two principal components (Dim 1 and Dim 2) accounted for 42.6% and 29.1% of the amino acid variation, respectively.

4. Discussion

4.1. Proximate composition

Evaluating the proximate profiles, which encompass parameters, such as protein, lipid, carbohydrate, fat, ash, and moisture content, is often imperative to ensure compliance with food and commercial regulations. Shrimps are known for their high perishability due to their elevated moisture and amino acid levels (Shamasunder and Prakash, 1994). In the current investigation, moisture content exceeding 81% was observed, indicating the freshness of deep-sea shrimps, aligning with previous studies where water content exceeding 70% signified freshness (Sriket et al., 2007; Chakraborty et al., 2022c).

The ash content provides insights into the shrimp's mineral composition richness (Wang et al., 2021). In this study, the ash content was similar in female and male shrimps indicating a lack of variation in mineral constituents. In a study carried out by Rosa and Nunes (2004) in the Atlantic Ocean, ash levels varied between 1.9% and 2.1% in *Aristeus antennatus* and *Parapenaeus longirostris*. Previous research by Fernandez et al. (2018) reported ash content ranging from 0.7% to 1.96% for deep-sea shrimps from the Arabian Sea, while Chakraborty et al. (2022c) indicated a range of 3% to 6% for shrimps from the same region. Remarkably, these earlier findings closely align with the results of the

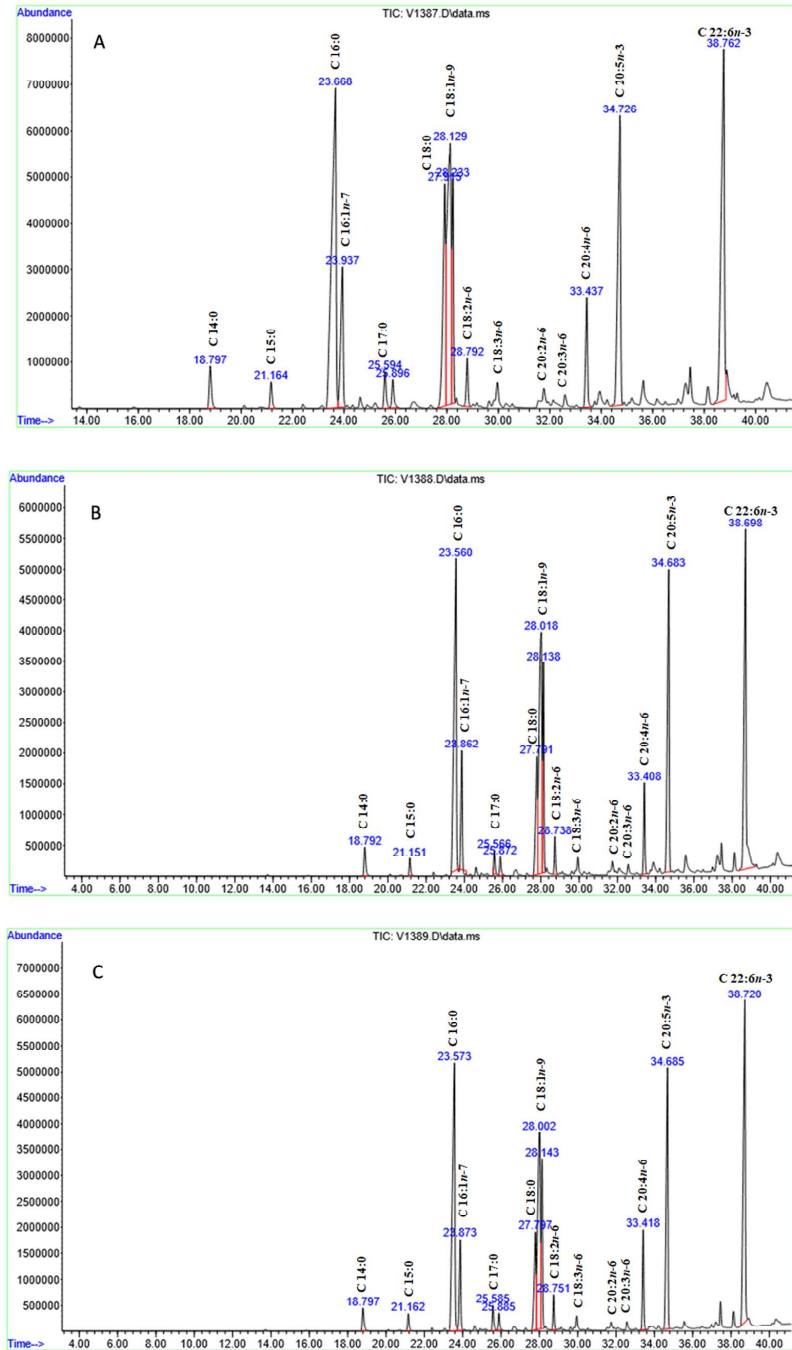


Fig. 2. Fatty acid composition in muscle tissues of *P. semilaevis* during pre-monsoon period. A, non-berried females; B, berried females; C, males.

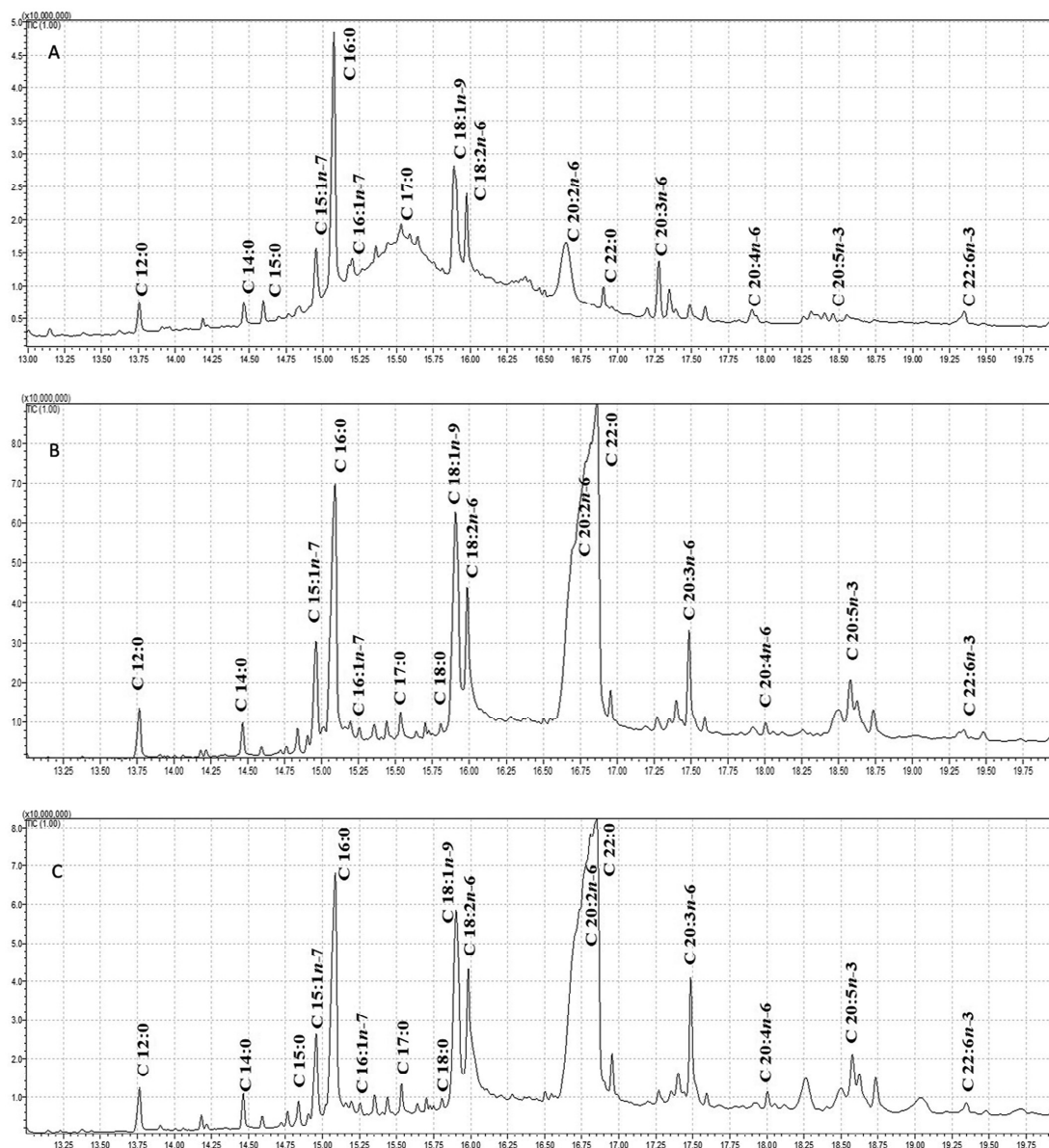


Fig. 3. Fatty acid composition in muscle tissues of *P. semilaevis* during post-monsoon period. A, non-berried females; B, berried females; C, males.

current study.

Among the organic nutrients, carbohydrates are typically the first to be utilized to generate the necessary energy. In this study, males exhibited lower carbohydrate levels than females, and among the female group, berried females displayed higher carbohydrate content.

When comparing the fat content in *P. semilaevis* (ranging from 0.77% to 0.85%) with that of other deep-sea shrimps from the same region, Chakraborty et al. (2022c) documented notably higher fat levels, such as 1.63% in *Aristeus alcocki*, 1.95% in *Heterocarpus chani*, 0.92% in

Plesionika quasigrandis, 1.53% in *Solenocera choprai* and 0.84% in *Metapenaeopsis andamanensis*.

From a nutritional perspective, protein is an important component in seafood, playing a critical role in supporting regular bodily functions and ensuring the growth and maintenance of body tissues. Notably, berried females exhibited lower protein levels in the tissue compared to males and non-berried females. This distinction can be attributed primarily to the greater allocation of protein for the development of eggs in berried females (Dinakaran et al., 2009; Rosa and Nunes, 2003).

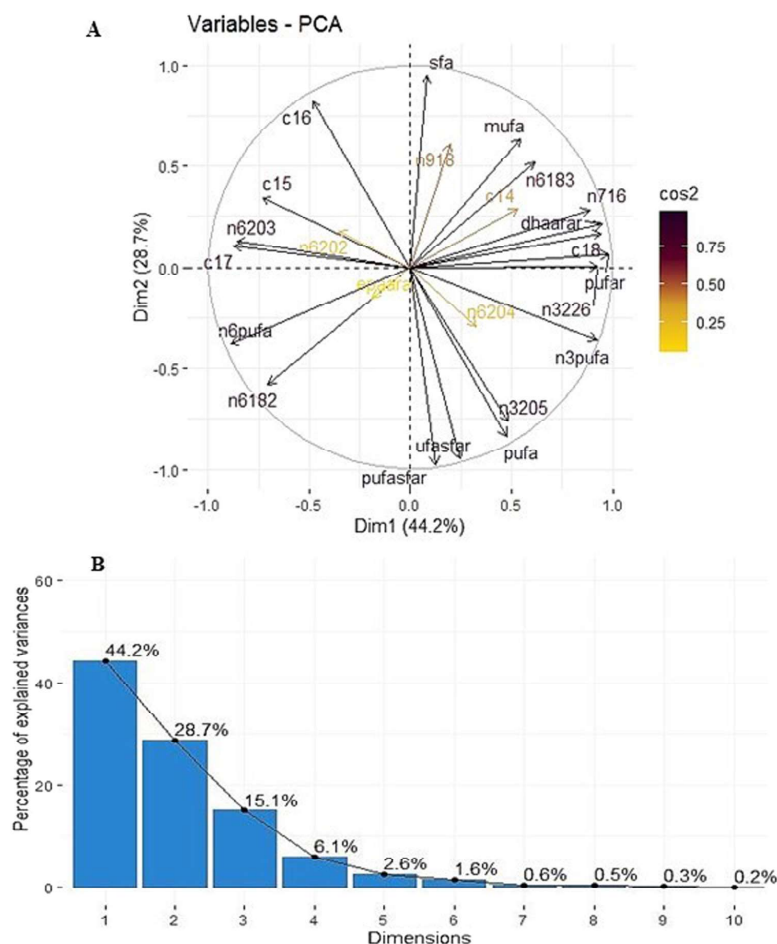


Fig. 4. (A): Principal component analysis of the fatty acids found in muscle tissue of *P. semillaevs* (B) Screen plot of 10 variables: Six variables with eigen values > 1 (1): pufar, *n*-3/*n*-6 ratio; (2): dhaaarar, DHA/ARA ratio; (3): c18; (18:00) (4): n3226; DHA (5): n6pufa; *n*-6 PUFA (6):n3pufa, *n*-3 PUFA.

Table 3
The mineral composition in muscle tissues of *P. semillaevs*.

Minerals	Male (mg kg ⁻¹)	Female (mg kg ⁻¹)
Na	9195.2 ± 140.72	9256.8 ± 90.5
Mg	378.7 ± 25.8	382.3 ± 30.01
Ca	2920.7 ± 58.5	2903.6 ± 81.9
Mn	1.57 ± 0.17	1.52 ± 0.07
Fe	33.7 ± 1.54	44.20 ± 0.94
Cu	4.6 ± 0.41	5.20 ± 0.029
Zn	15.36 ± 0.71	16.83 ± 0.28
Se	0.85 ± 0.05	0.82 ± 0.10
P	10294.5 ± 68.6	10419.8 ± 33.1
K	10645.1 ± 188.6	10607.4 ± 168.8

Data are presented as means ± standard deviation (SD).

Fernandez et al. (2018) reported a protein range of 18.81% to 22.33% in select deep-sea shrimps off the southwestern coast of India. In a recent study by Chakraborty et al. (2022c), deep-sea shrimps from the Arabian Sea, displayed protein content ranging from 9.8% to 12.7%. Notably, the protein content observed in *P. semillaevs* was greater than that of these

shrimps. Rao et al. (2016) reported a protein content of 14.92% in *Heterocarpus gibbosus* specimens collected from the west coast and 17.42% in samples gathered from the east coast. Discrepancies in protein content could arise from variations in growth stages, dietary factors, geographic location, and seasonal influences (Sikorski et al., 1990).

Lipids play a critical role in preserving the structural and physiological integrity of cellular and sub-cellular membranes. Typically, shrimp muscle contains lower lipid content, making it preferable for consumers (Bhavan et al., 2008). The lipid content in shellfish generally falls within the range of 0.3% to 3.2% (Oksuz et al., 2009). Chakraborty et al. (2022c) noted a lipid content range of 1.89% to 2.64% in other deep-sea shrimps from the Arabian Sea. In our study, the lipid content in the edible tissue of *P. semillaevs* was even lower, ranging from 1.14% to 1.47%. Furthermore, the total lipid level was found to be higher in female shrimps compared to male shrimps, aligning with the findings of Bhavan et al. (2010). The increased total lipid content observed in adult female shrimps may be attributed to the demands of specific physiological activities associated with reproduction (Bhavan et al., 2010).

The cholesterol levels in deep-sea shrimp are lower than those in shallow-water shrimps, as documented by Krzynowek and Panunzio

Table 4
The amino acid composition in muscle tissues of *P. semilaevis*.

Amino acids	NB (g100g ⁻¹)	B (g 100 g ⁻¹)	Male (g 100 g ⁻¹)
Essential amino acid (EAA)			
Histidine	0.52 ± 0.04	0.51 ± 0.03	0.50 ± 0.01
Isoleucine	0.97 ± 0.02	1.03 ± 0.03	0.98 ± 0.02
Leucine	1.65 ± 0.05	1.73 ± 0.04	1.65 ± 0.07
Lysine	2.49 ± 0.24	2.73 ± 0.10	2.17 ± 0.08
Methionine	0.36 ± 0.01	0.38 ± 0.01	0.36 ± 0.04
Phenylalanine	0.76 ± 0.04	0.7 ± 0.03	0.80 ± 0.01
Threonine	0.55 ± 0.01	0.56 ± 0.01	0.64 ± 0.01
Valine	1.02 ± 0.04	0.92 ± 0.02	0.98 ± 0.03
ΣEAA	8.31 ± 0.31	8.55 ± 0.11	8.08 ± 0.03
Non-essential amino acid (NEAA)			
Alanine	1.25 ± 0.11	1.29 ± 0.05	1.24 ± 0.01
Aspartic acid	2.11 ± 0.04	2.16 ± 0.17	2.14 ± 0.00
Glutamic acid	3.65 ± 0.20	3.67 ± 0.08	3.57 ± 0.01
Serine	0.8 ± 0.01	0.82 ± 0.01	0.86 ± 0.01
Glycine	1.27 ± 0.11	1.24 ± 0.03	1.18 ± 0.03
Tyrosine	0.63 ± 0.02	0.71 ± 0.02	0.66 ± 0.01
Cysteine	0.09 ± 0.01	0.12 ± 0.01	0.10 ± 0.02
Proline	0.25 ± 0.01	0.29 ± 0.01	0.29 ± 0.02
Arginine	1.75 ± 0.17	1.72 ± 0.01	1.66 ± 0.04
ΣNEAA	11.8 ± 0.61	12.01 ± 0.19	11.48 ± 0.05
Amino acid indices			
ΣAA	20.12 ± 0.91	20.56 ± 0.3	19.56 ± 0.02
ΣEAA/ΣNEAA	0.70 ± 0.01	0.71 ± 0.00	0.70 ± 0.01
Σ ARAA	1.39 ± 0.02	1.4 ± 0.05	1.46 ± 0.01
Σ SAA	0.44 ± 0.02	0.49 ± 0.01	0.43 ± 0.03
Leu/Ile	1.71 ± 0.09	1.68 ± 0.08	1.69 ± 0.05
Cys/ΣSAA	0.2 ± 0.01	0.24 ± 0.01	0.15 ± 0.02
Arg/Lys	0.7 ± 0.00	0.63 ± 0.02	0.77 ± 0.01
ΣEAA/ΣAA	0.41 ± 0.00	0.42 ± 0.00	0.41 ± 0.00
ΣNEAA/ΣAA	0.59 ± 0.00	0.58 ± 0.00	0.58 ± 0.00

Data are presented as means ± standard deviation (SD).

Abbreviations: NB, non-berried females; B, berried females; AA, amino acids; ARAA, aromatic amino acids; SAA, sulfur containing amino acids; Leu, leucine; Ile, Isoleucine; Cys, cysteine; Arg, arginine; Lys, lysine.

(1989) and Chakraborty et al. (2022c). The findings regarding cholesterol content in *P. semilaevis* align with values observed in other deep-sea shrimps from the Arabian Sea reported by Chakraborty et al. (2022c). These comparisons illustrate variations in proximate content among different shrimp species in the same geographical area.

4.2. Fatty acid analysis and nutritional indices

The primary source of energy for the growth of marine fishes and crustaceans is SFA, with a particular emphasis on palmitic acid (16:0) due to its higher caloric content (Chakraborty et al., 2022b). In *P. semilaevis*, the predominant SFA present is palmitic acid. In studies of deep-sea shrimps like *Parapenaeus longirostris* and *Plesionika martia* from the North Eastern Mediterranean Sea, palmitic acid emerged as the dominant saturated fatty acid in muscle tissue (Oksuz et al., 2009). The primary feeding period varies among species, as evident in observations of various shrimp species from the Arabian Sea (Paramasivam et al., 2020; Ambatt Padmanabhan et al., 2023; Sreelakshmy et al., 2023; Muralidharan et al., 2023). Interestingly, the concentration of SFA has been observed to rise during periods of increased feeding activity (Shirai et al., 2002). In the case of *P. semilaevis*, the pre-monsoon period stands out as a major feeding activity period (Sreelakshmy et al., 2023), during which higher levels of SFA are evident in males, berried, and non-berried females.

Palmitic acid is recognized as a significant source of metabolic energy during the egg formation process in females (Ramezani-Fard et al., 2016). Studies on ovarian maturation have indicated that deep-sea shrimps exhibit year-round spawning, with a peak occurring from January to April (Paramasivam et al., 2018; Sreelakshmy and Chakraborty, 2023). During the pre-monsoon period, which is the major reproductive period for *P. semilaevis* (Sreelakshmy and Chakraborty,

2023), females exhibited a higher percentage of palmitic acid in their fatty acid composition when compared to males. However, this trend of higher palmitic acid content in females was not observed during the post-monsoon period. This finding aligns with previous reports of spawning-associated variations in fatty acids, specifically palmitic acid (16:0), in female marine fish (Huynh et al., 2007). These findings suggest that the reproductive activities of female *P. semilaevis* during the pre-monsoon period may influence their fatty acid composition, specifically an increase in palmitic acid, to support their energy needs for egg formation and reproduction.

Moving on to MUFA, *P. semilaevis* was found to have oleic acid as the predominant MUFA, aligning with prior research indicating that the principal MUFA in marine lipids usually consists of 18 carbon atoms (Yanar & Celik, 2005; Chakraborty et al., 2022c). Oleic acid has been identified as important for energy metabolism during gonadal development (Huynh et al., 2007). Notably, in the present study, female shrimps exhibited higher levels of oleic acid than males. In humans, *n*-9 fatty acids play a role in reducing the risk of arteriosclerosis, cardiovascular disease, and stroke.

ARA plays a crucial role in the female reproductive cycle as a precursor to prostaglandin hormones essential for reproduction and vitellogenesis (Bell and Sargent, 2003). In the present study, the higher levels of ARA in females, especially in berried stages during the pre-monsoon period, indicate their reproductive maturity, coinciding with their spawning and hatching period from December to May (Sreelakshmy and Chakraborty, 2023).

Regarding *n*-3 PUFA, particularly EPA and DHA, their presence suggests better growth and survival of *P. semilaevis* in the wild. Elevated levels of EPA and DHA are associated with enhanced stress tolerance and increased membrane permeability (Farias et al., 2014). Oksuz et al. (2009) reported that the total PUFA in the edible portions of *P. longirostris* and *P. martia* were found in higher quantities when compared to the total SFA and MUFA. The current study aligns with these earlier findings, confirming the prevalence of PUFA in shrimps over other classes of fatty acids (Braganolo and Rodriguez-Amaya, 2001; Maia et al., 2022). The *n*-3 fatty acids are renowned for their multifaceted health benefits in humans, encompassing anti-inflammatory and anti-coagulant properties while also playing a vital role in bone formation and metabolism. DHA is particularly vital for pregnant and nursing mothers and young children, while EPA serves as a precursor to anti-inflammatory compounds necessary for efficient brain and cellular functioning (Chakraborty et al., 2014). Given that *P. semilaevis* contains substantial amounts of PUFA, it can indeed serve as a healthy dietary option, potentially contributing to overall well-being and mental health.

Chakraborty et al. (2022a) conducted a comparative analysis of the fatty acid profiles of *Aristeus alcocki*, *Solenocera choprai*, *Heterocarpus chani*, and *Plesionika quasigrandis*, captured along the southwest coast of India in the Arabian Sea, over different months. Their findings showed that *n*-3 fatty acids were most abundant during the period from December to February in the studied year, with a notable decrease in concentrations during March and April. In the present study, it was observed that the concentration of *n*-3 fatty acids was highest in the pre-monsoon samples (January to March) in comparison to the post-monsoon samples (September to November). Conversely, the concentration of *n*-6 fatty acids displayed an opposite trend, with higher levels observed during the post-monsoon period. This information underscores the significance of considering temporal factors when evaluating the nutritional profiles of these marine organisms, revealing seasonal variations in their fatty acid composition.

The ratio of *n*-3 to *n*-6 fatty acids is recognized as a critical biomedical marker for assessing the nutritional value of marine-derived lipids. An increased *n*-3/*n*-6 ratio is associated with a reduced risk of coronary heart disease and cancer (Chakraborty et al., 2014; Chakraborty et al., 2021). Notably, *P. semilaevis* exhibited a higher *n*-3/*n*-6 fatty acid ratio during the pre-monsoon period, which is indicative of a nutritious diet. Maintaining a proper balance and interaction between

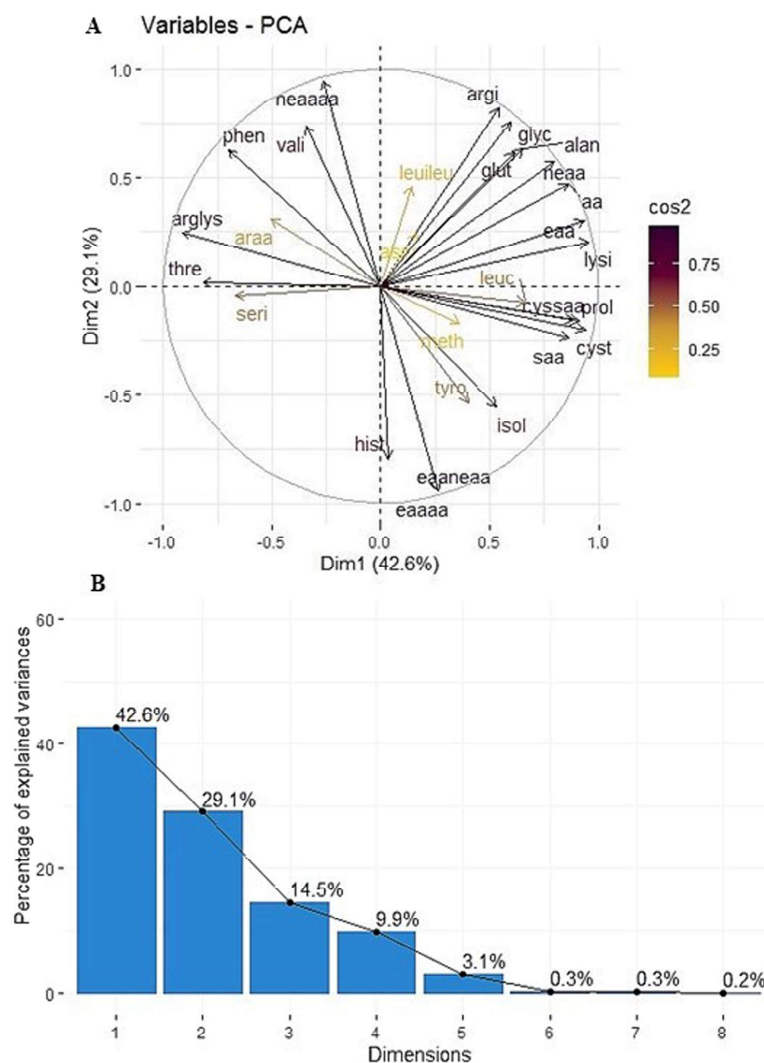


Fig. 5. (A): Principal component analysis of the amino acids found in muscle tissue of *P. semilaеvis* (B) Screen plot of 10 variables. Five amino acids with eigen values > 1 (1): lysi, lysine; (2): eaa; essential amino acids (EAA) (3): cyst, cysteine; (4): prol, proline; (5): arglys, Arg/Lys ratio.

n-3, *n*-6, and *n*-9 fatty acids is vital for overall health (Christensen et al., 2001). A healthy diet is expected to have a PUFA/SFA ratio exceeding 0.45 (HMSO, 2001) to reduce the risk of cardiovascular diseases. *P. semilaеvis* exceeded this recommended limit in males, berried, and non-berried females during both pre-monsoon and post-monsoon periods, making it a potential source of beneficial PUFAs. Foods with a lower PUFA/SFA ratio are generally considered unsuitable for consumption due to their potential to raise blood cholesterol levels. Thrombogenicity index (TI) and atherogenicity index (AI) are important parameters reflecting the metabolic effects of different fatty acids. Lower TI and AI levels are associated with a highly nutritious diet, which can potentially reduce the risk of cardiovascular diseases (Tonial et al., 2014). In the case of *P. semilaеvis*, the observed AI and TI values ranging from 0.48 to 0.63 and 0.22 to 0.42, respectively, suggest that this deep-water shrimp could be considered a healthy seafood choice.

4.3. Minerals

In *P. semilaеvis*, the most prevalent macro-mineral is potassium (K), followed by phosphorus (P), sodium (Na), calcium (Ca), and magnesium (Mg). These findings align with those reported by Oksuz et al. (2009) in their study on deep-sea shrimps, specifically *Parapenaeus longirostris*. Potassium plays a crucial role in the body, functioning in conjunction with Mg, Na and Cl as electrolytes to regulate intracellular osmotic pressure and maintain acid-base balance. In *Penaeus* species, K ranks as the second most abundant mineral, following Ca (Truong et al., 2023). In comparison to coastal shrimp, deep-sea shrimp have higher concentrations of Ca and Na while displaying lower levels of K (Fernandez et al., 2018).

P in conjunction with Ca, plays a significant role in vertebrates and comprises a substantial portion of the exoskeleton in crustaceans (Hynd,

2019). In a study focused on *Parapenaeus longirostris* from the Marmara Sea, Özden noted P concentrations ranging from 2685.9 to 3657.7 mg kg⁻¹, which is notably lower (Özden, 2010) compared to the phosphorus levels found in *P. semilaevis* (10294.5 ± 68.6 mg kg⁻¹ in males and 10419.8 ± 33.1 mg kg⁻¹ in females).

P. semilaevis exhibited similar Na and K levels to those observed in other deep-sea shrimps studied off the southwest coast of India by Fernandez et al. (2018). However, it displayed lower Ca quantities in comparison. Mg serves various functions, including maintaining membrane integrity, modulating neuromuscular transmission, and acting as a catalyst for a wide range of enzymes. In the case of *P. semilaevis*, the levels of Mg were found to be 378.7 ± 25.8 mg kg⁻¹ in males and 382.3 ± 30.01 mg kg⁻¹ in females, which were lower than the values reported in *Parapenaeus longirostris* and *Plesionika matia* (Özden, 2009; Oksuz et al., 2009).

Among micro-minerals, iron (Fe) emerged as the most prevalent element, followed by zinc (Zn), copper (Cu), manganese (Mn), and selenium (Se). Notably, in *P. longirostris*, the microelement concentrations were highest for iron, zinc, and copper, with values of 18, 6.1, and 2.2 mg kg⁻¹, respectively (Özden, 2009). Seafood serves as a reasonably good source of Fe and plays several critical roles in the body (Cámara et al., 2005). In *P. semilaevis*, the concentration of Fe in the tissues was 33.7 ± 1.54 in males and 44.2 ± 0.94 in females, while Fernandez et al. (2018) reported a range of 41.7 to 76.17 mg kg⁻¹ in other deep-sea shrimps from the same locality, with the lowest and highest values observed in *M. andamanensis* and *A. alcocki* respectively. The higher concentration of iron (Fe) observed in females compared to males implies a potential role for this element in the process of oogenesis (Méndez et al., 2001).

Cu and Zn are vital elements that play essential roles in the growth, cellular metabolism, and overall survival of most animals, including crustaceans (Candra et al., 2019). Notably, in crustaceans, such as shrimp, hemocyanin serves as the oxygen carrier and accounts for approximately 40% of the copper (Cu) stores (NRC, 2011). The levels of Cu (4.6 ± 0.41 mg kg⁻¹ in males and 5.20 ± 0.29 mg kg⁻¹ in females) and Zn (15.36 ± 0.71 mg kg⁻¹ in males and 16.83 ± 0.28 mg kg⁻¹ in females) observed in *P. semilaevis* are lesser than the Cu and Zn levels observed by Fernandez et al., (2018) in other deep-sea shrimps from the Arabian Sea. In contrast, Rao et al. (2016) found similar values for Cu at 4.11 ± 0.79 mg kg⁻¹ but notably higher values for Zn at 36.54 ± 1.06 mg kg⁻¹ in *P. spinipes* (later identified as *P. quasigrandis*) from the west coast. The elevation in Zn concentration within female shrimps further underscores its significance in the reproductive process. Regarding Mn concentrations, *P. semilaevis* exhibited levels akin to those reported in other deep-sea shrimps (Oksuz et al., 2009; Özden, 2009; Fernandez et al., 2018).

Selenium is a trace element that serves as a cofactor for the reduction of antioxidant enzymes, such as glutathione peroxidase, playing a critical role in protecting cells, tissues, and membranes against oxidative damage. In the case of *P. semilaevis*, Se concentrations were found to be 0.85 ± 0.05 mg kg⁻¹ in males and 0.82 ± 0.10 mg kg⁻¹ in females. These levels fall within the range observed by Özden (2009) for *P. longirostris* from the Marmara Sea. Notably, the Se values in the present study are higher than those reported by Plessi et al. (2001), Sirichakwal et al. (2005) and Burger and Gochfeld (2006) for other shrimp species.

The concentrations of the analyzed metals were found to be well within the regulatory limits, suggesting that the samples collected from deep-sea do not pose any threat to consumers (FAO, 1983; World Health Organization 1989; Food and Agriculture Organization/World Health, 1999; European Union, 2008).

4.4. Amino acid composition and nutritional indices

Amino acids serve as the fundamental building blocks of proteins, playing crucial roles in the construction of cell structures and serving as energy sources. Research conducted by Sikorski et al. (1990) on the

amino acid composition of prawns unveiled that glycine, alanine, serine, and threonine contribute to the sweet taste of prawns, while arginine, leucine, valine, methionine, phenylalanine, histidine, and isoleucine contribute to a bitter taste. Yanar and Celik (2006) observed that the most prevalent NEAA in *Penaeus semisulcatus* and *Metapenaeus monoceros* from the eastern Mediterranean were glutamic acid, aspartic acid, and arginine, aligning with our findings. Additionally, the major EAA noted in both studies are lysine, leucine, and valine.

Banu et al. (2016) analyzed amino acid content in the muscle of penaeid shrimps and reported higher quantities of EAA in comparison to NEAA in the muscle tissues. However, our present study indicates a significant increase in NEAA compared to EAA, consistent with the findings of Chakraborty et al. (2022c) in other deep-sea shrimps from the same locality.

The EAA/NEAA ratio in *P. semilaevis* falls within a balanced range of 0.70–0.71, underscoring the shrimps' status as excellent sources of protein (Chakraborty et al., 2022c). In comparison to other deep-sea shrimps found off the southwest coast of India, these shrimps also contain higher levels of aromatic amino acids (Chakraborty et al., 2022c). These amino acids are known initiators for catecholamine production and thyroid hormone synthesis. Additionally, they possess significant quantities of sulfur-containing amino acids, ranging from 0.43 to 0.49 g 100 g⁻¹. These amino acids play a pivotal role in lipid metabolism and have beneficial effects against atherosclerosis and metabolic disorders (Oda, 2006). The presence of sulfur-containing amino acids in muscle tissues of *P. semilaevis* suggests that protein derived from these deep-water shrimps can effectively complement dietary amino acid deficiencies. Leucine, a branched-chain amino acid, is known to stimulate protein synthesis in biological systems (Tipton, 2017). Notably, the leucine-isoleucine ratio in these shrimps falls within the limits prescribed by FAO/WHO (1990), ranging from 1.68 to 1.71. However, it's worth mentioning that excessive leucine intake may impact the biochemical pathways of tryptophan and niacin, potentially leading to pellagra (Krishnaswamy and Gopalan, 1971).

In the current study, *P. semilaevis* exhibits a Cys: ΣSAA ratio similar to that of other deep-sea species in the same locality. The cholesterolomic effects of proteins are closely tied to their amino acid composition and the Arg/Lys proportion (Rajamohan and Kurup, 1997). In the current study, the arginine-lysine ratio falls within the range of 0.70–1.68, aligning with the ratios found in meat and vegetables (Nurhan, 2007). This highlights the significance of these shrimps in maintaining a favorable cholesterolomic index. Notably, the EAA/AA ratio in *P. semilaevis* ranges from 0.41 to 0.42, above the threshold of 0.39, suggesting that *P. semilaevis* can be considered an ideal protein-rich food source (Chakraborty et al., 2022c).

5. Conclusions

The present study is the first to comprehensively analyze the nutritional composition of deep-sea shrimp *P. semilaevis*. The proximate composition, mineral analysis, fatty acid and amino acid profiling collectively reveal the presence of high-value nutrients in the edible tissues of shrimp. It presents a notably lower fat and lipid content in its edible tissue compared to several other deep-sea shrimp species from the same region. A higher PUFA content with lower thrombogenicity and atherogenicity indices indicates its potential to promote cardiovascular health. Significant quantities of aromatic and sulfur-containing amino acids, along with a favorable arginine-lysine ratio, underscores the potential of these deep-sea shrimps as an ideal protein-rich food source, capable of addressing amino acid deficiencies and promoting a favorable cholesterolomic index in the diet. The differences observed in muscle constituents between male, berried and non-berried female shrimps signify variances in sexual development and the associated energy demands for sustaining body physiology. This implies that gender has an impact on both the rate of growth and the quality of meat in *P. semilaevis*. When comparing this study to other shrimp species, it's

clear that different species offer varying nutrient benefits. This highlights the importance of biodiversity in shrimp consumption to meet diverse nutritional needs.

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Author statement

All authors have read and approved this manuscript. Everyone has contributed for this piece of work. None of the authors have any conflict of Interest.

CRediT authorship contribution statement

S Sreelakshmy: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Resources, Writing – original draft. **Chakraborty Rekha Devi:** Conceptualization, Formal analysis, Investigation, Project administration, Software, Supervision, Writing – review & editing. **Chakraborty Kajal:** Data curation, Formal analysis, Software, Visualization. **Dhara Shubhajit:** Data curation, Formal analysis, Software.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Data availability

Data will be made available on request.

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Feeding habits of the deep-sea shrimp *Plesionika quasigrandis* Chace, 1985 (Decapoda: Caridea: Pandalidae) in the southeastern Arabian Sea

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ABSTRACT

Species of *Plesionika* [Spence Bate, 1888](#) holds significant importance in the commercial harvesting of deep-sea shrimps along the southern coasts of India. Despite *Plesionika quasigrandis* [Chace, 1985](#) being a crucial resource on the southwest coast of India, there is a need for comprehensive information on its food and feeding habits. We investigated the diet of *P. quasigrandis* in relation to sex, size, and season. The species exhibited a diet primarily consisting of crustaceans, foraminiferans, and detritus. Both males and females showed a noteworthy reliance on detritus, as indicated by an index of preponderance values exceeding 45.8. The species displayed active scavenging behaviour alongside predatory dietary habits. We observed a decrease in feeding intensity from pre-monsoon to post-monsoon in both males and females. Permutational multivariate analysis of variance (PERMANOVA) revealed significant differences in the diets of *P. quasigrandis*, considering the combined effects of size and sex ($P < 0.01$). No significant distinctions were noted in the diet composition between males and females in relation to season.

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Occurrence of Deep-sea shrimp, *Hadropenaeus lucasii* (Spence Bate, 1881) from the southwest coast of India

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Abstract

The present study provides an integrative report combining morphological and molecular analysis of the deep sea shrimp species *Hadropenaeus lucasii* (Spence Bate, 1881) from the southwest coast of India. The present specimen was obtained from the depths of 200–300m from the commercial bottom trawlers operated off Sakthikulangara fishing harbour off Kollam, Kerala. A phylogenetic analysis was used to explore the relationships of the genus. DNA barcoding and phylogenetic analysis were used to explore the relationship of the genus *Hadropenaeus* based on mitochondrial gene (16S: OK571387, OK571388; COI: OK569849, OK569850) sequences of the present specimen with the sequences retrieved from NCBI GenBank revealed an interspecies genetic divergence of 0.0% to 0.6%.

Key words: Taxonomy, deep-sea, penaeid shrimp, phylogenetic, Southwest India

Introduction

The family Solenoceridae Wood-Mason & Alcock, 1891 comprises 10 genera distributed majorly, in tropical and subtropical zones inhabiting benthic habitats (Crosnier & Forest 1969; 1973; Pérez Farfante 1977; De Grave *et al.* 2009; Chan 2012). They are found in gravel or mud substrates between the continental shelf and the continental slope and also occur around oceanic islands. They are morphologically adapted to deep-sea lifestyle and support large vertical pressure variation and absence of light (Crosnier & Forest 1973; Farfante 1977).

Previous reports of Solenoceridae in India include five genera, *Solenocera*, *Haliporides*, *Hadropenaeus*, *Gordonella* and *Hymenopenaeus*. The genus *Hadropenaeus* is distinguished from other genera by the following characteristics: sub-cylindrical upper antennular flagellum, the epigastric tooth and the first rostral tooth separated by an interval equal to or slightly greater than interval between the first and second rostral teeth and rostrum deep, with ventral margin pronouncedly convex and absence of sub-marginal carina (Farfante 1977; Kim *et al.* 2010). *Hadropenaeus* includes four species, *H. lucasi*, *H. affinis*, *H. modestus*, and *H. spinicaudatus* occurring in temperate and tropical regions of the world. However, only *H. lucasii* was reported from India. Although previously reported, no proper taxonomic description is available on its morphology and molecular analysis. The present study accounts for a detailed taxonomic information of *Hadropenaeus lucasii* with morphological descriptions, molecular barcoding along with quality color photographs.

Materials and methods

On January 2020, a female deep-sea shrimp belonging to the genus *Hadropenaeus* was recorded in the deep-sea shrimp catches landed at Sakthikulangara (off Kollam 8°56'60.78"N/76°32'34.27"E) by bottom trawlers with the cod end mesh size (20 to 26 mm). The sample was preserved in 95% ethanol and the voucher specimen (ED 1.1.2.7) was deposited in the referral museum of the Central Marine Fisheries Research Institute (CMFRI), Cochin, India. The specimen was identified as *Hadropenaeus lucasii* (Spence Bate, 1881) based on the descriptions and illustrations provided by Kim *et al.* (2010), Bate (1881) and Pérez Farfante (1977). Images were taken using a stereomicroscope camera (Motic SMZ-168). The 16S and COI sequences of the mitochondrial region were amplified using universal primers (Palumbi, 1996; Folmer *et al.* 1994) and PCR purified products were sequenced by dideoxy chain termination method (Sanger *et al.*, 1977) using ABI Prism 3770 automated sequencer from Scigenom, India. The phylogenetic tree for the mitochondrial genes 16S and COI was built using a maximum likelihood method with 1000 bootstrap replicates (Felsenstein, 1993) using MEGA7 software.

Systematics

Order Decapoda Latreille, 1802

Suborder Dendrobranchiata Spence Bate, 1888

Superfamily Penaeoidea Rafinesque, 1815

Family Solenoceridae Wood-Mason in Wood-Mason & Alcock, 1891

Genus *Hadropenaeus* Perez Farfante, 1977

Hadropenaeus lucasii (Spence Bate, 1881)

Solenocera lucasii—Bate, 1881:185 [type locality: Kai Island, Indonesia]. *Pleoticus lucasii*: Bate, 1888: 227, pl. 42, fig. 4. *Hymenopenaeus lucasii*—Kubo, 1949: 213, figs. 8B, 20Q, 27K–N, 66O, P, 72C, I, 80H, 91, 92A–C. *Hymenopenaeus lucasi*—Crosnier, 1978: 115, figs. 37f–h, 39c, 43a, 44. *Hadropenaeus lucasii*—Pérez Farfante, 1977: 327, figs. 9, 16, 44C, 53–55; Hayashi, 1986: 43, 232, unnumbered fig.; 1992: 171, figs. 93, 94, 97. Miyake, 1998: 5, pl. 2, fig. 1; Dall, 1999: 560, fig. 5; 2005: 413. *Hadropenaeus lucasii* (Spence Bate, 1881); Kim *et al.* 2010: 321, fig. 1.

Material examined. Sakthikulangara (off Kollam 8°56'60.78"N; 76°32'34.27"E) fish landing center, Female specimen (Total length: 62 mm; Carapace length (CL): 15 mm; Rostral length (RL): 4 mm; Weight (W): 2 g, 200–230 m depth during January 2020.

Diagnosis of specimen from off Kerala: Rostrum short reaching up to the first segment of antennular peduncle. Rostral upper edge straight and almost horizontal, with six teeth including the epigastric tooth. The last two are more distant and above the gastric region. Epigastric tooth and first rostral tooth separated by equal intervals. Eye not large, carapace is glabrous. Postorbital, antennal, hepatic and branchiostegal spines well defined. Cervical sulcus prominent; hepatic sulcus shallow. Third abdominal segment has a well-developed rounded mid dorsal carina while keel like mid dorsal carina present on fourth to sixth somites. Telson has a pair of lateral immovable spines. First pereopod with long spine on basis and ischium and a small spine at mid-length of merus. Dactylus compressed. Second pereopod with long spine on basis. Fourth and fifth pereopods with anteromedian small spine on each coxa. Thelycum between the 5th pereopods having square like hollow plate and anteriorly 1 pair of boss with long setae, posteriorly strong plates are extend in both the sides (**Fig. 1**).

Coloration: Carapace reddish, abdomen and appendages pale reddish.

Distribution: Indo-West Pacific region: Mozambique to Indonesia, northwestern and eastern Australia, Madagascar, Japan to Hawaii and Wallis and Futuna Islands; 121–698 m (Dall, 2005; Crosnier, 1984) Southeastern waters of Jeju Island at 77 m (Kim *et al.* 2010).

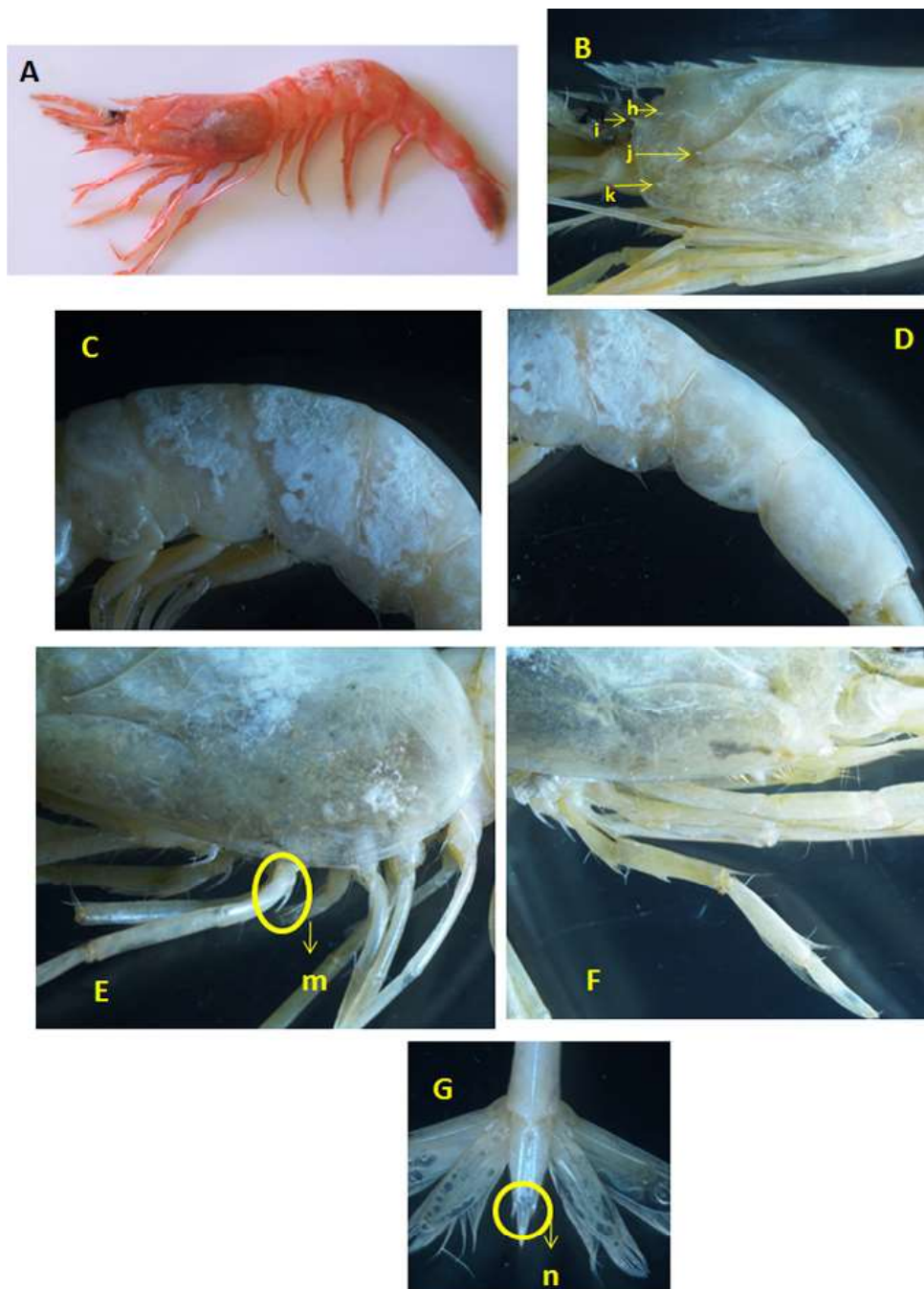


FIGURE 1. *Hadropenaeus lucasii* (Spence Bate, 1881) A : Female specimen. B: carapace. C: 3rd abdominal segment—rounded mid dorsal carina. D: 4–6th abdominal segment with keel and mid dorsal carina. E : Lower carapace. F: First pereopod with long spine on basis of ischium and small spine at mid-length of merus. G: Telson. h: Post orbital spine. i: Antennal spine. j: Hepatic spine. k: Branchiostegal spine. m: Second pereopod with long spine on basis. n: Pair of lateral immovable spines on telson.

Remarks: *Hadropenaeus lucasii* is closely allied to its two Atlantic congeners, *H. affinis* and *H. modestus*, but it may be distinguished from them by the possession of a conspicuous carina on the rostrum dorsal to the adrostral carina. The specimens analyzed herein do not differ much from the description of Kim *et al.* (2010), Bate (1881) and Pérez Farfante (1977). The present specimen is considerably larger than the one described by Kim *et al.*, (2010) (CL=8.4mm) and smaller than the one described by Bate (1881) (TL=76.2mm). The species described by Kim *et al.*, (2010) and Bate (1881) had seven rostral teeth including the epigastric tooth, while the present specimen has six rostral teeth, including the epigastric tooth.

Mitochondrial gene sequencing: The gene sequence obtained from the present specimen was deposited in GenBank (Accession Number: OK571387, OK571388) showed a sequence length of 480–540 bp for 16S ribosomal RNA (16S) and COI (Accession Number: OK569849, OK569850) with 600–610 bp. The present specimen sequences were compared with the NCBI sequences of the genus *Hadropenaeus* retrieved from the GenBank. The level of intraspecies genetic divergence within the specimens of the present and sequences deposited to GenBank was 0% (COI) and 0–0.6% (16S) and were used for constructing the phylogenetic tree (**Fig.2 & Fig.3**).

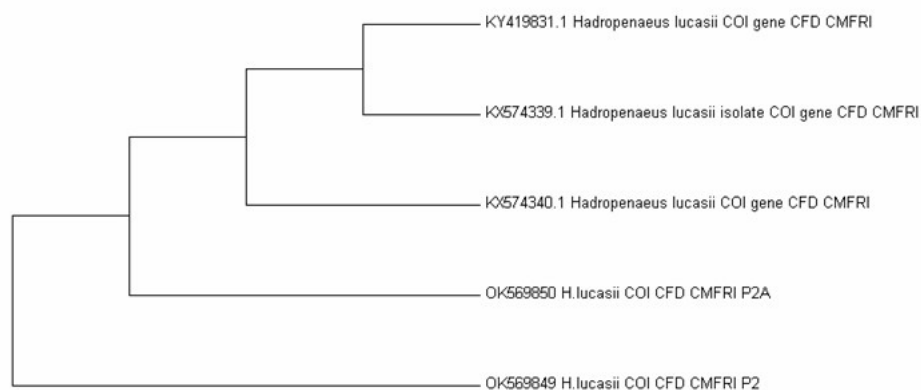


FIGURE 2. Phylogenetic tree of *Hadropenaeus lucasii* using Maximum Likelihood with 1000 bootstrap under the best fitting model GTR+G+I inferred from DNA sequences of 16S mitochondrial gene.

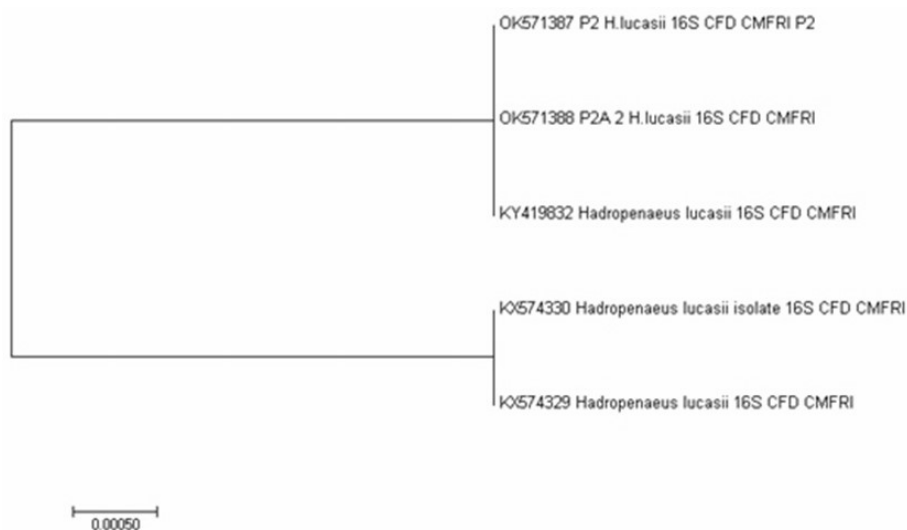


FIGURE 3. Phylogenetic tree of *Hadropenaeus lucasii* using Maximum Likelihood with 1000 bootstrap under the best fitting model GTR+G+I inferred from DNA sequences of COI mitochondrial gene.

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APPENDIX.

	<i>H. lucasii</i>	<i>H. affinis</i>	<i>H. modestus</i>
Scaphocerite	Scaphocerite reaching to distal margin of antennular peduncle or overreaching it by as much as 0.15 of its own length	Scaphocerite reaching distal end of antennular peduncle or surpassing it by less than 0.10 of its own length	Scaphocerite surpassing antennular peduncle by as much as 0.25 of its own length
Prosartema	Long, conspicuously overreaching distomesial margin of first article	Extending only to distomesial extremity of first antennular article	Conspicuously overreaching distomesial extremity of first antennular article
Fourth pereopod	Fourth pereopod exceeding carpoperite by almost length of dactyl and sometimes by as much as length of dactyl and 0.15 that of propodus.	Extending farther anteriorly than 'third pereopod; surpassing antennular peduncle by as much as length of dactyl and that of propodus; length of dactyl less than 0.5 that of propodus	Not extending so far anteriorly as third pereopod, reaching at most distal end of first antennular article; length of dactyl greater than 0.5 that of propodus
Coxa of fourth pereopods	bear a conspicuous anteromesial spine	Lacks a conspicuous anteromesial spine	Lacks a conspicuous anteromesial spine
Coxa of fifth pereopods	bearing conspicuous anterior spine.	Bearing strong anteromesial spine	Lacking anteromesial spine in adult, occasionally with Inconspicuous one in juvenile
Terminal portion of telson	Terminal portion length 3.3–4.0 times basal width;	Long. length 3.5–4.5 its basal width	Short, length 2.5–3.3 its basal width
Telsonic spines	lateral spines short, 1–1.4 times basal width of terminal portion.	Long. length more than 1.5 basal width of terminal portion of telson	Short, length not more than basal width of terminal portion of telson
Petasma	ventromedian lobule of the petasma is not produced into a distolateral projection; instead, its lateral portion is turned strongly inward; the distal plate of the ventrolateral lobule bears spinules along the entire terminal margin and is produced in a blunt, ventral projection	Ventromedian lobule with distomesial projection directed mesially; distal part of dorsolateral lobule sub elliptical	Ventromedian lobule with distomesial projection directed distally; distal portion of dorsolateral lobule subrectangular
Thelycum	Protuberance on sternite XIV roughly elliptical, low and does not project ventrally, paired convexities of sternite XIII with median ridge long, lacking tooth, sometimes ending in small knob at one or both extremities.	Protuberance of sternite XIV mammiform, with apical part directed ventrally; median keel of sternite XIII produced into anteriorly directed blunt tooth	Protuberance of sternite XIV subovate, with apical part directed anteriorly; median keel of sternite XIII produced into ventrally or posteriorly directed blunt tooth