

Review

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Review

Lobsters of the Southeastern Levantine Sea and the Northern Red Sea, an Up-to-Date Review

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Abstract

Despite the oligotrophic conditions of the southeastern Levantine Sea and northern Red Sea, six lobster species—five slipper lobsters (*Scyllaridae*) and one spiny lobster (*Palinuridae*) maintain permanent, reproducing populations in the study area. Additionally, there are isolated records of four other sporadic lobster species. In the southeastern Mediterranean, permanent species include the Mediterranean Slipper Lobster, *Scyllarides latus*, Small European Locust Lobster, *Scyllarus arctus*, and Pygmy Locust Lobster, *Scyllarus pygmaeus*. In the northern Red Sea, they include the Clamkiller Slipper Lobster, *Scyllarides tridacnophaga*, Lewinsohn Locust Slipper Lobster, *Eduarctus lewinsohni*, and Pronghorn Spiny Lobster, *Panulirus penicillatus*. This review synthesizes current knowledge of their biology and ecology, including distribution, habitat, reproduction and development, feeding, predators and anti-predatory adaptations, behavior, sensory modalities, environmental impacts, threats, and conservation. Recent advances focus mainly on larger, commercially valuable species (*S. latus*, *S. tridacnophaga*, *P. penicillatus*), while major gaps remain for oceanic post-embryonic stages and the nektonic niso postlarva, as well as for smaller, often cryptic species (*S. arctus*, *S. pygmaeus*, *E. lewinsohni*). Addressing these gaps will require targeted research, using modern methodologies, in coastal, deep, and open waters, coupled with citizen-science surveys. While many Indo-Pacific decapods have been established in the Mediterranean, no immigrant lobster species have successfully colonized Levant waters, despite rare records of three non-indigenous species (NIS). However potential NIS predators and shifts in mollusk compositions, the main prey of some native lobsters, may affect the latter. Large lobsters remain targeted by fisheries despite protective regulations, which are not always effective or obeyed. No-take marine protected areas (MPAs) or nature reserves can be effective if sufficiently large and well-managed. Habitat loss from marine construction can be partly compensated by stable, environmentally safe artificial reefs tailored to lobster behavioral ecology. The categories of the studied lobsters' species in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, last updated over fifteen years ago, should be re-evaluated.

Keywords: slipper lobsters; spiny lobsters; phyllosoms; biology; ecology; anthropogenic effects; overfishing; marine protected areas; management; future research

1. Introduction

Lobsters are crustaceans that, according to the classical taxonomy, belong to the suborder Macrura Reptantia, order Decapoda (all of which have 5 pairs of limbs), class Malacostraca, suborder Crustacea, order Arthropoda. Members of the latter group are characterized by a segmented body, two pairs of tentacles (antennae and antennulae) and biramous limbs that have undergone various specializations for feeding, grasping, walking, swimming, reproduction and sensory functions. Their body is covered with a hard exoskeleton composed mainly of chitin and calcium. Malacostracans include the largest crabs, including some species of lobsters, which are found exclusively in seawater.

Lobsters are generally divided into three infraorders. The first, **Astacidea**, includes the clawed lobsters' family, which comprise species of significant commercial importance, most notably the American lobster, *Homarus americanus*. The second, **Palinuridea**, contains the spiny lobster family,

which includes commercially valued species, and the slipper lobster family, some of which have economic value. Few members of the third group, Thalassinidea, have economic importance [1]. In more innovative classification approaches, lobsters are grouped into two main categories: those with claws (Homarida) and those without claws (Achelata), the latter encompassing the families Palinuridae, Scyllaridae and Synaxidae [1,2]. The present review focuses on clawed, spiny and slipper lobsters. The Levantine Sea is the easternmost part of the Mediterranean Sea (Figure 1), located far from the Mediterranean's connection to the Atlantic Ocean at the Gibraltar Straits. As a result, Levantine water has distinct physical and chemical, and therefore ecological, characteristics that are more extreme than the rest of the Mediterranean.

Environmental conditions in the Mediterranean change gradually from west to east: evaporation increases, precipitation decreases, salinity rises, water temperatures climb, nutrient levels in the photic zone drop, and primary productivity declines. These trends affect the entire food web, including fisheries, and result in the ultra-oligotrophic nature of the Levant Basin. Therefore, the southeastern Levantine coast is marked by low biological productivity and dynamic conditions, including continuous abiotic changes (e.g., rising water temperatures) and biotic shifts (e.g., the invasion of alien species). In recent decades, rapid population growth, particularly along coastal areas, has intensified human impacts, creating environmental threats, harming marine life, and generating conflicts between anthropogenic activities and the marine ecosystem [3].

Most indigenous marine biota in the Levantine Sea are of Atlantic origin, but since the opening of the Suez Canal in 1869, there has been a substantial influx of alien species from the Red Sea and Indian Ocean, a process known as Lessepsian (or Erythrean) migration (e.g., [4–6]). Levantine waters are warming at nearly twice the global average [7] and faster than other parts of the Mediterranean [8]. Climate change plays a key role in facilitating the spread of Lessepsian species [9]. Despite its oligotrophic nature and relatively low biomass, the Levant may host locally high biodiversity, driven by the prevalence of numerous species, including many non-indigenous species (NIS), and the presence of some unique habitats, such as hard substrates.



Figure 1. The study area. Background: part of *Blue Marble: Land Surface, Shallow Water, and Shaded Topography*. NASA Goddard Space Flight Center Image by Reto Stöckli, Robert Simmon and MODIS Groups; https://visibleearth.nasa.gov/images/57752/blue-marble-land-surface-shallow-water-and-shaded-topography_ (accessed on 11 February 2002). Courtesy of Professor Dov Zviely, Faculty of Marine Sciences, Ruppin Academic Center, Israel.

The coast of the Southeastern Levantine Sea and its adjacent inner shelf is divided into two main sedimentological provinces. The southern province consists of the margin of northern Sinai and of southern and central Israel, extending northward to northern Haifa Bay (Figure 1). This margin is relatively wide (ranging from about 50 km off Sinai to 10 km off Haifa) and the sea floor is generally smooth [3,10]. It is composed mainly of Nile-derived fine quartz sand and represents the northern flank of the Nile littoral cell, which extends roughly 650 km along the southeastern Mediterranean from Abu Quir Bay near Alexandria, Egypt, to Haifa Bay [3]. Since the construction of the Aswan dams, most sand supplied to this coastal system originates from erosion of the Nile Delta. The sediments are transported by longshore and offshore currents along the coasts of northern Sinai and Israel [11]. The northern province comprises the margins of northern Israel and Lebanon. It is narrow (3 to 12 km) and cut by numerous canyons. The latter are primarily submarine extensions of rivers of the Northern Israel and Lebanon [11]. The seabed here is dominated by hard substrates, with some areas covered by local coarse carbonate sand [12–14].

Several types of hard substrates occur along the Levantine coast, including *kurkar*, a local name for an aeolian, carbonate-cemented quartz sandstone, forming ridges parallel to the coastline. These ridges create rocky substrates rich in crevices and caves. Such complex submerged natural, as well as artificial, hard-bottom habitats, are important for many marine species, including certain lobsters' species (e.g., [15,16]). Hard substrates are more common along the northern coasts. *Kurkar* ridges occur underwater mainly from the shoreline to depths of about 30 m. Some of the *kurkar* substrates appear, in the intertidal zone, in the form of abrasion platforms, especially prevalent in the northern part of the region [3]. Another rocky feature is beachrock, which contains abundant marine-derived particles such as shells and coarse sediment, rapidly cemented by calcium carbonate within the intertidal zone. Beachrock outcrops may extend hundreds of meters in length, exceed 40 m in width, and reach about 1 m in thickness. There are also conglomerate and lime rocks along the Northern Province of the region.

The Gulf of Suez (GoS) and the Gulf of Aqaba (Eilat) (GoA) form the northern arms of the Red Sea, separated by the triangular Sinai Peninsula (Figure 1). The GoS, the northwestern arm of the Red Sea, is relatively shallow, with depths measured in tens of meters. Only in its southern part, off Ras Mohamed, does a deeper trench extend into the gulf from the Red Sea. The southern boundary of the gulf is defined by a line running from Ras Mohamed to Shadwan Island and Hurghada. This line roughly follows the 200 m depth contour, marking the point where the Red Sea proper begins [17].

The northeastern arm of the Red Sea, the GoA, is deep, with a maximum depth of 1,829 m. Its coasts are either very narrow or absent altogether. On the western side, large alluvial fans extend below the sea surface and are cut by numerous marine canyons. The eastern side drops steeply into deep basins [18].

Coral reefs are the most important habitats in the northern Red Sea. Although the open water is extremely oligotrophic, these reefs support high biological diversity and feature efficient nutrient recirculation. The spatial complexity of coral reefs includes structures such as caves, crevices, tunnels, holes, and cavities, which provide habitat for a wide range of marine life, including some lobster species. Bays in the northern Red Sea contain coral patches, seagrass beds, muddy substrates, and coral reefs.

Globally, the future stability and persistence of coral reefs is uncertain due to global warming and recurrent bleaching events, which reduce the resilience of these ecologically and socioeconomically important ecosystems [19]. The Sea Surface Temperature (SST) of the Northern Red Sea is warming at a rate of a few hundredths °C per year, comparable to the warming observed in the global oceans and the Mediterranean Sea [20]. Despite this, coral bleaching linked to rising sea temperatures has not yet been reported in the region. It has been suggested that the GoA, and possibly the GoS, may serve as reef refugia due to a unique combination of environmental conditions. This hypothesis is supported by experimental evidence showing an exceptionally high bleaching threshold for corals in the Northern Red Sea, as well as by ocean modeling that indicates potential dispersal of coral planula larvae through a selective thermal barrier. It is proposed that millennia of

natural selection at the southernmost end of the Red Sea have favored coral genotypes less susceptible to thermal stress, potentially delaying bleaching events in the GoA by at least a century [19]. Nevertheless, even in the northern Red Sea, increased anthropogenic pressures from tourism, shipping, ports, and industrial activities have negatively affected these sensitive and unique ecosystems.

Other important marine habitats in the northern Red Sea include seagrass meadows, such as those formed by the fern seagrass, *Halophila stipulacea* [21]. These meadows provide coastal protection and support high biodiversity. They also efficiently fixate carbon, making a significant contribution to mitigating climate change.

Salinity in the northern Red Sea ranges from ~ 39‰ in the south to ~ 41‰ in the north, around the GoS [22]. This is similar to the average salinity in the upper mixed layer (0–10 m depth) of the open Levant Sea, of 39.75‰ [3]. Despite the similarities in salinity and temperature regimes between the northern Red Sea and the southeastern Levantine Sea, far fewer species have migrated from north to south (anti-Lessepsian migration) compared with the south-to-north Lessepsian migration. Lessepsian migrants may outnumber anti-Lessepsian migrants by three or more orders of magnitude [9]. Fewer than 10 species are recognized as anti-Lessepsian, compared with nearly 500 Lessepsian species [23]. The Red Sea is open to southern seas, and non-indigenous species (NIS) of lobsters may also be introduced via ballast water from ships travelling to commercial ports such as Aqaba in Jordan, Eilat in Israel (both at the northern end of the GoA), and Duba (NEOM) on the northern Red Sea coast of Saudi Arabia. Similar introductions may occur via ships traveling to the main ports in GoS: Suez Port, Ain Sokhna Port, and Adabiya Port, as well as vessels transiting the Suez Canal.

Lobsters are currently important resources across the world's oceans, providing food security, employment, and valuable trade commodities. Humans have exploited lobsters since prehistoric times. They were a valuable food and economic resource for early coastal communities. Ancient Greek and Roman Mediterranean civilizations accumulated considerable knowledge about lobster biology and fisheries [24]. Despite their oligotrophic nature, the southeastern Mediterranean and northern Red Sea support a variety of spiny and slipper lobster species, some of which have been, and continue to be, harvested for food. Lobster use in ancient times varied widely, from complete prohibition in Jewish dietary laws to being regarded as a delicacy in the Roman world [25]. One of the earliest known depictions of a lobster is a wall carving in Egypt, illustrating Queen Hatshepsut's five-ship trade expedition to the Red Sea in the 15th century BC (e.g., [26]). This bas-relief mural on a temple wall in Deir el-Bahari, Egypt, depicts a spiny lobster alongside other mostly edible tropical marine animals. Some scholars suggest that this lobster represents the Pronghorn spiny lobster, *Panulirus penicellatus* [27].

The present article reviews the latest available information on the biology, ecology, distribution, reproduction, development, feeding, predation, environmental impacts, threats, and conservation of the known lobster species in the studied area.

2. Lobsters from the Southeastern Mediterranean Coast

Only slipper lobsters of the family Scyllaridae are known to be permanent residents along the Mediterranean coast of the Levant. These include the Mediterranean slipper lobster, *Scyllarides latus*, the Small European locust lobster, *Scyllarus arctus*, and the pygmy locust lobster, *Scyllarus pygmaeus*. They are also called "shovel-nosed" lobsters, a name that refers to their flattened, shovel-like antennae characteristic of slipper lobsters.

2.1. The Mediterranean Slipper Lobster

The Mediterranean slipper lobster, *Scyllarides latus* (Latreille, 1802) (Figure 2), is a relatively common species along the southeastern Mediterranean coast. The etymology of its scientific name derives from *skylarlos* (Greek) meaning a kind of crab, and *latus* (Latin) meaning broad [28,29]. According to the FAO, its common names include *Grande Cigale* or *Grosse Cigale* in French, and *Cigarra* or *Cigarra de Mar* in Spanish [1,29]. Other vernacular names for this species are: Flat Lobster (UK);

Magnosa, Cicala Grande (Italy); Cavaco, Lagosta de pedra (Portugal); Astakoudaki Megalo (Greek); Büyük Ayı Istakozu (Turkey); Cigale Noire (meaning "black cicada") and Farzit (Tunisia) [29]; additional common/local names include Cigale courte (Algeria); Feritah (Morocco); Caravida (Greece); Sapa (Spain); Homard plat, Macieta (France); Ccala hamra, Ccala seula (Malta) [30]; and Kapan Gushmani (referring to a spoon-shaped creature with connected, lumpy parts) in Israel (e.g., [31]).

Due to its considerable size and its economic and ecological importance, knowledge about *S. latus* is relatively well-established compared to other scyllarids species reported along the Levant coast. This is largely thanks to studies conducted mainly in Israel, Italy, Spain, and the Azores Islands. Nevertheless, several aspects of its biology and ecology remain unknown.



Figure 2. The Mediterranean slipper lobster, *Scyllarides latus* (photographed by Amit Zeevi on November 5, 2021, at 11:00 AM at a depth of 5 meters in the Akhziv-Rosh HaNikra Marine Nature Reserve on the northern coast of Israel).

The Mediterranean slipper lobster belongs to the genus *Scyllarides*, which includes 14 species found in temperate and tropical waters. These lobsters are members of the subfamily Arctidinae, which also includes the genus *Arctides*, comprising three species [32]. The family Scyllaridae is the most diverse among lobster groups in terms of both species number and variety, encompassing four subfamilies and at least 89 species. Slipper lobsters are taxonomically closely related to spiny lobsters (family Palinuridae) and furry lobsters (family Synaxidae); together, these families form the Achelata group of lobsters [1,2]. They differ from other decapod crustaceans in several ways, primarily due to their unique larval stage known as the phyllosoma (Figures 3 and 7). Additionally, their cephalothorax is flattened and features lateral lips, while the second pair of antennae are short and broadened into large plates—often mistakenly referred to as "shovels" or "fins."

Like other lobster species, *S. latus* is primarily nocturnal. During the day, it typically hides in dens, burrows, caves, and dark crevices within the rocky substrate [33]. However, initial data from a recent citizen science survey along the Mediterranean coast of Israel surprisingly revealed several instances of *S. latus* being observed during daylight hours. This species is found close to the coast on the shallow continental shelf (up to about 30 m depth) only part of the year, from around February to July, when seawater temperatures are relatively cool. During most of the summer and autumn, it is rarely seen in these shallow areas [15,34], likely migrating to deeper waters and returning to the shallows the following winter.

The maximum length of *Scyllarides latus* can reach is up to 45 cm, although it typically does not exceed 30 cm, with an average weight of about 1.5 kg. In recent decades, smaller sizes have been

reported, likely due to fishing pressure and fishermen's preference for larger individuals [33]. Notably, Atlantic specimens tend to be heavier than those from the southeastern Mediterranean [15]. Nonetheless, *S. latus* remains the largest lobster species in the southeastern Mediterranean Sea and has historically been, and continues to be, a target for fisheries. It is commonly found in rocky habitats at depths ranging from approximately 4 to 100 meters [1], though it has occasionally been reported at depths of up to 400 meters [35]. Its distribution spans the Mediterranean Sea as well as the central eastern Atlantic Ocean, from the coast of Portugal to Senegal, including Madeira, the Azores, Canary, and Cape Verde Islands [1]. The lobster is yellowish-brown in color, with the edges of its flattened antennae (the "shovels"), antennulae, and legs often displaying a bright purple hue (Figure 2).

2.1.1. Reproduction and Development

The breeding season in the study area lasts from April to July. The sexes are separate, with the female-to-male ratio in the population being roughly equal [35]. In adults, distinguishing females from males is straightforward by examining the ventral surface of the body. Females have larger, leafier, and broader pleopods (abdominal appendages) used to hold the eggs. Their fifth walking legs (pereiopods), which handle the eggs, are chelated (bearing pincers), whereas males' fifth legs lack pincers. The genital openings are located at the base of the third walking legs in females and at the base of the fifth in males. In the Levant, males with white gelatinous spermatophores at the base of the fourth and fifth walking legs have been observed both at sea and in the laboratory during early spring, when water temperatures reach at least 17°C [15]. Unlike some other lobster species, mating in this species is not associated with molting. In laboratory observations in the Levant, females were found carrying spermatophores 6–10 days before eggs appeared. Egg-bearing females have been reported both at sea and in the laboratory at water temperatures between 17° and 27°C. The eggs have a diameter of approximately 0.7 mm, and their number is directly proportional to the female's size, ranging from about 100,000 to 356,000 [32,34]. Such high fecundity is assumed as an adaptation to compensate for larval losses in the open sea and the variable recruitment of juveniles due to cyclical changes in the marine environment [36]. The eggs initially appear yellow orange (Figure 3) and darken brown as they develop. Along the Levantine coast, females carry their eggs on the abdomen for 4–6 weeks [15], while in the Atlantic Ocean, this period extends to 6–8 weeks [37] before the eggs are released into the water. It has been reported that females may lose some or all of their eggs if disturbed by predators or humans, either at sea or in laboratory settings [24,35].

The egg hatches into a "prelarval" stage called the naupliosoma, which measures about 1.3 mm in length. This stage does not feed and survives for no more than five hours before molting into the first stage of the phyllosoma larva [38]. The first stage of the phyllosoma larva lives for approximately six days and reaches about 1.8 mm long. It is a flat, transparent, leaf-like larva (Figure 3) that drifts in the pelagic zone, far from the shore. Feeding primarily on soft, gelatinous animals, it grows for nearly a year, undergoing 11 molts during this period. The final phyllosoma stage, which can reach up to 48 mm in length [38], then metamorphoses into the nisto, or post-larva. The nisto stage is neither fully planktonic nor entirely benthic; it represents the transition from life in the water column to life on the substrate. For many years, this stage was not observed in nature, but a lengthy search of museum collections uncovered a specimen in the Zoological Museum in Turin [39]. This tiny and rare specimen, measuring 38.7 mm (Figure 3), was collected in southern Italy in the early 20th century, likely from waters deeper than 800 m. It is assumed that individuals in this stage settle in deeper waters where they are better protected from predators. They then develop into small juveniles and gradually migrate along the bottom toward shallow adult habitats, molting and growing until they join the juvenile and adult population in coastal waters.

Although Mediterranean slipper lobsters mate and lay eggs that hatch readily in the laboratory, scientists have not yet been able to complete their full life cycle or successfully raise them from eggs in captivity.

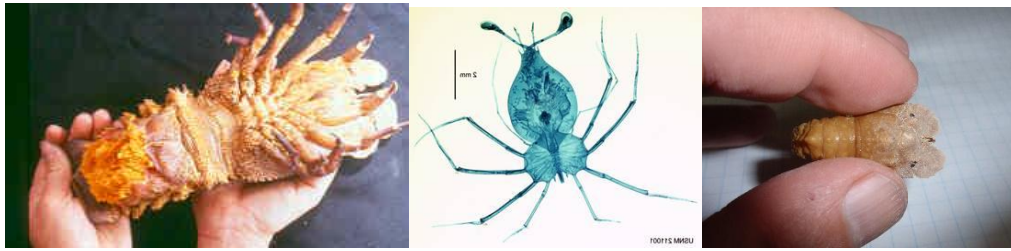


Figure 3. Left: Female *Scyllarides latus* with eggs (photographed by S. Breitstein, University of Haifa), Center: Phyllosoma larva of *Scyllarides* sp. (from the Martin Wiggo Johnson Phyllosoma slide collection of the Scripps Institute of Oceanography, Pelagic Invertebrate Collection website (<https://www.flickr.com/photos/siopiczp/collections/72157641176701533/>)) Right: nisto – young benthic stage of *S. latus* (photographed by J.J. Gottlieb, University of Haifa).

2.1.2. Food and Predators

The Mediterranean slipper lobsters feed mainly on clams [40], which they forage in the open area after sunset. They sometimes bring clams into their dens, probably those they have collected before dawn [15]. They open the clams with their strong pereiopods after investigating the clam using their antennulae and cutting the clam's closing muscles [41].

S. latus appears, at first glance, defenseless. Clawed lobsters, such as *H. americanus* (Figure 10), are equipped with large claws that may be used for defense (but also for gripping and cracking food), and the bodies of spiny lobsters, such as the Pronghorn spiny lobster from the northern Red Sea (Figure 15), are covered with spiny armor and have long, spiny antennae that may be used to ward off predators. Apparently, scyllarids have no morphological adaptations against predators. However, it turned out that they have both morphological and behavioral adaptations against predation. First, they usually hide during the day in horizontal dens, whose shade protects them from detection and physical harm, usually by diurnal predators. They prefer natural or artificial shelters (artificial reefs (AR), ships' wrecks) that have at least one extra escape opening in addition to the entrance [42]. They also tend to choose dens with small openings, which add to the physical protection of the dens as well as increase their shading. They often hide in dens with other individuals of their own species [41]. When they emerge from the dens in the evening to forage or for social interactions, their color blends with the rocky environment in the twilight light. If they are attacked, their thick armor may protect them from the initial assault of a typical diurnal predator such as the Mediterranean triggerfish, *Batistes carotinensis*, with its strong teeth. Their coarse carapace (exoskeleton) has been found to be at least twice as thick as that of clawed and spiny lobsters [43]. The special internal structure of the carapace [44] also makes it more resistant to mechanical damage than the carapace of lobsters from other families. During an attack, the slipper lobsters protect their mouthparts and delicate antennulae with their flat, stiff antennae ("shovels"), and their eyes converge into eye sockets protected by strong spines. Their short, strong legs, equipped with strong cloves, are used to cling to the rocky bottom or the walls of their den, to prevent the predator from turning them over and exposing their ventral side, where their carapace is thinner and more vulnerable. Measurements, using spring scales, have indicated that the clinging force of slipper lobsters to a rough, hard substrate (or the force required to detach the lobsters from such a substrate) ranges from 3 to 15 kg and is directly proportional to the size (weight) of the lobster. This clinging force is equivalent to 8 to 29 times the lobster's body weight [15]. Experiments at sea have shown that the survival of *S. latus* that hid during the day in dens in an AR was significantly higher than that of their conspecifics that were at the same time in the open, and most of them were prey upon by Mediterranean trigger fish [45].

If the "fortress defense" strategy fails, or if a predator manages to enter the den, the lobsters escape through alternative openings and switch to a rapid getaway swim. Slipper lobsters, which normally walk slowly on the substrate, use powerful tail flips in emergencies, rapidly propelling themselves backward by repeatedly striking their muscular and flexible abdomens. This burst-and-coast swimming style, characterized by large tail movements propelling the lobster quickly

backward, followed by a powerless glide, is also seen in some fast-swimming, negatively buoyant fish and other crustaceans. During acceleration, swimming speeds can reach up to three body lengths per second (about one meter per second), while during the glide phase speeds drop below one body length per second [46]. Escape swimming is short-lived and used only in emergencies to reach safety, such as an alternative den, due to its high energy demand. Lobsters can also abruptly change swimming direction, likely to confuse predators [32]. The flattened second antennae of *S. latus*, often mistaken for “shovels” or “flippers”, have movable joints that act as stabilizers or rudders to control swimming movements [46,47] (Figure 4). The tail fan (telson) may also contribute to steering and stabilization during swimming.

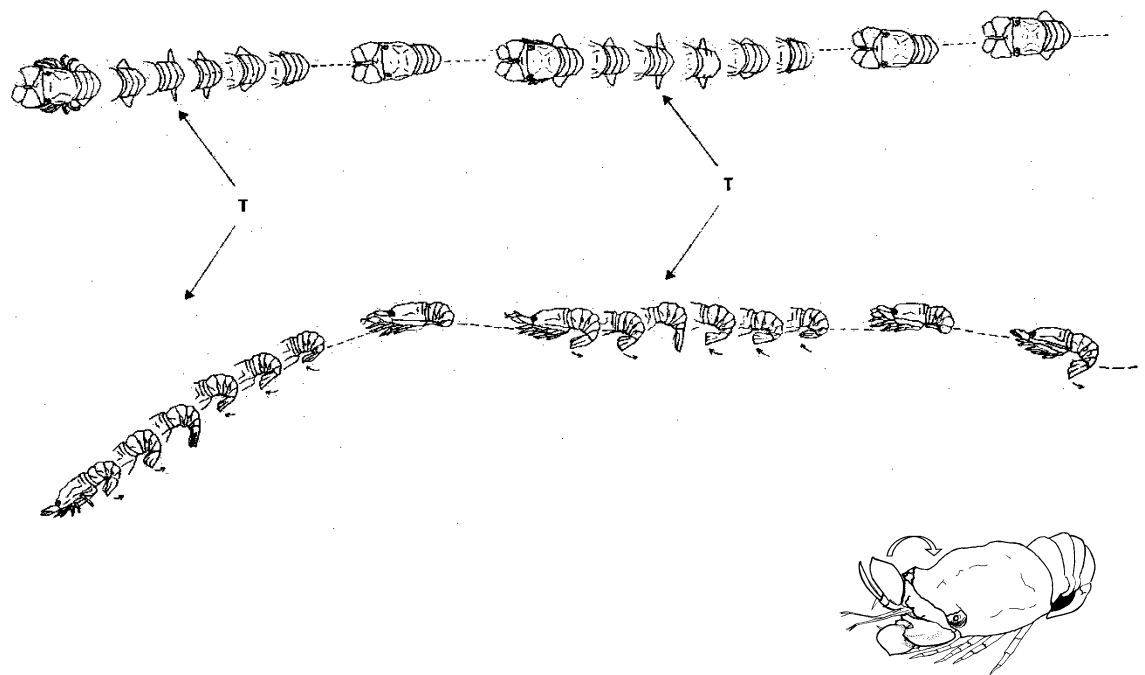


Figure 4. Demonstration of the Mediterranean slipper lobster's "burst and coast" swimming shown from above (top image) and from the side (middle image). T marks the start of the muscular abdomen movement (from [46] with permission). Bottom right: Illustration of the use of the flattened second antennae for steering while swimming (drawn, from video footage, by Rachel Pollak, University of Haifa).

Another potential predator of *S. latus* is the common octopus, *Octopus vulgaris*. The lobsters have frequently been observed sharing dens with Mediterranean moray eels, *Muraena helena*, without any evident predator-prey interactions between them [42]. It is speculated that this shared shelter may be mutually beneficial: since the octopus is prey for the moray, the lobsters might gain protection from the octopus by co-sheltering with the moray. Conversely, the moray may benefit from the presence of lobsters attracting octopuses to the den. However, these possible mutualistic relationships require further investigation.

2.1.3. Sensory Modalities

The sensory world of adult *S. latus* is less understood compared to other lobster groups. In other lobsters, chemical sensation is typically divided into near-field “taste” and far-field “smell.” However, observations of *S. latus* feeding behavior suggest that this distinction may not be as clear [41]. Lobsters possess tufts of sensory hairs (setae) across many parts of their bodies, but notably not at the tips of their legs. Despite this, *S. latus* can locate and retrieve clams buried several centimeters deep by using the claws of their walking legs, while simultaneously increasing the fluttering rate of their antennulae [15]. This behavior has also been observed in laboratory aquariums when clams were put into it.

The antennulae are covered with various types of sensory hair setae that likely serve as chemical and mechanical receptors [50]. The mechanical receptors are also used for hydrodynamic sensing during swimming, as are the numerous sensory hair setae located on the lobsters' “shovels,” which aid in steering during “take-off,” “landing,” and changes in direction. These sensory structures provide crucial feedback during escape swimming.

The ventral, and especially the dorsal, side of the *S. latus* exoskeleton, like those of other decapod crustaceans, is covered with numerous stiff sensory hair setae, which probably function as mechanical receptors.

The eyes, situated on stalks, also allow for backward vision. In response to a direct threat, they converge into foveae, each protected by a stiff spine. Anatomical studies of *S. latus* eyes [51] indicate that they resemble those of nocturnal decapod crustaceans and are adapted for vision in dim light. Additionally, these lobsters appear capable of perceiving polarized light—a crucial adaptation against predation, considering that several species of triggerfish, which are among the lobsters' predators, also possess this ability.

Statocysts are known in other lobster families and are used to maintain balance, but they have not yet been reported in slipper lobsters. The fact that *S. latus* responds immediately with a powerful “tail flip” of its muscular abdomen when turned over on its back [45] suggests that its statocysts are well developed.

Since *S. latus* appears capable of returning to the same preferred dens in hard substrate after a year [52] or even several years [34], how do they navigate such great distances? They may use magnetic cues or a geomagnetic “map,” as reported in spiny lobsters [53]. However, this aspect has not yet been studied in slipper lobsters.

Despite their French common name, *Cigale de Mer* [29], meaning “sea cicada,” which refers to the sound the lobster makes when rubbing its lobes together upon being taken out of the water, it remains unclear whether *S. latus* can hear or produce sounds like some other lobster species. Additionally, the sensory mechanisms of juvenile slipper lobsters are currently unknown.

2.1.4. Environmental Impacts, Threats and Conservation

The main threats to *S. latus* populations are overfishing, habitat loss, and climate change [31,32]. Due to its large size and high market value, *S. latus* is heavily fished throughout its range [54], including in the southeastern Levant. Fishing methods primarily include diving and the use of trammel and gill nets. The removal of large individuals with high reproductive potential poses a serious threat to the species' populations. In some areas of the western Mediterranean, such as Italy, it is estimated that the population may be unable to recover at all [55]. However, genetic studies comparing *S. latus* individuals from different sites in the eastern, central, and western Mediterranean, as well as the eastern Atlantic Ocean [56,57], have revealed little genetic variation across this broad distribution. This phenomenon, known as panmixia, refers to a population's ability to reproduce freely across a very wide geographic range spanning hundreds to thousands of kilometers. The researchers attribute this to the species' high fecundity and prolonged larval stage in the open sea. Given these findings, which indicate strong connectivity between geographically distant *S. latus* populations, researchers suggest that future conservation efforts should treat all populations as a single stock [57]. For example, larvae from healthy populations around the Balearic Islands in Spain

could potentially help restore depleted habitats in Italy, where Mediterranean slipper lobster populations have been nearly wiped out.

The main threats to the populations of *S. latus* are overfishing, habitat loss and climate change [31,32]. Due to its size and its high market value, *S. latus* is intensively fished throughout its range [54], including the southeastern Levant. Fishing is mainly done by diving and using trammel and gill nets. Removing large individuals with high reproductive potential from the sea is a serious threat to populations of this species. It is estimated that in some areas of the western Mediterranean, such as Italy, the population will not be able to recover at all [55]. However, genetic studies comparing individuals of *S. latus* from different sites in the eastern, central and western Mediterranean, and the eastern Atlantic Ocean [56,57] have indicated a lack of genetic variation between specimens of *S. latus* across the wide distribution range examined. This is a phenomenon of panmixia - the ability of individuals in a population to reproduce without restrictions over a very wide geographical range of hundreds to thousands of kilometers. The researchers explained this by the high fecundity of the *S. latus* and the prolonged larval stage in the open sea. Considering these findings, which indicated a high connectivity between geographically distant populations of *S. latus*, the researchers suggested [57] that future conservation strategies should manage all populations of this species together (as a single stock). For example, larvae from healthy populations of *S. latus* from the Balearic Islands in Spain may, therefore, restore suitable habitats in Italy where the populations of the Mediterranean slipper lobsters have been almost completely depleted.

In Israel, *S. latus* has been a protected species since 2005; however, illegal fishing continues. Due to the extensive marine area and insufficient number of inspectors/ rangers, the most effective method for protecting this species is through marine nature reserves. A study conducted in the Rosh Hanikra–Achziv Marine Reserve, a fully protected Marine Protected Area (MPA), and a comparable control area on Israel's northern coast [52] found that lobster abundance, density, and size were significantly higher within the protected reserve. Additionally, marked lobsters in the reserve tended to return to their dens during winter, unlike those in the control area. It is assumed that reserves may also benefit areas outside them by allowing adults, juveniles, and larvae to migrate into unprotected areas. Similar MPAs exist along the Mediterranean coast of Lebanon, such as the Palm Islands Natural Reserve in northern Lebanon (e.g., [58]), the Tyre Coast Nature Reserve in southern Lebanon [59], and the Sallum MPA, the first MPA on Egypt's Mediterranean coast [60].

The destruction of preferred habitats for *S. latus*, such as Submerged *Kurkar* Ridges (SKR) rich in caves, ravines, and natural dens [3], is another factor impacting their populations. Preserving these habitats is essential for the conservation and recovery of Mediterranean slipper lobsters and other threatened species. Environmentally safe and stable ARs, designed based on the lobsters' behavioral ecology, may provide effective hiding places and potentially serve as substitutes for destroyed natural habitats [61].

Rapid coastal urbanization, demographic growth, and industrial development can lead to chemical pollution in the shallow shelf. Elevated concentrations of trace metals, copper, zinc, and iron, were detected in *S. latus* specimens collected near Beirut compared to those from other coastal sites in Lebanon [62].

The sharp increase in seawater temperatures off the southeastern Levant coasts in recent years — due to climate change, reaching values above 31°C [3] may be harmful to *S. latus*. In laboratory conditions, lobsters' molting can be partial and complicated [63], sometimes resulting in death when kept for two months in seawater at 26°C or higher [41]. This may explain why lobsters migrate during the warm seasons to deeper, colder waters, which allow them to molt normally from a physiological standpoint. Molting involves shedding the old shell (exuvia) and growing a new one underneath, enabling the lobster to grow. However, during this time, the lobster's new outer shell remains soft, making it more vulnerable to predation. The migration to deeper waters may also be linked to reduced predation pressure in the darker depths. Information on the timing of molting is very limited and mainly based on a few reports of lobsters' exuviae found on the Israeli coast, mostly between November and February [15].

A laboratory study [64] indicated that slipper lobsters increase their activity as water temperature rises. These findings suggest that rising temperatures in the southeastern Mediterranean could affect the lobster's movements and seasonal distribution, potentially causing specimens to migrate to deeper waters earlier in the season. Climate change is also increasing the frequency and intensity of extreme weather events such as storms [3]. Notably, stranding of *S. latus* during two severe storms was recently reported off the northern coast of Israel [65].

The Mediterranean slipper lobster is classified as "Data Deficient" on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species [29]. Protecting a threatened species requires comprehensive information about its biology and ecology. However, because *S. latus* is primarily nocturnal and its populations are scattered, it is challenging for a small group of scientists to gain a complete understanding of its ecology. Consequently, the public, especially sea enthusiasts along the Mediterranean coast of Israel, was invited to assist in gathering data, such as the locations and timing of lobster exuviae and live sightings, through a "citizen science" approach [66]. Although the Israeli project has been brief, it has already yielded a few important reports that have contributed to expanding the biological knowledge of this species.

2.2. Locust Lobsters

Locust lobsters belong to a single subfamily, Scyllarinae, which included only one genus, *Scyllarus*, and at least 40 species. Most of these species are small and only a few have marginal commercial value, typically caught as by-catch [1]. Since 2002, some of the species have been assigned to other genera [67], but the two species known from the southeastern Mediterranean coasts remain in the genus *Scyllarus*.

2.2.1. The Small European Locust Lobster

The Small European locust lobster, *Scyllarus arctus* (Linnaeus, 1758) (Figure 5). Etymology of the scientific name: *skylarlos* (Greek) – a kind of crab or perhaps derived from *skulrow* (Greek) – torn or ragged (alluding to the antennal margins); *arctus* (Latin) –narrow (i.e., compared with other species), bear [28,29]. The FAO names for this species are - Petite Cigale (French) and Santiaguíño (Spanish)[1]. Other common or vernacular names include: Broad lobster (UK); Chambre, Petit scyllare (France); Cicala di mare, Magnosella (Italy); Lameiro, Lagosta da pedra (Portugal); Bujias, Cigarra, Toribo, Xuius (Spain); Chkal, Ziz il bahr, Petit cigal de mer, Cigal blnche (Tunisia); Astakouáki (Greece); Kapanit dubit (Israel)(refers to a small spoon-shaped bear-like lobster); Lesser slipper lobster (highlights its smaller size compared to other slipper lobsters) [30]. @@@

S. arctus is widespread throughout the Mediterranean Sea and the eastern Atlantic Ocean from the southern coast of the British Isles to the Azores, Madeira and the Canary Islands. It inhabits rocky substrates, often with caves, crevices and other shelters, as well as mudflats and seagrass beds, at depths of 4 - 50 m and occasionally beyond 200 m [35]. The species also occurs on ARs such as shipwrecks. Reports indicate seasonal migrations, with individuals moving to deeper waters in autumn and returning to shallower areas for breeding in spring. Total body length typically ranges from 5 - 10 cm, with a maximum body length of ~ 16 cm. *S. arctus* is of secondary importance, taken mainly as by-catch in coastal fisheries, for example along Spain's Atlantic coast [68]. @@@

The Small European locust lobster is a strikingly colorful species. Its rectangular cephalothorax bears three prominent central teeth. The body is reddish-brown with whitish scale tips and a dark brown spot in the center of each abdominal somite, though this marking is not sharply defined. The antennae ("shovels") are serrated. The abdominal joints are light blue with an orange stripe, forming a complex, fern-like pattern (Figure 5). The legs are yellow with dark blue stripes and red tips, while the bases of the eyes are orange red. Males are smaller than females. Like other slipper lobsters, this species is nocturnal, spending the day hidden in dens and caves where it is sheltered from predators, particularly benthic fish such as groupers



Figure 5. The Small European locust lobster, *Scyllarus arctus*, photographed by Dov Zingerman on 27 July 2019 at a depth of 18 m near Vela Luka, Croatia, in the Adriatic Sea.

2.2.1.1. Reproduction and Development

In the Mediterranean Sea, egg-bearing females have been observed year-round, with peak occurrences in March–April and July–September. Histological examinations confirm these as the main breeding periods. Each female carries 30,000–70,000 eggs, measuring 0.4–0.5 mm in diameter and yellow orange in color [35]. In laboratory conditions, larvae pass through 12–16 instars before molting to the benthic stage (nisto) after 192 days [35]. An oceanographic survey found that larvae are most abundant in eddies located about 250 km off the Israeli coast, which likely provide a suitable habitat for their early developmental stages [69].

2.2.1.2. Threats, Environmental Impacts and Conservation

S. arctus is listed as “Least Concern” on the IUCN Red List of Threatened Species [70] due to its wide distribution and the fact that it is only fished in part of its range. While local overexploitation does occur in some areas, and population declines have been recorded there, the species’ ecological characteristics have made it relatively resistant to extinction. This resilience is largely attributed to its high fertility and well-connected populations, supported by long-lived larvae that can survive for more than six months.

A 2009 assessment recommended continued monitoring of exploitation levels to detect potential increases in fishing pressure, alongside stricter enforcement and adjustments to current fishery management regimes [70]. For example, in northwestern Spain, the legal minimum body length for harvesting *S. arctus* (9 cm) ensures that sexually mature individuals have the opportunity to reproduce at least once a year. However, the area’s long reproductive cycle (about 11 months), combined with the near year-round presence of egg-bearing females and the prohibition on catching them, results in fishing being heavily biased toward males. This imbalance could reduce the reproductive potential of the stock due to a shortage of males [68].

The species is considered one of the most common crustaceans along the Lebanese coast [71], but it is likely less abundant in the southern waters of Israel and Egypt. It has not been recorded off the North African coast east of Morocco. Protection of *Posidonia* seagrass beds, a preferred habitat for *S. arctus* in areas where they occur, further enhances conservation of the species [70].

2.2.2. The Pygmy Locust Lobster

The pygmy locust lobster, *Scyllarus pygmaeus* (Bate, 1888) (Figure 6), is the smallest species of slipper lobster, with males reaching a maximum length of 54 mm and females up to 65 mm.

Etymology of the scientific name: *skylarlos* (Greek) – a kind of crab, or perhaps derived from *skulrow* (Greek) – torn or ragged (alluding to the antennal margins); *pygmaeus* (Latin) – dwarf or pygmy [28].
FAO names: in French – Cigale naine; in Spanish – Cigarra enana [1]. Other common or vernacular names include: nain cigale (France); Cicala minore (Italy) [30]; Kapanit Zutit (Israel) [72], meaning “small spoon-shaped miniature lobster.”

The pygmy locust lobster occurs at depths of 5–100 m [1], inhabiting sandy substrates, deep coral areas, and seagrass beds dominated by *Caulerpa prolifera* and Neptune grass, *Posidonia oceanica*, as well as caves in the Mediterranean Sea and around the Canary, Cape Verde, and Madeira Islands in the Atlantic Ocean. It has not been recorded off the coast of North Africa east of Morocco [1]. This species sometimes burrows into soft substrates and has also been collected at depths of up to 1,200 m [35]. In the Mediterranean Sea, it is considered less common, likely because individuals are sometimes misidentified as juveniles of the sympatric *S. arctus*, due to their similar serrated, flattened antennae (“shovels”). They can be distinguished mainly by size, *S. arctus* being larger, but also by specific morphological traits, such as the tubercle on the last thoracic sternite, which is flattened in *S. arctus* and conical in *S. pygmaeus* [73].

The coloration of *S. pygmaeus* is pale brownish or pinkish, with patches of darker setae (Figure 6) and bluish or orange stripes along the abdominal joints. The carapace is compact and bears small ridges. Their diet consists primarily of small live bivalves and occasionally dead fish.



Figure 6. The pygmy locust lobster, *Scyllarus pygmaeus*. Credit: Luis Sánchez Tocino (<https://litoraldegranada.ugr.es>), Granada University, Spain.

2.2.2.1. Reproduction and Development

In the western Mediterranean Sea, females carrying eggs have been observed year-round, with peak occurrence between April and July. In the eastern Mediterranean, the breeding season appears to be longer, and females with eggs have even been recorded in December at depths of 27–82 m [74]. Little is known about the larvae and early benthic stages. Recently, a stage VII phyllosoma larva of this species was reported from the Levant (Figure 7). It was collected far from shore, in the central part of the Israeli exclusive economic zone, at a depth of 0.5–1 m in waters with a bottom depth of 1,100 m [75]. This constitutes the first record of the larva of *S. pygmaeus* in the eastern Mediterranean Sea.

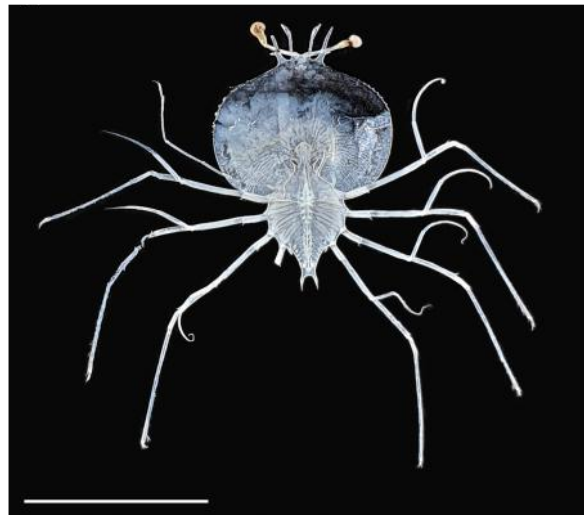


Figure 7. Dorsal view of a *Scyllarus pygmaeus* phyllosoma larva (stage VII), collected on 12 December 2022 using a horizontal tow with a Bongo plankton net (mesh size 65–200 μm) at a depth of 0.5–1 m, offshore in the central Israeli Exclusive Economic Zone (bottom depth 1100 m), southeastern Mediterranean Sea. Scale bar: 1 cm. (Photograph by Prof. T. Guy-Haim).

2.2.2.2. Threats, Environmental Impacts and Conservation

S. pygmaeus is classified as "Least Concern" on the IUCN Red List of Threatened Species. This is due to its wide distribution in the Mediterranean and eastern Atlantic, its small size and lack of economic interest. There is a local decline in the population in certain areas [76].

2.3. Occasional Species on the Mediterranean Coast

Only three lobster species have been recorded on the southeastern Mediterranean coasts, each reported just once. These include an adult male ornate spiny lobster, *Panulirus ornatus* (Fabricius, 1798) (Figure 8), caught in 1988 near the Haifa Port breakwater [77]; and a complete exuvia of an adult female long-legged spiny lobster, *Panulirus longipes longipes* (A. Milne Edwards, 1868) (Figure 9), found in the Haifa coastal waters in 2018 [78]. Both specimens were likely Lessepsian migrants [3]. In late 2022, two American clawed lobsters, *Homarus americanus* (H. Milne Edwards, 1837) (Figure 10), were reported on Arches Beach in Caesarea [79], on Israel's central coast, probably originating from lobsters imported from North America for restaurants in Israel.



Figure 8. Ornate spiny lobster, *Panulirus ornatus* (Credit: Prof. Clive Jones, James Cook University, Australia).



Figure 9. Exuvia of an adult female long-legged spiny lobster, *Panulirus longipes longipes* (Photographed by E. Friedmann, Israel).



Figure 10. Agonistic interaction between two American clawed lobsters, *Homarus americanus* (photographed by Michael Tuval in very shallow water, 20–30 cm deep, off the coast of Caesarea, Israel, on 30 December 2022).

3. Lobsters from the Northern Red Sea

On the coasts of the GoA and GoS there are representatives of both the families of slipper lobsters, Scyllaridae, and spiny lobsters, Palinuridae. Lobsters of the later family are characterized by a very long thick, spiny antennae that are longer than the body length and the four front pectoral legs without chelae.

3.1. Clamkiller Slipper Lobster

The Clamkiller Slipper Lobster, *Scyllarides tridacnophaga* Holthuis, 1967, closely resembles its Mediterranean congener, *S. latus*. Likewise, it is primarily nocturnal, hiding in dens during the day

[80]. The etymology of its scientific name derives from Greek: *skylarlos* meaning a kind of crab, and *tridacnophaga* combining *tridacna* (referring to giant clams) and the suffix *-phaga* (meaning "eater" or "devourer"), reflecting its habit of preying on giant clams [29]. FAO common names include "Clamkiller slipper lobster" (English), "Cigale de mer" or "Cigale Marie-carogne" (French) and in Saudi Arabia and Egypt (Arabic) "sartan al-baḥr 'abu shḥāṭa" (the sea crab abu shkhta) and "Saltu'un malikat al-rukhawiyat" (literally, Crab of the Queen of Mollusks). In Hebrew, it is called "Kapan Hatsdafot" (literally, The Clams' Slipper Lobster) [72].

This species is the largest slipper lobster in the Northern Red Sea, with a maximum length up to 40 cm, though the average size is about 30 cm. It typically inhabits coral reef areas or rocky substrates in shallow waters, ranging from 5 to 112 meters deep, and has also been found in seagrass meadows, such as those dominated by *Halophila stipulacea*, and sandy bottoms. Its geographical distribution spans the Indo-Pacific region, from the western Pacific Ocean along the western coasts of Thailand, India, and Pakistan, extending to East Africa (Somalia and Kenya), the Gulf of Aden, and the Red Sea [1].

The color of *S. tridacnophaga* is generally reddish to yellowish-brown, featuring a mottled pattern on the dorsal side and pale orange on the ventral side (Figure 11). Most of the bumps on the shell, as well as the edges of the flattened antennae, are reddish. The flagella at the tip of the orange antennulae are deep purple. The legs are orange, with purple joints. The upper part of the first abdominal segment is mostly smooth and bears three large, sharply defined red spots—one central and two lateral—all round in shape (Figure 12). The spaces between the spots are approximately as wide as the spots themselves. In contrast, the Mediterranean *S. latus* displays a central red spot surrounded by a yellow ring, flanked on each side by two prominent, non-round red spots separated by very narrow spaces [80].



Figure 11. The Clamkiller Slipper Lobster (*Scyllarides tridacnophaga*) on fern seagrass (*Halophila stipulacea*). Photographed by Amit Zeevi in Eilat, Gulf of Aqaba, Israel, at 10 m depth on May 14, 2022.

3.1.1. Food

S. tridacnophaga is able to open giant clams of the genus *Tridacna*. These clams anchor themselves to hard substrates using byssal threads. The lobster manipulates the clam to expose its dorsal surface, where the byssal thread attachments protrude, and then plunges its dactyls (the terminal segments of the legs) into this vulnerable area, causing the clam to gape. It likely destroys the adductor muscle or damages the nervous system that controls shell closure. At this stage, the lobster overturns the shell, inserts its legs to further wedge the valves open, and feeds on the living tissues [81]. In addition to giant clams, it also preys on other clams and scavenges dead fish [1]. Individuals sometimes forage in groups of three or more and exhibit gregarious sheltering during the day.

3.1.2. Reproduction

The breeding season occurs during the spring and summer months. During courtship, *S. tridacnophaga* rely on their senses of smell and touch. Fertilization is usually external, with the female carrying the eggs until they hatch, after which the larvae are released. The Marine Science Station (MSS) in Aqaba, Jordan, has successfully maintained several clamkiller slipper lobsters in captivity. At the field laboratory of the Central Marine Fisheries Research Institute (CMFRI) in Madras, India, four individuals, both males and females, were kept. Reproduction occurred in late June, producing round eggs approximately 0.5 mm in diameter. The eggs were initially light yellow, gradually turning orange and then rusty brown. Adult growth is slow, particularly in males [82].

Recently, a single-file queue of three *S. tridacnophaga* was observed in the evening on a sandy bottom north of a shipwreck in Eilat, Israel, at the northern edge of the GoA (Figure 12). This behavior resembles the queuing reported for Caribbean spiny lobsters, *Panulirus argus*, during their autumnal mass migrations (e.g., [83]). It remains unclear whether this behavior is related to foraging, reproduction, defense, migration, or other activities.

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3.1.3. Threats, Environmental Impacts and Conservation

S. tridacnophaga is listed as “Least Concern” on the IUCN Red List of Threatened Species. However, due to its large size, it is caught in Kenya, either by diving or as bycatch in trawl fisheries, and probably also in other parts of its range. A continuing decline in the number of adult individuals has been reported [84]. It is also occasionally entangled in ghost nets (discarded or abandoned fishing gear).



Figure 12. A single-file queue of three Clamkiller Slipper Lobsters, *Scyllarides tridacnophaga*, on a sandy bottom north of the Sun Boat diving site, Eilat, northern Gulf of Aqaba, Israel, at a depth of 8 m on 8 June 2025 (video by Ziv Regev; still image prepared by Eran Shushu Spanier).

3.2. The Lewinsohn Locust Slipper Lobster

The Lewinsohn Locust Slipper Lobster, *Scyllarus lewinsohni* (Holthuis, 1967) [85], has since been reclassified as *Eduarctus lewinsohni* (Holthuis, 1967) [85,86].

Etymology – The genus name *Eduarctus* combines part of the name *Eduard*, honoring Eduard von Martens, for whom the type species was named, with the generic name *Arctus* De Haan, 1849. The word *arctus* (Latin) means “narrow” (i.e., compared with other species) or “bear” [28]. The species name *lewinsohni* commemorates the late Israeli crustacean expert Chanan Lewinsohn [85]. Its Hebrew name is “Kapanit Lewinsohn” (Lewinsohn locust lobster) [72].

Very little is known about this small species. On the IUCN Red List of Threatened Species, it is listed as “Data Deficient,” with a noted decline in the number of mature individuals in its fragmented population. However, this assessment dates back to 2009 [85].

Due to its small size, it has no commercial value and is not threatened by fishing. It has been recorded at depths of 20–82 meters in the Red Sea north of Bab-el-Mandeb (the southern entrance to the Red Sea), in the southern GoS, and in Eilat, Israel, the GoA. The cephalothorax measures 6–12 mm in length, with a maximum overall size estimated at 3–4 cm. Like other locust lobsters, its carapace is highly compressed and features small ribs on the surface. The coloration of *E. lewinsohni* is reddish-brown on the sides of the cephalothorax, marked with several large white spots and a few smaller dots of similar color. The abdominal segments display a complex red and white fern-like pattern in the center and along the sides [85]. The legs are yellow with dark lines (Figure 13).



Figure 13. Lewinsohn locust lobster (*Eduarctus lewinsohni*), Eilat, northern Gulf of Aqaba, Israel, at approximately 5 m depth on the shallow reef opposite the Interuniversity Institute for Marine Sciences, 9 August 2019. Estimated total length: 3–4 cm. (Photographed by Dr. Gil Koplovitz).

3.3. Evidence of a New Species of Pygmy Slipper Lobster in Eilat the Gulf of Aqaba—*Biarctus sordidus*

A phyllosoma larva of a pygmy slipper lobster species, previously unknown in the Red Sea [87], was recently sampled in the northern GoA (Figure 14). The distribution of this species, the pygmy slipper lobster, *Biarctus sordidus* (Stimpson, 1860), whose English name is similar to the Mediterranean *Scyllarus pygmaeus*, was previously known only from the Far East to the Persian Gulf [85]. Etymology: *Bi-* means “life” (Greek), *arctus* means “narrow” or “bear” (Latin), referring to its comparatively narrow shape [28,29]. *Sordidus* (Latin) means “dirty” or “foul.” The taxonomy of *B. sordidus* has changed over time. Initially, it was classified as *Scyllarus sordidus* and *Arctus sordidus*, but subsequent studies reclassified it as *Biarctus sordidus* [85,88]. This species is closely related to other slipper lobsters, with its classification based on both morphological and molecular data. The larva was collected using a plankton net towed horizontally at a depth of 0.5–1 m, over a bottom depth of 700 m. The specimen was identified as a phyllosoma stage III/V of *B. sordidus* based on morphology and DNA barcoding. Researchers suggest that previous Red Sea biodiversity surveys may have confused *B. sordidus* with its congener *B. pumilus*, which is known from the Red Sea [85]. An additional/alternative explanation for the late detection of *B. sordidus* is that the species was recently introduced via ballast water of a merchant ship that arrived at the port of Eilat, Israel at the north edge of the GoA, or the close-by port of Aqaba, Jordan from the Far East. This is despite the fact that there is still no report of the transfer of phyllosoms via ballast water.



Figure 14. Ventral view of a phyllosoma stage III/V larva of the pygmy slipper lobster, *Biarctus sordidus*, sampled on 17 April 2024 off Eilat, Israel, in the northern Gulf of Aqaba (29°28'N, 34°55'E). The specimen was collected at a bottom depth of approximately 700 m using a plankton net (200- μ m mesh size, 50 cm opening diameter) towed horizontally at 0.5–1 m depth. Scale bar: 500 μ m (Photographed by Prof. T. Guy-Haim).

3.4. The Pronghorn Spiny Lobster

The Pronghorn Spiny Lobster, *Panulirus penicillatus* (Olivier, 1791) is the largest spiny lobster in the Northern Red Sea. Its maximum body length is about 40 cm or more, the average length of an adult lobster is about 30 cm, and males are larger than females [1]. Etymology: The genus name *Panulirus* is likely derived from the Greek "pan" (all, whole) and "oura" (tail), possibly describing the lobster's large, fan-like tail. It may also be an anagram (a word formed by rearranging the letters of a different word) of the lobster genus *Palinurus* [28]. The species name, *penicillatus*, is derived from the Latin "penicillus," meaning "paintbrush" or "pencil" [28], likely referring to the brush-like tufts of setae (bristles) found on its legs and body (Figure 15). FAO names: Pronghorn spiny lobster (English), Langouste fourchette (French), Langosta horquilla (Spanish) [1]. Other common /vernacular names are: Common spiny lobster, Red lobster, Golden lobster, Rock lobster, Double spined lobster, Fourspine rock lobster, Coral cray, Socorro spiny lobster, and "Jirad albahr hasir" (Arabic) in Saudi Arabia [89] and "Mekhoshtan Kotsani" in Hebrew [90] (literally: has spiny tentacles).

The body of this lobster is elongated, with the second pair of antennae extending beyond the length of the body. It is very spiny and lacks banding [1]. The legs (pereiopods) do not have pincers, and the front of the cephalothorax features large spines that protrude above the eyes. *P. penicillatus* displays striking coloration (Figure 15). Its body color varies widely, ranging from yellowish-green and greenish brown to dark rusty-brown or bluish black. The head, thorax, and abdomen are mottled with tiny whitish spots, with two fairly large whitish spots located on the sides of the first abdominal segment. The abdominal appendages (pleopods) are dark with light margins, while the legs display longitudinal yellowish-white lines or stripes set against a darker greenish or reddish background. The tail fan at the end of the abdomen is very wide, predominantly bright blue or greenish-gray, and edged with vivid orange.

This species has an extremely wide circumtropical distribution, ranging from the Red Sea and the western Indian Ocean to the eastern Pacific Ocean [1]. Despite its broad range, biological knowledge about this species remains limited compared to other spiny lobsters.

During the day, it hides in rock crevices and beneath the outer edges of coral reefs, typically in fixed locations, becoming primarily active at night. It inhabits shallow waters between 1 and 16 meters deep, most commonly at depths less than 4 meters, though it has occasionally been observed in deeper waters (e.g., [91]). The pronghorn spiny lobster favors rocky substrates in clear waters, away from river mouths, often in areas with wave breaks, as well as on arid beaches and small islands [92].

It usually shelters alone, but gregarious behavior has been observed, with groups often exceeding 20 individuals [93], a tendency also noted in some other spiny lobster species (e.g., [94]).



Figure 15. The pronghorn spiny lobster, *Panulirus penicillatus*, Coral Coast Nature Reserve, Eilat, northern Gulf of Aqaba, Israel, 22 July 2015, at a depth of 2.5 m. Estimated length (excluding antennae) ~ 40 cm (Photographed by Bader Levi).

3.4.1. Reproduction and Development

The sex ratio did not differ significantly from 1:1 [92,93]. Females reach sexual maturity in the wild at a cephalothorax length (CL) of 50 mm. The breeding season in the GoA spans from February to October, during which females lay 2–4 clutches. The number of eggs is directly proportional to cephalothorax length. The incubation period for the eggs is approximately 35 days at temperatures between 24 and 27 °C [92]. Phyllosoma larvae of this species have been successfully reared in aquaria from hatching until they metamorphosed into active pueruli, which can swim freely and settle on substrates when near suitable shallow habitats. In the laboratory, completing this life cycle required 8–10 months and involved 20 molting stages [95]. In terms of size distribution and size-specific fecundity, the Saudi Red Sea population closely resembles those in the GoA and the Philippines but differs markedly from populations in Palau and Enewetak [96].

3.4.2. Food and Anti-Predatory Adaptations

The pronghorn spiny lobsters are generalist feeders, primarily consuming benthic invertebrates such as mollusks, crustaceans, and sea urchins, whose hard parts they break with their strong upper jaws. Their diet may also include polychaetes, brittle stars, and fish remains. In some regions, they also feed on algae. Lobsters inhabiting carbonate reefs tend to consume more mollusks than those from granite reefs, and larger lobsters likely feed closer to the coast or rely more on detritus feeders than smaller individuals [97].

There are no specific reports on their predators. However, based on known predators of other lobster species, large fish such as the orange-lined triggerfish, *Balistapus undulatus*, and groupers may prey on adult *P. penicillatus* in the northern Red Sea. The lobsters' diurnal sheltering and nocturnal activity serve as anti-predator adaptations against daytime predators. *P. penicillatus* has a notably large head equipped with considerable defensive mechanisms in the wild [98]. It is protected by numerous spines on its shell and by long, spiny antennae that may be used to fend off predators. The seaward reef margin preferred by this species may also present a lower risk of predation. Additionally, the robust pereopods characteristic of *P. penicillatus* enable it to forage effectively in

strong surge conditions, likely providing a selective advantage that allowed this species to colonize and thrive in this habitat, which may serve as a refuge from predators [97].

3.4.3. Threats, Environmental Impacts and Conservation

P. penicillatus is fished throughout its wide range, primarily caught by hand or spear gun during daytime skin and SCUBA diving, or using torchlight near the surface at night. Traps have proven ineffective for this species, whereas trammel nets tend to yield better results [1]. Overexploitation has caused local declines in some areas, including the Northern Red Sea. Despite this, the species is classified as "Least Concern" on the IUCN Red List of Threatened Species due to its broad distribution. A 2009 assessment concluded that fishing did not significantly impact on the global population [99]. However, since this assessment is now almost 16 years old, current fishing levels should be re-monitored to detect any increases in exploitation and to provide an updated measure of the species' abundance. *P. penicillatus* is protected in Israeli waters of the GoA, with particularly effective protection within nature reserves MPAs) such as the Eilat Coral Nature Reserve (e.g., [100]), the Aqaba MPA in Jordan [101], and Egyptian marine reserves in the GoA, including Abu Galum Managed Resources Protected Area, Nabq Managed Resources Protected Area, and Ras Mohammed National Park [60]. Several studies have documented positive effects of MPAs on lobsters, including increased abundance, density, biomass, catch-per-unit-effort (CPUE), and size [102]. However, this trend was not observed for *P. penicillatus* within the Galapagos Marine Reserve, where populations declined, likely due to weak enforcement and illegal fishing [103]. No significant changes in lobster size or size-frequency distribution were detected after more than 11 years of protection. Scientists suggest that poaching inside MPAs is a major factor limiting the recovery of lobster populations in this region.

4. Discussion and Conclusions

Despite the oligotrophic nature of the Southeastern Levantine Sea and the Northern Red Sea, six species (five slipper lobsters and one spiny lobster) maintain permanent reproductive populations in the study area, along with single reports of four additional sporadic lobster species. Biological knowledge of the permanent lobster species in this region has expanded in recent years, particularly for the larger, commercially valuable species (*S. latus*, *S. tridacnophaga*, and *P. penicillatus*). However, even for the adult stages of these species, there remain significant gaps in understanding their genetics, life history, reproduction, behavior, sensory biology, diet and feeding habits, predators and anti-predator adaptations, movement, physiology, growth, distribution, fisheries, and conservation status. This lack of information is even more pronounced for the post-embryonic oceanic stages, the naupliosoma in some, perhaps all species, and the free-living phyllosoma larvae, whose larval period can range from a few weeks to over nine months depending on the species. Data on the nektonic niso postlarvae, which settle and initiate the benthic juvenile phase, are rare. Biological knowledge of the smaller and often cryptic species (*S. arctus*, *S. pygmaeus*, and *E. lewinoi*) is even more limited.

To bridge this knowledge gap, focused studies employing modern technologies, such as underwater video cameras, Remotely Operated Vehicles (ROVs), acoustic tagging, and DNA barcoding, are needed both in coastal waters and in the deep, open sea. However, because lobsters are widely dispersed across time and space, it is challenging for a limited number of scientists to systematically collect data across such vast marine and coastal areas. Therefore, the scientific community must engage the general public active along coasts and at sea—professional and sport fishermen, skin and SCUBA divers, and beachgoers—through Citizen Science initiatives (e.g., [66,104]). Since lobster distributions often cross international borders, international Citizen Science surveys are necessary whenever possible. The findings from the few existing Citizen Science studies on lobsters emphasize the importance of integrated approaches to monitoring cryptic, sometimes low-density species like lobsters.

Notwithstanding four remote records of different lobster species from other biogeographic regions, mainly the Indo-Pacific, there is currently no evidence of established reproductive

populations of these species in the new areas. Many Lessepsian crustaceans have formed viable, permanent reproductive populations in the Mediterranean, where crustacean NIS are the second-most abundant invertebrate group, comprising more than a hundred species belonging to the order Decapoda [105,106]. Some of these species contribute positively to commercial fisheries, while others outcompete native commercial crustaceans. However, no lobster NIS has established a permanent reproductive population in the study area. It has been suggested [107] that the passage of lobster sensitive propagules via ship ballast water is unlikely due to the long and complex life cycle of these crustaceans. Additionally, it is doubtful whether the delicate planktonic early stages of lobsters can survive and complete their development under the environmental conditions of the destination regions.

However, Lessepsian migration may impact Mediterranean lobsters indirectly through changes in their food sources and predators. A recent study reported a significant collapse in marine mollusk populations in the eastern Mediterranean over the past decades [108]. The authors attributed this decline primarily to seawater warming, which has rendered conditions unsuitable for native mollusk populations. They described this event as the largest climate-driven, regional-scale biodiversity loss documented in the oceans to date. Furthermore, they predict that as climate warming continues, this native biodiversity collapse will worsen and spread geographically, with only Lessepsian species entering through the Suez Canal potentially mitigating the decline. Restoration to historical baselines, they argue, is unlikely. How will such a dramatic shift in mollusk populations affect lobsters, which heavily rely on mollusks, especially bivalves, as a food source? Lessepsian predators may also influence Mediterranean lobsters. For example, the lionfish, *Pterois miles*, was first recorded in the eastern Mediterranean in 2012. Since then, its population density has increased dramatically, making it extremely common in the coastal waters of the Levant, from very shallow areas to depths greater than 100 m. *P. miles* has a high reproductive potential: individuals reach maturity within a year, and adults are capable of spawning year-round, with peak spawning during summer. Lionfish in the Levant grow faster and larger than in their native range, and females outnumber males. As generalist predators, lionfish consume a wide range of teleost and crustacean prey, including species of high economic value [109]. Given their effectiveness in preying on benthic fish and invertebrates, they are assumed to prey on juvenile *S. latus* and probably also on adults of smaller scyllarid species. For instance, a 17 mm juvenile Spanish slipper lobster (*Scyllarides aequinoctialis*) was found in the gut contents of a 310 mm invasive red lionfish (*Pterois volitans*) in Belize [110]. Additionally, the highest attack rates and shortest handling times by adult *P. volitans* were observed for the Norway lobster (*Nephrops norvegicus*) [111]. However, this assumption regarding *P. miles* in the Levant still needs to be confirmed by stomach content analyses.

The most effective “predator” of lobsters, although evolutionarily recent, is *Homo sapiens*. Lobsters have been targeted by fisheries from prehistoric times through the 21st century [24]. However, modern fishing pressure has sometimes been too intense, leading in some cases to the depletion of local lobster populations to levels from which they cannot recover (e.g., [55]).

One approach to protecting lobster populations primarily involves regulating fishing seasons, limiting lobster size, controlling fishing gear (such as traps and nets), and setting harvesting quotas to promote sustainable practices. In some cases, lobsters have even been declared protected species, making their removal from the sea illegal. However, these regulations are not always effective or enforced, due to the vastness of marine inspection areas relative to the limited number of inspectors/rangers [102], as well as insufficient public education among those active at sea.

Another approach is to establish MPAs or nature reserves. The protection offered by no-take MPAs can lead to significant improvements in four key criteria within their boundaries compared to fished control areas outside the reserves: biomass, density, individual size, and species richness [112]. Several studies have demonstrated positive effects on lobsters within MPAs, including increased abundance, density, biomass, catch-per-unit-effort (CPUE), and individual size [102]. The single quantitative study on the effect of an MPA on *S. latus* in the southeastern Mediterranean highlighted some of these positive outcomes [52]. These benefits may also extend to lobster fisheries, as MPAs

can supply propagules, juveniles, and adults to unprotected areas through the “spillover” process. However, this aspect was not examined in the recent study on the effect of a no-take reserve on *S. latus* in the southeastern Mediterranean [52] and warrants further investigation. Some reserves fail to show positive effects, potentially due to factors such as MPAs being too small relative to the home ranges of lobster species, their location, size, shape, protection of lobster predators, ineffective enforcement against illegal fishing, and “edge effects” (e.g., [103]). Therefore, there is a clear need for more and larger MPAs to protect lobsters (and other important or threatened species) in the study area, alongside stronger enforcement in existing marine reserves. In cases where lobster fishing is allowed, establishing a minimum legal size for the fishery and protecting egg-bearing females should be strictly enforced.

Additional important aspect of lobster conservation in the study area is the destruction of their preferred natural habitats, such as the morphologically complex SKR, which provides natural dens for lobsters [3]. Marine construction activities, such as building ports, can cause significant damage to SKR. For example, during the construction of the new Bay Port in Haifa Bay, a 2.2 km long and up to 19 m deep entrance channel was excavated through SKR to accommodate the newest giant ships [3], resulting in the loss of a considerable portion of natural lobster habitat. Extensive underwater sand dredging associated with port construction may also cause silting. With the influence of wind and currents, this silting can be carried to nearby SKR areas, disrupting the vital filtration processes of bivalves [3], which, as previously mentioned, are an important food source for lobsters. To mitigate the loss of essential natural habitats, environmentally safe and stable ARs can be deployed. These should be designed based on the behavioral ecology of the specific lobster species, considering factors such as the size, number, and configuration of the ARs, as has been successfully implemented in the southeastern Mediterranean [113] and the GoA [114]. The best practice would be, rather than crushing natural rock (*kurkar* or coral rocks) and pumping out the fragments, to cut large pieces of natural rock and use this durable material to build the ARs.

The lobster species discussed in this review were previously classified by the IUCN Red List as either “Data Deficient” or “Least Concern” [55,70,76,84,86,99]. However, these assessments were made at least 15–16 years ago and are due for updating. Given the environmental changes and new data accumulated since then, it is timely to re-evaluate these IUCN statuses.

Finally, unfortunately, in recent years, parts of the study area have been affected by war activities. Missiles, detonated drones, and other explosive devices have landed in coastal waters and exploded. What impact have these events had on lobsters, their habitats, and fisheries? No direct studies have specifically examined this subject in lobsters. However, research on other marine animals (e.g., [115]) indicates that underwater blasts can cause significant harm, ranging from direct physical injury to behavioral disturbances and ecosystem damage. Explosions generate powerful shock waves that may damage internal organs, rupture cell membranes, and even cause death. Additionally, these blasts can destroy habitats and disrupt animals’ abilities to communicate, find food, and navigate their environment. The severity of the impact depends on factors such as species, size, and proximity to the explosion. Recent studies (e.g., [116]) on the effects of seismic surveys using sub-surface air guns, which create intense sound waves penetrating the substrate, have shown that these sound waves can affect lobster physiology and short-term behavior. For example, Western rock lobsters, *Panulirus cygnus*, exposed to air guns exhibited short-term behavioral changes related to predator avoidance, and fewer tagged lobsters were recaptured by commercial fishers.

On the other hand, civilian anthropogenic pressure from commercial and sport fishermen, divers, and others, on lobsters is considerably reduced during wartime due to restrictions on non-military activities at sea (e.g., [117]). However, this reduction in civilian pressure is not expected to offset the significant damage caused by underwater warfare explosions on lobster populations.

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