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Fouling of the slipper lobster, *Scyllarides latus*, by cyclostome and ctenostome bryozoans in the Mediterranean Sea off Malta

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ABSTRACT: A Mediterranean slipper lobster, *Scyllarides latus* (Latreille, 1802), was found near Malta in the Mediterranean Sea. It was conspicuously fouled by bryozoans which is a rare occurrence for lobsters in general, including this species. Based on its size, it was estimated to be an adult with an age of eight years and is eight months post-molt. Five erect branching *Crisia* sp. cyclostome bryozoan colonies, three encrusting lichenoporid cyclostome bryozoan colonies, and a few small ctenostome colonies were found on the dorsal surface of the lobster. The potential costs and benefits of this rare epibiotic relationship for the lobster and the bryozoans are reviewed. The goal of this paper is to describe this rare relationship between epizoic bryozoans and a slipper lobster.

1 INTRODUCTION

Epibiosis is the ecological relationship between organisms growing attached to a living surface such as the bryozoans on the lobster in this study. We follow the terminology of Wahl (1989) and refer to the slipper lobster as the basibiont (i.e. the motile host arthropod substrate) and the bryozoans as the epibiont (i.e. the sessile organism attached to the basibiont's exoskeleton). Fouling refers to the more general colonization process of a solid surface, living or dead, by epibionts (Wahl 1989). Here we use epibiosis and fouling interchangeably. Some epibionts are opportunists that simply require a hard substrate, others are obligate symbionts. Epibiosis is important because fouling epibionts degrade the functionality of ship hulls, heat exchangers, and water intake pipes (Hellio & Yebra 2009). The presence of epibionts like bryozoans can cover hosts' eyes, inhibit hosts' wound healing, decrease hydrodynamic efficiency of hosts, and result in an unappealing appearance of the affected lobster tails (the main consumable part of all lobsters), which lowers their commercial value (Zha *et al.* 2017).

A variety of organisms can foul the exoskeleton of lobsters, including bryozoans, hydroids, barnacles, serpulid worms, molluscs and many microorganisms (Key *et al.* 2021). Epibionts on lobsters are not as common as on other basibionts. This has been attributed to grooming by the host to remove settling larvae (Phillips *et al.* 1980; Quinn *et al.* 2009) and molting. Because lobsters typically do not have a terminal molt, they continue to molt throughout life, casting off any accumulated epibionts (Shields 2011). Thus, fouling of lobsters, such as reported here, is unusual.

The objective of this study is to describe a rare occurrence of bryozoans fouling the Mediterranean slipper lobster *Scyllarides latus* (Latreille, 1802).

2 MATERIALS AND METHODS

A Mediterranean slipper lobster, *Scyllarides latus* (Latreille, 1802) was noticed during a SCUBA dive on 27 July 2021 as it was conspicuously fouled by bryozoans (Figure 1A). It was found 40–50 m off the north coast of the island of Gozo, Malta in the Mediterranean Sea (36.080874°N, 14.241772°E) at a depth of 21.3 m (Figure 2). The water temperature was 23°C. For photographic documentation, a Canon PowerShot G7 X Mark II (Canon, Tokyo, Japan) in a Fantasea (Fantasea Photo and Marketing Ltd., Blaine, Washington, United States) underwater housing was used with an additional +7 diopter for higher magnification.

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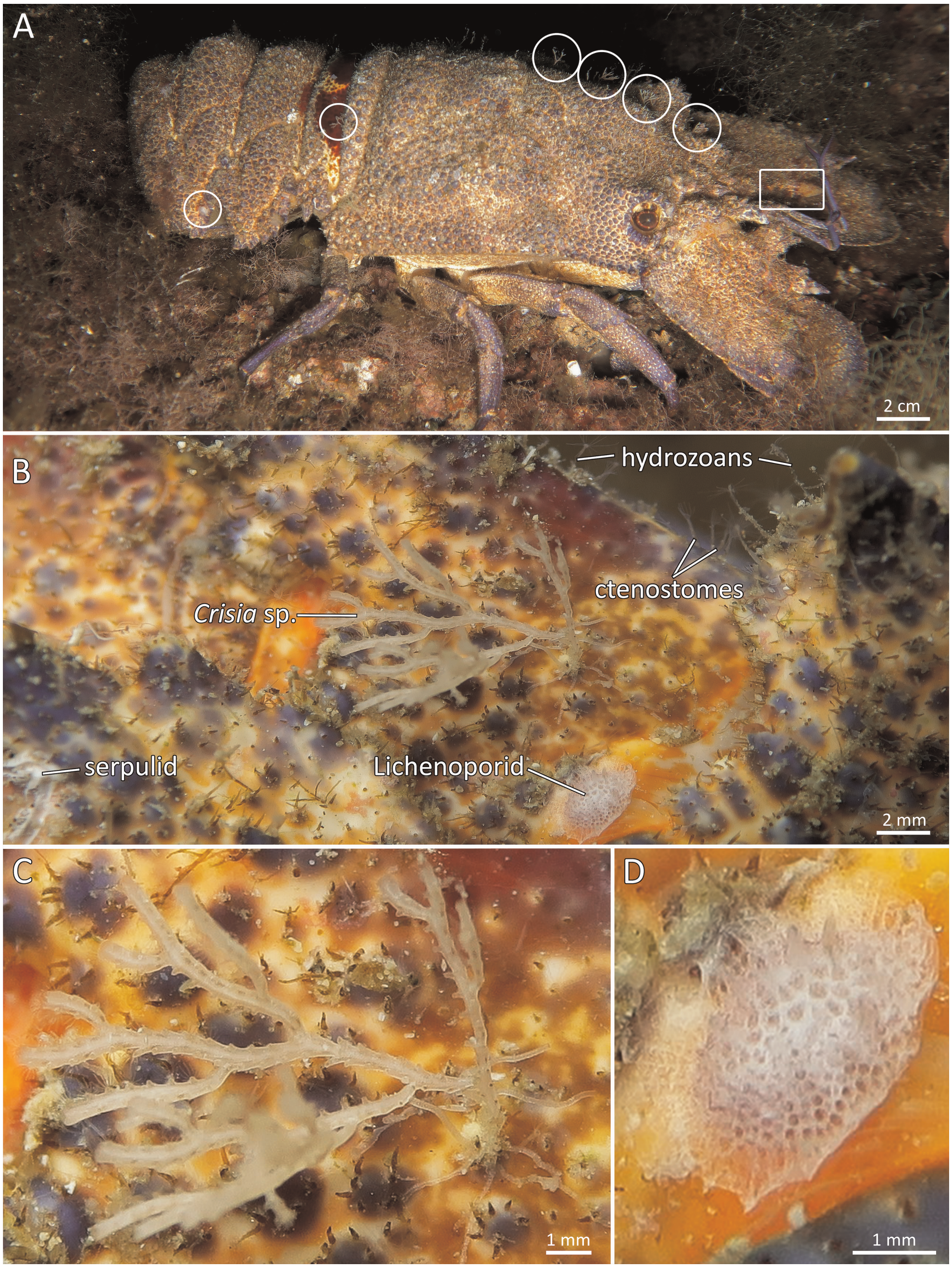

Figure 1. The Mediterranean slipper lobster, *Scyllarides latus*, examined in this study. A, bryozoan colonies on host's carapace circled. B, closeup of rectangle in A showing the diversity of epibionts. C, close up of erect *Crisia* sp. colony in B. D, close up of encrusting lichenoporid colony in B.

This lobster's main defense mechanism is their fortress strategy (Lavalli *et al.* 2007). This involves clinging tenaciously with their sharp pointed stout legs to a rough substrate protected by their broad flattened heavily armored carapace, similar to a limpet (Barshaw & Spanier 1994a, 1994b; Spanier & Lavalli 1998). Their clinging force is up to 150 N, equivalent to 29 times their body weight (Spanier & Lavalli 1998). Therefore, to prevent damage to the delicate erect bryozoan colonies, the lobster was not pried off its rocky substrate. Thus, we were unable to photograph the ventral surface

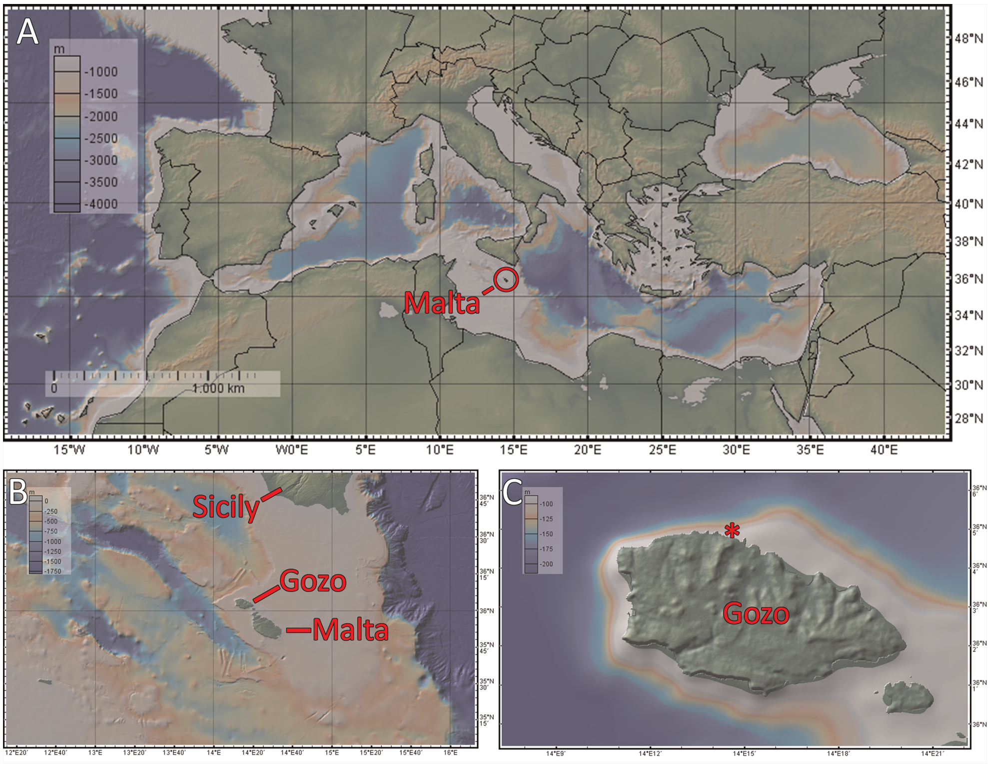

Figure 2. Bathymetric maps of the Mediterranean Sea. A, general location of Malta marked by a red circle. B, close-up of the Strait of Sicily showing islands of Malta and Gozo relative to Sicily. C, close-up of the Island of Gozo with the exact locality of the investigated slipper lobster (*Scyllarides latus*) marked by a red asterisk (36.080874°N, 14.241772°E). Maps were generated with GeoMapApp 3.6.14 using the Global Multi-Resolution Topography synthesis by Ryan *et al.* (2009).

and to observe the sexual orifices and the sexually dimorphic shapes of the pereiopods on the ventral surface (Romeo *et al.* 2004; Spanier & Lavalli 1998). Therefore, we did not determine the sex of the lobster.

3 RESULTS

Compared to other lobsters in the vicinity, the host lobster was fully mature and 25–30 cm in total length. Total length is not the usual size metric in lobsters; carapace length is the standard metric (Phillips *et al.* 1980). Using Martins (1985, fig. 3) to predict carapace length from total length in *S. latus*, our lobster would have had a carapace length of ~10 cm.

We counted five erect branching *Crisia* sp. cyclostome bryozoan colonies, three encrusting lichenoporid cyclostome bryozoan colonies, some small unidentified ctenostome bryozoan colonies, three encrusting serpulids, and some small hydrozoans (Figure 1B). All were growing on the dorsal surface of the host lobster, specifically the carapace and the enlarged flattened left second antennae. As stated above, we did not have access to the ventral surface. With only field photographs and no prepared SEM images, we could not determine the exact species of the bryozoans. The erect *Crisia* sp. colonies were up to 1 cm tall (Figure 1C). The *Crisia* colonies were either *C. sigmoidea* Waters 1916 or *C. oranensis* Waters 1916. The disc shaped lichenoporids were either *Disporella* sp. or *Patinella radiata* (Audouin 1826) and were up to 3 mm by 4 mm (Figure 1D).

4 DISCUSSION

A carapace length of 10 cm indicates an individual of 8 years of age (Bianchini & Ragonese 2007, fig. 9.1). An 8 year old lobster is an adult, and adult individuals of *S. latus* typically molt annually over the winter months, November to February (Bianchini *et al.* 2001; Martins 1985; Spanier *et al.* 1988; Spanier & Lavalli 1998). Therefore, based on the July date of our lobster, it was probably seven months, but up to eight months, post molt. The more recently *S. latus* has molted, the "cleaner" the carapace is (i.e. free from epibionts) (Bianchini *et al.* 2001; Spanier & Lavalli 1998). The lobster in this study was likely 58–67% of its way through its molt cycle, and thus an older, more fouled host.

We used Smith's (1992) experimental data on bryozoan colony growth rates to estimate the age of the largest (i.e. 1 cm tall) *Crisia* colony in this study. Smith (1992) did not include this weakly calcified genus in her study but did include another weakly calcified erect cheilostome species, *Caberea zelandica*. A 1 cm tall colony, weighing 0.020 g (Smith 1992, tbl. A1.3), and growing at 0.030 g/year (Smith 1992, tbl. 1D.2) would have been 8 months old. Even though these species are from different clades and environments, it adds credence to the estimate of the host lobster being up to 8 months post molt, assuming the host lobster was fouled by the bryozoan larvae soon after molting. This is possible as the carapace of *S. latus*, like other slipper lobsters without defensive claws and spines, hardens within 3–24 hours as compared to the prolonged post-molt soft condition of clawed lobsters (Barshaw *et al.* 2003; Horne & Tarsitano 2007).

The key for a successful epibiotic relationship, from the bryozoan perspective, is that the epibiont must reach reproductive maturity in less time than it takes for the basibiont to complete its molt cycle. Were the bryozoan colonies big enough to have sexually reproduced to make this host lobster basibiont a viable substrate? There is no data relating erect colony size to timing of sexual maturity, and no ovicells or embryos were visible on the colonies. But there is such data for encrusting cheilostome species, and it ranges widely. For example, *Rallocytus ridiculs* reaches sexual maturity at only four zooid size, many interstitial species reach sexual maturity by <10 zooids, *Drepanophora* sp. by 30 zooids, *Parasmittina* sp. and *Stylopoma spongites* by 150 zooids, but *Stylopoma* sp. not until it has 4600 zooids (Grischenko *et al.* 2018; Herrera *et al.* 1996; Jackson & Wertheimer 1985; Winston & Hakansson 1986). The encrusting cyclostome colonies were ~100 zooids in size. Thus, it is possible that these bryozoan colonies may not have reached sexual maturity before their host molted.

Most of the epizoic bryozoans in this study were cyclostomes. Cyclostomes are not as common as epizoans compared to cheilostomes and ctenostomes. For example, in a study of bryozoan fouling of crabs, cyclostomes were reported in only 10% of the cases of syn-vivo bryozoan fouling of extant crabs (Key *et al.* 2017, tbl. 3). Dick *et al.* (1998) reported an unidentified lichenoporid cyclostome and *Crisia* sp. fouling the snow crab *Chionoecetes bairdi*. The lichenoporids were found encrusting the dorsal and ventral surfaces, whereas the *Crisia* colonies were only on the ventral legs (Dick *et al.* 1998). In the crab fossil record, cyclostomes made up 16% of the cases (Key *et al.* 2017, tbl. 4). Cyclostomes have also been reported fouling fossil nautiloids (Turek 1987; Wyse Jackson & Key 2014) and trilobites (Tetreault 1992, 1997).

It is not surprising that one of the cyclostomes fouling the lobster was *Crisia* sp. as *Crisia* is one of the most species rich bryozoan genera in the Mediterranean (Harmelin 1968; Rosso 2003; Rosso & Di Martino 2016). In the Mediterranean, *Crisia sigmoidea* and *C. oranensis* are known to encrust rocks, sea grasses, sponges, and corals (Harmelin 1968) but not motile animals such as lobsters. In the south Pacific, erect crisiid colonies were reported on the red rock lobster *Jasus edwardsii* (Key *et al.* 2021).

Disporella and *Patinella* are just two of the many encrusting bryozoan genera in the Mediterranean (Rosso 2003; Rosso & Di Martino 2016). Encrusting bryozoans are much more common epibionts than erect bryozoans (Key *et al.* 2021). So, why were there more erect colonies (i.e. five) than encrusting colonies (i.e. three) on the host lobster in this study? It may be a function of the closely spaced setal tufts of the conspicuous and high tubercles that cover the surface of this lobster's carapace (Figure 1C) (Spanier & Lavalli 2013, fig. 13.18). These would have made an erect growth habit easier with its smaller surface area of attachment on the host lobster's carapace.

The incidence of epibionts on crustaceans is also a function of host grooming (Fernandez-Leborans 2010). *Scyllarides latus* does groom itself using mouthparts and legs to clean different parts of its body (Barshaw & Spanier 1994b; Lavalli *et al.* 2007, 2018; Spanier & Lavalli 1998). But those parts are generally ventral appendages, not the dorsal carapace where the bryozoans in this study were found.

What are the costs of this epibiotic relationship to the lobster and the bryozoans? Possible detrimental effects to the host include: (1) increased weight; probably not a major problem due to the almost neutral buoyancy of the bryozoans, (2) increased drag; probably not a major problem due to the encrusting nature of some of the colonies and the slow walking movement of the host, (3) shared doom (i.e. when a predator of either the host or the epibiont kills both (Wahl & Hay 1995)) (e.g. predation of bryozoans probably not a major problem as the epizoic bryozoan lifestyle may reduce susceptibility to predation via camouflage), and (4) increased susceptibility to predation (e.g. if the bryozoan colonies increase the host's weight and drag, decrease hosts functionality by overgrowing eyes or decreasing its flexibility, and attract predators of the bryozoans which may also eat the host) (Key & Barnes 1999; Key *et al.* 1995, 1996a, 1996b, 1999, 2000, 2010).

Possible detrimental effects to the bryozoans include: (1) being cast of by molting of the host, (2) abrasion of colonies by host crawling into crevices, (3) abrasion of colonies during mating, and (4) shared doom (e.g. predation of host) (Key & Barnes 1999; Key *et al.* 1995, 1996a, 1996b, 1999, 2000, 2010).

What are the benefits of this epibiotic relationship to the lobster and the bryozoans? The bryozoans may have provided camouflage to the host lobster as suggested by Martins (1985). For example, Vance (1978) documented a decrease in predation by starfish on clams, which were covered by bryozoans. Some crustaceans such as the decorator crabs purposefully camouflage themselves with bryozoans (Parapar *et al.* 1997; Stachowicz & Hay 2000). Camouflage is important for this species of lobster as it has no defensive claws or spines like other lobsters (Barshaw *et al.* 2003). The main predators of *S. latus* are humans through the over exploitative commercial fishery (Fisher 1973; Fisher *et al.* 1981; Martins 1985; Spanier 1991) and a variety of bony fishes, especially triggerfishes, *Balistes* spp. (Barshaw & Spanier 1994a, fig. 2; Barshaw *et al.* 2003; Lavalli & Spanier 2001; Martins 1985, Spanier & Lavalli 1998). Slipper lobsters such as *S. latus* are already camouflaged due to their flattened morphology and coloration (Barshaw & Spanier 1994a; Ogren 1977). This camouflage is enhanced in *S. latus* by the presence of its numerous attached epizoans including serpulids, hydroids, barnacles, bivalves, bryozoans, and foraminiferans (Martins 1985; Spanier & Lavalli 1998). Due to the minimal surface area coverage of the host by the bryozoans, the benefit of camouflage to the host is minimal.

Are the bryozoans receiving any benefit? There are a variety of benefits for a sessile encrusting animal living on a motile host. They include increased geographic range and substrate space. Living on a motile host provides the sessile bryozoans with free transport for avoiding predators, improve gamete dispersal, and increase geographic range. Hard substrate space is a limiting factor for bryozoans, especially encrusting bryozoans (Jackson 1977; Lidgard & Jackson 1989; McKinney 1995; Taylor 2016). Therefore, any increase in hard substrate space (e.g. motile host basibionts) should reduce competition for substrate space and result in an increase in bryozoan diversity as documented by Balazy & Kuklinski (2013). Finally, the host's carapace setae may provide camouflage for the small encrusting lichenoporids.

An additional benefit accrues to the bryozoans if the host is the encrusting animal's predator such as the bryozoans that foul predatory pycnogonids (Key *et al.* 2013). Other lobsters eat bryozoans, including the clawed lobster *Homarus* (Lawton & Lavalli 1995) and the spiny lobsters *Jasus* and *Panulirus* (Castaneda-Fernandez-de-Lara *et al.* 2005; Edmunds 1995; Fielder 1965; Lindberg 1955). The diet of *S. latus* consists of molluscs, mainly bivalves, but also including gastropods, but not bryozoans (Barshaw & Spanier 1994b; Martins 1985; Spanier 1987, 1991; Spanier *et al.* 1988), so it is doubtful this benefit accrues to the bryozoans here.

Weighing all these potential costs and benefits to the host lobster and the fouling bryozoans, the relationship is best described as commensalism. Overall, this is a one-sided commensal symbiotic relationship, best described as phoretic (i.e. hitchhiking relationship) for the bryozoans. This is the most commonly documented type of symbiosis between lobsters and bryozoans (Key & Hendrickx 2022; Key *et al.* 2021).

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REFERENCES

Audouin, J.V. 1826. Explication Sommaire des Planches de Polypes de l'Egypte et de la Syrie, Publiees par Jules-Cesar Savigny. In J.V. Audouin (ed.), *Description de l'Egypte, ou Recueil des Observations et des Recherches Qui ont été Faites en Egypte Pendant L'expédition de l'armée Française … Histoire naturelle*, 1 (4): 225–244. Paris: Imprimerie Impériale.

Balazy, P. & Kuklinski, P. 2013. Mobile Hard Substrata – an Additional Biodiversity Source in a High Latitude Shallow Subtidal System. *Estuarine, Coastal and Shelf Science* 119: 153–161.

Barshaw, D.E. & Spanier, E. 1994a. Anti-predator Behaviors or the Mediterranean Slipper Lobster *Scyllarides latus*. *Bulletin of Marine Science* 55: 375–382.

Barshaw, D.E. & Spanier, E. 1994b. The Undiscovered Lobster: A First Look at the Social Behaviour of the Mediterranean Slipper Lobster, *Scyllarides latus* (Decapoda, Scyllaridae). *Crustaceana* 67: 187–197

Barshaw, D.E., Lavalli, K.L. & Spanier, E. 2003. Offense Versus Defense: Responses of Three Morphological Types of Lobsters to Predation. *Marine Ecology Progress Series* 256: 171–182.

Bianchini, M.L., Bono, G. & Ragonese, S. 2001. Long-term Recaptures and Growth of Slipper Lobsters, *Scyllarides latus*, in the Strait of Sicily (Mediterranean Sea). *Crustaceana* 74: 673–680.

Bianchini, M.L. & Ragonese, S. 2007. Growth of Slipper Lobsters of the Genus *Scyllarides*. In K.L. Lavalli & E. Spanier (eds), *The Biology and Fisheries of the Slipper Lobster*: 199–220. Boca Raton: CRC Press.

Castañeda-Fernández-de-Lara, V., Serviere-Zaragoza, E., Hernández-Vázquez, S. & Butler IV M.J. 2005. Feeding Ecology of Juvenile Spiny Lobster, *Panulirus interruptus*, on the Pacific coast of Baja California Sur, Mexico. *New Zealand Journal of Marine and Freshwater Research* 39: 425–435.

Dick, M.H., Donaldson, W.E. & Vining, I.W. 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the Region of Kodiak Island, Alaska. *Journal of Crustacean Biology* 18: 519–528.

Edmunds, M. 1995. The Ecology of the Juvenile Southern Rock Lobster, *Jasus edwardsii* (Hutton, 1875) (Palinuridae): 1–164. Tasmania: University of Tasmania, PhD dissertation.

Fernandez-Leborans, G. 2010. Epibiosis in Crustacea: an Overview. *Crustaceana* 83: 549–640.

Fielder, D.R. 1965. The Spiny lobster, *Jasus lalandei* (H. Milne-Edwards), in South Australia. III. Food, Feeding, and Locomotor Activity. *Australian Journal of Marine and Freshwater Research* 16: 351–367.

Fischer, W. (ed.) 1973. FAO Species Identification Sheets for Fishery Purposes. *Mediterranean and Blacks Sea (fishing area 37)*. Volume 2. Rome: Food and Agricultural Organization.

Fischer, W., Bianchi, G. & Scott, W.B. (eds) 1981. FAO Species Identification Sheets for Fishery Purposes. *Eastern Central Atlantic (fishing areas 34, 47 in part)*. Volume 5. Ottowa: Department of Fisheries and Oceans.

Grischenko, A.V., Gordon, D.P. & Melnik, V.P. 2018. Bryozoa (Cyclostomata and Ctenostomata) from Polymetallic Nodules in the Russian Exploration Area, Clarion-Clipperton Fracture Zone, Eastern Pacific Ocean – Taxon Novelty and Implications of Mining. *Zootaxa* 4484: 1–91.

Harmelin, J.G. 1968. Contribution à l'étude des Bryozoaires Cyclostomes de Méditerranée: Les *Crisia* des côtes de Provence. *Bulletin du Muséum National d'Histoire Naturelle* 40: 413–437.

Hellio, C. & Yebra, D. 2009. *Advances in Marine Antifouling Coatings and Technologies*. Oxford (UK): Woodhead Publishing.

Herrera, A., Jackson, J.B.C., Hughes, D.J., Jara, J. & Ramos, H. 1996. Life-history Variation in Three Coexisting Cheilostome Bryozoan Species of the Genus *Stylopoma* in Panamá. *Marine Biology* 126: 461–469.

Horne, F.R. & Tarsitano, S.F. 2007. The Mineralization and Biomechanics of the Exoskeleton. In K.L. Lavalli & E. Spanier (eds), *The Biology and Fisheries of the Slipper Lobster*: 183–198. Boca Raton: CRC Press.

Jackson, J.B.C. 1977. Competition on Marine Hard Substrata: The Adaptive Significance of Solitary and Colonial Strategies. *The American Naturalist* 111: 743–767.

Jackson, J.B.C. & Wertheimer, S.P. 1985. Patterns of Reproduction in Five Common Species of Jamaican Reef-associated Bryozoans. In C. Nielsen & G.P. Larwood (eds), *Bryozoa: Ordovician to Recent*. 161–168. Fredensborg: Olsen & Olsen.

Key, M.M., Jr. & Barnes, D.K.A. 1999. Bryozoan Colonization of the Marine Isopod *Glyptonotus antarcticus* at Signy Island, Antarctica. *Polar Biology* 21: 48–55.

Key, M.M., Jr. & Hendrickx, M.E. 2022. *Biflustra irregulata*: A Tsunami Debris Rafted Indo-Pacific Bryozoan Found in Eastern Pacific. *Zootaxa* 5128: 340–354.

Key, M.M., Jr., Hyžný, M., Khosravi, E., Hudáčková, N., Robin, N. & Mirzaie Ataabadi, M. 2017. Bryozoan Epibiosis on Fossil Crabs: A Rare Occurrence From the Miocene of Iran. *Palaios* 32: 491–505.

Key, M.M., Jr., Jeffries, W.B. & Voris, H.K. 1995. Epizoic Bryozoans, Sea Snakes, and Other Nektonic Substrates. *Bulletin of Marine Science* 56: 462–474.

Key, M.M., Jr., Jeffries, W.B., Voris, H.K. & Yang, C. M. 1996a. Epizoic Bryozoans and Mobile Ephemeral Host Substrata. In D.P. Gordon, A.M. Smith & J.A. Grant-Mackie (eds), *Bryozoans in Space and Time*: 157–165. Wellington: National Institute of Water and Atmospheric Research.

Key, M.M., Jr., Jeffries, W.B., Voris, H.K. & Yang, C. M. 1996b. Epizoic Bryozoans, Horseshoe Crabs, and Other Mobile Benthic Substrates. *Bulletin of Marine Science* 58: 368–384.

Key, M.M., Jr., Jeffries, W.B., Voris, H.K. & Yang, C. M. 2000. Bryozoan Fouling Pattern on the Horseshoe Crab *Tachypleus gigas* (Müller) from Singapore. In A. Herrera Cubilla & J.B.C. Jackson (eds), *Proceedings of the 11th International Bryozoology Association Conference*: 265–271. Balboa: Smithsonian Tropical Research Institute.

Key, M.M., Jr., Knauff, J.B. & Barnes, D.K.A. 2013. Epizoic Bryozoans on Predatory Pycnogonids from the South Orkney Islands, Antarctica: "If You Can't Beat Them, Join Them". In A. Ernst, P. Schäfer & J. Scholz (eds), *Bryozoan Studies 2010*: 137–153. Berlin: Springer-Verlag.

Key, M.M., Jr., Schumacher, G.A., Babcock, L.E., Frey, R.C., Heimbrock, W.P., Felton, S.H., Cooper, D.L., Gibson, W.B., Scheid, D.G. & Schumacher, S.A. 2010. Paleoecology of Commensal Epizoans Fouling *Flexicalymene* (Trilobita) from the Upper Ordovician, Cincinnati Arch Region, USA. *Journal of Paleontology* 84: 1121–1134.

Key, M.M., Jr., Smith, A.M., Hanns, B. & Kane-Sanderson, P. 2021. Rare Report of Bryozoan Fouling of Rock Lobsters (*Jasus edwardsii*: Decapoda: Palinuridae) from the North Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research* 1–13 (online). https://doi.org/10.1080/00288330.2021.1977344

Key, M.M., Jr., Winston, J.E., Volpe, J.W., Jeffries, W. B. & Voris, H.K. 1999. Bryozoan Fouling of the Blue Crab, *Callinectes sapidus*, at Beaufort, North Carolina. *Bulletin of Marine Science* 64: 513–533.

Latreille, P.A. 1802. Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes: Ouvrage Faisant Suite Aux Oeuvres de Leclerc de Buffon, et Partie du Cours Complet D'histoire Naturelle Rédigé par C.S. *Sonnini* 3: 1–468.

Lavalli, K.L., Malcom, C.N. & Goldstein, J.S. 2018. Description of Pereiopod Setae of Scyllarid Lobsters, *Scyllarides aequinoctialis*, *Scyllarides latus*, and *Scyllarides nodifer*, with observations on the Feeding During Consumption of Bivalves and Gastropods. *Bulletin of Marine Science* 94: 571–601.

Lavalli, K.L. & Spanier, E. 2001. Does Gregariousness Function as an Antipredator Mechanism in the Mediterranean Slipper Lobster, *Scyllarides latus*? *Marine and Freshwater Research* 52: 1133–1143.

Lavalli, K.L., Spanier, E. & Grasso, F. 2007. Behavior and Sensory Biology of Slipper Lobsters. In K.L. Lavalli & E. Spanier (eds), *The Biology and Fisheries of the Slipper Lobster*: 133–181. Boca Raton: CRC Press.

Lawton, P. & Lavalli, K.L. 1995. Postlarval, Juvenile, Adolescent, and Adult Ecology. In J.R. Factor (ed.), *Biology of the Lobster: Homarus americanus*: 47–88. San Diego: Academic Press.

Lidgard, S. & Jackson, J.B.C. 1989. Growth in Encrusting Cheilostome Bryozoans: I. Evolutionary Trends. *Paleobiology* 15: 255–282.

Lindberg, R.G. 1955. Growth, Population Dynamics and Field Behaviour in the Spiny Lobster, *Panulirus interruptus* (Randall). *University of California Publications in Zoology* 59: 157–248.

Martins, H.R. 1985. Biological Studies of the Exploited Stock of the Mediterranean Locust Lobster *Scyllarides latus* (Latreille, 1803) (Decapoda: Scyllaridae) in the Azores. *Journal of Crustacean Biology* 5: 294–305.

McKinney, F.K. 1995. One Hundred Million Years of Competitive Interactions Between Bryozoan Clades: Asymmetrical But Not Escalating. *Biological Journal of the Linnean Society* 56: 465–481.

Ogren, L.H. 1977. Concealment Behavior of the Spanish Lobster, *Scyllarides Nodifer* (Stimpson), with Observations on its Diel Activity. *Northeast Gulf Science* 1: 115–116.

Parapar, J., Fernandez, L. Gonzalez-Gurriaran, E. & Muino R. 1997. Epibiosis and Masking Material in the Spider Crab *Maja squinado* (Decapoda: Majidae) in the Ria de Arousa (Galicia, NW Spain). *Cahiers de Biologie Marine* 38: 221–234.

Phillips, B.F., Cobb, J.S. & George, R.W. 1980. General Biology. In J.S. Cobb & B.F. Phillips (eds), *The Biology and Management of Lobsters. vol. I, Physiology and Behavior*: 1–82. New York: Academic Press.

Quinn, R.A., Smolowitz, R. & Chistoserdov, A. 2009. Eukaryotic Communities in Epizootic Shell Disease Lesions of the American Lobster (*Homarus americanus* H. Milne Edwards). *Journal of Shellfish Research* 28: 913–922.

Romeo, T., Florio, G., Lentini, F., Castriota, L., Falautano, M., Consoli, P., Pelusi, P. & Greco, S. 2004. Morphometric Aspects of *Scyllarides latus*. *Mediterranean Marine Science* 5: 65–71.

Rosso, A. 2003. Bryozoan Diversity in the Mediterranean Sea. *Biogeographia* 24: 227–250.

Rosso, A. & Di Martino, E. 2016. Bryozoan Diversity in the Mediterranean Sea: an Update. *Mediterranean Marine Science* 17: 567–607.

Ryan, W.B.F., Carbotte, S.M., Coplan, J.O, O'Hara, S., Melkonian, A., Arko, R., Weissel, R.A., Ferrini, V., Goodwillie, A., Nitsche, F., Bonczkowski, J. & Zemsky, R. 2009. Global Multi-resolution Topography (GMRT) Synthesis Data Set. *Geochemistry, Geophysics, Geosystems* 10(3): Q03014, https://doi.org/10.1029/2008GC002332

Shields, J.D. 2011. Diseases of Spiny Lobsters: A Review. *Journal of Invertebrate Pathology* 106: 79–91.

Smith, A.M. 1992. *Aspects of the Sedimentology of New Zealand Bryozoans and Mixed Carbonate-clastic Deposits: A Contribution to the Temperate Shelf Carbonate Model [dissertation]*. Waikato: University of Waikato.

Spanier, E. 1987. Mollusca as Food for the Slipper Lobster *Scyllarides latus* in the Coastal Waters of Israel. *Levantina a Journal of Malacology* 68: 713–716.

Spanier, E. 1991. Artificial Reefs to Insure Protection of the Adult Mediterranean Slipper Lobster, *Scyllarides latus* (Latreille, 1803). In C.F. Boudouresque, M. Avon & V. Gravez (eds), *Les Espèces Marines Protégées en Méditerranée*: 179–185. France: GIS Posidonia.

Spanier, E. & Lavalli, K.L. 1998. Natural History of *Scyllarides latus* (Crustacea: Decapoda): A Review of the Contemporary Biological Knowledge of The Mediterranean Slipper Lobster. *Journal of Natural History* 32: 1769–1786.

Spanier, E. & Lavalli, K.L. 2013. Commercial Scyllarids. In B.F. Phillips (ed.), *Lobsters: Biology, Management, Aquaculture and Fisheries*: 414–466. Oxford: Blackwell.

Spanier, E., Tom, M., Pisanty, S. & Almog, G. 1988. Seasonality and Shelter Selection by the Slipper Lobster *Scyllarides latus* in the Southeastern Mediterranean. *Marine Ecology Progress Series* 42: 247–255.

Stachowicz, J.J. & Hay, M.E. 2000. Geographic Variation in Camouflage Specialization by a Decorator Crab. *American Naturalist* 156: 59–71.

Taylor, P.D. 2016. Competition Between Encrusters on Marine Hard Substrates and its Fossil Record. *Palaeontology* 59: 481–497.

Tetreault, D.K. 1992. Paleoecologic Implications of Epibionts on the Silurian Lichid Trilobite *Arctinurus*. In S. Lidgard & P.R. Crane (eds), *North American Paleontological Convention Abstracts and Program*: 289. Knoxville: Paleontological Society and University of Tennessee.

Tetreault, D.K. 1997. Trilobite Behavior in the Silurian. *Second International Trilobite Conference, Abstracts with Programs*: 48–49. St. Catharines: Brock University.

Turek, V. 1987. On Some Epizoans of Mollusk Shells from the Upper Silurian (Pridoli) of the Barrandian area. *Vestnik Ustredniho Ustavu Geologickeho* 62: 105–111.

Vance, R.R. 1978. A Mutualistic Interaction Between a Sessile Marine Clam and its Epibionts. *Ecology* 59: 679–685.

Wahl, M. 1989. Marine Epibiosis. 1. Fouling and Antifouling – Some Basic Aspects. *Marine Ecology Progress Series* 58: 175–189.

Wahl, M. & Hay, M.E. 1995. Associational Resistance and Shared Doom: Effects of Epibiosis on Herbivory. *Oecologia* 102: 329–340.

Waters, A.W. 1916. Some Species of *Crisia*. *Annals and Magazine of Natural History*, 8th series 18: 469–477

Winston, J.E. & Håkansson, E. 1986. The Interstitial Fauna of the Capron Shoals, Florida. *American Museum Novitates* 2865: 1–98.

Wyse Jackson, P.N. & Key, M.M. Jr. 2014. Epizoic Bryozoans on Cephalopods Through the Phanerozoic: a Review. *Studi Trentini di Scienze Naturali* 94: 283–291.

Zha, H., Lewis, G., Alfaro, A., Wang, S., Dong, Y., Grandiosa, R. & Jeffs, A. 2017. Immune Status of the Spiny Lobster *Jasus edwardsii* with Tail Fan Necrosis. *Diseases of Aquatic Organisms* 126: 229–238.