THE INTIMATE RELATIONSHIP BETWEEN BOXER CRABS AND SEA ANEMONES: WHAT IS KNOWN AND WHAT IS NOT

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Abstract   Crabs of the xanthid subfamily Polydectinae (boxer crabs) have the remarkable habit of holding another animal, usually a sea anemone, in each of their claws. Some boxer crab species hold nudibranchs and holothurians. Boxer crabs are the only known crab species to have effectively lost all ability to use their claws in typical fashion, having formed what appears to be an obligate dependence on the animal held in its claws. Several, although not all, of the associated anemone species are known to occur free-living. Due to the anemones being held in the 'hands' of the crab, it is easy to envision how the stinging anemones are used for defence and food gathering. Boxer crabs have been mentioned often in this regard in popular culture and are commonly kept by marine aquarists. However, since their first appearance in the literature over 200 years ago, very few systematic studies have been conducted into the particulars of this symbiosis. Recent laboratory studies have expanded on various aspects of the natural history of boxer crabs, as well as the discovery of additional species in this subfamily. This review covers the literature on the boxer crab–anemone association, using the more extensively studied hermit crab–anemone association as a point of comparison. The review covers many aspects of the symbiosis, including the cost and benefits to each of the partners, the defensive value of the anemones to the crab, how the crabs locate their anemones, their respective morphological adaptations, anemone splitting and theft, as well as distribution and phylogeny. Due to their small size, most of the experimental work conducted to date has been limited to the laboratory. Recent advances in video recording as well as other tracking methods may allow for a closer look at this association in the wild, laying out the path to answering the many questions in this fascinating partnership.

Keywords: boxer crab, sea anemone, symbiosis, asexual reproduction, tool use, defense, Lybia, Alicia

Introduction

Members of the xanthid crab subfamily Polydectinae are the only group of crabs whose claws have lost the ability to fulfil typical functions such as food gathering, burrowing and grooming, since they have become specialized for holding anemones (Figure 1D). Other brachyuran crabs that carry anemones do so by placing them on their carapace or appendages. They often hold them with their fourth and or fifth walking legs without loss of claw function (see reviews by Guinot et al. 1995,
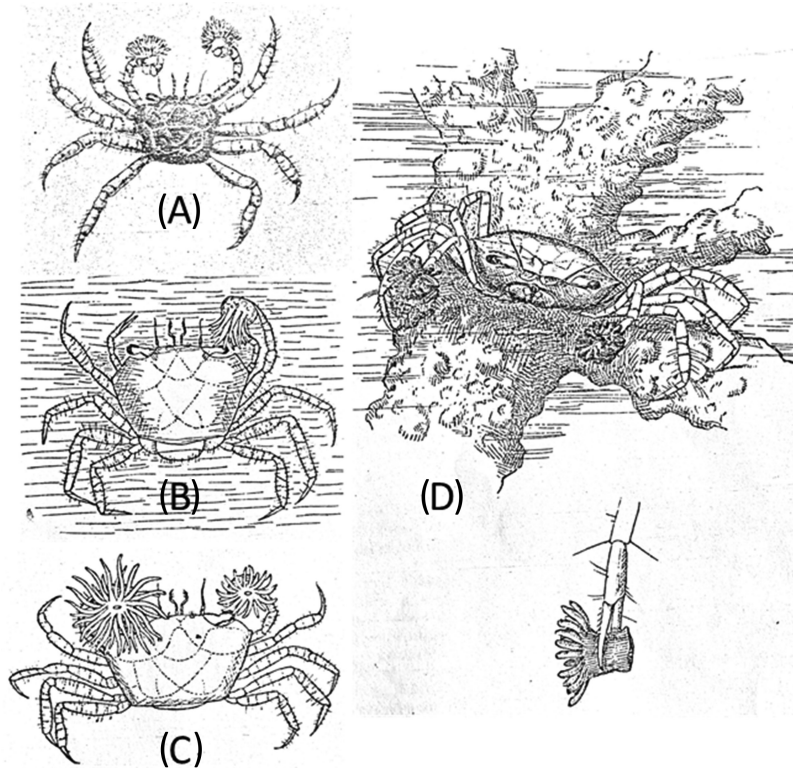
Figure 1 Early descriptions of polydectine crabs associated with anemones. (A) *Lybia tessellata* holding an actinian in each claw. After Richter (1880). (B) *Lybia edmondsoni* detaching a fixed actinian with its first walking leg (Duerden 1905). (C) *Lybia edmondsoni* holding an expanded actinian in each claw (Duerden 1905). (D) *Lybia tessellata* on a live coral, bearing in each claw an anemone, and an enlarged claw holding an anemone (Borradaile 1902).

Guinot and Wicksten 2015). The dependence of boxer crabs on their associated invertebrates to replace their claws renders these partnerships so interrelated and unique.

The first description of the association between a polydectine, *Lybia tessellata* (initially designated as *Melia tessellate*; see Appendix 1 for further details on polydectine crabs) and anemones was published at the end of the nineteenth century, as a small footnote by Mobius to a taxonomic study of the Crustacea of Mauritius and the Seychelles Islands (Richter 1880). *Lybia tessellata* was described as holding a living anemone *Actinia prehensa* (Moebius), in each of its claws by means of delicate hooks, slightly embedded in the anemone column (Figure 1A). It was suggested that the anemone's stinging cells assisted the crab in securing food. A detailed study of this association was carried out in Hawaii at the beginning of the twentieth century (Duerden 1905) (Figure 1B and C). Even though this study was based on only three specimens of boxer crabs (two in the genus *Lybia* and one *Polydectus cupulifer*), it contributed much to our understanding of the crab–anemone relationship. Duerden (1905) dealt with crab–anemone partner specificity, the mechanism of anemone acquisition, defensive movements carried out by the crab with its anemones, feeding behaviour of the crab and anemone, as well as the cost and benefit of the association for both crab and anemone. Due to their peculiar behaviour of holding anemones, crabs of

the genus *Lybia* have received since then much attention from the public, receiving such popular names as 'boxer crabs', 'pom-pom crabs' and 'cheer leaders'. Boxer crabs despite their small size are very photogenic, often featured in popular books on coral reefs and annual calendars. These crabs, and particularly *Lybia tessellata,* are also popular in the ornamental crustacean trade (Calado et al. 2003; Calado, 2020). In contrast to the interest in boxer crabs from the non-scientific community, little systematic research has focused on these partnerships. Ross (1983) in his review on symbiosis in crustaceans emphasized that since the pioneering study by Duerden (1905) very little research addressed the behaviour of these creatures and more research is needed on the relationship between boxer crabs and their anemones. Several studies have recently been published on these partnerships (e.g. Karplus et al. 1998, Mendoza and Ng 2011, Schnytzer et al. 2013, 2017).

This review examines all the information available on Polydectine crabs and their associated anemones and other invertebrates, emphasizing what is known and what should be investigated in the future. We review the first accounts of boxer crabs and the studies that followed, covering what is known about their taxonomy, morphology, distribution, partner specificity and associated behaviours, as well as phylogeny and evolution. Throughout this review, the relationship of hermit crabs and other crustaceans with their associated anemones is contrasted with that of boxer crabs to better understand the peculiarity of the latter. This association is unique since the crabs cause temporary morphological changes in their claw-held associates, as well as inducing their asexual reproduction, at least in the case of the more commonly held anemones, raising interesting questions about the ultimate costs and benefits to each partner.

Taxonomy and distribution of boxer crabs and associated anemones

The Polydectinae is a small subfamily of the Xanthidae (124 genera and 639 species) with only 11 species and 3 genera (Figure 2). Within the subfamily, *Lybia* has eight species; *Tunebia* has two species; and *Polydectus* is monotypic (Table 1; Appendix 1). The morphology and taxonomy of the Polydectinae have been extensively reviewed by Guinot (1976) and Serène (1984). Results from Lai et al. (2011) using molecular data and developmental comparisons of first stage zoea are consistent with the adult morphological parameters which remain diagnostic. Guinot (1976), in her study of the Polydectinae, summarized the major morphological traits to include form of carapace, morphology and position of the antennas, mouth appendages, structure of the pincers and the ability to grasp anemones (Figure 2). Guinot (1976) recognized three species groups within *Lybia* based on the structures of the carapace, anterolateral border, the endopod of the first and third maxillipeds, male first pleopod and chelipeds. The first group consists of *Lybia tessellata* (Figure 2A) and *Lybia edmondsoni* (Figure 2D). Both these crabs are conspicuously coloured (Figure 3A and C). *Lybia tessellata* has a wide Indo-West Pacific distribution and *Lybia edmondsoni* is apparently endemic to Hawaii. The second group consists of *Lybia plumosa* (Figure 2F) and *Lybia leptochelis* (Figure 2E); both are cryptically coloured and occur in the Indian Ocean. *Lybia denticulata* was left by itself, regarded as intermediary between the genera *Polydectus* (Figure 2I and J) and *Lybia*. The status of *Lybia australiensis* (Figure 3F), *Lybia caestifera* and *Tunebia hatagumoana* (Figures 2G and 3E) was left undecided. *Lybia tutelina* was subsequently defined from New Caledonia by Tan and Ng (1994; Figure 2H). Mendoza and Ng (2011) erected *Tunebia* for *Tunebia hatagumoana* and *Tunebia tutelina*. Both species appear to have a relatively limited distribution, *Tunebia hatagumoana* occurring in Japan and the Philippines (Mendoza and Ng 2011) and *T. tutelina* in New Caledonia. To date, both species have only been found in relatively deep water of not less than 70 m.
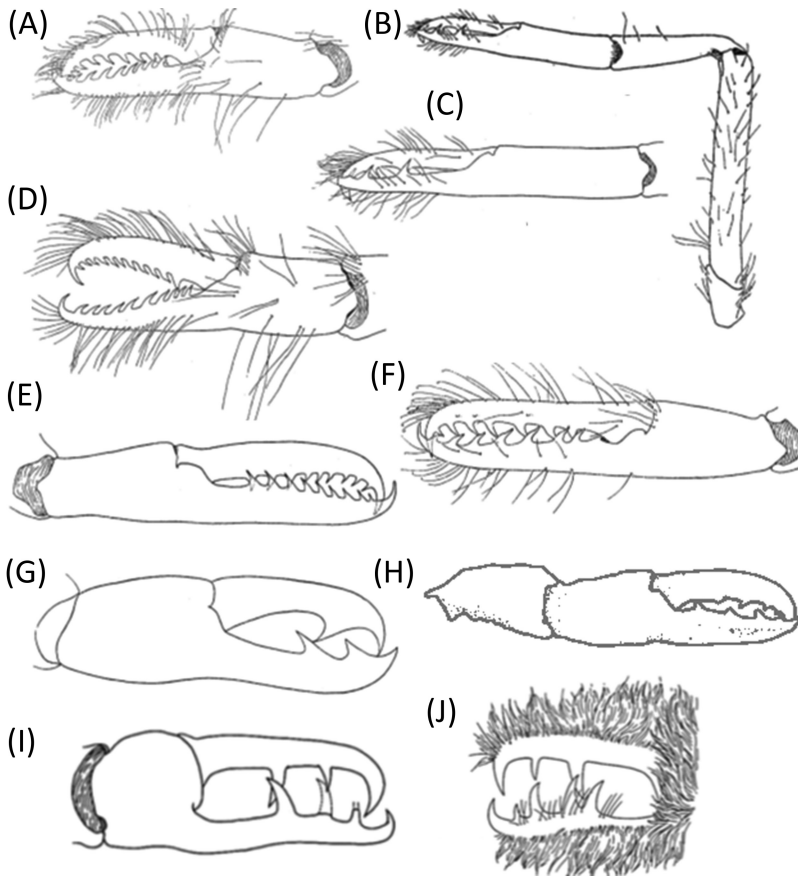
Figure 2 Chelipeds of Polydectine crabs. (A) *Lybia tessellata*. (B and C) *Lybia denticulata*. (D) *Lybia edmondsoni*. (E) *Lybia leptochelis*. (F) *Lybia plumosa*. (G) *Tunebia hatagumoana*. (H) *Tunebia tutelina*. (I and J) *Polydectus cupulifer*. (A–F) After Guinot (1976); (G) after Guinot & Wicksten (2015); (H) after Tan & Ng (1994); (I and J) after Guinot & Wicksten (2015).

Thus far, there have been no studies that focused on the ecology of boxer crab–anemone associations. These partnerships were only briefly mentioned in overviews of non-scleractinian anthozoans of the shallow Red Sea (Fishelson 1970), the shallow benthic fauna of the Red Sea (Fishelson 1971) and the fauna of the coral reefs of northern Mozambique (Kalk 1959). Their habitat and depth distribution has been often briefly mentioned in taxonomic studies (Table 1). In most cases, boxer crabs live in the shallow littoral zone, under rocks, basalt slabs and coral rubble during the day, leaving their shelters at night for foraging.

The taxonomy of the anemones carried by Polydectine crabs has not been well studied. In 6 out of 11 recognized species of boxer crabs the identity of their symbiotic anemones is unknown (Table 1). According to Crowther (2013), the difficulty in the identification of these symbiotic anemones is due to their small size and changes in morphology (e.g. lack of body outgrowths) which are different from that of the fully grown non-associated anemones and important for their classification. Cutress (1977) suggested that several misidentifications of symbiotic anemones associated with boxer crabs may have arisen due to the altered morphology of held anemones.

The anemones of the family Aliciidae are typically involved in symbiosis with zooxanthellae. They typically possess branched outgrowths from the column which harbour these intracellular
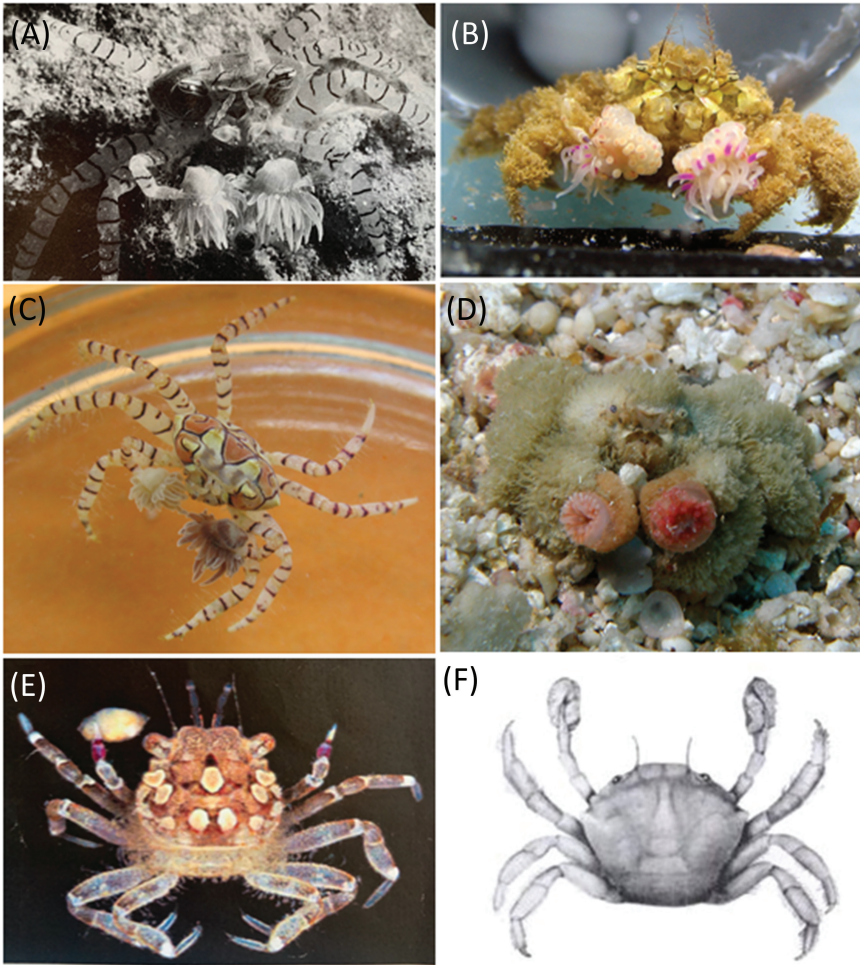
Figure 3 Polydectine crabs and associated invertebrates. (A) *Lybia edmondsoni* holding in each claw a *T. producta* (Karplus et al. 1998). (B) *Lybia leptochelis* holding in each claw an *Alicia* sp. (C) *Lybia tessellata* holding in each claw a *Triactis producta* anemone: the right claw anemone is bleached, and the left claw anemone is dark due to the presence of symbiotic zooxanthellae. (D) *Polydectus cupulifer* holding unidentified anemones. Taken by Kaoru Imagawa. (E) *Tunebia hatagumoana* holding a nudibranch in one claw (Lai et al. 2011). (F) *Lybia australiensis* holding unidentified anemones (Ward 1933).

photosynthetic algae and spherical defence structures that contain nematocysts (Crowther 2013). This family consists of four genera, *Lebrunia*, *Triactis, Phyllodiscus* and *Alicia*, and a total of nine species (Crowther 2013). Two of these species are associated with boxer crabs, *Triactis producta* and *Alicia* sp. The former is highly venomous (Levi et al. 1970) and has a wide Indo-West Pacific distribution. This species is involved in more partnerships with boxer crabs than any other anemone, occurring in four out of the five associations with boxer crabs whose anemones were positively identified. *Alicia* sp. has been found in the Red Sea only in association with *Lybia leptochelis*. A further six species of anemones have also been identified in association with boxer crabs, albeit to a lesser extent; *Boloceractis prehensa* (Fam. Boloceroididae), *Actinia prehensa* (Fam. Actiniidae), *Bunodeopsis* sp. (Fam. Boloceroididae) *Sagartia pugnax* (Fam. Sagartiadae), *Phelia* sp. and *Telmatactis decora* (Fam. Isophellidae; see Table 1). Members of the families Isophellidae

Table 1 Boxer crabs and associated anemones

Species	Distribution	Habitat & depth	Associated anemones	References
Lybia australiensis (Ward 1933)	New South Wales Australia	Under large rock	Unknown	Guinot (1976)
Lybia caestifera (Alcock 1898)	Western Indian and eastern Pacific Ocean	Shallow water	Unknown	Lee et al. (2008)
Lybia denticulata (Nobili 1906)	Red Sea	Unknown	Unknown	Guinot (1976)
Lybia edmondsoni (Takeda & Miyake 1970)	Hawaii[a]	Under basalt & coral rocks 6–20 m[a]	*Triactis producta*[a]	Karplus et al. (1998)[a], Takeda & Miyake (1970)[b]
Lybia leptochelis (Zehntner 1894)	Indian Ocean[b]	Under rocks in the shallow sublittoral[b]	*Triactis producta*[a] *Alicia* sp.[b]	Fishelson (1970)[a] Schnytzer et al. (2013)[b]
Lybia plumosa (Barnard 1947)	Indian Ocean[a]	Coral pools Shallow water[b]	*Triactis producta*[c]	Guinot (1976)[a] Kalk (1959)[b] Giman (2008)[c]
Lybia pugil (Alcock 1896)	Indian Ocean[a]	Unknown	Unknown	Guinot (1976) Mendoza & Ng (2011)
Lybia tessellata (Latreille 1812)	Indian Ocean & Western Pacific[f]	Living coral branches,[g] under dead coral and stones,[i] intertidal,[h] 4 m[b]	*Triactis producta*[a] *Boloceractis prehensa*[b] *Actinia prehensa*[c] *Bunodeopsis* sp.[d] *Sagartia pugnax*[e]	Giman (2008)[a] Jeng (1994)[b] Richter (1880)[c] Duerden (1905)[d] Verrill (1928)[e] Guinot (1976)[f] Borradaile (1902)[g] Serène (1984)[h] Tweedie (1950)[i]
Tunebia hatagumoana (Sakai 1961)	Japan[a] The Philippines[d]	Unknown 60[a]–100 m[b]	*Gymnodoris* sp. (nudibranch) Unknown anemone[c]	Sakai (1961)[a] Miyake (1983)[b] Baba & Noda (1993)[c] Mendoza & Ng (2011)[d]
Tunebia tutelina (Tan & Ng 1994)	New Caledonia	Unknown 74–76 m	Unknown	Tan & Ng (1994)
P. cupulifer (Latreille 1812)	Indo-Pacific[d]	Under coral & stone blocks,[a] intertidal & several m[d]	*Phelia* sp.[a] *Sagartia pugnax*[b] *Telmatactis decora*[c] Small holothurians[d]	Duerden (1905)[a] Edmondson (1946)[b] Schmitt (1965)[c] Guinot (1976)[d]

and Sagartiadae possess acontia or stinging threads, which are expelled by the anemones in defence against predators. Some of the species in the list may actually be synonyms and misidentifications of *Triactis producta* (Cutress 1977, 1979, Crowther 2013). According to Cutress (1979), the *Bunodeopsis* sp. identified by Duerden (1905) as the anemone carried by crab number one in his study, is almost certainly a misidentification of *Triactis producta*. Forty specimens of *Lybia edmondsoni* examined in Hawaii all carried *Triactis producta* (Cutress 1977). As aforementioned, the small specimens and fragments carried in the chelae of *Lybia* are often not of typical morphological form (lacking, outgrowths, changes in size, etc.) and are not readily identified. The 'sagartiids' carried by Duerden's (1905) second crab are likely young *T. decora*, the species usually carried in the chelae of *Polydectus cupulifer* (Figure 3D).

   In addition to anemones, boxer crabs occasionally collect and hold in their claws other small invertebrates. Most notably, *Tunebia hatagumoana* appear to almost always hold small nudibranchs of the genus *Gymnodoris,* possibly *Gymnodoris citrina* (Sakai 1961, Baba & Noda 1993), although

Sakai (1961) reported one specimen found holding an unidentified anemone. *Tunebia hatagumoana* have been observed holding nudibranchs in both Japan and the Philippines (Mendoza & Ng 2011); however, a majority of the studied specimens are preserved, impeding on the identification of small soft tissue animals held by the crabs. *Polydectus cupulifer* usually hold sea anemones but has also been retrieved holding small unidentified holothurians in each claw (Guinot 1976). Little is known about the nature of the association of these crabs with nudibranchs or holothurians. The notion that they hold animals such as nudibranchs which are typically far more mobile than anemones is intriguing.

Schnytzer (2008; see Appendix 2) documented a novel relationship between *Lybia leptochelis*, who always hold a pair of *Alicia* sp., and another anemone, typically twice the size or more of the claw-held
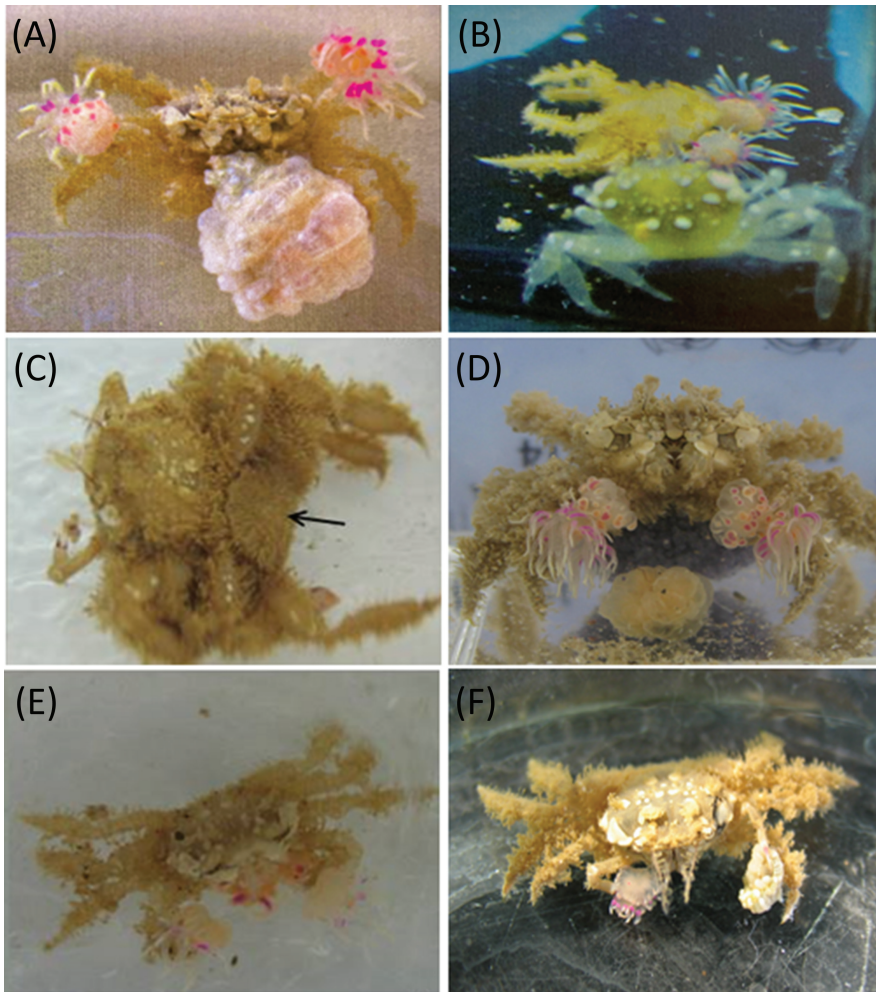

Figure 4 *Lybia leptochelis* and associated anemones. After Schnytzer (2008). (A) The crab is holding an *Alicia* sp. in each of its claws and retaining an *Anthopleura elatensis* with the aid of its walking legs. (B) Newly moulted crab in the front, behind is the moult with both anemones still secured in the claws. (C) Mating *Lybia leptochelis*. The black arrow points at the female abdomen. (D) Female crab with attached purple eggs holding two large anemones with a large *Anthopleura elatensis* in front of the crab. (E) A crab with four *Alicia* sp., two held in the claws and two retained with the walking legs. (F) *Lybia leptochelis* holding a typical *Alicia* sp. anemone in the right claw, and what appears to be a fragmented *Anthopleura elatensis* in the left claw.

anemones (Figure 4A; Supplemental Video 1). About a quarter of all collected *Lybia* crabs were found retaining an additional anemone *Anthopleura elatensis* with the aid of their walking leg(s). Although the fourth walking leg was usually used to hold the anemone, occasionally, further walking legs were used, depending on the size of the anemone. The larger the anemone the more legs used to hold it. In the laboratory, this anemone was retained for several weeks at least. The most common 'additional anemone' was *Anthopleura elatensis,* but occasionally a crab was found retaining *Boloceroides mcmurrichii* and once a *Paractis paldella. Anthopleura elatensis* appeared also to be the most commonly found anemone in the crab's habitat occurring in clonal groups of four to six under rocks that are similar to those under which the crabs are found. The function of retaining these relatively large anemones by boxer crabs is unknown. Possible functions include chemical or physical camouflage, 'active' defence or perhaps they are holding a food reserve (Schnytzer 2008). Identifying anemones held by crabs using classical morphological techniques is both time-consuming and uncertain. There is a very large gap in our knowledge regarding the taxonomy of anemones associated with boxer crabs. Such a gap could be closed by the application of molecular techniques. Contrasting the DNA of a small symbiotic unknown anemone to that of a large, fully developed and identified non-associated anemone should provide the answer. This procedure was successfully applied by Giman (2008; see Appendix 3) and Crowther (2013) for the identification of *Triactis producta* held by several species of crabs.

Morphological adaptations for holding and wielding anemones

The claws of polydectine crabs are structured to efficiently hold live anemones, sea slugs or small holothurians. The chelipeds exhibit no sexual dimorphism. These chelipeds are slender with long fingers armed with spiniform recurved hooks on their cutting margins (Figure 2). The hooks are directed obliquely inwards and gradually increase in size from those near the tip of the finger to the proximal ones. The tips of both fingers are strongly curved downwards and upwards, respectively. The anemones are held tightly by the middle of the column below the tentacles, with the sharp hooks of the fingers dug into the anemone tissue. The anemones are usually held with the pedal disc facing up and the tentacles facing down. The shape of the chela and fingers and the number and shape of the hooks along the cutting margins are species specific for polydectine crabs (Figure 3) (Guinot 1976, Guinot & Wicksten 2015, Davie et al. 2015).

The adaptive and comparative morphology of boxer crabs has been studied extensively using light microscopy (Guinot 1976). The use of SEM (Scanning Electron Microscope) has never been employed to this end. Since the claws are occupied with holding anemones, boxer crabs must use their walking legs to perform behaviours such as food gathering (Duerden 1905), food theft (Schnytzer et al. 2013), intraspecific fighting (Karplus et al. 1998), anemone detachment (Duerden 1905) and even the carrying of additional anemones (Schnytzer 2008). These observations led to the hypothesis that the crabs may have sensory adaptations enabling them to feel if, when, how and where they are holding their symbiont and/or other anemones, as well as the collection or theft of food particles. A SEM study using three representatives of *Lybia*, male and female specimens of *Lybia leptochelis, Lybia tessellata* and *Lybia plumosa*, revealed that the claws, particularly on the inward-facing 'hooks' used for retaining anemones, and tips of the walking legs (Figure 5), particularly the first, have numerous pores on them. Two main types of pores were observed on the legs,
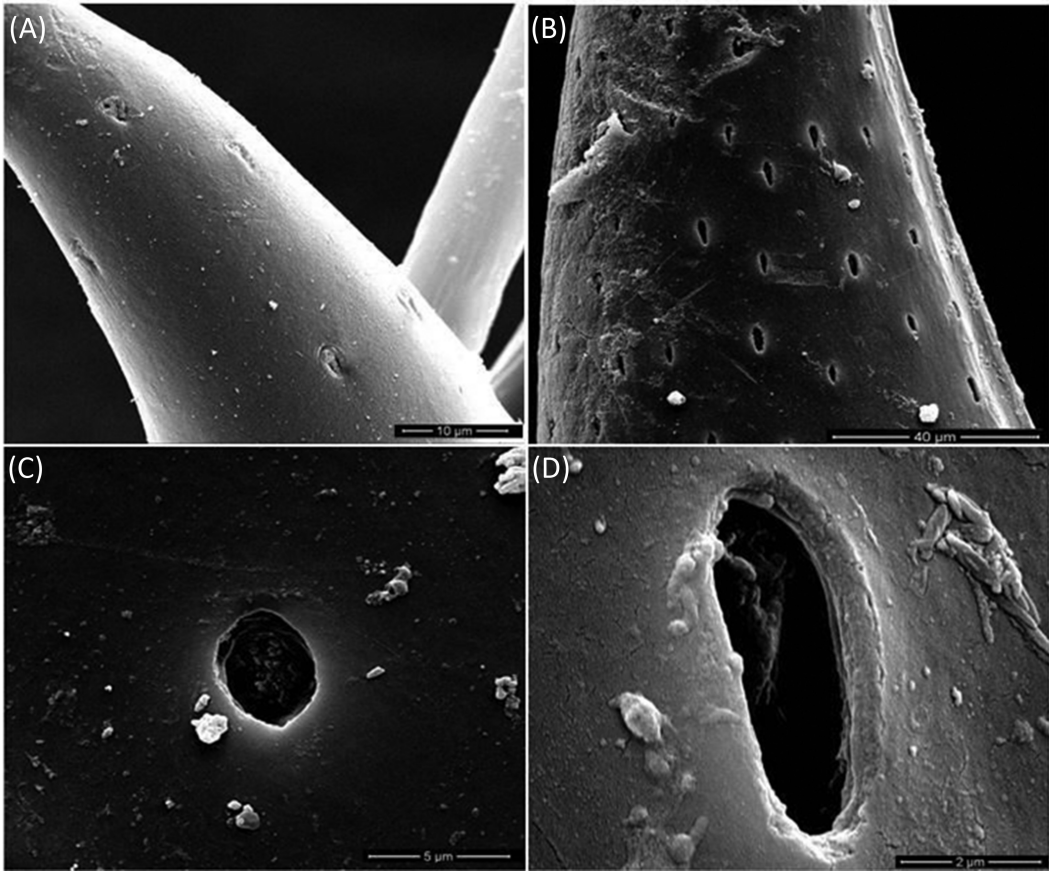
Figure 5 SEM images of possible *Lybia tessellata* sensory pores. (A) Tip of claw. (B) Tip of first walking leg. (C) Close-up of round-type pore. (D) Close-up of oblong-type pore. All images were taken from *Lybia tessellata*.

one rounder and one more oblong (Figure 5C and D), and one type of pore was observed on the claws. Similar structures, such as hair peg and campaniform organs, are known to have mechano-sensory and chemosensory functions in other brachyuran crabs (Davie et al. 2015). Some variances in the number and distribution of pores were observed between the *Lybia* species tested. Although further work is required, *Lybia* crabs provide a promising model for studying the functioning of putative crustacean sensory organs in the performance of their unique behaviours (Schnytzer 2008).

The range of motion of each of the segments of crustacean chelipeds is usually restricted to a single plane. Each plane is typically positioned so that it is perpendicular to that of its neighbour (Davie et al. 2015). However, the propodal-carpal joint in polydectine crabs is different, allowing much more freedom of movement and precision (Guinot 1976). This capacity allows boxer crabs to precisely wield their anemones to target a source of disturbance, as described by Duerden (1905).

Outside the Polydectinae, *Diogenes edwardsii* is the only hermit crab which places an anemone, *Sagartia paguri,* on top of its claw, but without impending the grasping ability of its chelae. All other hermit crabs place their anemones atop of their shells. When *Diogenes edwardsii* withdraws into its shell, the anemone is pulled back into the aperture facing the outside. As the crab emerges from its shell the anemone comes out first, usually fully expanded (Ross 1975).

Measurements of field-collected *Lybia leptochelis* revealed a size range of maximal carapace width of adults between 4 and 13 mm (Schnytzer et al. 2017) and that of *Lybia edmondsoni* ranged

between 10.5 and 14 mm (Karplus et al. 1998). *Alicia* sp. pedal disc diameters range between 0.5 and 3 mm. Within this range, there is a positive correlation between *Lybia leptochelis* carapace width and the mean pedal disc diameter of the associated anemone (Figure 6A) (Schnytzer et al. 2017). There appear to be no signs of handedness (Figure 6B). There seems to be an optimal anemone size for the crab to carry. The correlation between carapace width and anemone diameter is unlikely to be the result of acquiring the right size of anemone, but probably due to the crab regulating the size of anemone (Schnytzer et al. 2017). Overly large anemones may cause an excessive strain on the delicate propodal-carpal joint. *Polydectus cupulifer* is the only boxer crab which can handle anemones near its own size (e.g. *Teliopsis* sp.; Guinot 1976). According to Guinot (1976), the propodal-carpal joint of *Polydectus cupulifer* is different from that of other boxer crabs and has a more robust structure.
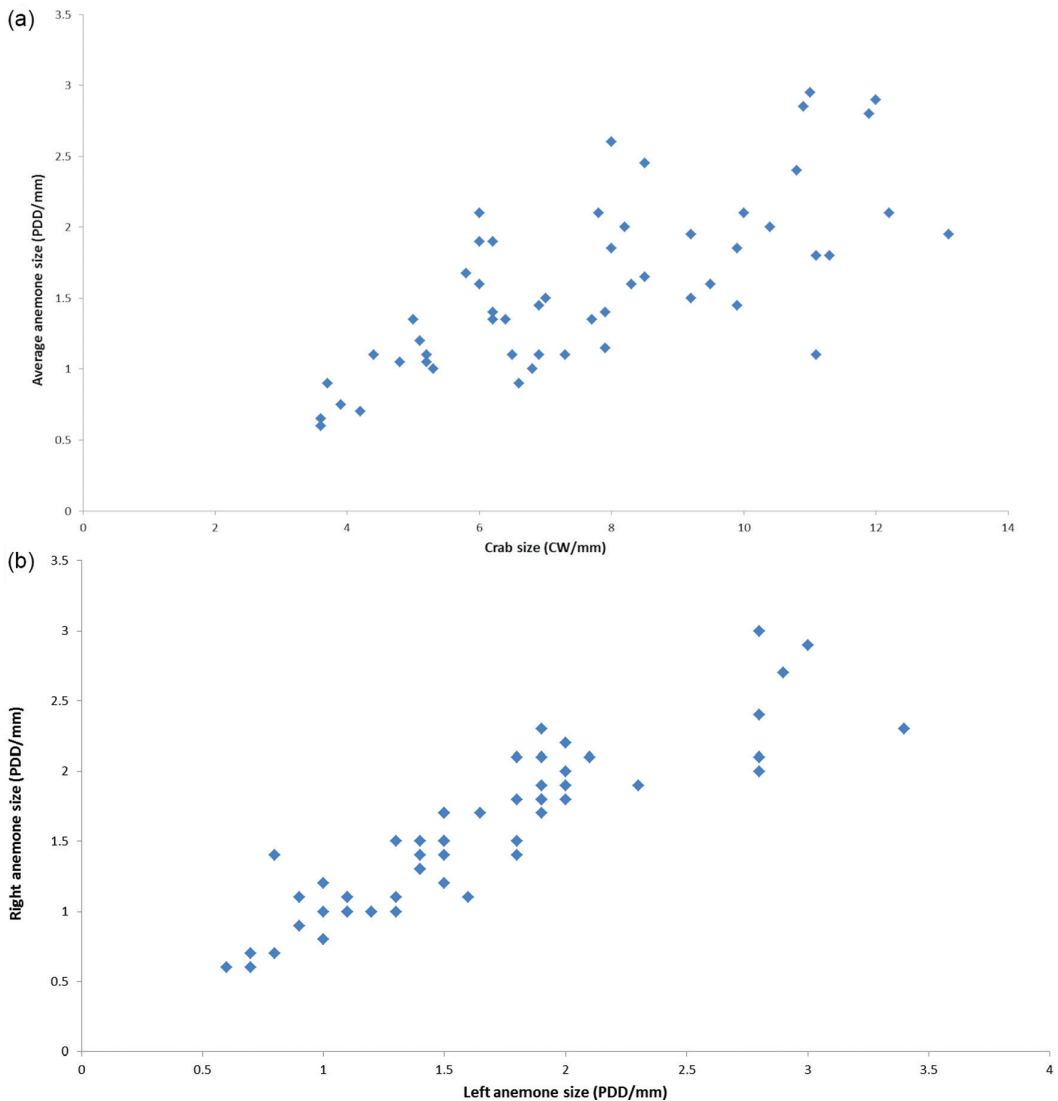

Figure 6 *Lybia leptochelis* and *Alicia* sp. size relationships. (a) Correlation between pedal disc diameter of held anemones (i.e. average of left and right anemones) and crab carapace width, as observed in nature. (b) Correlation between pedal disc diameter of left- and right-held anemones as observed in nature. CW– carapace width, PDD– pedal disc diameter. After Schnytzer et al. (2017).

Alterations in associated anemones

Anemones held by boxer crabs undergo with time alterations in size, structure and colouration in comparison with free-living specimens. As will be discussed in the following sections, unique behaviours such as food restriction, splitting (induction of asexual reproduction) and intraspecific theft of whole and fragmented anemones, all presumably contribute to these alterations and changes. *Triactis producta* held by *Lybia tessellata* also differ from free-living specimens by lacking column outgrowths (Figure 7). Anemones with outgrowths would render their handling difficult, thus the crabs either choose anemones that lack column outgrowths, or the crabs impede their formation (Crowther 2013). A further possibility is that the anemones held by the crab are too small for outgrowth development. *Triactis producta* held by *Lybia edmondsoni* became bleached
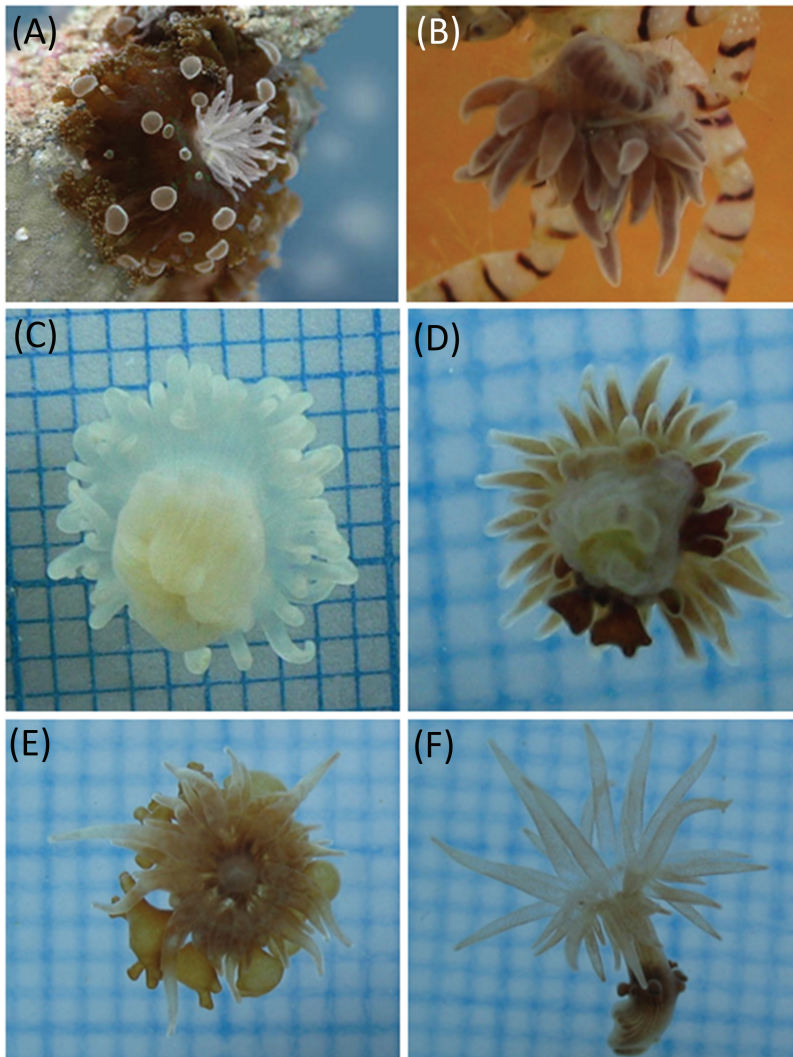

Figure 7 *Triactis producta* wild vs. crab held morphology. (A) Free-living *Triactis producta* in nature. (B) Crab held, with photosymbiotic zooxanthellae. (C) Bleached anemone, immediately after removal from crab. (D) Two weeks post-removal from crab, kept under LD lighting conditions. (E) Two months post-removal from crab – top view. (F) Two months post-removal from crab – side view.

(Figure 7C) due to loss of zooxanthellae because of the sheltering of the crab in the dark during the day. In comparison, free-living anemones are dark brown, except for their frosty white tips, due to thriving zooxanthellae exposed to sunlight (Figure 7A; Cutress 1977). Experimentally, a small whitish coloured *Triactis producta* lacking any outgrowths from the column was removed from *Lybia tessellata*. When fed and exposed to light, gradually this anemone increased in size, became darker and developed outgrowths of its column (Figure 7D-F; Yanagi and Iwao 2012). Furthermore, *Lybia edmondsoni* have been observed mouthing their held anemones, whereby the crabs will bring the anemones in contact with their mouth appendages. It was suggested that this activity affects the anemone structure, giving its pedal disc a cone shape, making it easier to handle (Karplus et al. 1998). Boxer crabs may also control the morphology of other invertebrates held in their claws. Nudibranchs (*Gymnodoris* sp.) held by *Tunebia hatagumoana* are small and have no visible gills or oral tentacles compared with free-ranging gymnodorids (Baba & Noda 1993). Baba & Noda (1993) note that this species of *Gymnodoris* most closely resembles *Gymnodoris citrina*; however, they were unable to confirm this due to the structural changes possibly due to being held by the crab.

Crab and anemone activity rhythms

The activity rhythm of boxer crabs in the field has been briefly described based on limited observations. *Lybia* crabs presumably spend the days hidden in crevices and under stones in shallow tropical reefs, whereas at night they emerge from their shelters to scavenge (Crowther 2011). *Lybia edmondsoni* was observed during night dives by Debelius (1984) in the stony infra littoral of Hawaii. The crabs were active moving on top of rocks as long as they were not targeted by the underwater flashlight causing them to freeze.

Triactis producta, a common associate of *Lybia tessellata and Lybia edmondsoni,* has a diurnal activity rhythm. This anemone is associated with photosynthetic zooxanthellae and gains most of its nutrition from its symbionts. *Triactis producta* is attached to firm substrate such as dead or live scleractinian corals (particularly *Porites* and *Acropora*) and rocks at depths of 1–15 m in areas of strong light penetration (Levi et al. 1970).

The activity rhythm of *Lybia leptochelis* associated with *Alicia* sp. was studied in the laboratory under controlled light conditions (Schnytzer 2008). *Lybia leptochelis,* with and without anemones, were maintained in isolation in small aquaria, each equipped with a shelter (see Schnytzer et al. 2013). The crabs displayed a distinct nocturnal activity rhythm. They spent about 80% of the time inside the shelter during the day and about 20% at night. Time spent in locomotion was relatively high at night and reduced while inside the shelter during the day. Minor grooming (i.e. grooming with the third maxilliped) occurred both inside and outside the shelter whereas major grooming (i.e. grooming with the chelipeds, involving the temporary removal of an anemone from the claw) occurred only inside the shelter. Major and minor grooming occurred during both day and night. The same activity patterns were displayed by crabs with anemones and after the anemones had been removed. In the case of *Lybia* crabs associated with *Triactis producta* (e.g. *Lybia edmondsoni* and *Lybia tessellata*), the presumed nocturnal activity of the crabs probably enforces its own activity rhythm on that of the anemone, causing it to bleach due to loss of zooxanthellae. That said, previous work on bleached *Entacmaea quadricolor,* a common host of symbiotic clown fish, has shown that they do not lose their ability to deploy toxic nematocysts when bleached (Hoepner et al. 2019).

Boxer crab and anemone feeding and growth

Feeding in anemones is diverse, ranging from complete metabolic dependence on symbiotic zooxanthellae to predation of benthic and planktonic organisms, suspension feeding and a combination of some of the above (Schick 1991). *Triactis producta* and *Alicia* sp. are both associated with boxer crabs but differ in their feeding habits. Aquarium studies revealed that *Triactis producta* largely

depends on photosynthetic algae embedded in its tissues. *Daphnia* and *Artemia* feed is usually refused in the aquarium. Glutathione has been found to produce a feeding response in most anemones but fails to do so in *Triactis producta* (Levi et al. 1970).

   Alicia sp. lacking zooxanthellae, as revealed by Pulse Amplitude Modulation (PAM) fluorometry measurements, epifluorescent microscope observations and histological work, depend largely on predation and scavenging (Schnytzer 2008, Schnytzer et al. 2013).

   Boxer crabs use their associated anemones in three different strategies to facilitate feeding:

A. *Stunning of prey. Lybia tessellata* and *Lybia leptochelis* crabs in aquaria attacked live small fishes and amphipods using their anemones to stun and immobilize them. Elusive prey could then be captured and consumed (Schmitt 1965). By contrast, *Lybia leptochelis* holding *Alicia* sp. in the laboratory did not use its anemones for stunning large prey (Supplemental Video 3; Schnytzer et al. 2013). That being said, when presented with live brine shrimp, however, the shrimp will adhere to the *Alicia* sp. tentacles and cease to move shortly thereafter. Indeed, free-living *Triactis producta* colonies are known to cause serious stings even in humans (Levi et al. 1970), whereas *Alicia* sp. that were kept in the lab and held on many occasions caused no apparent discomfort (Schnytzer et al. 2013).

B. *Anemones used to collect food.* Duerden (1905) reported in his classical study on the crab–anemone feeding reactions that *Lybia edmondsoni* robbed food from their held anemones *Bunodeopsis* sp. and *Sagartia* sp. He observed that the crabs perform a 'mopping' action with the anemones using them as tools for gathering food. The crabs were described removing food particles adhering to the walls of the polyp (Supplemental Video 2). Pieces of meat attached to the anemone oral disc were removed by the crab with their first pair of walking legs. In cases that the food fragments have already been swallowed by the polyp, the crab extracted the food from the stomodeum of the anemone. The crab might have detected the presence of food on the anemone by movements of the anemone during ingestion and or due to stimulation by meat juices emanating from the food particles.

C. *Anemones distanced from food. Lybia leptochelis* associated with *Alicia* sp. attempts to reduce the amount of food ingested by the anemones by distancing the held anemones from the food and removing any food captured by the anemones (see the following section for further details; Supplemental Video 3; Schnytzer et al. 2013). This is of course in contrast to the more active use of anemones exhibited by *Lybia tessellata* and *Lybia edmondsoni.*

Supplemental Video 2   *Lybia tessellata* holding out its *Triactis producta* to capture food (dead *Artemia*), then proceeds to remove particles from anemone tentacles (Schnytzer 2008).

Supplemental Video 3   *Lybia leptochelis* holding its *Alicia sp.* anemones away from presented food (dead *Artemia*). Any food particles that are caught by the anemone are then removed by the crab for its consumption (Schnytzer et al. 2013).

Only one study has systematically assessed the impact of lone and crab-held anemone feeding and growth (Schnytzer et al. 2013). This study included four experimental groups. The first group included fed *Lybia leptochelis* holding *Alicia* sp. anemones which shrunk significantly over the course of the experiment. The crabs reduced the amount of food ingested by the anemones by distancing them and removing food captured by the anemone. The successful removal of food by the crab was due to their much more rapid response to the food compared with the response of the anemones. The second experimental group consisted of fed crabs without anemones and made almost no use of their vacant claws. If a crab would try to use its modified chelae to grasp and lift an *Artemia* they failed in their attempts. However, they were successful, as were the anemone-bearing animals, in pushing and shoving presented food into their mouths with the first pair of walking legs. No growth was recorded for the crabs since none of them moulted during the study.

Experimental group three consisted of anemones that were 'freed' from the crabs ingested up to four *Artemia* per feeding session (Figure 8A; Supplemental Video 4) and ate about 8 times more than the crab-held anemones. These anemones underwent remarkable changes in morphology, colour and size, with a 250% expansion in pedal disc diameter. Experimental group four consisted of 'free' starved anemones shrunk in size until they disappeared altogether, probably due to lack of zooxanthellae, being dependent on predation for survival (Figure 8B). The relationship between *Lybia leptochelis* and *Alicia* sp. is an extreme example of a kleptoparasitic interaction. *Lybia* preserves the minute size of its associated anemones by food reduction much as gardeners produce 'Bonsai' trees (Figure 8C). The boxer crab thus maintains a 'Bonsai' symbiont that is conveniently carried around as a tool to trap its food and provide protection.

Boxer crab reproduction

No information is available on the breeding and larval culture of boxer crabs (Calado et al. 2003, Calado 2020). The demand for boxer crabs and particularly *Lybia tessellata*, *Lybia edmondsoni* and *Polydectus cupulifer* in the ornamental crustacean trade is supplied exclusively by capture of crabs in the field, damaging and depleting natural populations.

Our limited knowledge of the reproductive biology of *Lybia leptochelis* has been accumulated partly by chance as a by-product of other projects. While collecting boxer crabs, we noticed that during the winter months only a single crab was found under a rock, whereas, during the summer on many occasions two, and sometimes even more crabs, were found under the same rock. On two such occasions both crabs were collected and found to be a male and a female. On one such occasion the pair proceeded to mate shortly after being brought to the laboratory. As they were to be used for a separate study, the anemones were removed from the crabs, leaving only small fragments in their claws. Within several minutes the crabs encountered one another. Both crabs held their claws away from the opposing crab, while their bodies and appendages were in close contact. Several minutes later the male lifted its pleon from his cephalothorax, whereas about 20 minutes later the female lifted her broad and round abdomen exposing the pleopods. The crabs remained copulated for about two and a half hours (Figure 4C) and subsequently disengaged. Approximately 2 weeks following the mating, the female laid a grey egg clutch of several hundred eggs which gradually turned purple over the course of about 2 weeks. *Lybia leptochelis* females hold significantly larger anemones than males (Schnytzer et al. 2017). Possibly the larger size of their anemones contributes additional protection to the eggs attached to the female pleopods (Figure 4D). Hatching of zoea larvae was observed several times in the laboratory. The larval hatching is assisted by the female leading to larval dispersal. The morphology of zoea 1 of *Lybia plumosa* was described by Clark and Paula (2003), which also predicted this species has four different zoeal stages, typical for other related xanthids. There seems not to be a strict 'high season' of settling since ovigerous females were seen all year round at the collection sites except in the middle of the winter, with small individuals found throughout the year (unpublished data).
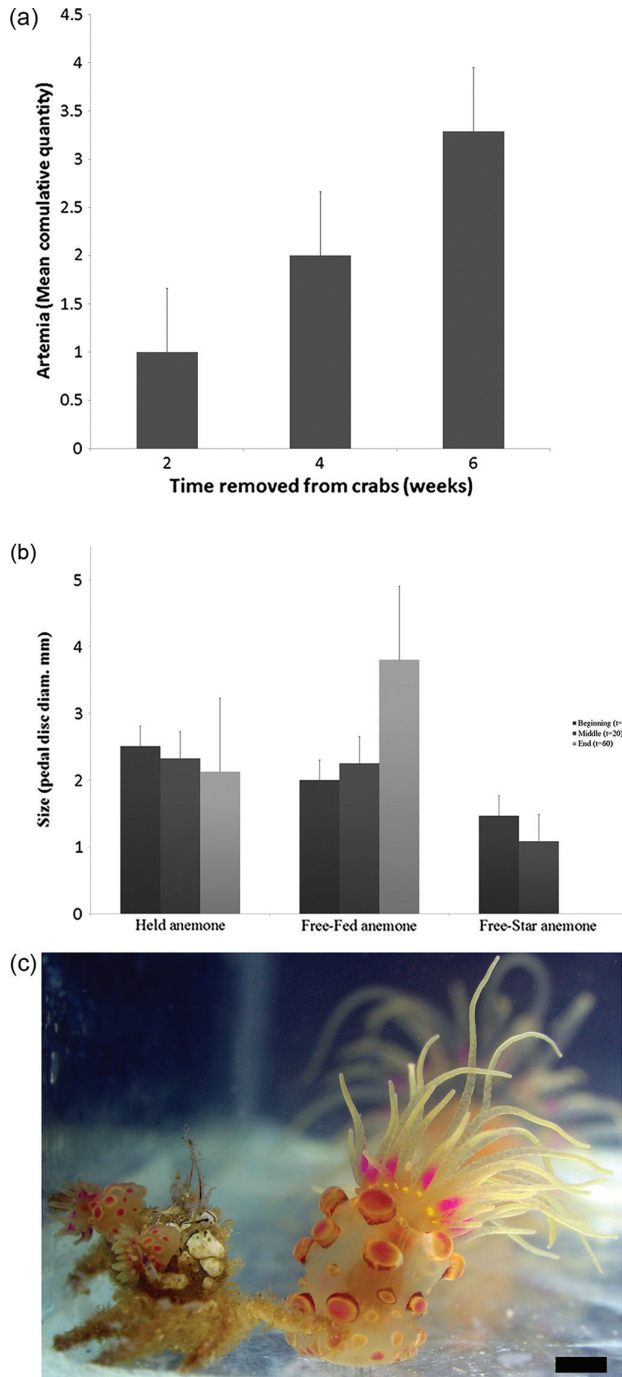
Figure 8 Growth of *Alicia* sp. while being held or removed from *Lybia leptochelis*. (a) The quantity of *Artemia* consumed by free *Alicia* sp. anemones per feeding trial following 2, 4 and 6 weeks after removal from the crab. (b) Anemone pedal disc diameter before (0 days), during (20 days) and after (60 days) the feeding experiment in anemones held by crabs, free anemones fed to satiation and starved anemones. (c) *Lybia leptochelis* holding a small *Alicia* sp. anemone in each of its claws (left side) and a large *Alicia* sp. grown free from the crabs for 3 months (right side). Scale bar = 2 mm.

Anemone location by boxer crabs

According to Duerden (1905), *Lybia edmondsoni* is not able to locate its associated anemones from a distance. He observed the crabs apparently moving aimlessly in the proximity of the anemone (i.e. *Bunodeopsis* sp. and *Sagartia* sp.) and only after coming in physical contact with the anemone did the crab seize it.

In contrast to Duerden (1905), in a recent study (Schnytzer 2008) *Lybia leptochelis* was found both visually and chemically attracted to its associated anemone *Alicia* sp. (Supplemental Video 5). In a tank in which anemones were in a cell behind a transparent partition, both crabs with and without anemones were attracted to the anemones, spending significantly more time close to a cell containing sea anemones, in comparison with the cell without anemones.

Chemical attraction of the crabs to the anemones was tested in an elongated aquarium that contained two permeable black nylon bags, one with anemones and one left empty, that were placed at either end. A significant majority of the tested crabs, both with and without anemones, were attached to the sacs that contained the anemones. Some crabs were even found to have torn the bag open and were holding two anemones. A similar experiment was carried out with *Anthopleura elatensis*, the anemone that is often carried by *Lybia leptochelis*. Once again, the crabs with and without anemones were chemically attracted to this anemone. Many of the questions concerning the chemical attraction of *Lybia leptochelis* such as the chemical nature of the anemone compound that attracts the crab and the specificity of the chemical attraction are still unknown. The differences in the positive findings of Schnytzer (2008) on the optical and chemical attraction in *Lybia leptochelis* to the lack of such attraction in *Lybia edmondsoni* as described by Duerden (1905) may be due to differences in the tested species or differences in the testing procedures, being more quantitative in the former and of a general descriptive nature in the latter.

A comparison with the study on the chemical attraction of the hermit crab *Dardanus venosus* to its associated anemone *Calliactis tricolor* by Brooks (1991) is of interest. In contrast to *Lybia*, hermit crabs were only attracted to anemones if they had no anemone on their shell. It was suggested that when carrying an anemone possibly all their chemoreceptors were saturated with specific molecules resulting in random movement of the crab with regard to the anemone. The chemical attraction of *Lybia leptochelis* was the same irrespective whether it held anemones. In preliminary observations, we found that *Lybia leptochelis* and *Lybia tessellata* will replace a small anemone with a larger one when available, perhaps explaining their attraction to anemones even when holding them.

Initiation of the partnership

How young boxer crabs initially find anemones is largely unknown. No one has documented acquisition in the wild by any polydectine. Our group as well as others have observed in the laboratory the hatching of *Lybia* crabs and vertical transfer, i.e. anemones passing from parent to larvae, does not appear to occur following the observation of many hatching events in the lab. Furthermore, the zoea lack the claws or other appendages to hold the anemones during their initial stages post-hatching (Clark & Paula 2003, Schnytzer 2008). It is perhaps easier to understand the initiation of the partnerships between *Triactis producta* and its associated boxer crabs such as *Lybia tessellata* and *Lybia edmondsoni* as they have been observed in close proximity in the wild. This anemone is by far the most common associate of boxer crabs, has a wide Indo-West Pacific distribution and occurs in well illuminated shallow water often in rock crevices or vertices of branching scleractinian corals

(Fishelson 1970). Large specimens of *Triactis producta* are often surrounded by smaller individuals, possibly the product of asexual reproduction (Crowther 2013). *Lybia tessellata* megalopa larvae may be chemically attracted to the large colonies of *Triactis producta*. A newly settled crab could presumably remove the small anemones located at the base of the large anemones with their maxillipeds and first walking legs. Subsequently the crabs with their newly acquired anemones would move into shallow water. It is important to note that various *Lybia* take part in intraspecific anemone theft and anemone splitting, the relative importance of these behaviours in *Lybia* anemone acquisition is unknown.

With regard to *Lybia leptochelis*, the most pressing question is whether the crab-held *Alicia sp.* also occur free-living or they are perhaps obligate symbionts of the crab only occurring in association. A limited histological study on the morphology of *Alicia* sp. taken from *Lybia leptochelis* indicated that they may be an undescribed species of *Alicia* (Fautin & Crowther pers. comm.). Furthermore, very small crabs (i.e. 2–3 mm c.w.) already possess two tiny anemones which indicates that the association between boxer crabs and anemones is formed very early in the crab's life cycle. We have searched for free-living *Alicia* sp. in the vicinity of the habitat of *Lybia leptochelis* without success. *Alicia* sp. is hard to miss since it is very conspicuous, having bright violet spots forming a ring at the base of the tentacles, a vibrant orange coloured mouth and orange-red coloured outgrowths around its column and base. However, anemones living in fissures and crevices are hard to detect, more so when such predatory anemones, such as *Alicia* sp., are nocturnal (Kruzic et al. 2002, Katsanevakis & Thessalou-Legaki 2007) and are presumably contracted during the day. We may cautiously assume that anemone splitting, and theft are part of the crab–anemone acquisition mechanism in nature. This is supported by the genetic identity of anemone pairs held by individual crabs collected at sea, as well as the size similarity of left- and right-held anemones (Schnytzer et al. 2017). However, it is reasonable to assume that splitting and theft are not the full picture of the acquisition mechanism. The discovery of free-living *Alicia* sp. will allow to investigate their genetic structure and the role they play in the initiation of these partnerships.

Mechanism of anemone acquisition and temporary release

Removal of sea anemones from substrate

The removal of symbiotic anemones attached with their pedal disc to the substrate has been described in detail in two species of boxer crabs, *Lybia edmondsoni* (Duerden 1905) and *Lybia leptochelis* (Supplemental Video 5; Schnytzer 2008). In both species, the anemone removal progressed in three phases: probing, detachment and readjustment. In the probing stage, the crab touched the anemone stalk and pedal disc with its first walking legs and third maxillipeds, administrating tactile stimulation to the anemone which leads to its relaxation. In the detachment stage the crab introduces its first walking legs under the pedal disc, loosening the anemone attachment (Figure 1B). In the event the crab encounters a large anemone it may make use of additional walking legs to aid in the detachment and acquisition of the anemone. During the probing and detachment stages, the crab claws, whether empty or holding anemones, were not involved. Only after detachment was completed did the crab use its chelae to grasp the anemone. The chelae seized the anemone in any position initially. However, to achieve what we perceive as the 'optimal holding position' the anemone was temporary

Supplemental Video 5   *Lybia leptochelis* without anemones (previously removed) grabbing newly presented *Alicia sp.* anemone (Schnytzer 2008).

held with the third maxillipeds and first walking legs. Finally, the anemone was re-grasped by the chela at the middle of the stalk with the oral disc facing down.

The process of anemone removal from the substrate and its placement on a hermit crab shell has been studied in great detail. Special attention was given to the active vs. passive role filled by the crab and anemone, respectively, and the particular mechanism employed by different pairs of associated hermit crab–anemone species in the initiation phase of the association (Ross & Sutton 1961, 1968, Ross 1967, 1974). The comparison between boxer and hermit crabs in relationship with symbiotic anemones during the probing and detachment stages is of interest. Unlike hermit crabs that make use of the claws and walking legs during the probing and detachment stages, boxer crabs do not use their claws but only their first walking legs and maxillipeds even when they are not holding anemones and could potentially make use of their claws. The tactile stimulation by hermit crabs has been experimentally replaced by tactile stimulation of the anemones with rods as well as by an electric current (Ross & Sutton 1968).

Theft of anemones

The first record of anemone theft by boxer crabs was reported by Karplus et al. (1998) observing *Lybia edmondsoni* holding *Triactis producta*. Schnytzer et al. (2017) demonstrated that anemone theft was a frequently practiced behaviour among *Lybia leptochelis* associated with *Alicia* sp. The interactions between pairs of crabs matched in size and sex, each consisting of one individual with two anemones and the other without anemones were tested. In 73% of the encounters intense fighting occurred culminating in anemone theft. Crabs of both genders, with or without anemones, were equally likely to initiate a fight. The time from encountering one another until the start of fighting was not affected by crab gender or whether the initiator was deprived or possessed an anemone. Fight duration was variable and was not related to gender or contest outcome (i.e. removal of an entire anemone or of a fragment).

In a typical contest, the individuals first approached one another. The crab with the anemones held its anemones at a distance away from the other (Figure 9A). Next, the initiator gently touched the other crab with the tip of its first walking leg for about a minute (Supplemental Video 6; Figure 7B). Following this gentle leg contact the two crabs typically proceeded to a back-to-back configuration (Figure 9C). Following this, the crabs rapidly locked their walking legs and commenced a close physical struggle (Figure 9D), grasping one another with their legs forming a tight ball (Figure 9E). During these phases, both crabs distanced their claws (either holding anemones or vacant) as far as possible from the other (Figure 9E). Next, the crab without anemones strived to move into a dominant position, typically on top of the crab holding anemones. The crab without anemones then tried to hold one of the opposing crab's claws and to lock it with the aid of its walking legs. No use was made of its unoccupied delicate claws. Upon achieving a claw lock of the opposing crab, the crab without anemones tried to remove the anemone held by the other crab using its first walking leg to pry at the claw holding the sea anemone. After it has been pried open sufficiently, the attacking crab for the first time used its vacant claw to take hold of the anemone (Figure 9G). Sometimes, an entire anemone was taken and sometimes only a fragment was torn off. Never was a contest witnessed with two whole anemones removed. Typically, after a whole anemone or a fragment was stolen, the contest was over (Figure 9H). No crabs were injured or killed in fights. In about a half of the contests an entire anemone was stolen, in a third an anemone fragment was taken, occasionally the crab stole two fragments. Splitting (see the following section) occurred in all cases that a single anemone or fragment were stolen. Presumably splitting is not induced when both claws are occupied. Contests were staged between very small juveniles deprived of their anemones and fully grown crabs with anemones. In all cases it was the small crab which initiated the fight and, in all instances, managed to come away with a fragment or a full anemone.
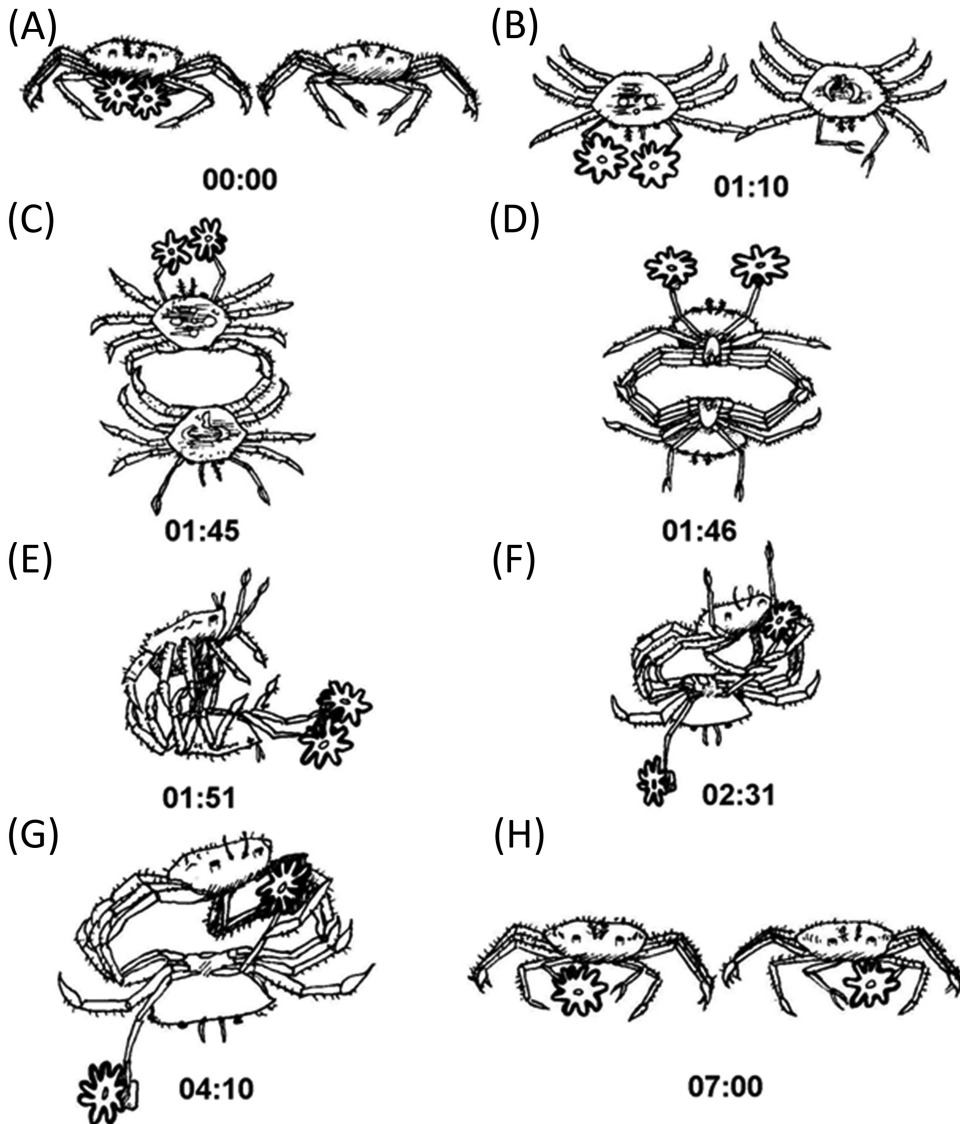
Figure 9 Sequence of typical anemone theft by *Lybia leptochelis*. Line drawings from video. (A) The crab with anemones holds them at a distance away from the other crab. (B) The initiator gently touches the other crab with the tip of its first walking leg for about a minute. (C) The crabs then typically proceeded to move into a back-to-back configuration. (D) The crabs then rapidly lock their walking legs and commence a close struggle grasping one another with their legs forming a tight ball. Note that during these phases both crabs distanced their claws (holding anemones or vacant) as far as possible from the other. (E) The crab without anemones strives to move into a dominant position, typically on top of the crab holding anemones. (F) The crab without anemones then tries to hold one of the opposing crab's claws and lock it with the aid of its walking legs. No use was made of its unoccupied delicate claws. (G) Once a claw lock of the opposing crab without anemones is acheived, it proceeds to remove the anemone held by the other crab. At first, it made use of its first walking leg to pry at the claw holding the anemone. After it has been pried open sufficiently, the attacking crab for the first time used its vacant claw to take hold of the anemone. (H) The crabs post contest holding a whole or fragmented anemone. Time presented in mm:ss. See text for elaboration of theft sequence. After Schnytzer et al. (2017).

Supplemental Video 6 *Lybia leptochelis* anemone theft. Two equally sized crabs are placed together, one with and one without anemones. The crab without anemones then proceeds to steal a large fragment (Schnytzer et al. 2017).

Supplemental Video 7 *Lybia leptochelis* anemone theft. Disproportionate matchup between small crab without anemones and a large crab with anemones. The small crab proceeds to steal an anemone fragment (sped up X2; Schnytzer et al. 2017).

In contrast to boxer crabs, very little intraspecific stealing of anemones was demonstrated for three species of Mediterranean hermit crabs, *Dardanus arrosor, Paguristes oculatus* and *Pagurus alatus* (Ross 1979). The rare intraspecific stealing was not immediate, almost never seen and was suggested to be due to some inhibiting influence deterring stealing from conspecifics. In contrast, stealing of anemones from conspecifics was very common among boxer crab, in line with the crucial role of the anemone in the boxer crab life. Moreover, in Giraud's (2011) study, only large *Dardanus pedunculatus* removed the anemone *Calliactis tricolor* from small conspecifics, whereas the reverse never occurred. In contrast, small boxer crabs removed anemones from conspecifics irrespective of the existing size difference, again indicating the importance of the anemone to the boxer crab (Supplemental Video 7).

Splitting

Duerden (1905) and Karplus et al. (1998) reported that *Lybia edmondsoni* may split its associated anemone *Triactis producta* into two fragments that later regenerate. Splitting was further studied in *Lybia leptochelis* associated with *Alicia* sp. demonstrating that splitting is common in this species and has implications for both the initiation of the anemone–boxer crab partnership as well as the genetic structure of associated anemone populations (Schnytzer et al. 2017). *Lybia leptochelis* of both genders that had either their left or right anemone removed were monitored. Splitting was a highly significant response performed by the crabs in 77% of the trials. The torn anemone fragments typically had less than a 10% size difference. The complete splitting process was observed several times (Figure 10; Supplemental Video 8). Splitting started with the crab holding the anemone with its claw, across the column, with the pedal disc facing upwards. The crab then took hold of the anemone with its free claw, thus holding the anemone in the aforementioned conformation between both claws. Next, the crab slowly began stretching the anemone between both claws in an outward motion, utilizing its front walking legs to surgically tear the anemone in half. Occasionally, the crab momentarily ceased the stretching to re-grasp the anemone in a central position as far as possible, so that the final splitting will produce two equal parts. Once the anemone was split into two, the remaining strands of connecting tissue were cut by the front walking legs. All split anemones fully regenerated within 4–7 days.

To establish whether splitting is a common occurrence in the wild, the genetic relatedness of anemone pairs taken from wild-caught crabs was tested. Anemones removed from freshly collected crabs were used for DNA analysis employing AFLP (Amplified Fragments Length Polymorphism; Amar et al. 2008, Douek et al. 2011, Brazeau et al. 2013). Pairs of anemones from a given crab were genetically identical. Furthermore, there was genetic identity between most pairs of anemones held by different crabs, with only three genotypes showing slight genetic differences. The resemblance of
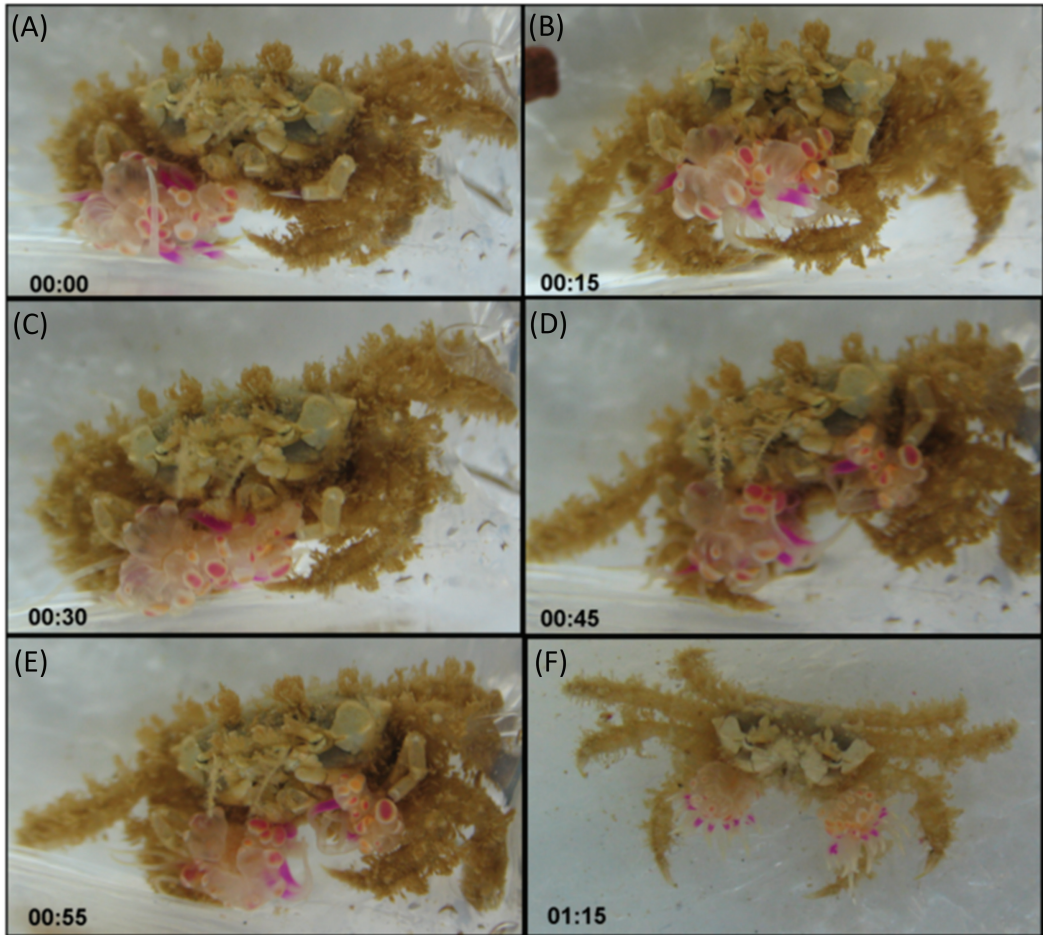
Figure 10 Sequence of anemone splitting by *Lybia leptochelis*. Time presented in hh:mm format. (A) The crab holding an anemone in one claw; the second is vacant. (B) Typical anemone splitting conformation with pedal disc up and oral disc down. (C) Stretching of anemone between both claws and use of front walking legs to tear it down the middle. (D) Tearing of anemone into two. (E) Final strand of anemone tissue are cut with front walking legs. (F) The crab holding two identical clones of the original anemone. After Schnytzer et al. (2017).

Supplemental Video 8 *Lybia leptochelis* splitting *Alicia* sp. (sped up X16; Schnytzer et al. 2017).

the DNA profiles between the three anemone groups is probably the result of asexual reproduction not involving the crab (Giman 2008). Measurement of the pedal disc diameter of the anemones held in the left and right claw of a crab revealed a highly significant size correlation (Figure 6B). This size correlation between anemone pairs from wild-caught crabs further support the notion of wide-spread splitting in natural populations of *Alicia* sp. anemones. This is a unique case in which one animal induces asexual reproduction of another, consequently also affecting its genetic diversity.

The phenomenon of splitting anemones appears to be unique to boxer crabs as it has not been documented among hermit crabs or any other crustacean associated with anemones.

Temporary release of anemones – moulting

Verril (1928), in his study of Hawaiian shallow water anthozoans, stated that when boxer crabs shed their shells they must be 'intelligent' enough to remove and transplant the actinian to their new claw, but he doubts that this operation has been seen. Jeng (1994) suggested that *Lybia tessellata* when moulting deliberately release the anemones, setting them aside until the new shell hardens, then retaking them. A different sequence of events has been observed in *Lybia leptochelis*. While keeping this species in captivity over several years, we frequently witnessed moulting in *Lybia leptochelis* (Supplemental Video 9; Schnytzer 2008). Sexually mature adult crabs moult about once every 2–3 months, during both day and night. The crabs withdrew from their old exoskeleton leaving the anemones held in the claws of the exuvia (Figure 4B). After a short period of time, an hour at most, from when the crab had fully moulted it would move rapidly towards the moult and within an hour take back its anemones one at a time. Great care was taken by the crab to remove the anemones complete and unharmed, each to its original claw. For approximately 30 minutes after retaking its anemones the crab would exhibit acclimatization signs in the form of claw 'twitching' (see section on 'Boxer crab immunity'). In contrast to boxer crabs which retake their original anemones after moulting, the spider crab *Inachus phalangium* (Inachidae) switches to a new host following each moult. This crab leaves its relatively large host *Anemonia sulcata* prior to moulting and following its night-time moulting will move to another nearby anemone (Wirtz & Diesel 1983, Landmann et al. 2016).

Temporary release of anemones – grooming

Many decapod crustaceans spend considerable amounts of time grooming, with their claws in many cases playing an important role (Bauer 1981). Highly conserved grooming behaviours were observed to take place in *Lybia leptochelis* and *Lybia tessellata* and have two distinct forms of grooming, defined as major and minor (Schnytzer 2008). Major grooming was only performed inside the shelter (Supplemental Video 10). During which the crab held one of their anemones in a raised position, facing the entrance of the shelter. The second anemone on the inner side of the shelter was held down on the substrate, and in a highly conserved sequence, the anemone was released from the claw and held tightly by the first walking leg on the same side as the claw. The tip of the leg was pressed against the pedal disc of the anemone and the mouth and tentacular region were folded between the joints of the leg. The crab then proceeded to move the free claw towards the mouth appendages and used the vacant claw to brush over its antennules, antennae, eyes and

Supplemental Video 9 *Lybia leptochelis* moulting and retaking *Alicia* sp. anemones (video shortened for convenience; Schnytzer et al. 2017).

Supplemental Video 10 *Lybia leptochelis* performing major grooming. *Lybia leptochelis* in shelter, releasing one anemone, holding it with walking legs and then proceeding to clean claw and facial appendages before retaking the anemone (Schnytzer 2008).

general frontal region. It repeated this process several times. The crab then retakes the anemone in its claws. The retaking of the anemone can take some time, the crab would rotate it vertically and horizontally until it was in the correct conformation. The anemones were almost always held across the middle of the column with the pedal disc facing up and the mouth region facing down. On some occasions, the crab moved to the other side of the shelter and proceed to remove the other anemone and implement the same sequence of actions. The unique aspect of major grooming is that the claw function of holding the anemones was temporarily abandoned in favour of grooming. A transition from holding to any other activity (e.g. feeding, fighting or anemone detachment) was not observed in boxer crabs, including minor grooming which only involves grooming with the third maxilliped without anemone removal.

Anemone swapping

The swapping of anemones has been described for two species of boxer crabs, *Lybia edmondsoni* (see Duerden 1905) and *Lybia leptochelis* (see Schnytzer 2008). Duerden (1905) twice observed a crab holding in one claw an intact *Bundeopsis* sp. and a fragment in the other, replacing the fragment with an intact anemone. The fragment was once replaced by an intact *Bunodeopsis* and once by an intact *Sagartia*. After dropping the fragment, the crab cleaned its free chela before grabbing the intact anemone. *Lybia leptochelis* holding two intact *Alicia* sp. in their claws were exposed to a single *Alicia* sp. larger as well as smaller than those held in their claws. Anemones larger than those carried by the crab were swapped following their examination by the crab with its first walking legs and maxillipeds. Anemones smaller than those held in their claws were invariably not swapped. A crab holding an *Aiptasia* sp. would swap it in favour of an *Alicia* sp.; however, the reverse never occurred.

Boxer crab immunity

The studies of crustacean immunity from cnidarians is mainly focused on palaemonid shrimps associated with giant anemones. Palaemonids that were isolated for several days from their anemone, or whose integument was wiped, undergo a process of acclimatization when returning to the anemone. The shrimp gradually approach the anemone, first retreating after being stung, but gradually being less and less stung until being able to move freely over the entire anemone without releasing any response (Levine & Blanchard 1980, Crawford 1992, Karplus 2014). However, the anemone shrimp *Periclimenes brevicarpalis,* after isolation from the anemone *Entacmaea quadricolor*, did not require any acclimation behaviour before entering its host without being stung (Fautin et al. 1995). Three mechanisms have been suggested for preventing the discharge of nematocytes while the shrimp are in close contact with anemones: (1) The shrimp covers its body with the anemone secretions, becoming chemically camouflaged (Levine & Blanchard 1980, Giese et al. 1996). (2) The shrimp, upon contact with an anemone, may secrete a chemical that acts on its own and inhibits nematocyte discharge by binding to a receptor site of the nematocyte (Crawford 1992). (3) Similar to the previous hypothesis except that the chemical secreted by the shrimp combines with an anemone-derived substance to inhibit nematocyte discharge (Crawford 1992).

Unlike the shrimp dynamic acclimation process, boxer crabs undergo acclimation to their anemones while continuously holding them. For approximately 30 minutes after retaking its *Alicia* sp. a freshly moulted *Lybia leptochelis* would exhibit acclimation signs in the form of claw 'twitches'. 'Twitches' were produced at a rate of 1–2 times a minute. These movements were analogous to what might be expected when a person is stung by an anemone. 'Twitching' was never observed a day following anemone retake. It is not known which of the three mechanisms suggested to prevent nematocyte discharge operates in *Lybia leptochelis*. However, the second suggested mechanism is highly unlikely since shrimp that produce their own secretion to inhibit nematocyte discharge are not affected by ecdysis in the retake of their anemones.

Boxer crab–anemone partner specificity

The earliest observations related to partner specificity in the boxer crab–anemone associations were carried out in Hawaii by Duerden (1905). In this pioneering study, one of two captured specimens (presumably *Lybia edmondsoni*) was holding a pair of *Bunodeopsis* sp. anemones, and the other specimen was holding a pair of *Sagartia* sp. anemones. The two species of anemones were found to be interchangeable, in that following removal of their anemones and exposure to anemones previously held by the other specimen, the crabs readily accepted the other species of anemone. In another experiment an additional crab–anemone combination, namely crabs that held in each claw a different species of anemone, was formed. Duerden (1905) concluded that in all his experiments the crabs appeared to seize one or the other species with equal readiness. A lack of partner specificity was thus demonstrated among the two species of carried anemones.

The evaluation of the level of partner specificity of boxer crab–anemone associations is speculative since many of the anemones have not been identified and few crabs from specific species were collected (Table 1). However, looking at Table 1, there are at least some crab species such as *Lybia tessellata* and *Polydectus cupulifer* which seem to be host generalists, found in association with five species of anemones in the former and three species of anemones and a holothurian in the latter. Nonetheless, in a specific locality, crabs often seem to hold anemones of only a single species. One hundred examined *Lybia leptochelis* from the northern Red Sea invariably held *Alicia* sp. in their claws, except for one case of a crab that held a fragment of an unidentified anemone, clearly not *Alicia sp.*, presumably *Anthopleura elatensis* (Schnytzer et al. 2013; Figure 4F).

Some insight concerning partner specificity may be gained by attempting to form in the laboratory associations between boxer crabs and anemones which do not occur in their natural habitat. Guinot (1976) reported that *Polydectus cupulifer* in the absence of *Sagartia pugnax* agreed to hold in aquaria an anemone of the genus *Teliopsis* sp., almost as large as its own size. *Lybia leptochelis*, which typically hold *Alicia* sp., had their anemones removed and were presented with *Aiptasia* sp. Crabs without anemones treat *Aiptasia* sp. in captivity in a similar way to *Alicia* sp., including holding and splitting. However, several crabs that were holding *Aiptasia* sp. were found to lose them after one to several months. This occurred possibly due to the lack of intake of photosynthetic metabolites due to bleaching when carried by the night-active crabs or due to feeding on these anemones which was observed on several occasions (Schnytzer 2008). It is noteworthy that *Aiptasia* sp. occurs in the Red Sea but not in the same habitat as *Lybia leptochelis* and has not been observed associated with boxer crabs in the wild.

Boxer crab intraspecific fighting

The involvement of anemones in boxer crab intraspecific fighting was studied in *Lybia edmondsoni* associated with *Triactis producta* (Karplus et al. 1998). Contests were staged between pairs of crabs matched to size and gender. Five out of the 15 recorded acts were performed with anemones (Figure 11). Three of these acts – 'twitch' (i.e. a rapid and short (1–3mm) lateral extension of the propodus), 'wave' (i.e. slow movement of chela or chelae in the horizontal plane) and 'extend' (extension of chelipeds with anemones) – comprised nearly 50% of all acts performed by the crabs. Both males and females avoided proximity and contact with their adversaries. Even when extending one claw at close range crabs invariably did so with the claw farthest away from the opponent. Actual contact between anemones and an opponent was extremely rare and seemed to occur due to an accidental movement of one of the crabs. Short contacts between legs during agonistic interactions (e.g. 'single-leg contact' and 'full grapple' (Figure 11A)) seem to have replaced the usual ritualized intertwining of the chelae reported in several other brachyurans (Schone 1968, Warner 1970, Lindberg 1980) and forcefully grasping (Huber 1987). There was no sexual dimorphism in claw dimensions since this structure is involved in anemone holding in both genders. Likewise, there was a marked similarity
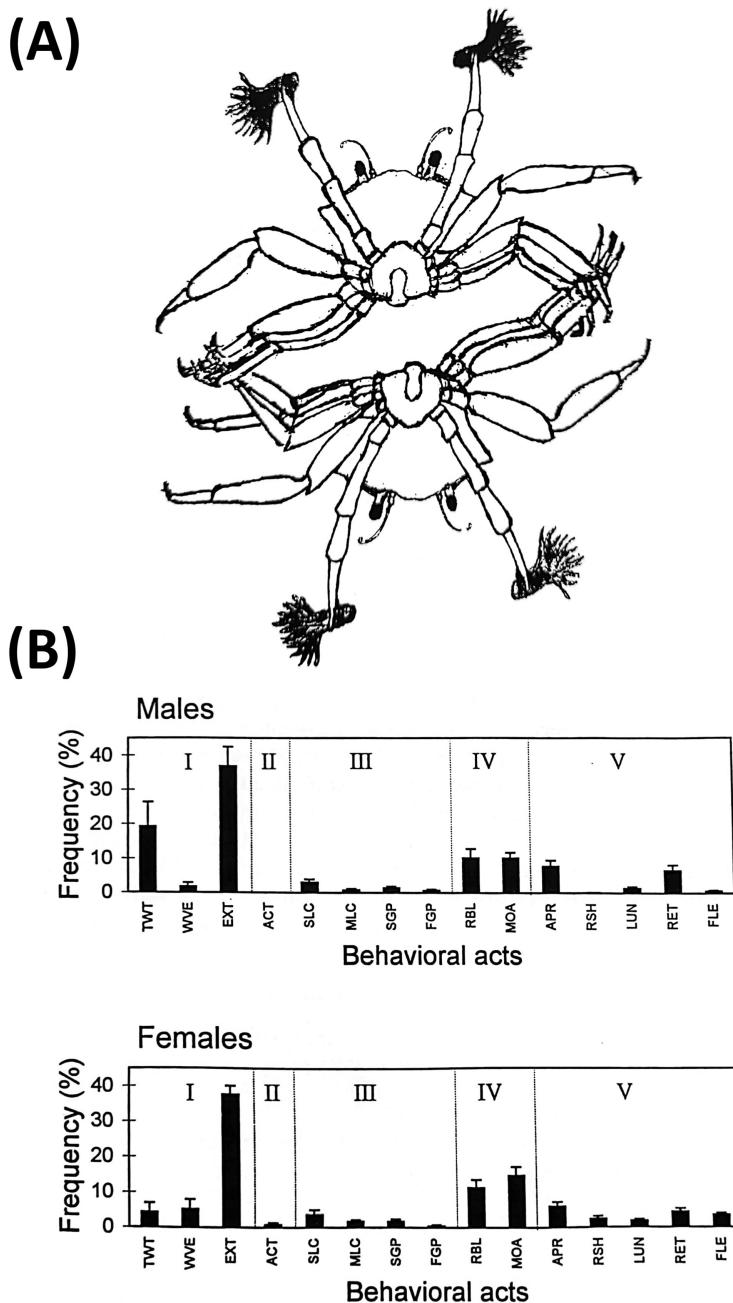
Figure 11 Intraspecific fighting behaviour of *Lybia edmondsoni*. (A) Two fighting males in the full grapple position (FGP). Walking legs are interlocked while the anemones *Triactis producta* are extended in opposite directions. (B) Mean frequency with standard error of 15 different acts during intraspecific aggressive encounters presented separately for males and females. I. Non-contact acts carried out with anemones (i.e. TWT – twitch; WVE – wave; EXT – extend). II. Contact acts carried out with anemone (i.e. act-anemone contact). III. Other acts with physical contact between crabs (i.e. SLC – single-leg contact; MLC– multiple-leg contact; SGP – semi-grapple; FGP – full grapple). IV. Maintenance activities (i.e. RBL – rub legs; MOA – mouth anemone). V. Acts increasing and decreasing distance between crabs (i.e. APR – approach; RSH – rush; LUN – lunge; RET – retreat; FLE – flee). After Karplus et al. (1998).

in the fighting behaviour of male and female crabs during contests. Several hypotheses were raised for the lack of use of anemones as a contact weapon during intraspecific contests:

1. *Triactis producta is a valuable resource to Lybia edmondsoni.* The anemones are not used in combat to prevent their damage or removal by the opponent.
2. *Triactis producta is highly toxic to L. edmondsoni.* Crabs avoid their use in fighting due to their high potential of severely harming the winner and loser of fights (Maynard-Smith & Price 1973), similar to fighting poisonous snakes (Shaw 1948, Thomas, 1961, Carpenter et al. 1976).
3. *Triactis producta are non-toxic to L. edmondsoni.* The anemones constitute an inefficient weapon and therefore are not used in combat.

So far, it is unclear which of the three hypotheses, or a combination of them, underlies the lack of anemone use in intraspecific fighting.

Boxer crab anti-predator defence

The involvement of anemones in boxer crab defence by deterring predators has been suggested several times (Borradaile 1902, Duerden, 1905, Jeng, 1994, Karplus et al. 1998, Davie et al. 2015). According to Verril (1928) the anemones serve as a protective living shield against fishes and perhaps other predators which fear the venomous stings of the actinian tentacles. When threatened, *Lybia* crabs perform a waving display by waving both chelipeds from side to side for a few seconds while either holding anemones (Jeng 1994) or nudibranchs (Baba and Noda 1993), bringing their defensive partners closer to the threatening object (Duerden 1905, Baba and Noda 1993). However, the claims concerning the anemone function to deter predators has so far not been supported by systematic experimentation. Preliminary observations on interactions of *Lybia leptochelis* associated with *Alicia* sp. with two species of fishes and a crab were carried out (Schnytzer 2008). A juvenile sciaenid *Argyrosomus regius*, a predator of small crustaceans, was placed in an aquarium with *Lybia leptochelis*. The fish, several times the size of the crab, very soon swam towards the boxer crab and came very close to it. The crab in response raised its anemones and struck the fish near the eye (Figure 12B). The fish appeared to 'shiver' for a brief moment and then retreated, not coming close to the crab again. Furthermore, *Lybia leptochelis* was introduced into an aquarium that contained a juvenile puffer fish, several times the size of the crab. The puffer fish several times slowly approached *Lybia leptochelis*. In one of these occasions the boxer crab struck at the puffer fish that retreated (Supplemental Video 11). An average sized *Lybia leptochelis* (c.w. 6–10 mm) was placed in the same aquarium with an Indo-Pacific crab, *Pilodius areolatus* several times its size. The crab approached the boxer crab which subsequently touched it with one of its anemones. The crab did not appear to be affected but did stop harassing the crab. In a single observation a *Lybia tessellata* (presumably holding *Triactis producta*) was approached by a juvenile octopus, about twice the size of the crab. The crab pointed its anemones at the octopus and touched it, causing the octopus to retreat (Figure 12A; Vaninni, pers. comm.). The crab's use of its anemones in anti-predatory defence is completely different from its avoidance of contact during intraspecific fighting.

Further experiments with boxer crabs with and without anemones exposed to different predators are needed to establish the protective role of the anemones. Similar experiments were carried out with hermit crabs with anemones attached to their shells and hermit crabs without anemones, exposed to predators (Ross 1971, McLean & Mariscal 1973, Brooks 1988). These studies clearly demonstrated the role of the anemones in helping to protect hermit crabs from octopuses and crabs.
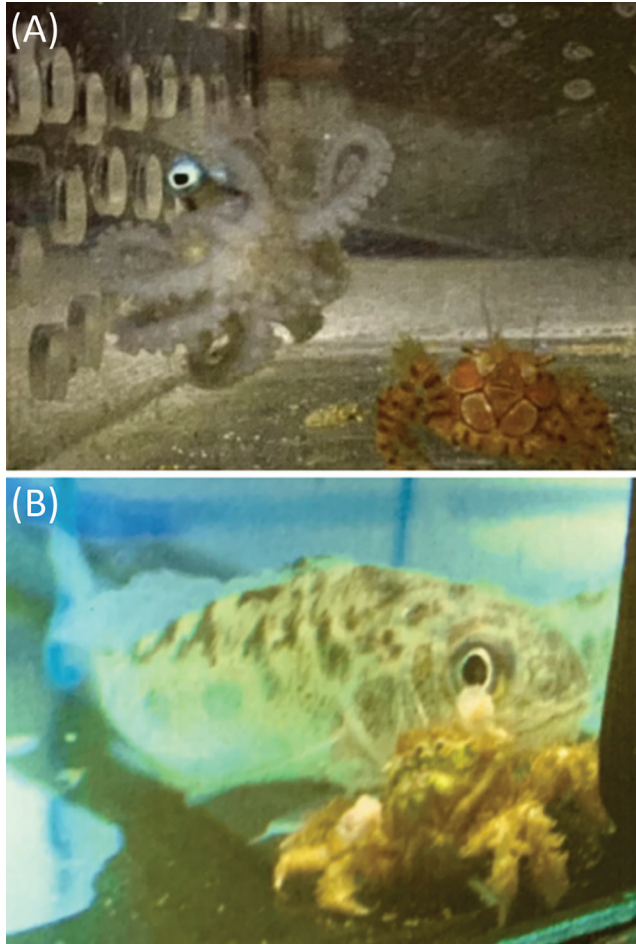
Figure 12   Boxer crabs deterring predators. (A) *Lybia tessellata* probably holding *Triactis producta* induced a retreat in a juvenile octopus by touching it (Vannini pers. com.). (B) *Lybia leptochelis* extending its left anemone towards the eye of an approaching sciaenid *A. regius.* After Schnytzer (2008).

Obligatory vs. facultative partnerships

The partnership between boxer crabs and anemones appears to be obligatory, as there is only one reference of several cases pertaining to the finding of several boxer crabs in the wild without symbiotic anemones (Borradaile 1902). In other references, each covering large numbers of at least 50 examined specimens (Richter 1880, Fishelson 1970, Karplus et al. 1998, Schnytzer et al. 2013),

Supplemental Video 11   *Lybia leptochelis* deterring Pufferfish. PBS 2018. https://www.youtube.com/watch?v=BUdpqFQYeZA; BBC 2018. https://www.bbc.co.uk/programmes/p06fnfmj/player.

crabs invariably held anemones in their claws. Furthermore, almost all specimens of these crabs in museums were preserved with their anemones (Guinot 1976). *Lybia* spp. were reared in captivity for several months without anemones (Karplus et al. 1998, Schnytzer et al. 2013). It is not surprising that they managed to survive under laboratory conditions considering the lack of predators and availability of food. However, in the wild, boxer crabs are not expected to survive given the lack of protection from predators and the lack of efficient means of collecting food.

Several *Lybia leptochelis* kept up to 1 year in captivity never lost their *Alicia* sp. anemones (Schnytzer 2008). This long adherence to their preferred anemone is a further indication of the obligatory boxer crab–anemone relationship. In contrast, hermit crabs which are facultatively associated with anemones, loose their anemones, frequently damaging and eating them following several months of captivity in the absence of predators. Chemical effluent from a tank containing an octopus reactivated the hermit crab habit of transferring anemones to its shell (Balasch & Mengual 1973, Ross & Von Boletzky 1979, Brooks & Mariscal 1986).

Anemones are probably facultatively associated with boxer crabs, given the fact that several of them such as *Triactis producta* (Fishelson 1970), *Phelia* sp. (Duerden 1905) and *Sagartia pugnax* (Verril 1928) have been observed free-living. Although *Alicia* sp. has so far not been observed free-living (Schnytzer et al. 2017), it will be quite surprising if it is not.

Costs and benefits from the partnership

Boxer crabs benefit from their association with anemones in three main ways: (1) Predator defence (Schnytzer 2008); (2) Stunning prey for feeding (Schmitt 1965) and food collection (Duerden 1905; Schnytzer et al. 2013); (3) Intraspecific ritualized fighting (Karplus et al. 1998). The presence of the anemones held by the crab claws emphasize and render more conspicuous the ritualized movements of the boxer crabs (e.g. behaviours such as wave and twitch), which would presumably be an unimpressive display by the crabs vacant, thin and feeble claws.

Anemones may also be involved in crab camouflage and conspicuousness. *Lybia tessellata* has derived its name from the special tessellated pattern of its carapace consisting of red and white polygons bordered with black lines. The crab legs are white with red to black rings (Figure 3C). The very conspicuous colour and patterns on *Lybia tessellata* (Figure 1D), as well as *Lybia edmondsoni*, may help them to blend into their colourful natural background as a form of disruptive camouflage (Ng pers. comm.). Alternatively, this colouration may be involved in aposematism, advertising its symbiotic anemone venom to deter potential predators. So far, no systematic work has confirmed aposematism in decapods (Caro 2018). In contrast, some of the polydectine crabs are cryptically coloured and indeed typically occur in rocky and muddy areas more suited to their colouration. *Polydectus cupulifer* possess a very thick covering of soft setae all over its external surfaces and has therefore been called 'teddy bear crab' (Figure 3D). The sediment that adheres to these setae conceal the form of the crab making it look like a lump of mud (Verril 1928, Chen and Hsueh 2007). The anemones carried by this crab possibly also add to its concealment.

Tool use by boxer crabs, related to benefits from the partnership, was already addressed close to the discovery of the association (Borradaile 1902, Duerden 1905). Since then, boxer crabs have been listed among tool users. Recently, they have been grouped together with elephants and lemurs as tool waving animals (Shumaker et al. 2011). Among invertebrates, only ants, crabs and octopus are known to construct tools (Shumaker et al. 2011), which raises the question: Do the modifications seen in anemones and nudibranchs held by Polydectine crabs constitute as tool construction? Broader invertebrate tool use is more common; however, the foregoing of the 'hands' or 'claws' which are permanently replaced by another animal are unknown outside of Polydectine crabs. There is, however, a comparable and interesting, yet little studied association between *Tremoctopus violaceus*,

the blanket Octopus, which has special dorsal arm suckers to which they attach *Physalia physalis* (Portuguese man o' war) tentacles, obviously providing them with a formidable weapon (Jones 1963, Norman et al. 2002). It is important to note that there they make use of tentacle strands and not the whole animal. The main problem, which is out of the scope of this study to discuss, is the issue of invertebrate cognition and to what extent and where the definition 'tool use' is applicable (Hansell & Ruxton 2008). In a recent review of tool use in animals (Amodio et al. 2018), boxer crabs were classified as stereotyped in contrast to flexible tool users. In stereotyped tool use the actions are absent prolonged individual practice and social influences showing little variation within species and genera. However, the use of a single tool (i.e. anemone) for different purposes in boxer crabs is exceptional among stereotyped tool users. The question as to the possible ontogenetic changes in the crab, such as individual practice and experience while handling anemones, has still to be resolved.

The major cost of the partnership to the crab is the loss of the common grasping function of its claws, which are highly adapted for the sole purpose of anemone holding. These functions are replaced or compensated for by the crabs' walking legs and maxillipeds. A further potential cost is the utter dependence of the crabs on their held anemones and consequently the availability and abundance of their anemones which dictates the distribution of each particular boxer crab species.

Benefits to anemones from their association with boxer crabs, have been suggested to relate to changes in the crabs' position, with increased oxygen supply and greater proximity to potential food items, though not necessarily ingesting them (Duerden 1905). Anemones are also dispersed by the crabs and occasionally forced to reproduce asexually. Other than this, the anemone pays a heavy toll for being associated with the crab, namely, growth suppression due to food deprivation and prevention of sexual reproduction (Schnytzer et al. 2017). Furthermore, it appears that in cases where *Lybia* hold anemones in symbiosis with zooxanthellae, they bleach over time due to the nocturnal activity of the crabs, resulting in a loss of one of their primary methods of nutrition (i.e. photosynthesis). As already stated by Duerden (1905), the advantage for the actinian appears largely negative. Many, but not all, of the anemones associated with Polydectine crabs, such as *Lybia tessellata*, *Lybia edmondsoni* and *Polydectus cupulifer* are found free-living. It would appear that the crab is essentially a parasite of the anemone as the anemones are also found commonly free-living and thus has little or nothing to benefit from being held by the crabs which limit their food intake and suppress growth (Yanagi & Iwao 2012, Schnytzer et al. 2017). It is compelling to suggest that the association is of a parasitic nature. In contrast, *Alicia sp.* associated with *Lybia leptochelis*, has not been found free-living to date and so we must be cautious about defining the nature of that particular association. In the case of *Tunebia Hatagumoana*, typically found holding gymnodorid nudibranchs, it is all the less clear what gain could come to a mobile predatory slug. Overall, the nature of this association appears to be of a parasitic nature, with very little if any gain to the crabs 'partners'. Such is the case with many other crab–anemone associations that have been documented, in which there is a highly intimate association, such as *Dorippoides facchino* and the anemone *Carcinactis* (Holthuis & Manning 1990) which are known to collect small anemones and grow with them simultaneously. Yet, it appears that none of those studies have experimentally assessed the cost and benefit to each of the associates and so we must be cautious with such comparisons.

Evolution of the boxer crab–anemone partnership

The reconstruction of the evolution of a complex behavioural relationship is always complicated and speculative. According to Duerden (1905), there were no simpler or intermediate stages of the boxer crab–anemone partnership which could suggest the lines along which the evolution has taken place. A change from predation to association has been suggested by Imafuku et al. (2000) for hermit crabs and could also be applied to the boxer crab–anemone partnership evolution. Hermit crabs, according to Imafuku et al. (2000), occasionally feed in captivity on their symbiotic anemones particularly during starvation. These crabs also eat non-symbiotic anemones. The complex behaviour

of removing firmly attached anemones likely shifted from detachment for feeding to detachment for placement on the shell for protection. Boxer crabs also feed occasionally in captivity on non-symbiotic as well as symbiotic anemones (Schnytzer 2008). In the case of the symbiotic *Alicia sp.* this was observed to happen when the crabs were already holding a pair of anemones and were provided with a surplus of anemones. The partnership between *Lybia leptochelis* and *Anthopleura elatensis* carried by its walking legs, may have originated as a food reserve, perhaps representing an early phase in the boxer crab–anemone partnership. In addition, a very small *Lybia leptochelis* of about 3 mm c.w. was collected holding in its claws two *Alicia* sp. as well as two additional similar sized anemones of the same species held in the fold of the two first walking legs (Figure 4E). The carrying of *Alicia* sp. by the legs as well as the claws, may provide a clue as to the evolutionary pathway of associated anemone holding mechanism.

Molecular analysis of the Xanthidae using three concatenated mitochondrial 12S rRNA, 16s rRNA and cytochrome oxidase I (COI), and the nuclear marker histone H3 was carried out on a large number of xanthid crabs, containing five species of the subfamily Polydectinae (Lai et al. 2011). The four *Lybia* species included in the study were split into two sister clades, each with two species. One clade included *Lybia edmondsoni* and *Lybia tessellata* as sister species and the other *Lybia hatagumoana* and *Lybia leptochelis*, with *Polydectus cupulifer* basal to them. The subfamily Polydectinae appears to be monophyletic, indicating that the partnership between boxer crabs and anemones evolved once among the sampled boxer crabs nested among non-associated xanthid crabs.

An additional molecular phylogeny was carried out by Giman (2008) on the subfamily Polydectinae using the three mitochondrial genes used by Lai et al. (2011) and Giman (2008), and two species of *Lybia*, *Lybia plumosa* and *Lybia caestifera*, that were not included in Lai et al. (2011). Included in this study were also *Lybia tessellata* from four different localities (i.e. Japan, Indonesia, Kenya and Somalia). In this study, based on the combined trees, the subfamily Polydectinae was resolved as a monophyletic group within the Xanthidae (Figure 13). The molecular analysis supports separation of *Lybia* into two clades, the setose carapace clade (i.e. *Lybia caestifera, Lybia plumosa, Lybia leptochelis*) with *Polydectus cupulifer* forming a sister group to this clade. The smooth crabs, *Lybia edmondsoni* and *Lybia tessellata*, forming a separate clade. The most intriguing result was that of *Lybia tessellata* from Somalia. The genetic distance found in the specimens from Somalia is enough to doubt its inclusion within the species *Lybia tessellata* (Figure 13). According to Guinot (pers. comm.) *Lybia tessellata* from Somalia looks different from the other *Lybia tessellata* and may be a different species. The three setose species (i.e. *Lybia caestifera, Lybia plumosa, Lybia leptochelis*) are closely related, sharing almost identical sequences (Giman 2008).

The evolution of the claws for only holding anemones is hard to comprehend according to Duerden (1905) since while holding anemones by the claws, the same claws have to be used for seizing and conveying food to the mouth as in most other decapods. The solution to this dilemma is in the plasticity of the periopod function. In decapod crustaceans the walking legs may change their function and replace that of lost appendages reflecting possible convergent evolution. For example, in the giant freshwater prawn, *Macrobrachium rosenbergii*, the amputation of the second pair of large claws resulted in the involvement of the small first pair of claws in intraspecific fighting behaviour. The small claws usually mainly involved in food acquisition and grooming were used in the absence of the large claws in the performance of aggressive acts (Karplus et al. 1992). Similarly, with the evolution of the boxer crab claws for holding anemones, the walking legs, particularly the first pair, took over the functions of feeding, anemone detachment and intraspecific fighting. The capacity for such a compensatory mechanism enabled the benefits of using the sea anemones to outweigh the costs of neutralizing the claws and thereby the evolution of boxer crab – anemone partnership.
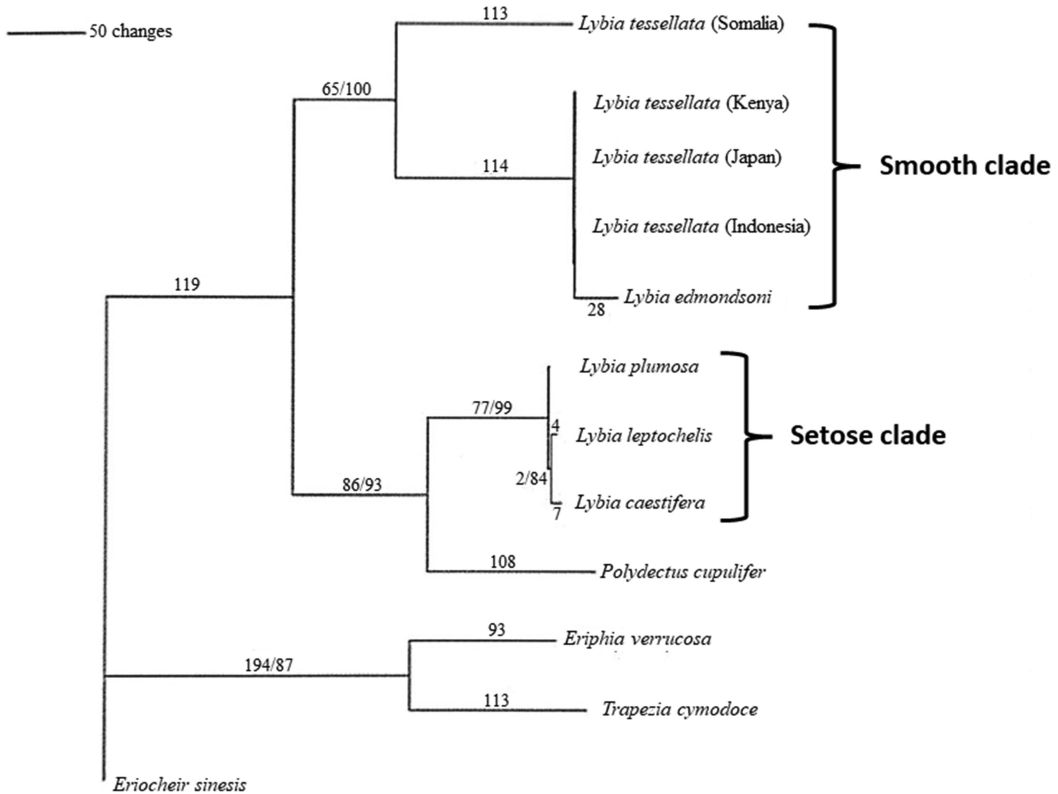
Figure 13 Phylogeny of polydectine crabs based on three combined mitochondrial genes (12S + 16S + COI). The tree was built according to the ML method using GARLI software. Left numbers are branch length, and right numbers are bootstrap values based on 100 replications. After Giman (2008).

Recommendations for future research

Several recent studies have contributed significantly to the limited knowledge to date on this association, followed by increased attention in the popular literature to boxer crabs. Nevertheless, important knowledge gaps remain, including the following:

a. There are substantial gaps in the ecology of boxer crabs and their associates. Some species, such as *Lybia leptochelis*, are known to occur at disparate locations, with little information of their distribution in between. There are some indications, both morphological and molecular, that *Lybia tessellata* from different locations may not be the same species. For other species such as *Lybia australiensis* and *Lybia denticulata*, *Lybia pugil* and *Tunebia tutelina*, the entire body of knowledge is based on one or two preserved museum samples. Others, such as *Tunebia hatagumoana*, have only been recorded on several occasions and always from relatively deep (60–80 m) trawls, their specific macro- and microhabitat/s are unknown. However, there is some anecdotal evidence of their occurrence in shallower water, like other boxer crabs. Due to their small size, cryptic behaviour and camouflage, it is difficult to find boxer crabs, certainly most of which are not as colourful as *Lybia tessellata* and *Lybia edmondsoni*.

b. The occurrence and ecology of some boxer crab associates is well known (e.g. *Triactis producta*). However, due to the external changes in the held associates, it is often unclear

which species is being held. In the case of *Alicia* sp. held by Red Sea *Lybia leptochelis*, the form and size of the crab-held anemones is nothing at all like that of lab-grown and lab-fed anemones. Indeed, they have never been found free-living. So too for the gymnodorids held by *Tunebia hatagumoana*, nothing is known about the exact species held and where or if they occur free-living.

c. The benefits gained by the crabs holding anemones are clear. The cost and benefit for the anemones (and other invertebrates) is less evident. Although there appears to be no long-term morphological damage to the anemones, no studies have been conducted on their reproduction abilities, especially sexual, in and out of association. Furthermore, for those species harbouring photosynthetic zooxanthellae (thus making it a triple symbiosis), the possible effects of being held by the reclusive crabs are even less clear. So too in the case of nudibranchs and holothurians, typically found free-living. Further growth as well as histological studies are required to better understand this.

d. Boxer crabs are often mentioned regarding the aquarium trade and hobby. They are a popular species (especially the 'common' and colourful *Lybia tessellata*) and are widely available from pet store suppliers worldwide. All the animals sold to date are wild-caught. Further studies on the crab's reproduction and aquaculture methods may be quite beneficial to the sustainability of boxer crabs.

e. Although some work has been done on the visual and chemosensory abilities of boxer crabs, particularly for adult *Lybia leptochelis*, the mechanisms involved in the initiation of the association, especially at the post-larval stage, as the crabs metamorphose into megalopa and settle, are unknown. It is reasonable to assume that they may navigate to the general area of settlement and then home in on their associates rapidly and precisely. Further lab and field experiments are required to understand this. Current advances in video recording as well as tagging methods may finally enable these studies to be carried out, which were always impeded by the crabs' small size.

f. The idea of holding an anemone for defensive purposes is apparently obvious. However, little experimental, and no field work, has shown this. Further studies are required to fully establish the protective value of holding anemones. Regarding the nudibranchs and holothurians that some *Lybia* have been found holding, the utility is even more mysterious, as at least in the case of the gymnodorids held by *Tunebia hatagumoana*, as it is unclear what sort of defensive mechanisms they have. Nothing is known about the species of holothurians held by boxer crabs.

g. There is evidence from Japan (Yanagi pers. comm.) that Okinawan *Lybia caestifera* are found holding several species of anemones, including an *Alicia sp.* very similar to the one held by Red Sea *Lybia leptochelis*. In addition, *Lybia caestifera* have been observed to hold with their legs an *Anthopleura sp.*, again very similar to the one held by Red Sea *Lybia leptochelis*. These similarities, in such disparate regions, and in different species, warrant further research.

h. From a molecular perspective, most of the research on this association has focused on the identity and phylogeny of the partners in the association, with no functional work conducted. This association could prove to be a promising model for understanding the underlying molecular mechanisms governing and regulating such symbioses. For example, one can envision various transcriptomic and proteomic studies, testing both the crabs and anemones, in and out of association, experimentally parted, and wild-caught for those animals that occur free-living, in order to discover which genes and proteins are involved in the symbiosis.

i. Past morphological studies have focused primarily on the species-specific claw differences, as well as other macro-level markers. Little work has been conducted using electron

microscopy. The finding of putative sensory pores in abundance on both the tips of legs and claw 'teeth', which are typically embedded in the held associates, warrants further functional studies.

Conclusions

Since their first recording over two centuries ago, boxer crabs have fascinated scientists and enthusiasts alike, presumably due to their easily anthropomorphized form, holding in both claws' 'little tools'. It is something about their unique appearance that induces this curiosity. However, so few studies have been conducted, practically none in nature. The current body of knowledge has established, especially in one or two representative species, the fundamentals of the association; however, further comparative work is much required. Due to the particular nature of the association, such apparent morphological changes, both short and long term, in both associates, are uncommon in other 'macro'-scale associations, making this an important model for further research.

The crab's habit to steal and split their anemones raises many questions regarding costs and benefits as well as long-term effects on associated anemone distribution and longevity, a topic which has received much recent attention. Boxer crabs and their associates may prove to be a flagship model for intensive aquaculture research and development, in limiting the continued collection and depletion of wild populations. Preliminary lab work and observations indicate that this is quite possible. They could follow the giant footsteps of the ever-popular panda in promoting conservation.

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