

INTRODUCTION

Earth is the third planet from the Sun and the fifth largest of the eight planets in the solar system. It is also the largest of the solar system's four terrestrial planets. It is unique among all the planets in our solar system as it has a large amount of water, because of which the planet is also called the "Blue Planet." Water covers over 71% of the Earth's surface, of which 96.54% of free water is present in the oceans. Oceans are considered the earth's life support system because they help in regulating oxygen and carbon dioxide levels in the atmosphere, influence climate and weather, serve as a reservoir for water, and support majority of the lifeforms on Earth. In fact, life itself originated from the seas. Researchers have been studying oceans since ancient times, but their importance to human well-being has only recently been recognised (Honeyborne and Brownlow, 2017).

Oceans support a huge diversity of life forms that differ in their forms, functions and sizes (McIntyre, 2010). A field of biology that studies these marine organisms is known as marine biology. Marine biology is a broad field of study that can be further divided into two parts: functional biology and ecology. Functional biology basically includes the development of understanding about the routine biological activities of organisms like locomotion, feeding, reproduction and foraging, as well as the biochemical and cellular processes carried out for respiration, digestion, etc. On the other hand, ecology is a field of study that includes the understanding of interactions between organisms and their physical or biological environment and how such interactions will affect the distribution and abundance of the organisms. Functional biology and ecology are so closely related in nature that it almost becomes impossible to clearly distinguish the two, since almost all functional forms have some sort of ecological impact too (Levinton, 2021).

The studies in the field of marine biology were initiated at a time when there were no such separate fields of scientific specialties. That is why the earliest biologists were "natural philosophers" who tried to recognise the life habits and general anatomy of marine biota. The initiation of such studies can be credited to Aristotle (384–327 B.C.) and his companions, who recorded the distribution and life history of marine organisms. Since Aristotle was the pioneer

in the field of marine biology, he is often referred to as the "Father of Marine Biology." Although Aristotle was the pioneer of marine biology, Linnaeus (1707–1778) was one of the most prominent contributors as he established the modern scheme of classifying organisms. On the basis of his experiences, Edward Forbes (1815–1854) was the first naturalist to give a marine biological hypothesis according to which life does not exist deeper than 300 fathoms (1800 feet). Another great naturalist, Charles Darwin (1809–1881), during his five-year voyage on the H.M.S. Beagle (1831–1836) sailing around the world, conducted an extensive collection of marine organisms. On the basis of that collection, he made many important contributions, including a book on coral reefs as well as the first systematically perfect classification of barnacles, which was so precise that it has remained unchanged to date. Later, C. Wyville Thomson and a great naturalist, John Murray, led another voyage on the H.M.S. Challenger around the world, which provided the first global insight into the marine diversity of the oceans. Their collections were so enormous that it required 50 volumes to describe the tremendous number of organisms sampled during the expedition (Levinton, 2021). With the significant efforts and marine expeditions of many such naturalists and marine biologists, the current data reflects an estimated number of marine species ranging from 250,000 (Groombridge and Jenkins, 2000) to 274,000 (Reaka-Kudla, 1997), with body forms ranging from bacteria to baleen whales. Ocean habitat can be divided into two major zones: the benthic zone and the pelagic zone. For the suitability and description of ecosystems, these zones can be further subdivided on the basis of the distance from the shore as well as the depth of the water. As compared to the pelagic zone, the benthic zone, which is the seafloor, represents a greater variation in habitats, which differ from one another in terms of the type of substrate, degree of immersion (tidal vs. subtidal), temperature, depth and light availability.

The pelagic zone is the entire water column of the oceans, which is inhabited by floating and swimming marine organisms. The pelagic zone can be further divided into two regions: the neritic region, which lies above the continental shelf, and the oceanic region, which starts from the edge of the continental shelf and expands to the deepest region of the ocean. The oceanic zone can be further subdivided into several other zones on the basis of light

penetration, which plays a vital role in shaping the distribution of life forms. The zones are: the **epipelagic zone**, which extends from the water surface to a depth of 150 m of water; the **mesopelagic zone**, which lies between 150 m and 2000 m of water; the **bathypelagic zone**, which ranges from 2000 m to 4000 m of depth; the **abyssopelagic zone**, which extends up to 6000 m of depth; and the **hadalpelagic zone**, which comprises the seabed and the bottom most part of the oceans (Figure 1) (Levinton, 2021).

Benthic refers to the bottommost substratum of any waterbody, and it supports a wide diversity of organisms as a result of varying habitats. Benthic zones can be further divided into five zones on the basis of the depth of the oceanic floor. Starting from the landward side, the first zone is the **intertidal zone**, which is a transitional area between terrestrial and aquatic habitat and comprises less than 1% of the total benthic environment. The **subtidal** or **sublittoral zone**, which exists between 0 and 150 m of depth and accounts for approximately 8% of the total benthic environment. The third zone is the **bathyal zone**, extending from 150 to 2000 m of depth and comprising around 16% of the benthic environment. The fourth zone is the **abyssal zone**, which extends from 2000 to 6000 m deep and accounts for approximately 74% of the total benthic environment. The fifth and last zone is the **hadal zone**, which extends beyond 6000 m up to the deepest part of the ocean and comprises only 1% of the total benthic environment (Figure 1) (Levinton, 2021).

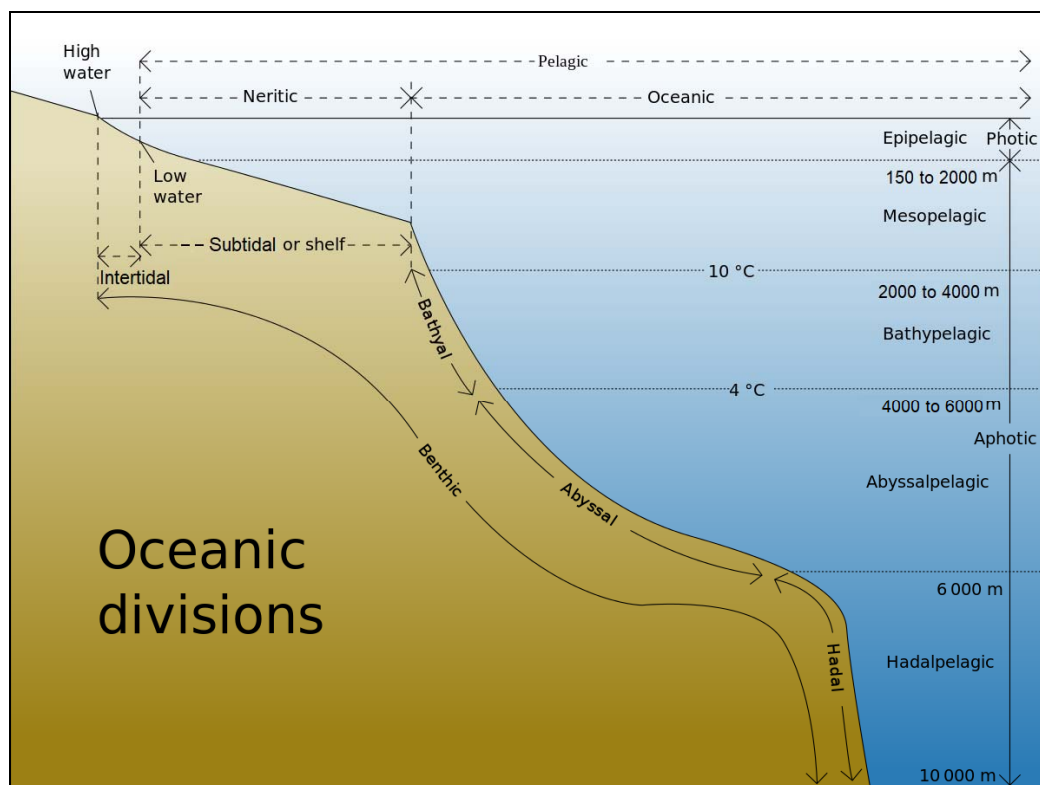


Figure 1. Classification of marine environment. (Source: Xu et al., 2008).

These different zones of the oceanic environment also vary in terms of the diversity of organisms. The difference in the diversity of organisms is due to variations in several environmental factors, including sunlight, temperature, salinity of water, waves, tides, currents, and many more, which tend to affect marine life significantly (Venkatraman et al., 2012). The benthic zone harbours a greater diversity of marine life forms as compared to the pelagic zone (Angel, 1993). Only 11 of the 35 marine phyla are represented in the pelagic realm, with the majority occurring in the benthos, which is the archetypal habitat (Angel, 1993). Because of the presence of sunlight, the littoral, sublittoral, epipelagic, and mesopelagic zones have the greatest diversity of organisms. Beyond these zones, light cannot penetrate farther, and the diversity of organisms decreases in the aphotic zone since organisms here require special adaptations to survive in a dark, cold, and high-pressure environment.

The marine organisms can be classified by their general habits as follows:

Planktons– organisms living suspended in water and include bacteria, protists, plants and animals, which are often less than one millimetre in size. **Neuston**–

microscopic organisms that are found at the sea surface. **Nekton**– animals that live in the water column, and they are powerful swimmers as they can swim against the current or through turbulent water. Their size can range from small shrimp to gigantic whales. Some marine organisms tend to live wholly or partly within the substrate of the ocean by making burrows or similar structures and are known as **infaunal** organisms, which include clams, tubeworms, etc. Infaunal species usually dominate communities on soft substrates, and they are most diverse and abundant in subtidal regions. There are a few infaunal species in hard substrate communities as well; rock-boring clams are one example. Organisms that live close to the surface of the ocean bed or remain attached to the substratum fall under the category of **epifaunal** organisms, which includes oysters, barnacles, and other such animals. Epifauna are found on almost all types of substrates, but they are predominantly developed on hard substrates, moreover, they are the most abundant and diverse organisms found in rocky intertidal areas and coral reefs. A third category can be added to include those animals that live in association with the seafloor but also swim temporarily above it; crustaceans such as prawns and crabs, or flatfish such as sole fish, form the **epibenthos** (Figure 2). Since a large scale of the planet's animal population is found in the ocean, we can say that "Earth's ecology is the ocean's ecology" (Barnes and Hughes, 1999).

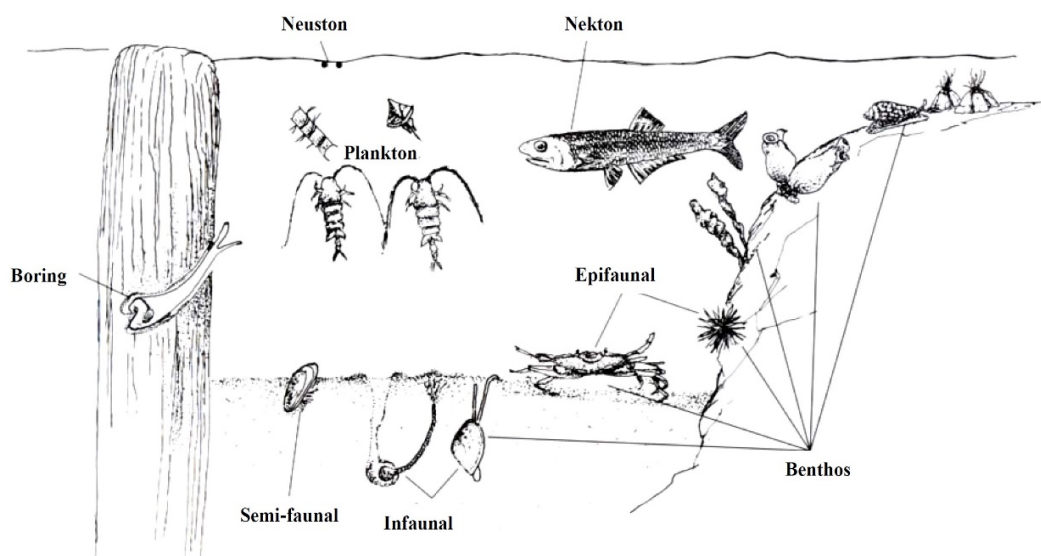


Figure 2. General habit of marine organisms (Source of figure: <http://site.iugaza.edu.ps>).

Each of the different regions of marine environments has a unique set of habitats. Among these regions, the coastal region, which includes intertidal and subtidal areas on and above the continental shelf (at a depth of 200 m) and immediately adjacent to land, shows maximum habitat variation like coral reefs, mangroves, tidal wetlands, sea grass beds, barrier islands, estuaries, peat swamps, and a variety of other habitats (Angel, 1993; Levinton, 2021).

Intertidal zone

The coastal region includes intertidal and subtidal areas on and above the continental shelf (at a depth of 200 m) and immediate adjacent lands. Marine biodiversity is higher along coasts than in the open ocean since there is a greater range of habitats near the coast (Gray, 2001). The intertidal region is the transitional area from land to sea, and although it contributes to a very small part of the oceanic environment, it presents enormous diversity and richness of marine plants and invertebrate communities, along with a few bird species and inshore fish species (Lalli and Parsons, 2012). This region shows maximum habitat variation, like coral reefs, mangroves, tidal wetlands, seagrass beds, barrier islands, estuaries, peat swamps, and a variety of other habitats. This is due to the fact that the marine fauna originated in benthic sediments. The terms intertidal and littoral are synonyms for the coastal region that is periodically exposed to air by falling tides and rising submerged water levels. The intertidal region shows various distinctive ecosystems like rocky shores, sandy beaches, and mudflats, each of which supports specially adapted species to survive in the region. Out of these various habitats, the rocky intertidal area supports rich epifaunal diversity (Lalli and Parsons, 2012).

Intertidal organisms are adapted to harsh extremes and have developed special adaptations that allow them to survive in such fluctuating environments and physical stresses as temperature fluctuation, aerial exposure, salinity, and hydrodynamic forces. Water becomes available due to tidal action, but salinity can range from very low during the monsoon due to the accumulation of fresh water from rain to extremely high during the summer due to the evaporation of water and dry salt accumulation with drying between tidal inundations. The action of waves can dislodge residents in the littoral zone. With the intertidal

zone's high exposure to the sun, the temperature can range from extremely hot with full sun to near freezing in colder climates (Davenport and Davenport, 2005). Instead of being harsh environment to survive, the intertidal zone presents high diversity of organisms as high amount of nutrient influx takes place from land and sunlight penetrates evenly in the shallow waters, allowing certain organisms to flourish at the bottom, including plants, seaweeds and corals. These organisms further provide shelter and food to other life forms. Also, the regularly incoming tides bring a fresh supply of oxygen, planktons and other nutrients to the intertidal zone (Nugroho et al., 2020).

Intertidal zonation

Organisms in the intertidal region are grouped in distinctive bands, where some species reside high in the intertidal region while others are grouped at the lower intertidal mark. Such a type of zone patterning is visible among all the rocky shore communities, however, in the pattern of zonation, the species composition of subzones may vary depending upon geographical location, tidal range, aerial exposure, wave action pattern, and so on. In the earliest attempt, zonation was based on the most abundant organisms present in the particular regions. And therefore, Audouin and Milne-Edwards (1832), who probably were the first to classify both the plant and animal zones, recognised four principal zones, which were: a balanoid zone (a zone of top-shells), limpets and dogwhelks zone, a coralline zone, and a laminarian zone. For detailed studies of zonation, the upper and lower limits of the most abundant plants and animals have been related by surveying methods to the tidal constants and to a fixed measure on land (Johnson and York, 1915; Johnson and Skutch, 1928). The method is useful for the calculation of the time spent by an organism under water or exposed to the air. Stephenson and Stephenson (1949) proposed a general scheme for the zonation of marine organisms on rocky coasts, which they considered to have worldwide application. Vertical zonation is the most important process or phenomenon observed in the intertidal zone, in which organisms are distributed into specific belts or zones from the upper intertidal to the lower intertidal zone, each of which is characterised by distinct features of its own (Stephenson and Stephenson, 1949; Ellis, 2003). According to this scheme

of zonation, the intertidal region was basically subdivided into three zones: the Littorina zone (or supralittoral fringe), the Balanoid zone (or midlittoral fringe) and the sublittoral fringe (or infralittoral fringe). Zonation is a very sensitive phenomenon that responds immediately to the slightest changes in the amount, form, and strength of the wave action to which rocky faces may get exposed. Other factors, like the slightest shade or the slightest more sun, a difference in the slope of a rock or other such types of changes, can affect the zonation in their own way (Stephenson and Stephenson, 1949). However, this zonation scheme was complicated as in various parts of the world's coastal regions, there are enormous variations in the tidal range and behaviour, along with the degree of wave action occurrence. Therefore, it cannot be expected to have same zones in their simple form such that they can be so obvious on a first inspection of the coast (Cranwell and Moore, 1938; Stephenson and Stephenson, 1949). Lately, Snively (1978) gave the best zonation model, which divided the intertidal region into four zones from highest to lowest as follows: the spray zone, the high tide zone, the middle tide zone, and the low tide zone.

Spray zone (upper littoral): This subzone outlines the stretch above high tide. It is the highest reaches of the intertidal region, where wave splashes are felt only during the strongest winter storms at high tides; otherwise, this zone remains more terrestrial and dry except for rain. The zone is mostly influenced by heat, light, and fresh water. Organisms residing in this region include limpets, other gastropods, and barnacles (Figure 3) (Stephenson and Stephenson, 1949).

High intertidal zone: This subzone is situated just below the spray zone, which is waterlogged only during high tides. This zone is influenced by the heat, wind, and sunlight as well as the water cover and salt content. Since the abundance of water is not very high for a large amount of marine diversity to flourish, only those organisms can survive that have specific adaptations to tolerate high temperatures. Organisms that are predominantly found in this subregion are green algae, anemones, chitons, mussels, snails, whelks, barnacles, isopods, crabs, sea stars, brittle stars, and some marine vegetation. Another very interesting organism that is found in this subregion are the hermit crabs. Their successful survival in the harsh conditions of the subregion is made possible by

their behavioural adaptation of occupying empty shells as their portable home. Hermit crabs have evolved this behavioural adaptation, which functions excellently in protecting them from desiccation due to the water present in their occupied shell. Subsequently, hermit crabs are found more commonly as compared to common crabs in the high tide zone. Due to the availability of regular water, organisms here flourish much more than in the spray zone (Figure 3) (Stephenson and Stephenson, 1949).

Middle intertidal zone: This subzone is the part of the seashore that is submerged and flooded by the semi-daily tides twice a day, allowing periodic exposure to air. Temperature affects this region less because of the short time exposure to direct sunlight, and salinity is also just slightly above the oceanic level. Consequently, the wave action in this subregion is generally more extreme as compared to the high tide and spray zones. As a result of the regular availability of water, this region generally has a higher population of marine vegetation, especially seaweeds. Comparatively, in this subzone, more complex and larger organisms can be found. Here, the diversity of organisms includes barnacles, anemones, chitons, crabs, isopods, limpets, mussels, sea lettuce, sea palms, sea stars, snails, sponges, whelks, and green algae. Rock pools can also serve as a favourable habitat for some small fish, shrimp, krill, sea urchins, and zooplankton. Along with being more populated, the subzone possesses a greater diversity of organisms as compared to the high tide and splash zones (Figure 3) (Stephenson and Stephenson, 1949).

Low intertidal zone: This subzone is almost always covered with seawater and exposed to air only at the lowest low tides and for a longer period of time at the lowest low tides. The subzone is comparatively more stable since the temperature and salinity of the water do not fluctuate more. This area is flourishing with a variety of life forms and a significantly greater variety of marine vegetation, which is the most distinct characteristic of this subzone. Along with this, it also sustains a great biodiversity of other organisms, including abalone, anemones, chitons, crabs, hydroids, isopods, limpets, mussels, nudibranchs, sculpins, sea cucumber, sea lettuce, sea palms, sea stars, sea urchins, shrimp, snails, sponges, surf grass, tube worms, green algae, and brown

seaweed. Organisms in this region mostly don't need not to adapt for exposure to longer periods of dryness and desiccating temperatures. As this subzone has more energy in its localised ecosystem, creatures in this area can grow comparatively larger. Also, the water coverage is greater in this region, while it is shallow enough to allow plenty of light to carry out photosynthesis. The salinity in this subregion remains almost constant as compared to the other zones, and therefore the marine vegetation can also grow to much greater sizes. As this subregion is still shallow, it provides protection from large predators like larger fish (Figure 3) (Stephenson and Stephenson, 1949).

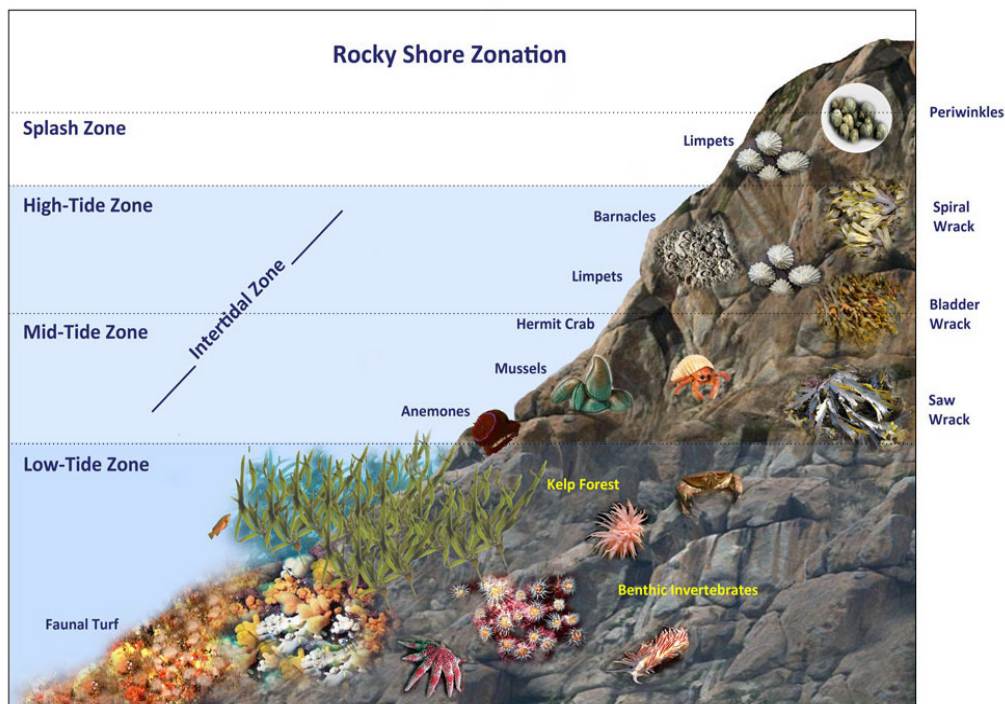


Figure 3. Intertidal zonation pattern showing intertidal distribution of marine organisms. (image source: hoopmanscience.pbworks)

It is often believed that zonation is a result of wave action, but that is not always true. Zonation can even occur in static water bodies, such as lakes and ponds, where there is no tidal action. The chief cause of zonation is the presence of an interface between air and water. Below the water's surface, light penetrates in a gradient fashion, influenced further by other gradients such as changes in sedimentation with increasing depth. Above the water level, zonation is controlled by the degree to which surrounding rock surfaces are exposed to certain parameters like water spray, moisture formed by evaporation, etc.

Therefore, it can be believed that tides are not the sole reason for zonation, but they can strengthen the pattern of zonation, making it more marked (Stephenson and Stephenson, 1949). On the other hand, Doty (1957) believed that although factors like temperature, wind, rain, and waves might have some effect on zonation, only tidal variation has profound effects on biological zonation. Zonation does vary with time and topography, and therefore the listing of zones as above is only for the convenience in order to understand the complex biological circumstances that are not outlined by exact boundaries.

For survival in different regions of the intertidal zone, organisms develop special types of adaptations. For the majority of intertidal species, there is a general correlation between physical tolerance and shore position (Palumbi et al., 2019). Organisms residing in the spray zone or upper intertidal region, which receives water only during the highest high tide, face desiccation as the major limiting factor. Temperature, wind, and humidity are the three major environmental factors that contribute to desiccation, and these factors can alter rapidly. Therefore, several organisms residing in this zone, like barnacles and bivalves, close their shells tightly to retain moisture, while certain organisms that crawl or walk occupy crevices and cracks to protect themselves from overexposure to heat (Newell, 1979). While moving further to the lower shores, competition becomes a major limiting factor. Here in the lower intertidal zone, competition can be for space, food, light, shelter, etc. Obtaining a suitable microhabitat becomes challenging as a result of the high density of organisms, which leads to inter- and intra-specific competition for suitable resources (Wetthey, 1983). Also, the rate of predation increases in the lower intertidal region as compared to the spray zone and the upper intertidal region. Differences in community structure over geographical space have long been a major concern for ecologists. Though variations in species diversity are perhaps the most striking differences and have certainly received the most attention, other aspects of community structure, including space utilisation patterns, species composition, trophic structure, and body size structure, can also vary.

Crustaceans and Other Decapoda

The invertebrate phylum Arthropoda is derived from the Greek words “arthron” meaning joint, and “pod” meaning appendage, which is one of their key characteristic features as a phylum. Arthropoda is the most diverse phylum, which roughly constitutes about 1.2 million species of all living species in the world’s terrestrial and marine environments out of approximately 1.8–2.0 million known species (Bouchet, 2006). Arthropods are well adapted to all ecosystems and play an important role in the food chain and food web. Arthropods are predated by several consumers, like amphibians, fish, reptiles, birds, and mammals (Sanchez-Contreras and Vlisidou, 2008). Crustacea is a subphylum that comes under the phylum Arthropoda and represents a highly diverse group of marine organisms in terms of morphology, physiology, life history, and ecological adaptation (Martin and Davis, 2001). Global diversity of crustacean species comprises around 67,000 species (Ahyong et al., 2011), which places them in the fourth position in terms of overall species diversity (Martin and Davis, 2001). The morphological diversity among crustaceans is remarkable, and it is believed to be even greater than the diversity of insects. The group includes marine organisms like crabs, lobsters, crayfish, shrimp, prawns, krill, woodlice, and barnacles. Crustaceans originated about 500 million years ago during the Precambrian period and have undergone dynamic species radiation, occupying various aquatic habitats in the ecosystem (Zhang et al., 2007). As a result of this, today these organisms are found in a wide variety of habitats, including marine, limnic, and terrestrial regions ranging from the deepest part of the oceans to the high mountain regions and from the Polar Regions to the tropics (Vogt et al., 2018). The Crustacean adult forms range in size from one tenth of a millimetre in maximum diameter (a tantulocarid parasite) to four metres across (a Japanese king crab), with their maximum ages ranging from a few days to more than 70 years (Vogt, 2012).

Crustaceans play a vital role in supporting aquatic ecosystems. The planktonic forms, like some copepods and krills, feed upon the microscopic plants floating in the sea. Intern these planktons are consumed by other larger fish, seabirds, or whales, and in this way supporting the food web. Crabs play an

important role as predators, and the continuing struggle among them and their prey leads to the acquisition of new adaptations. For example, the massively ornamented shells of marine gastropods are thought to be protective against the predatory activities of crabs, which in turn develop larger and more powerful pincers. Besides that, crustaceans can be parasitic, where they parasitize a wide range of other aquatic animals, ranging from sea anemones to whales and even other larger crustaceans (Boxshall and Hayes, 2019).

Decapoda Latreille, 1802, is just an order of the superorder Eucaridæ in the subclass Eumalacostraca of the class Malacostraca of the subphylum Crustacea (Poore, 2004), which are also called the insects of the sea. While insects are diverse and common on land, decapods are diverse and common in the marine habitats. It is the most species-rich, diverse, visible, popular, and economically important group of all crustaceans (Abele, 1974). Recently, the decapod diversity was estimated at around 14,756 species (2,725 genera) living, while the fossil species stood at 3,300 species (De Grave et al., 2009). It includes some popular organisms such as shrimps, lobsters, freshwater crayfish, hermit crabs, and “true” crabs, some of which support seafood and marine industries worth billions of dollars each year to the world’s economy (Shen et al., 2013). Decapod crustaceans are important members of tropical benthic communities. The greatest diversity of Decapoda is observed in the shallow waters; however, a few species have been reported from 5000–6000 m of depth too. Besides the fact that the largest and most abundant species are used as food sources for human consumption, they also contribute to the size, complexity, and functioning of ecosystems. Every marine habitat includes major predatory species of decapod crustaceans that play an important role in regulating the trophic relationships of benthic communities, while the smaller species provide a food base for other marine creatures (Hendrickx and Harvey, 1999). Many species are scavengers, while a few are filter feeders. Consequently, this is a promising study group, as the establishment of these animals in such habitats derives from the evolution of adaptive population strategies (Mantelatto and Sousa, 2000). Order Decapoda consists of the following infraorders: **Stenopodidea** Bate, 1888; **Caridea** Dana, 1852; **Astacidea** Latreille, 1802; **Glypheidea** Winkler, 1883; **Axiidea** de Saint Laurent, 1979; **Gebiidea** de Saint Laurent, 1979; **Achelata** Scholtz and Richter,

1995; **Polychelida** Scholtz and Richter, 1995; **Brachyura** Linnaeus, 1758 and **Anomura** MacLeay, 1838 (De Grave et al., 2009).

The infraorder Anomura represents a highly diverse group of decapod crustaceans, which includes hermit crabs, mole crabs, king crabs, squat lobsters, and porcelain crabs (Bracken-Grissom et al., 2013). They can be easily distinguished by their morphological characteristics, which include having their last thoracic plate free from the carapace on the ventral side, the fifth pair of pereopods (walking legs) greatly reduced such that only the previous four pairs are visible, as well as having their second antennae (antennule) placed just outside the eyestalks. The fossil record of nearly all extant families proves their existence from the Norian/Rhaetian period (late Triassic) (Chablais et al., 2011) to the Holocene period. They are found inhabiting a variety of ecosystems, which include freshwater, anchialine caves, terrestrial habitats, and hydrothermal vent habitats. They can also be found from the oceanic surface waters to great depths of more than 5000 m (Macpherson and Segonzac, 2005). The morphological and ecological diversity of anomurans is of significant scientific interest. They also represent a vital economic commodity, as is obvious in the major commercial fisheries, which include some king crab and squat lobster genera (Dawson, 1989; Lovrich, 1997; Wehrtmann and Acuna, 2011) and the common use of hermit crabs as pets in the aquarium trade. As currently defined, extant Anomura contains seven superfamilies, 23 families, 242 genera, and more than 3300 species (Baba et al., 2008; De Grave et al., 2009; Ahyong et al., 2010; Boyko and McLaughlin, 2010; McLaughlin et al., 2010; Osawa and McLaughlin, 2010; Schnabel and Ahyong et al., 2010; WoRMS, 2022). However, these numbers may increase as a result of subsequent descriptive studies. Although the monophyly of Anomura is widely accepted (Porter et al., 2005; Tsang et al., 2008), the explanation of internal relationships among families, genera, and species using modern methods is dynamic and under constant debate (McLaughlin et al., 2007; Lemaitre and McLaughlin, 2009; McLaughlin and Lemaitre, 2009; Ahyong et al., 2010; Schnabel and Ahyong et al., 2010; Tsang et al., 2011; Bracken-Grissom et al., 2013).

The ecology of most organisms involves a set of complex interdependencies where a given species is generally reliant upon the resources produced by one or more other species. One such example of ecological reliance is best presented by hermit crabs (Laidre, 2011). Hermit crabs are an interesting group of crabs known for their unique behavioural adaptations among the various Anomura groups. They are the most successful group of marine organisms found in the intertidal zone, as they have evolved both their biology and behaviour in order to match their habitat characteristics. Hermit crabs are decapod crustaceans, most of which lack a calcified pleon, and hence they require protection from physical factors like desiccation and biological factors like predation (Reese, 1969; Williams and McDermott, 2004). In order to obtain protection by building their own hard exoskeleton, these crustaceans generally occupy empty gastropod shells or pseudoshells, which are generally termed as "portable homes," which serve as protection from both desiccation and predation. It is a behavioural adaptation that is classified as a form of animal tool use (Beck, 1980). Along with that, the asymmetrical twisting of a hermit crab's pleon is especially suitable for shell occupation. The occupied shells seem to satisfy a variety of essential survival and reproductive functions for hermits, including prevention from desiccation, protection against parasites and predators, and shelter from abrasive sand and other environmental stresses (Vance, 1972; Hazlett, 1981; Lancaster, 1988a).

The hermit crab's body can be majorly divided into two morphological parts: the cephalothorax and abdomen. The cephalothorax is formed by the fusion of the head and thorax of the crab. The carapace is partially or completely calcified and is formed by branchiostegites. The shield is a calcified structure that is delineated laterally and posteriorly by the cervical groove. The appendages in the cephalothoracic region include a pair of antennae, antennules, ocular peduncles, and five pairs of legs (McLaughlin et al., 2007). Antennules possess a series of chemoreceptive setae (Snow, 1973) that are used by the hermit crab to sense taste and smell. The antenna possesses a five-segmented peduncle and a long; sometimes setate antennal flagellum originating from the distal terminal part of the fifth peduncular segment. Antennae serve the functions of touch and feel-sensing. The mouth parts of hermit crabs are formed by three paired

thoracic appendages, viz., mandibles, maxillules, and maxillae (McLaughlin et al., 2007). The abdominal appendages are called pleopods. The numbers of these pleopods may vary from species to species of the hermit crab. As compared to males, the pleopods are well developed in females, as they are used for the purpose of holding the egg mass (Alcock, 1905). Furthermore, these pleopods are commonly used by both the sexes for the purpose of holding the occupied shell so that they cannot be dragged out by the predators easily (Figure 4).

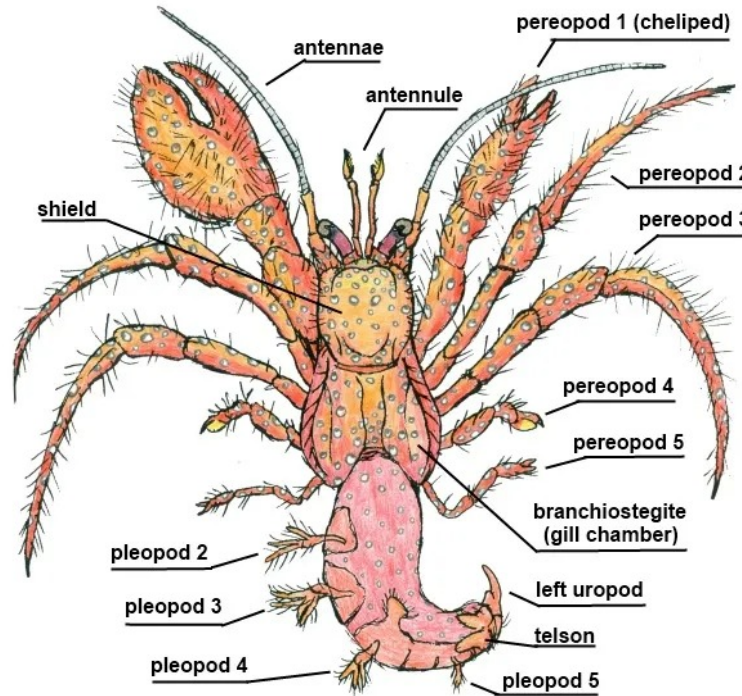


Figure 4. External morphology of hermit crab. (Source: https://la-france-qui-bosse.com/wear_rm)

Hermit crabs are represented by approximately 2002 described species worldwide (Appeltans et al., 2012). They are uniquely different from other macrobenthic fauna for their dependence on empty gastropod shells or pseudoshells in order to protect their soft abdomen (Reese, 1969), which they are generally unable to procure from living gastropods with some exceptions (Randall, 1964; Rutherford, 1977). Hermit crabs are best known from intertidal areas, where they are conspicuous and ecologically important scavengers and predators (Whitman et al., 2001). They are distributed throughout the tropical, subtropical, and temperate seas, occupying semi-terrestrial to abyssal habitats (Rahayu et al., 2008).

Hermit crabs are common inhabitants of intertidal habitats such as rocky shores, mangroves, and mudflat areas, where they can occur in high abundance. For hermit crabs, intertidal habitats are favourable as there is continuous replenishment of detritus as a food source and refuge from specialised predators (Reese, 1969). To exploit these advantages, hermit crabs may also employ behavioural adaptations against desiccation (Reese, 1969; Bertness, 1981a; Taylor, 1981; Turra and Leite, 2000). A small percentage of hermit crabs use bivalve and scaphopod shells, hollowed cylinders of wood (Forest, 1987; Lemaitre, 1995; McLaughlin and Lemaitre, 1997), or hollowed-out fragments of stone (Pope, 1953; Mayo, 1973), while others live in immobile domiciles provided by calcareous tubes of polychaetes or vermetid gastropods (Gherardi and Cassidy, 1994; Gherardi, 1996; Rodrigues et al., 2000), corals (McLaughlin and Lemaitre, 1993), or sponges (Forest, 1987). Some, such as the fully calcified coconut crab, *Birgus latro* (Linnaeus, 1767), exist without a shell for most of their terrestrial lives, although shells are utilised by its megalopa and young crabs (Reese, 1968; Greenaway, 2003). Hermit crabs, on a worldwide basis, influence a whole community of associates in habitats ranging from terrestrial to the deep sea. And therefore, it is believed that hermit crabs are allogenic engineers that transform "living or non-living materials from one physical state to another." (Jones et al., 1997). Apart from their role as allogenic engineers, they play an important ecological role in the marine ecosystem. Understanding the ecology of these marine organisms can strengthen our understanding of the marine ecosystem as well as the effects of changing environments and anthropogenic pressure.

Hermit crabs are one of the most ecologically important and easily recognisable invertebrates inhabiting intertidal and subtidal habitats (Schembri, 1982). They generally act as active scavengers, and most of them are omnivores, feeding on organic matter and helping in the recycling of nutrients, which suggests that they are a very crucial part of the food web. They provide a food base for a variety of other organisms. Smaller individuals are consumed by other larger crustaceans, fishes, and birds, while some terrestrial hermit crabs, like the coconut crab or robber crab from the family Coenobitidae, are consumed by humans. Few species are used as pets in aquariums, while some other species

are used as bait. Almost all aspects of the biology of hermit crabs are greatly influenced by their strong association with their adopted gastropod shells. Not so surprisingly, the majority of biological studies of hermit crabs are focused on their association with gastropod shells. Even studies on their behaviour ecology, which are primarily concerned with shell occupation, indicate that shell selection and shell exchange are unquestionably shelter-related (Hazlett, 1981). Also, the visual display mechanisms used by the crabs are somehow directly or indirectly associated with the distribution of the shell resource (Hazlett, 1966, 1974). Hazlett (1981) suggests that most of the ecological studies on hermit crabs are focused on their interaction with gastropod shells, and comparatively very little work has been carried out on the hermit crab as a component of marine ecosystems.

Around 2934 crustacean species have been reported from India (Venkataraman and Wafar, 2005), with the number steadily increasing as new records and species are discovered. Recently, a few groups of scientists have started preparing a taxonomically valid checklist of Indian crustaceans, revealing the Indian diversity as follows: 231 species of anomuran crabs (58 genera, 15 families and 05 superfamilies) (Patel et al., 2022a), 144 species of barnacles (75 genera, 19 families) (Trivedi et al., 2021), 72 species of stomatopods (35 genera, 10 families and 5 superfamilies) (Trivedi et al., 2020), 910 species of brachyuran crabs (361 genera and 62 families) (Trivedi et al., 2018), and 437 species of prawn (30 families and 131 genera) (Radhakrishnan et al., 2012). The hermit crab fauna of Indian waters is one of the most scarcely studied groups of decapod crustaceans. Total 115 species (26 genera) of hermit crab are reported from Indian waters (Trivedi and Vachhrajani, 2017; Patel et al., 2022a) out of which maximum species belongs to family Diogenidae (81 species, 11 genera) followed by Paguridae (20 species, 7 genera), Parapaguridae (6 species, 3 genera), Coenobitidae (6 species, 2 genera) and Pylochelidae (2 species, 2 genera).

Genus *Clibanarius* Dana, 1852, comes under the family Diogenidae of the superfamily Paguroidea of infraorder Anomura, which currently comprises 60 species worldwide (McLaughlin et al., 2010). The species of the genus *Clibanarius*

are mainly found in various types of tropical or subtropical intertidal habitats, including mangrove forests, coral reefs, rocky substratum, sand and mud flats, etc. (Southward and Southward, 1977; Hirose et al., 2010; Ismail, 2010). Also, a species of *Clibanarius fonticola* is the only hermit crab species found in a completely freshwater habitat (McLaughlin and Murray, 1990). In India, taxonomic studies suggest that the genus *Clibanarius* represents one of the diverse genera of hermit crabs, comprising 18 species, of which 11 are found on the coast of Gujarat (Trivedi and Vachhrajani, 2017; Patel et al., 2020a, 2022a). Although *Clibanarius* is one of the most commonly occurring genera, there is currently very little information available regarding the ecology of hermit crabs as a result of a lack of ecological studies focused on hermit crabs.

REVIEW OF LITERATURE

Before the current research effort began, several studies and specific topics were examined with the help of a survey of related literature. Because of their unique behavioural adaptations, hermit crabs have drawn the attention of many scientists, and they have been the subject of several studies conducted all over the world.

International review

The intertidal zone or the littoral zone are synonyms for the coastal zone, which gets periodically exposed during the low tide time (falling tides) and submerged during the high tide time (rising tides) (Lalli and Parsons, 2012). The intertidal regions mark the transition from land to sea, and although they make up only a very small part of the total world ocean, they support rich and diverse communities of marine plants, birds, inshore species of fish, and invertebrates (Lalli and Parsons, 2012). This region represents one of the complex biotic systems that experiences significantly varying physico-chemical conditions and periodically changing habitat, influencing the biotic communities drastically (Stillman and Somero, 2000). Water is available with the tides on a regular basis, but it varies from less saline with rain to highly saline and dry salt with drying between tidal inundations. Moreover, the action of waves can dislodge residents in the littoral zone. With the intertidal zone's high exposure to the sun, the temperature ranges from very hot with full sun to near freezing in colder climates. Organisms in the intertidal zones are adapted to such an ever-changing environment of harsh extremes. Adaptation in the littoral zone is for making use of nutrients delivered in large quantities from the sea on a regular basis, which are actively moved to the zone by tides (Rebach, 1974; Taylor, 1981; Barnes, 2002; Turra and Denadai, 2003).

Microenvironments found on the rocky shores, including cracks, crevices, exposed areas, and tide pools, facilitate a great proliferation of species (Benedetti, 2001). In the earliest attempts to describe zonation, it was usual to name the zones after the most prominent or most abundant organism present. Thus, Audouin and Milne-Edwards (1832), who appear to have been the first to

classify the intertidal zone on the basis of the presence of dominant plants and animals. The intertidal zone can be divided into three major zones: the upper intertidal, the middle intertidal, and the low intertidal, which vary in terms of organism availability. It is observable that the upper limit is usually determined by physical factors (temperature, desiccation, modes of transportation, etc.), while the lower limit is usually determined by biological factors (competition and predation) (Reese, 1969; Williams and McDermott, 2004). Due to the different zonation patterns, it can harbour different types of organisms (Tomanek and Helmuth, 2002).

Hermit crabs constitute one of the most visible groups of organisms successfully and efficiently flourishing in the intertidal environment. They can do so as a result of their behavioural adaptation, which includes the use of shells, which enables them to thrive in the intertidal habitat (Reese, 1969). As hermit crabs are scavengers and feed upon detritus matter (Bolt, 1961; Roberts, 1968), the intertidal waves continuously replenish the organic material and provide a continuous source of food for them. They have also adapted for reproduction as well as movement in the littoral region, which eased their successful exploitation of the intertidal habitat. Generally, the factors that affect the distribution of a species in turn also affect its abundance in the same manner (Brown, 1984). The distribution of hermit crabs in the intertidal region is also governed by the complex interaction of biotic and abiotic factors. Species membership and geographical location determine the macro-environment and distributional pattern, while photoperiod, migration, aggregation, and dispersal interact to determine the micro-distribution within the larger, overall pattern. Of course, physiological tolerances to environmental extremes of temperature, salinity, and desiccation are of great importance, especially in those species and environments where the extreme conditions cannot be avoided or lessened by behaviour (Reese, 1969).

During his study on the distribution pattern of hermit crabs in the intertidal and subtidal zones, Barnes (1997) found that the highest numbers of species were occurring in the lower shore as compared to other zones. Vance (1972) and Kellogg (1977) have carried out one of the most detailed studies on

the resource partitioning by the hermit crab populations. In a study carried out on the coexistence of three sympatric species of intertidal hermit crabs, Vance (1972) observed that the species were occupying different habitats, which probably played an important role in the coexistence of the sympatric species. On the other hand, Kellogg (1977) studied habitat partitioning and also carried out substrate selection experiments. However, he did not quantify the habitat partitioning in the field, and the sample size for his study was very small. Studies suggest that habitat partitioning, a mechanism important to reduce inter- or intra-specific competition for common resources, governs the zonal segregation of hermit crab species along the intertidal region (Abrams, 1980, 1987a, b; Bertness, 1981a). Subsequently, species that inhabit the same habitat occupy varying microhabitats, which leads to separation in their finer distribution (Abrams, 1980; Bertness, 1981b).

The differences in the spatial distributions may also be the result of differential resistance of the species to predation (more intense in the lower fringe) and physical stress (which mostly affects the upper fringe) (Bertness, 1981a). Upper intertidal species are more exposed to desiccation risks; among them, species of the genus *Clibanarius* survive dehydration longer than species of *Calcinus* (Gherardi, 1990). Second, the supply of empty snail shells may vary (or be the same) between crab species sharing (or not sharing) the same general habitat due to the differential mobility of hermit species (Kellogg, 1977) and abiotic forces that move empty shells (Hazlett, 1981). A third concern is that hermit crab habitat segregation patterns can be the product of differences in larval settlement (Nyblade, 1974). A single intertidal species can produce enough larvae to saturate the shell supply of a given habitat (e.g., the upper intertidal) and thus cause the settling preferences of the other hermit crab species to shift away from there (Abrams et al., 1986). Thus, when studying competition between resource consumers, attention should be directed towards both the movement patterns of hermit crab species and the population biology and dynamics of the resource (Abrams, 1980), two points that have often been neglected.

The life history of hermit crabs consists of a free-swimming larval stage with a duration of several weeks to several months (Nyblade, 1974) and an adult stage, which may last many years. As adults, hermit crabs are almost always found inhabiting gastropod shells. These shells become available when the resident snail dies. The shell appears to protect the crab's soft abdomen from predators (Reese, 1969; Vance, 1972), helps prevent desiccation in the intertidal environment (Reese, 1969), protects the female's eggs before the larvae are hatched (Fotheringham, 1976a), and is an essential part of the sexual behaviour of most species (Hazlett, 1966). In common with other decapod crustaceans, hermit crabs undergo a planktonic larval (zoea) stage, which becomes a megalopa (glaucothoe) after several molts, settles, and metamorphoses into the benthic adult crab. Hermit crabs inhabit a wide range of environments, from polar to tropical seas and from supratidal to deep ocean canyons. They play important roles as predators, scavengers, detritivores, and even filter-feeders (Schembri, 1982), and their manifold symbioses can enrich the biodiversity of their habitats today and probably in the past (Reiss et al., 2003).

Gastropod shells are an indispensable resource for hermit crabs (Asakura, 1991). The empty shells are likely to be buried in the substratum unless they are used by hermit crabs (Stachowitsch, 1977; Creed, 2000; Pretterebner et al., 2012). Hermit crabs are therefore often termed "ecosystem engineers," because by using gastropod shells, they affect the abundance and distribution of other invertebrates (Jones et al., 1994; Gutierrez et al., 2003; Williams and McDermott, 2004; Pretterebner et al., 2012). The connection between hermit crabs and shells affects almost all aspects of their biology (Hazlett, 1981), including their growth, survival, and fecundity. Shell volume (Bertness, 1980), colour (Partridge, 1980), weight (Reese, 1996), and species (Elwood et al., 1979) have been shown to be related to preferences (Rodrigues et al., 2000).

The majority of the time, populations are exposed to special environmental forces that force them to diverge from one another and display distinct gene frequencies that are maintained through geographic isolation from other populations. Thus, populations serve as a reflection of the limitations imposed by the environment to which they are exposed. Studies that allow for

comparisons among these groups are carried out to understand how various environmental factors affect them (Turra and Leite, 2000). Population studies have mostly concentrated on describing them. Most of the research usually addresses issues with recruitment, dispersion, density, sex ratio, sexual dimorphism, and sexual behaviour. Species that live with one another may respond to environmental factors similarly, yet cohabitation and subsequent competitive exclusion may have the reverse effect (Bach et al., 1976). For hermit crabs exposed to various shell supplies, Bertness (1981a) described the adaptability in population biology.

Predation (Paine, 1966; Connell, 1970; Janzen, 1970), physical stress (Andrewartha and Birch, 1954; Wolcott, 1973), disturbance (Connell, 1978), and competition (Grinnell, 1917; Hutchinson, 1957; Mac Arthur, 1958; Gause, 2019) have all been proposed as the major aspects regulating the distribution and abundance of populations as well as the structure of plant and animal communities. However, several studies have shown the significance of how these factors together impact populations and communities (Connell, 1961; Dayton, 1971; Menge, 1976; Buss and Jackson, 1979). Most ecological theory makes the assumption that a species comprises individuals with similar characteristics or whose characteristics are influenced by size or age. However, there are notable discrepancies in the ecological functions played by male and female individuals in many species. Such gender-wise variations may be significant in defining both the nature of interspecies interactions as well as population management within a species (Abrams, 1988).

Studies on the population structure of hermit crabs have been well described by some researchers (Markham, 1968; Ameyaw-Akumfi, 1975; Fotheringham, 1975; Bertness, 1981a, b; Gherardi, 1991; Negreiros-Fransozo and Fransozo, 1992; Gandolfi, 1996; Turra and Leite, 1999). In general, they have suggested that in population males mostly attain larger sizes as compared to females as a result of which the sex ratio in smaller and intermediate sizes is generally skewed for females whereas it is skewed for males in larger sizes (Bertini and Fransozo, 2000; Garcia and Mantellato, 2001). Factors responsible for such an unequal sex ratio can probably be attributed to differential mortality

and growth rates between sexes, migrations, or a faster growth rate of males in relation to females (Wenner, 1972). Females have lower growth rates than males due to the use of inadequate shells and a higher energy allocation to reproduction (Markham, 1968; Abrams, 1988). Also, the search for and utilisation of shells is a major adaptation for hermit crabs, which influences the population size, with one sex (generally males) being more successful in obtaining the shells (Bertness, 1981b).

Numerous studies have been conducted in both the field and laboratory on various biological aspects of hermit crabs, mostly focusing on behaviour, including the usage of gastropod shells and habitat preference (Garcia and Mantelatto, 2001). However, studies on the reproductive biology of hermit crabs started in recent years only (Bertini and Fransozo, 2000; Turra and Leite, 2000), which suggests that hermit crabs may show a seasonal or continuous pattern of reproduction and may exhibit sexual dimorphism, with males on average being larger than females (Mantelatto and Garcia, 2000; Mantelatto and Martinelli, 2001), which may provide an advantage in competition for resources. Female-biased local populations of intertidal and shallow water hermit crabs have often been reported (Ameyaw-Akumfi, 1975; Fotheringham, 1975; Abrams et al., 1986; Asakura, 1987, 1992; Abrams, 1988; Lowery and Nelson, 1988; Murata et al., 1988; Hazlett, 1989) whereas even or male-biased populations have rarely been reported (Fotheringham, 1980; Asakura, 1987; Johnson and Ebersole, 1989). It has been discovered that the availability and abundance of gastropod shells used by hermit crabs have a significant impact on their reproductive activity. Additionally, reproductive peaks might differ across populations in response to interspecies competition, shell availability, and the response of the hermit crab population to environmental conditions of the habitat (Reese, 1968; Ameyaw-Akumfi, 1975; Fotheringham, 1976a).

Despite high diversity, the reproductive biology of hermit crabs is still poorly known, although there are many studies on different biological aspects, mostly related to behavioural characteristics such as use of gastropod shells and habitat selection (Tunberg et al., 1994; Barnes, 1999; Mantelatto and Garcia, 1999; Turra and Leite, 2001; Litulo, 2007). However, according to Litulo (2005b)

studies on the reproductive biology of hermit crabs have only been conducted for species found in Europe (Carlson and Ebersole, 1995; Manjón-Cabeza and Garcia-Raso, 1998; Pessani et al., 2000; Macpherson and Raventos, 2004) and the South American region (Fransozo and Mantelatto, 1998; Bertini and Fransozo, 2000; Turra and Leite, 2000; Garcia and Mantelatto, 2001; Branco et al., 2002; Martinelli et al., 2002; Litulo, 2007). Year-round reproductive seasons have been reported in the tropical hermit crab species *Clibanarius zebra*, *Calcinus laevimanus*, and *Calcinus latens* (Reese, 1968), *Clibanarius chapini* and *Clibanarius senegalensis* (Ameyaw-Akumfi, 1975) and *Clibanarius clibanarius* (Varadarajan and Subramoniam, 1982). Among temperate species on the Pacific coast of Northern America, very long reproductive seasons are also known, such as 11 months in *Pagurus armatus* and *Pagurus granosimanus* and 10 months in *Pagurus beringanus* and *Pagurus hirsutiusculus* (Nyblade, 1987). Lancaster (1988) also suggested the occurrence of a year-round reproductive season in the European species, *Pagurus bernhardus*. Between species, differences in reproductive output have been suggested as a mechanism that allows coexistence, with the competitively inferior species balancing the dominant one (Nyblade, 1974).

The global sex ratio of hermit crabs did not differ from the 1:1 ratio, but significant deviations were recorded monthly, with females appearing in larger numbers in relation to males, which is a frequent phenomenon in hermit crabs. Several causes have been postulated for this discrepancy, with the most commonly reported being differences between sexes in longevity and maturation time, differential migration, mortality, and sex reversal (Werner, 1972; Turra and Leite, 2000; Branco et al., 2002; Litulo, 2005b). In hermit crabs, females often tend to be more abundant than males (Werner, 1972; Litulo, 2005a). Turra and Leite (2000) postulate that this trend may be explained by high mortality rates acting on males or by habitat partitioning, differential feeding restrictions, and spatial dispersion between sexes.

Irrespective of their taxonomic group, hermit crabs may reproduce continuously, with or without peaks, or they can confine it to certain species phases (a seasonal pattern) (Manjón-Cabeza and Garcia-Raso, 1998; Macpherson

and Raventos, 2004). Such traits may be seen even in sympatric species (Turra and Leite, 2000; Macpherson and Raventos, 2004). As per Giese (1959), species with extended breeding seasons or continuous breeders could produce a number of successive broods year-round, or they could breed simultaneously, in which case a few individuals are still maturing while others are preparing to spawn, while some others are already doing so, and the remainder have already finished spawning. In tropical and subtropical regions, reproductive patterns may be continuous or seasonal. The limited fluctuations in temperature, precipitation, sunlight, and nutritional supply that affect reproduction and larval development account for this. According to the hypothesis given by Turra and Leite (2000), the existence of seasonal reproductive patterns in tropical waters and continuous reproductive patterns in temperate waters might be dependent on the life histories of the population. When evaluating the reproductive characteristics of a species or population, several elements, including competition, shell usage, and abiotic factors, should be taken into account.

According to Giese (1959), the continuous breeders or species having an extended breeding season may generate numerous consecutive broods throughout the year or they are breeding asynchronously, which means that some individuals are in the earlier stages of their maturation, some other individuals are getting ready for the purpose of spawning, whereas some individuals are already spawning, and the remaining have already spawned. According to Sastry (1983), temperature may function as a metabolic, biochemical, and hormonal modulator, initiating the ecdysis, mating, and gonad growth processes. Oocyte maturation is known to slow down at low temperatures, necessitating a longer incubation time. On the other hand, rain may provide intertidal anomuran populations with a selection advantage since increased rainfall rates may alter the salinity of the water, increase nutrient content, favour planktonic larval development, and boost the primary production of the saltwater (Litulo, 2004).

Regardless of the family they belong to, hermit crabs may exhibit year-round (with or without peaks) or seasonal reproduction patterns (Tunberg et al., 1994; Fransozo and Mantelatto, 1998; Manjon-Cabeza and Garcia-Raso, 1998;

Branco et al., 2002; Macpherson and Raventos, 2004). Hermit crab species in the tropical region breed for extended lengths of time, likely as a result of very low fluctuations in temperature, nutrient input, and rainfall that are believed to be very crucial for breeding and larval development (Litulo, 2004). Although the majority of hermit crab species exhibit seasonal patterns of reproduction, those situated in tropical and subtropical waters exhibit both seasonal and continuous patterns of breeding (Litulo, 2004).

Temporal variation in abundance of individuals in warm waters of tropical and subtropical regions is not marked (Mantelatto and Fransozo, 1999; Turra et al., 2002). Seasonal migration in temperate hermit crabs is reported from intertidal to subtidal areas in the summer to compensate with fluctuating temperatures (Asakura and Kikuchi, 1984; Asakura, 1987). The tropical intertidal and shallow subtidal hermit crabs also undergo seasonal vertical migration from shallow and colder waters to deep and warmer waters during the winter months (Fotheringham, 1975; Rebach, 1978, 1981). This migration is effective in protecting the hermit crabs from freezing air temperatures. Although few species can withstand the usual winters in the littoral zone, the function of seasonal migration is not directly related to the physical characteristics of the littoral zone, since the cold hermit crab will become slow in withdrawing into its shell, which makes it vulnerable to warm-blooded predators such as small mammals or shore birds (Fotheringham, 1975). Migration into deeper water in the reproductive season has been reported in many species (Allen, 1966), including hermit crabs (Kikuchi, 1962; Asakura and Kikuchi, 1984; Asakura, 1987). Many studies have indicated that salinity is readily decreased by rainfall in the upper intertidal zones of rocky shores (Lewis, 1964; Carefoot, 1977; Newell, 1979), and that a lower distribution of female hermit crabs can be an adaptation to avoid low salinity in the upper intertidal area (Abram, 1988; Imazu and Asakura, 1994).

Availability of gastropod shells in different zones can also be another aspect of migration, like larger *Clibanarius vittatus* requires larger gastropod shells, which are available in the sublittoral zone (Fotheringham, 1975). Hermit crabs may have a seasonal (Lowery and Nelson, 1988; Lancaster, 1990; Fransozo

and Mantelatto, 1998; Bertini and Fransozo, 1999) or continuous reproductive pattern (Bertini and Fransozo, 2000; Turra and Leite, 2000). Reproductive season occurs during warmer months in tropical and subtropical regions when the availability of food sources is abundant (Fransozo and Fransozo, 1992). Continuous breeding is very common in tropical waters, but seasonal breeding is an important strategy in temperate and sub-tropical waters (Turra and Leite, 2000). Such a seasonal or continuous pattern is associated with the optimum temperature required for successful breeding (Turra et al., 2002). Despite the large number of studies conducted on the shell preference of hermit crabs, information on the population ecology and intertidal distribution of hermit crabs is scanty and the population biology of these organisms is still poorly known (Litulo, 2005a).

Hermit crabs occupying gastropod shells (Figure 5) not only provide them with motile shelter, but the use of shells also affords micro-climatic conditions that can enhance the hermit crab's physiological tolerance (Reese, 1969). Hermit crabs are generally dependent on empty shells; however, some studies suggest that hermit crabs are capable of removing the live gastropod from their shell and can acquire the shell (Randall, 1964; Rutherford, 1977). However, recent experiments conducted by Laidre (2011) proved that neither marine nor terrestrial crabs are able to remove live gastropods from their shells.

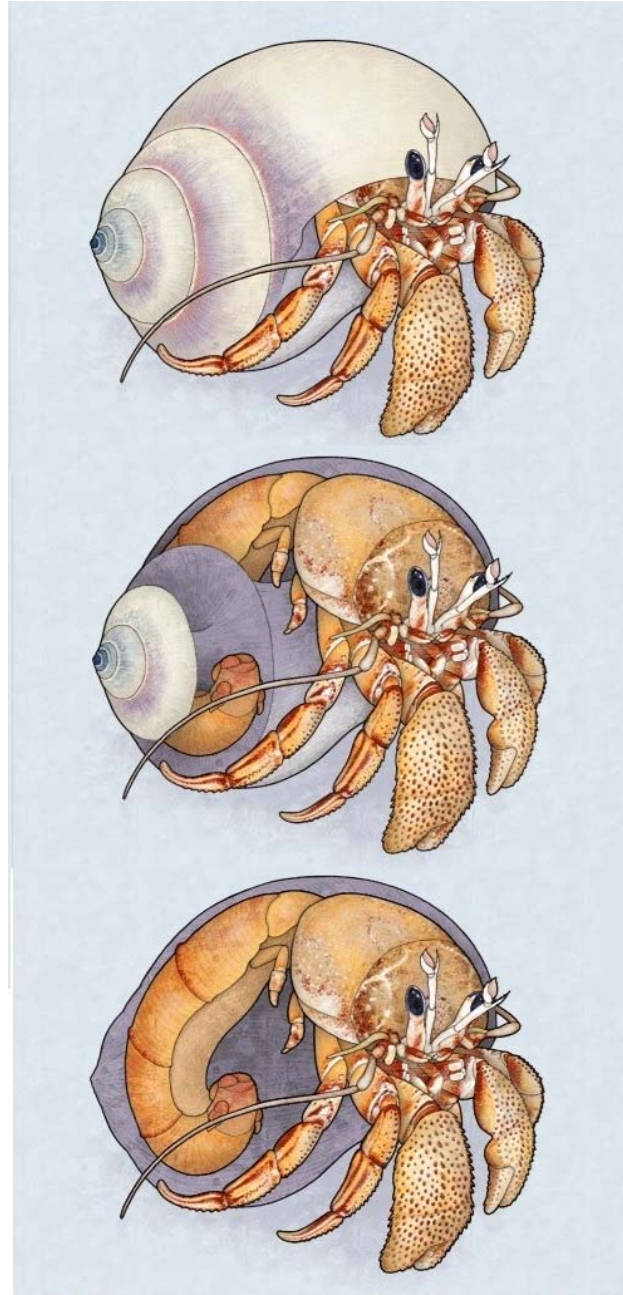


Figure 5. Internal arrangement of hermit crab in an empty gastropod shell.
(Source: www.rkherman.net)

The selection of a proper shell also imparts a role in reproductive success (Childress, 1972; Hazlett, 1989) as well as the energy expenditure for locomotion (Osorno et al., 1998). The preference is given to certain types of shells that can provide them these advantages and enhance their fitness (Markham, 1968). The dependence of hermit crabs on the shells they inhabit has long been a subject of

fascination for ecologists. The selection of gastropod shells is not random and hermit crabs show preferences for certain types of shells that can prove advantageous and increase their fitness (Markham, 1968; Bertness, 1980). Different gastropod shells provide different benefits and disadvantages for hermit crabs. Shell assessment can be based on various morphological aspects such as shell length, shell aperture length, shell aperture width, shell weight, shell volume, hydrodynamic characters, the presence of epibionts, etc. (Bertness, 1981c; Hahn, 1998; Argüelles et al., 2009).

Ideally, a hermit crab continually switches to larger shells as it grows, thereby maintaining a shelter that adequately protects it from predators and provides enough space for a female hermit crab's brood (Childress, 1972; Hazlett, 1981). The ability of hermit crabs to seek out and occupy shells that provide optimal fit is well documented (Scully, 1979; McClintock, 1985; Wada et al., 1997). Hermit crabs choose shells according to species or shape (Jensen and Sato, 2005; Mantelatto et al., 2007), size (Hazlett, 1992), shell condition (McClintock, 1985; Pechenik et al., 2001), the previous experience of the crab (Meireles et al., 2008; Alcaraz and Kruesi, 2009), morphological characteristics of the crab (Scully, 1979; Côté et al., 1998), and the developmental and reproductive stage of the crab (Elwood et al., 1979). Shell selection is also dependent on environmental conditions like wave action (Argüelles et al., 2009). The size, type, and condition of the shell used by a hermit crab have been shown to be determinants of its growth, fecundity, motility, and survivorship (Bertness, 1981b; Herreid and Full, 1986; Angel, 2000; Bach and Hazlett, 2009). Accordingly, hermit crabs are not only selective for shell size (Angel, 2000; Turra and Leite, 2004; Mantelatto et al., 2007) and weight (Briffa and Elwood, 2005), but also for shells of particular snail species (shell type) (Vance, 1972; Hazlett, 1981; Worcester and Gaines, 1997).

The pattern of shell use is known to be dependent on shell preference (Bertness, 1980; Biagi et al., 2006; Mantelatto et al., 2007; Meireles et al., 2008) and shell availability (Turra and Leite, 2001; Argüelles-Ticó et al., 2010; Arce and Alcaraz, 2011). Shell availability is a major limiting factor, as the hermit crabs cannot acquire shells from live gastropods in nature, and hence, they need to

search for the best available empty shells or fight inter- or intra-specifically to obtain an appropriate shell (Childress, 1972; Fotheringham, 1976b; Hazlett, 1980). Shell availability depends on the abundance of gastropods in the habitat or the rate of mortality of gastropods in the habitat (Scully, 1979), as well as inter- of intraspecific competition for shell (Abrams, 1986).

Preferred shell types have been shown to increase hermit crab fitness relative to non-preferred shell types (Dominciano et al., 2009). In hermit crabs, in particular, shell selection is not by chance but based on the adequacy and availability of resources (Reese, 1962; Conover, 1978) and is affected by both shell size and species (Abrams, 1978; Conover, 1978; Blackstone, 1985; Lively, 1988; Siu and Lee, 1992; Ohmori et al., 1995; Hahn, 1998; Rodrigues et al., 2000; Mantelatto and Dominciano, 2002; Mantelatto and Meireles, 2004). Previous studies conducted by Abrams (1978); Elwood et al. (1979); Siu and Lee (1992); Ohmori et al. (1995); Hahn (1998); Dominciano and Mantelatto (2004); Biagi et al. (2006) found that the hermit crabs in the laboratory preferred those shell species that are most occupied in the field. Nonetheless, the lack of a shell species preference for *Pagurus samuelis* (Stimpson, 1857) and *P. granosimanus* under laboratory conditions was found by Orians and King (1964) for *P. samuelis* (Stimpson, 1857) and *P. granosimanus* (Stimpson, 1858), by Siu and Lee (1992) for *Clibanarius bimaculatus* (De Haan, 1854), by Garcia and Mantelatto (2001) for *Calcinus tibicen* (Herbst, 1791) and by Meireles and Mantelatto (2005) for *P. brevidactylus* (Stimpson, 1859). It was found that hermit crabs were more dependent on size of shell instead of species of shell while carrying experiments in lab conditions. The strong association between hermit crabs and their adopted shelters has influenced greatly almost all aspects of their biology (Hazlett, 1981). There is substantial evidence that shell availability can limit local hermit crab population size (Vance, 1972; Kellogg, 1976; Spight, 1977; Bertness, 1981a; Halpern, 2004).

Optimal gastropod shells that serve as "mobile homes" for hermit crabs provide protection from predators and, to a lesser extent, other hermit crabs, as well as protection from desiccation. The availability of such optimum shells in some populations is supposed to be a limiting factor for population growth

(Provanzano, 1960), and therefore, in some instances, the hermit crabs are observed to be occupying pseudoshells (Figure 6). In several instances, the supply of shells is so limited that all the shells except the most damaged ones are occupied by hermit crabs (Childress, 1972). Therefore, shell availability becomes a major concern for their growth (Fotheringham, 1976c; Bertness, 1981c; Blackstone, 1985) and reproduction (Fotheringham, 1976b; Bertness, 1981a). It is found that the availability of accurate-size empty shells is generally not enough for the hermit crabs in a population (Reese, 1969; Spight, 1977), however, in some regions, they can be abundantly available (Scully, 1979; Turra and Leite, 2001). It is believed that the availability of gastropod shells can directly affect the abundance of the hermit crab population (Kellog, 1976; Spight, 1977). Occupying shells of insufficient size increases the hermit crab's risk of both desiccation and predation. The mortality of hermit crabs increases during low temperatures due to desiccation when the occupied shells are too small (Taylor, 1981), and they become more vulnerable to predation when they cannot retreat completely inside the shell (Vance, 1972). Occupying a suboptimal shell (a shell too small) can have a negative impact on hermit crabs, leading to decreased somatic growth and increasing the threat of predation. However, decreased growth can be an advantageous strategy that enables the habitant hermit crab to retract completely inside the shell (Angel, 2000). Bertness (1980) suggested that the availability of shells provides insight into the relative abundance of different gastropod species in the area, the death rate of the species, the cause of mortality, as well as the architecture and size of the shells.



Figure 6. Hermit crabs occupying variety of pseudoshells (Source: <https://www.ranker.com/list/trash-crustacean-shells/eric-vega>).

The availability of shells can be reduced due to breakage of shells or removal of shells from the area due to wave actions (Bertness, 1980). Also, the coexistence of hermit crab species can influence the amount of shell availability, leading to competition (Reese, 1969; Bertness, 1981a). As a result of limited availability of useful optimum gastropod shells in nature, hermit crabs compete intra- or interspecifically for the suitable shells. Such competition often involves highly ritualised and aggressive displays and shell-fighting behaviour (Hazlett, 1966). Dowds and Elwood (1983) have described the shell fight of hermit crabs very descriptively. Barnes (1997), during his study, found that the species were forming large gatherings, which he termed "clustering," which was believed to be occurring for shell exchange among the individuals. He observed that the clustering was occurring on the elevated nearby surface in the intertidal region. He also noticed that the majority of the clusters were made up of a single hermit crab species, and in some cases, more than 90% of the individuals belonged to a single species. The size of the clusters varied significantly, from having only 105 individuals to as many as 1104 individuals. Similar phenomena were also

observed at the study sites of the present research work, where clustering behaviour was observed commonly and the size of clusters varied from 39 to 876 individuals.

Intraspecific (Abram, 1988; Turra and Leite, 2001) and interspecific (Gherardi and Nardone, 1997; Barnes, 1999) shell partitioning is common in hermit crab populations. The pattern of shell use in nature is dependent on shell availability (Turra and Leite, 2001) as well as crab preferences (Bertness, 1980). Therefore, understanding the preference for shells of the coexisting species can explicate the shell utilisation pattern in nature (Kellog, 1976; Bertness, 1981b). Several reasons are postulated for such differences in shell use patterns, including differences in the sizes of individuals among coexisting individuals (Manjon-Cabeza and Garcia-Raso, 1999; Turra and Leite, 2001), microhabitat segregation (Mitchell, 1975; Floeter et al., 2000), and particular abilities to obtain a new shell in competition (interspecific competition) or by active searching (exploitation/competition) (Bertness, 1981c).

Turra and Leite (2002), in a study, found that two hermit crab species, *C. vittatus* and *C. sclopetarius*, utilized similar shell species but of different dimensions as well as physical damage and degree of encrustation. It was also found that another species, *C. antillensis*, had a different habitat preference as compared to the other two species, while *C. vittatus* and *C. sclopetarius* showed microhabitat segregation, which might be an important aspect of coexistence. Similar microhabitat segregation is observed in various other studies (Mitchell, 1975; Kellogg, 1977; Gherardi, 1990; Gherardi and Nardone, 1997). Intraspecific shell partitioning is also observed in several populations where male individuals use larger shells as compared to female individuals (Imazu and Asakura, 1994; Asakura, 1995; Gherardi and Nardone, 1997; Patel et al., 2020b, c). Such differences in shell utilisation can be the consequence of larger sizes attained by male individuals as compared to female individuals (Turra and Leite, 2000). Additionally, it is also found that larger individuals utilise fewer species of shells as compared to smaller individuals (Reddy and Bisewar, 1993; Imazu and Asakura, 1994; Turra and Leite, 2001, 2002), suggesting the importance of shell availability on the shell utilisation pattern. It is found that hermit crabs occupy

the shells of the most abundantly coexisting gastropod shells, which shows the effect of shell availability on the shell utilisation pattern of hermit crabs (Reese, 1969; Wilber and Herrnkind, 1982; Leite et al., 1998).

There is strong evidence that most species experience a shortage of good-quality empty gastropod shells, which serve as mobile microhabitats for the crabs (Hazlett, 1981). Turra and Leite (2001) noted that using a suboptimal shell can directly affect fecundity and that species with larger eggs select relatively bulkier shells in order to gain more space within the shell. Occupying a shell too small for the optimum requirement can greatly reduce the reproductive potential of the hermit crab (Childress, 1972; Fotheringham, 1976c; Bertness, 1981d). It is also observed that when hermit crabs occupy suboptimal shells, the degree of protection against predation decreases (Vance, 1972), as well as decline in the success rate of agonistic interactions (Childress, 1972). It can be inferred that hermit crabs attempt to obtain and maintain a shell of optimum size in order to achieve protection from predators, the best growth rate, and the highest fecundity (Dowds and Elwood, 1982). Similarly, a larger shell makes the crab more vulnerable and reduces its chances of survival. Thus, it is required to occupy a shell having an optimum shell weight/body weight ratio and an optimum shell volume/crab size that provides maximum fitness to the individual (Reese 1962; Orians and King 1964; Hazlett 1970).

Several species show significant differences regarding their roles as male and female individuals. These differences among sexes are potentially important in determining the nature of population regulation within a species as well as the nature of interactions among species. Ecologists have majorly tried to understand and quantify the difference in resource use between species (Schoener, 1974a, b), but relatively few studies are carried out to understand the differences in resource use by different sexes of a species. It has been found that the preference of gastropod shells changes in different hermit crab categories (juveniles, males, non-ovigerous females, and ovigerous females) since all the shells are not available in all sizes (Biseswar and Reddy, 1993; Arguelles-Tico et al., 2010). It is also observed that the shell preference of a hermit crab can vary with changing geographical location based on the specific condition of the

habitat, which needs different solutions for the purposes of mobility, protection, and/or reproduction (Arguelles-Tico et al., 2010). The relationship between hermit crabs and gastropod shells has been the main subject of both eco-ethological studies (Hazlett, 1981) and models describing animal assessment and decisions (Elwood and Neil, 1992).

National review

The Indian Ocean is found to be a region of high biodiversity, with one of the countries in the region, India, rated as one of the mega-biodiversity centres of the world. The exclusive economic zone (EEZ) of the country has an area of 2.02 million km², comprising 0.86 million km² on the west coast, 0.56 million km² on the east coast, and 0.6 million km² around the Andaman and Nicobar Islands (Venkatraman and Raghunath, 2015).

The first publication on the anomuran crabs of Indian waters is credited to Heller (1865). In his publication, he listed around 14 hermit crab species collected from the Nicobar Islands during the "Novara" expedition. Later, Henderson (1893) published a paper on anomuran crabs from the Gulf of Mannar in Tamil Nadu, recording species belonging to superfamilies like Galatheoidea, Hippoidea, and Paguroidea. The first catalogue of hermit crabs was prepared by Alcock (1905), describing several species new to science. Later, Southwell (1909) reported three species: *Diogenes investigatoris* (Alcock, 1905), *Clibanarius humilis* (Dana, 1851) and *Clibanarius infraspinus* (Hilgendorf, 1869) from the collections of Mr. James Hornell from Okha Mandal in Gujarat state, India. Kemp (1915) described six new species of hermit crabs from his collection at Chilika Lake. Kamalaveni (1950) examined a collection of hermit crabs in Indian museums and described a new species, *Diogenes waltirensis* (Kamalaveni, 1950). She has also described a new genus, which is now accepted as a junior synonym of *Dardanus pedunculatus* (Herbst, 1804). Sarojini and Nagabhushanam (1972) listed 22 species of hermit crabs from the Waltair coast of Andhra Pradesh, with one species, *Pagurus indicus* (Sarojini and Nagabhushanam, 1972), being new to science. From the coastal region of Maharashtra, Sankolli (1962) described a new species, *Pagurus kulkarnii* (Sankolli, 1962), while two new species, *Diogenes macLaughlinae* (Nayak and

Neelakantan, 1985) and *Diogenes karwarensis* (Nayak and Neelakantan, 1989), were described by Nayak and Neelakantan (1985, 1989) from the coastal areas of Karnataka state.

From the published literature, it can be inferred that the east coast of India is studied more as compared to the west coast of India. However, in recent times, several new records (Dineshbabu et al., 2011; Reshmi and Bijukumar, 2010, 2011, 2013; Reshmi, 2014; Trivedi et al., 2015b; Trivedi and Vachhrajani, 2016a, b, c) and new species (Komai et al., 2012, 2013a, b, 2015; Trivedi et al., 2016; Kachhiya et al., 2017; Patel et al., 2020a) of hermit crabs have been published in the past decade, which enriches our understanding of the hermit crab fauna of the west coast.

Hermit crab fauna in Indian waters accounts for a total of 115 species belonging to 26 genera and five families, out of which the most species are reported from the family Diogenidae (81 species, 11 genera), followed by Paguridae (20 species, 7 genera), Parapaguridae (6 species, 3 genera), Coenobitidae (6 species, 2 genera), and Pylochelidae (2 species, 2 genera) (Patel et al., 2022a). In the case of hermit crab diversity, the east coast of India is reported as more diverse, with 81 species (22 genera, 5 families), as compared to the east-west coast of India, which has 73 species (19 genera, 4 families). Total 30 species and 4 genera which were confined to the west coast were reported, whereas 39 species, 7 genera and the family Pylochelidae were confined to the west coast of India. There were a total of 42 species of 12 genera that were reported to be common on the entire coast of India (Trivedi and Vachhrajani, 2017).

Ecological studies on the hermit crab fauna of Indian waters are very scanty. Ramesh et al. (2009) worked on the habitat diversity of *Clibanarius longitarsus* (Dehaan) in the Vellar estuary on the southeast coast of India and found that the distribution and availability of gastropod shells affect the distribution and abundance of hermit crabs. In a study carried out on the metamorphosis of *C. olivaceus* Henderson, 1893, Khan and Natrajan (1981) observed different larval stages, including five zoeal stages and a glaucothoe stage. Manjulatha and Babu (1991) worked on the mouth parts' morphology and

feeding mechanism in *C. longitarsus* and observed that the mouth parts are used for both microfeeding as well as macrofeeding. In a study carried out on *Diogenes miles* (Herbst, 1791), it was observed that the species has a specific breeding season in the summer months (Sankolli and Shenoy, 1993). Moreover, the larval forms were also identified, including three zoeal stages and a megalopa stage. The results of the reproduction of *C. clibanarius* were compared between the east coast (Cochin) and the west coast of India by Varadarajan and Subramoniam (1982). They found that on the east coast, the species was breeding continuously without showing any seasonal pattern, while on the west coast, contrasting results were observed with the species breeding between the months of September and March as a result of variation in the sea water temperature.

The Gujarat coastline, being the longest of all the Indian states, extends about 1650 km, which comprises around 21% of the Indian coast line. The state coastline can be divided into three coasts as a result of two indentations, viz., the Gulf of Kachchh, the Saurashtra coast, and the Gulf of Khambhat (Singh, 2002). The state possesses diverse coastal habitats, including mangroves (1031 km²), coral reefs (130.2 km²), mudflats (21913.7 km²), sand/beaches (106.1 km²), salt marshes (1003.9 km²), other vegetated areas (1059.9 km²), rocky areas (20.7 km²) and salt pans (459.5 km²) as the major ecosystems (Garg et al., 1998). As a result of these diverse coastal habitats, the Gujarat coast supports a great diversity of marine organisms. Out of these three major coasts, the Saurashtra coast possesses the richest diversity of organisms, including around 120 species of macrofauna (Vaghela, 2010). A few species of hermit crabs, viz., *Clibanarius nathii*, *C. ransoni* and *C. rhabdodactylus* are commonly found in the intertidal regions of the Saurashtra coast (Vaghela and Kundu, 2012; Patel et al., 2022b). Recently, in a study carried out on the diversity of marine decapod crustaceans, a total of 255 species (134 genera, 45 families) were reported. This included various infraorders, including Brachyura (163 species, 93 genera, 29 families), Caridea (52 species, 28 genera, 12 families), Anomura (39 species, 12 genera, 3 families), Gebiidea (2 species, 2 genera, 2 families), Stenopodidea (1 species, 1 genus, 1 family), and Axiidea (1 species, 1 genus, 1 family) (Gosavi et al., 2021).

A total of 18 species (4 genera, 2 families) of hermit crabs are reported from the coastal regions of Gujarat, (Trivedi and Vachhrajani, 2017; Patel et al., 2020a, 2022a). In a study carried out on the taxonomy of the genus *Clibanarius* (Family: Diogenidae), total seven species were identified, viz., *C. infraspinatus* (Hilgendorf, 1869), *C. longitarsus* (De Haan, 1849), *C. rhabdodactylus* Forest, 1953, *C. rutilus* (Rahayu, 1999), *C. signatus* (Heller, 1861), *C. virescens* (Krauss, 1843) and *C. zebra* (Dana, 1852) collected from various coastal regions of Gujarat (excluding the Gulf of Kachchh coast). Later, one more species, *C. ransoni*, was recorded from the Saurashtra coast (Patel et al., 2020a), while the records of *C. zebra* are kept as doubtful records as the species is restricted to the southwestern Pacific region (Patel et al., 2022a). Out of these, *C. rhabdodactylus* Forest, 1953, is one of the most commonly occurring species on the rocky shores of the Saurashtra coast (Trivedi et al., unpublished data). *Clibanarius rhabdodactylus* has been so far reported from the Philippines (Malay et al., 2018), South Japan (Osawa and Yoshida, 2009), and Gujarat, India (Kachhiya et al., 2017). The species was earlier considered *C. zebra* var. *rhabdodactylus*, which was later described as a new species by Forest (1953).

Few ecological studies on hermit crab species on the Gujarat coast have been conducted, with the majority of them focusing solely on behavioural ecology. Vaghela and Kundu (2012) studied the spatiotemporal variation in the hermit crab population along the four major rocky shores (Dwarka, Mangrol, Veraval, and Kodinar) of the Saurashtra coast and observed that the species was not showing any spatial or temporal variation in the population in all the study sites. In one such study, the effect of various abiotic and biotic factors like salinity, temperature, substratum preference, and pH on the density, abundance, and temporal distribution of two hermit crab species, *C. zebra* and *C. nathii*, was studied at the Saurashtra coast (Desai and Mansuri, 1989). The shell utilisation pattern of *C. zebra* was studied along different coastal sites in Saurashtra, where it was found that the species was occupying 23 species of gastropod shells with a maximum utilisation of six gastropod species (Trivedi and Vachhrajani, 2014a). In one more such study, the shell utilisation pattern of *Diogenes custos* in the intertidal zone of the Gulf of Kachchh was studied, and it was observed that the species was occupying 49 species of gastropods, with the majority occupying

only six gastropod species (Patel et al., 2020b). Apart from that, the shell utilisation pattern of *C. rhabdodactylus* has also been studied along the Gulf of Kachchh and was observed to occupy 36 different species of gastropod shells, with only five species being highly occupied (Thacker et al., 2021). Although *C. rhabdodactylus* has a widespread distribution along the Gujarat coast, the ecological aspects of the species have not been well studied so far.

Clibanarius rhabdodactylus can be easily identified by the stripes on different body parts. Dark-brown stripes adorn the eye-stalk, shield, and walking legs. Carapace has four longitudinal bands on the dorsal surface. Cheliped subequal; right slightly bigger. Ambulatory legs with merus and carpus having three stripes on the lateral surface; propodus and dactylus having five stripes; three on the lateral surface and two on the dorsal surface (Figure 7). The species closely resembles *C. zebra* (Dana, 1852). However, *C. zebra* has no stripe on the dactyl of the ambulatory legs, while *C. rhabdodactylus* has five prominent stripes on the dactyli (Miyake, 1956). *Clibanarius rhabdodactylus* has affinities with *C. signatus* from Pakistan, the Persian Gulf, the Gulf of Oman, the Gulf of Aden, and the Red Sea (Poupin et al., 2013). But it is distinct by having only one longitudinal stripe on the ocular peduncle and four longitudinal stripes on the cephalic shield (Moradmand and Sari, 2007).



Figure 7. Dorsal habitus of *Clibanarius rhabdodactylus* Forest, 1953.

Origin of the study

Out of the three coasts of Gujarat State, the Saurashtra coastline is around 850 km long, which provides varied coastal habitats that range from the muddy, sandy, to rocky intertidal zones (Trivedi et al., 2015), which support a rich diversity of hermit crabs (Kachhiya et al., 2017). Some studies are available on the diversity and distribution of hermit crabs on the Gujarat coast (Desai and Mansuri, 1989; Vaghela and Kundu, 2012; Trivedi et al., 2015; Kachhiya et al., 2017; Patel et al., 2020a). However, studies available on the ecology of hermit crabs are scanty and started recently (Patel et al., 2020b, c, 2021; Thacker et al., 2021). Out of the eight hermit crab species of *Clibanarius* Dana, 1852, found on the Gujarat coast, *Clibanarius rhabdodactylus* is one of the most commonly occurring species along the rocky intertidal coast of Gujarat (Trivedi et al., unpublished data). The species is found on the entire Saurashtra coast, starting

from Okha to Diu, with higher occurrences recorded in Veraval, Sutrapada, and Dhamlej located on the coastal area of Gir Somnath district of Gujarat state (Trivedi et al., unpublished data). Although the species *C. rhabdodactylus* is commonly occurring on the Saurashtra coast, the population ecology, behaviour and biology of the species are not well studied. Therefore, the present study is designed to understand the population structure, intertidal distribution as well as the shell utilisation pattern of *C. rhabdodactylus* along the Saurashtra coast of Gujarat.

Objectives of the study

1. To study population ecology of *Clibanarius rhabdodactylus*.
 - a) To study the population structure of *Clibanarius rhabdodactylus*.
 - b) To study the seasonal variation in intertidal distribution pattern of *Clibanarius rhabdodactylus*.
2. Study of behavioural ecology of *Clibanarius rhabdodactylus*.
 - c) To study the shell utilisation pattern of *Clibanarius rhabdodactylus*.