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Settlement of the barnacle *Balanus trigonus* Darwin, 1854, on *Panulirus gracilis* Streets, 1871, in western Mexico

Michel E. Hendrickx[1] orcid.org/0000-0001-9187-6080
Evlin Ramírez-Félix[2] orcid.org/0000-0002-5136-5283

1 Unidad académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. A.P. 811, Mazatlán, Sinaloa, 82000, Mexico

2 Oficina de INAPESCA Mazatlán, Instituto Nacional de Pesca y Acuacultura. Sábalo-Cerritos s/n., Col. Estero El Yugo, Mazatlán, 82112, Sinaloa, Mexico.

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Abstract

A large number of specimens (2765) of the acorn barnacle *Balanus trigonus* Darwin, 1854, were observed on the spiny lobster *Panulirus gracilis* Streets, 1871, in western Mexico, including recently settled cypris (1019 individuals or 37%) and encrusted specimens (1746) of different sizes: <1.99 mm, 88%; 1.99 to 2.82 mm, 8%; >2.82 mm, 4%). Cypris settled predominantly on the carapace (67%), mostly on the gastric area (40%), on the left or right orbital areas (35%), on the head appendages, and on the pereiopods 1–3. Encrusting individuals were mostly small (84%); medium-sized specimens accounted for 11% and large for 5%. On the cephalothorax, most were observed in branchial (661) and orbital areas (240). Only 40–41 individuals were found on gastric and cardiac areas. Some individuals (246), mostly small (95%), were observed on the dorsal portion of somites. Of the encrusting individuals, 18% were dead with no clear pattern in localization, but less common (7%) on dorsal than on lateral portions (right, 18%; left, 32%). Larger specimens (up to 11 mm) were observed in other lobsters from different catches. Previous presence of Cirripedia in decapod crustaceans, size range in the material examined, settlement patterns, and growth of the barnacles are discussed.

Keywords

Balanids, Crustacea, infestation, spiny lobster, eastern Pacific

CORRESPONDING AUTHOR
Michel E. Hendrickx
michel@ola.icmyl.unam.mx

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Introduction

The Cirripedia include free-living, commensal and parasitic species, almost exclusively marine, but some species occur in estuaries and coastal lagoons, and with a sedentary life-style (Newman and Abbott, 1980; Brusca and Brusca, 2003). Species of cirripeds belonging to the Thoracica are mostly found in shallow water although they have been collected down to 600 m depth. Most species in this group are encrusted to hard substrates, and there are some burrowing and obligate symbiotic species (Newman and Abbott, 1980; Van Syoc and Winther, 1999; Achituv and Newman, 2002).

Acorn barnacles, or Sessilia, are fixed on natural hard substrates like rock, wood, and shells, or on artificial substrates, like plastic, wood, concrete structures, and ship hulls. They also settle on selected groups of living animals, ranging from other invertebrates like medusae, corals, echinoderms, crabs, and stomatopods, to marine turtles, dolphins, whales, crocodiles, and sea snakes (Monroe and Garrett, 1979, Newman and Abbott, 1980; Karuppiah *et al*., 2004). Acorn barnacles as epibionts on decapod crustaceans have been mostly noted on true crabs (*e.g*., spider crabs, cancrids, portunids) and on lithodids, although they are known to occur also on shrimps (Dendrobranchiata and Caridea), lobsters and hermit-crabs; they have also been found on stomatopods (Dvoretsky and Dvoretsky, 2009; Giri and Wicksten, 2001).

Eastern Pacific acorn barnacles (Balanomorpha) are relatively well known and have been documented by Pitombo and Ross (2002). These authors included 92 living shallow-water species in a distribution checklist from Alaska to Chile. Brusca (2005) listed 30 species of Balanomorpha occurring in the Gulf of California, Mexico. As in the case of Sessilia, goose barnacles (Pedunculata) are able to attach to similar hard substrates, either natural or artificial. Some species also attach to soft tissues of decapod crustaceans like gills and appendage articulations (Williams and Moyse, 1988; Jeffries *et al*., 2005; Hendrickx and Innocenti, 2019).

During routine observation of lobster catches in local fisheries, one large specimen of *Panulirus gracilis* Streets, 1871, fished in March 2017, turned out to be the host of a very large series of balanids attached to the carapace and limbs. The present study reports on this association between *P. gracilis* and the encrusting barnacle *Balanus trigonus* Darwin, 1854, for the first time evaluating and analyzing its abundance and location on the host.

Material and Methods

The specimen of *P. gracilis* was caught by local fishermen with a gillnet, in March 2017, at a depth of about 13 m, in the SE Gulf of California, off Mármol (north of Mazatlán; approximately 23°26'N, 106°40'W). It was kept deep frozen for a couple of days and, prior to the examination, was unfrozen and briefly (about 2 days) kept in approximately 8% formaldehyde solution, then thoroughly washed with freshwater and stored in 70% ethanol. Carapace and appendages covered with cirripeds were photographed in order to count and measure the encrusting specimens. The specimen was deposited in the holdings of the Regional Collection of Marine Invertebrates (ICML-EMU-12481) at the Universidad Nacional Autónoma de México (UNAM), in Mazatlán, Mexico. Epibionts included specimens of the acorn barnacle *Balanus trigonus* in different development stages, *i.e*., cypris larvae, juveniles and pre-adult specimens. Large specimens were used to confirm identification to species level based on literature (Brusca, 1980) and by comparing material to identified specimens in the local collection. Identification of these large specimens were confirmed by William Newman. Small juveniles and large specimens feature the basic characters of *B. trigonus*, therefore it is assumed that all the specimens observed belonged to that species. Specimens were counted using digital grid and close-up photographs of carapace areas heavily infested, or by direct observation. Three size classes (basal largest diameter) were used for juveniles and pre-adults: <1.99 mm, 1.99-2.82, >2.82 mm. Because the only species of cirriped found in encrusting stages was *B. trigonus*, cypris and very small specimens were all assumed to belong to this species.

Results

A total of 2765 specimens of *B. trigonus* was found on one specimen (total length, 247 mm; carapace length, 80 mm) of a non-ovigerous female of *P. gracilis*. The barnacle specimens included 1019 cypris larvae and 1746 encrusted specimens in three size classes (small size, <1.99 mm, 1551 specimens; medium size, 1.99 to 2.82 mm, 133 specimens; large size, >2.82 mm, 62 specimens) (Tab. 1).

Of the 1019 cypris larvae observed on the entire animal, 67% were found on the cephalothorax (Fig. 1A–C), with a majority of these attached to the gastric (40%) and to the combined left and right orbital areas (35%). The rest were attached to the cardiac (7%) and branchial areas (18%; both sides) (Tab. 1). No cypris were found on the tergites of the abdominal somites, but 20 specimens were located on the ventral side of somite 1 (3) and 2 (17). A large amount of cypris also settled on the head appendages (Fig. 1E), with a remarkable symmetry: left and right antennula, 8 and 3 specimens; left and right antenna, 103 and 111 specimens, respectively. Eyes were totally devoid of

Table 1. Distribution of *Balanus trigonus* Darwin, 1854, in different body parts and appendages of *Palinurus gracilis* Streets, 1871.

Body parts/Appendages		Cypris	Small (<1.99 mm)	Medium (1.99–2.82 mm)	Large (>2.82 mm)
Gastric region		273	23	14	4
Cardiac region		49	13	17	10
Branchial region	Left	68	272	25	10
	Right	52	303	32	19
Orbital region	Left	122	78	5	5
	Right	118	104	7	1
Antennula	Left	8	22	0	1
	Right	3	25	0	0
Antenna	Left	103	48	0	0
	Right	111	87	9	2
Pereiopod 3	Left	0	0	0	0
	Right	0	17	0	0
Pereiopod 4	Left	0	12	0	0
	Right	0	0	0	0
Pereiopod 5	Left	0	6	0	0
	Right	0	4	0	0
Eye	Left	0	1	0	1
	Right	0	17	1	0
Horn	Left	33	0	0	1
	Right	12	61	2	1
Somite 1	Dorsal	0	67	1	0
	Ventral	3	38	0	0
Somite 2	Dorsal	0	94	2	1
	Ventral	17	5	0	0
Somite 3	Dorsal	0	45	3	1
	Ventral	0	0	0	0
Somite 4	Dorsal	0	16	3	0
	Ventral	0	0	0	0
Somite 5	Dorsal	0	5	1	0
	Ventral				
Somite 6	Dorsal	0	7	0	0
	Ventral	0	0	0	0
Crest	1	7	65	7	5
	2	0	40	0	0
Pleopod 1	Left	3	18	0	0
	Right	4	7	0	0
Pleopod 2	Left	1	7	0	0
	Right	2	5	0	0
Pleopod 3	Left	6	2	0	0
	Right	1	4	1	0
Pleopod 4	Left	0	0	0	0
	Right	2	0	0	0
Uropod	Left	5	8	0	0
	Right	15	17	0	0
Telson		3	8	3	0

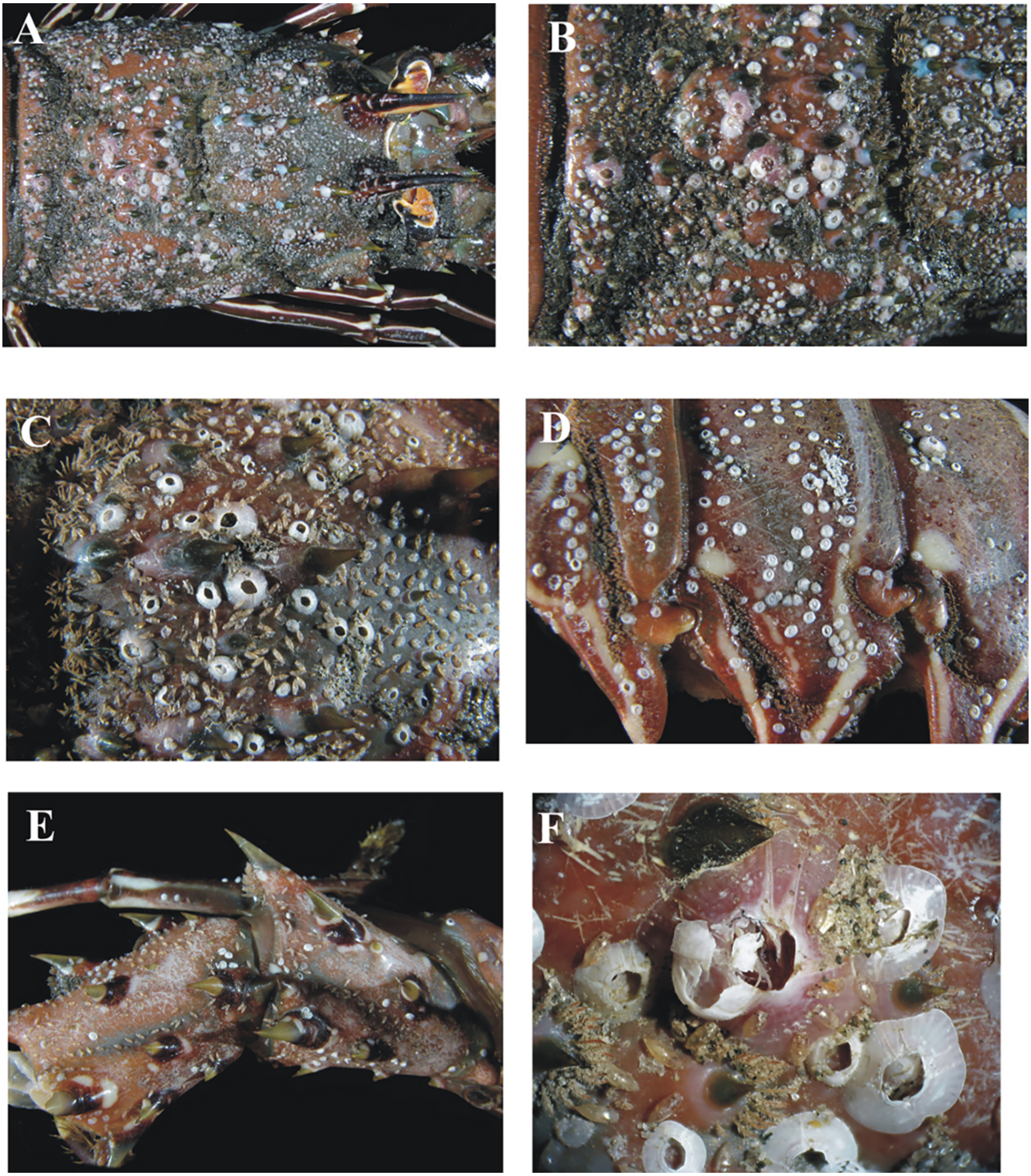

Figure 1. Photographs of selected portions of the carapace and appendages of *Panulirus gracilis* Streets, 1871, showing accumulation of individuals of *Balanus trigonus* Darwin, 1854. A. Cephalothorax, dorsal. B. Same, detail of gastric area. C. Same, detail of cardiac area; note the accumulation of the cypris larvae. D. Lateral portion of somites 1-3. E. Antenna 2; note the settlement pattern of the cypris larvae. F. Detail of carapace showing cypris larvae and encrusting individuals.

cypris, as were pereiopods 4 and 5. On the contrary, pereiopods 1, 2 and 3 were used as settlement areas for some cypris (10 on the right and 9 on the left appendages). Despite their small size compared to other parts of the carapace, orbital spines (frontal "horns") were colonized by 33 (left) and 12 (right) cypris. Telson and uropods were also colonized by up to 17 cypris (Tab. 1). Where cypris were very dense, the individuals formed a regular pattern, leaving a similar distance between individuals (Fig. 1C).

Among the 1746 specimens of *Balanus*-shaped specimens, the majority (942 specimens, 54%) occurred on the cephalothorax (gastric, cardiac, branchial, and orbital areas) (Fig. 1). Encrusting individuals were mostly small (84%); medium-sized specimens accounted for 11% and large specimens for 5%. Very high concentrations of individuals were observed on the branchial areas (661 individuals, left and right combined). Orbital areas were colonized by 240 individuals, while only 41 and 40 individuals were found on the gastric and cardiac areas, respectively. A large number of individuals (246) were observed on the dorsal and lateral portions of the somites (Fig. 1D), more abundantly on somites 1-3 (87%) than on somites 4-6 (13%). These 246 individuals were mostly small (95%). Ventral portions of somites 1 and 2 were colonized by fewer specimens, 43 in total, all of small size (Tab. 1).

High numbers of encrusted barnacles on appendages correspond to the smallest juvenile stages (*i.e.*, <1.99 mm; 368 in total or 24%) and were observed predominantly on the antennulae (47) and antennae (135) (Fig. 1E). Pereiopods and pleopods had fewer fixed barnacles, and all correspond to the small size class except for one medium-sized specimen in pleopod 3. These small specimens were observed on pereopods 3, 4 and 5, and on pleopods 1, 2 and 3. On the appendages, the two large size classes were much less represented: 9 specimens for the 1.99-2.82 mm class and 4 for the >2.82 mm class (Tab. 1). Telson and uropods were also colonized by small barnacles, including a few specimens (3) of the medium-sized class on the telson (Tab. 1).

When all areas and sizes were included, 18% of the balanid-shaped individuals on the carapace were dead. There was no clear pattern in the localization of low or high percentages of dead individuals on the carapace, but dead barnacles were less common (7%) on the dorsal portion of the carapace than on the lateral portions (18% on the right; 32% on the left). The presence of dead individuals is considered significant as they obviously had to go through the complete settlement process earlier to our observations, and then grow up to the size they attained before they died.

In addition to the large series of small specimens observed on *P. gracilis* (see above), isolated individuals were collected or observed on other lobsters. Two barnacle specimens of about 8–9 mm diameter were collected on March 29, 2017, in the same area, both in the gastric region of one specimen of an immature female of *P. gracilis* (CL 91 mm) (Fig. 2A) and one mature female of *Panulirus inflatus* (Bouvier, 1895) (CL 70 mm) (Fig. 2B). Another lobster individual (Fig. 3A, B) of *P. gracilis* had two large specimens (approximately 11 mm) attached to the right carapace frontal horn and a series of eight specimens (approximately 5 to 9 mm) attached on the sternum. There were no cypris or small balanids (recently settled) attached to the carapace of these two spiny lobsters.

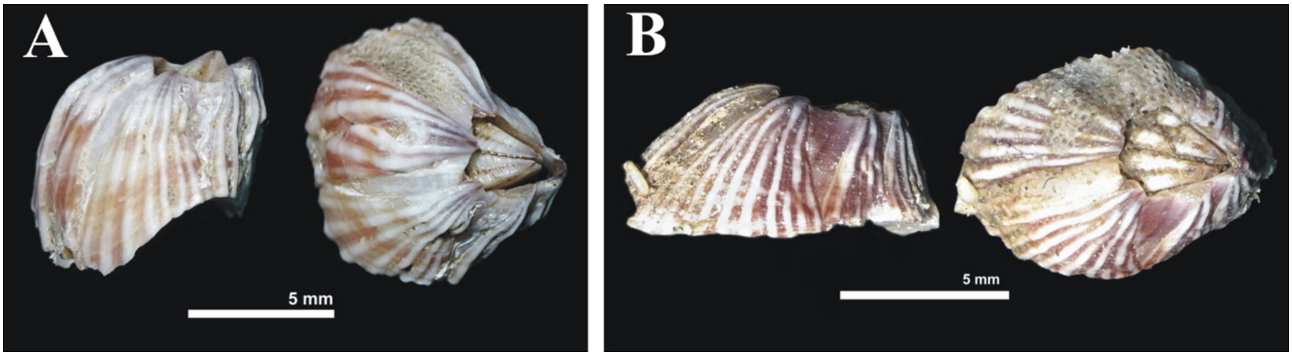

Figure 2. Large specimens of *Balanus trigonus* Darwin, 1854, collected on spiny lobsters. A. On the gastric area of an immature female of *Panulirus gracilis* Streets, 1871 (CL 91 mm). B. On the gastric area of one mature female of *P. inflatus* (Bouvier, 1895) (CL 70 mm).

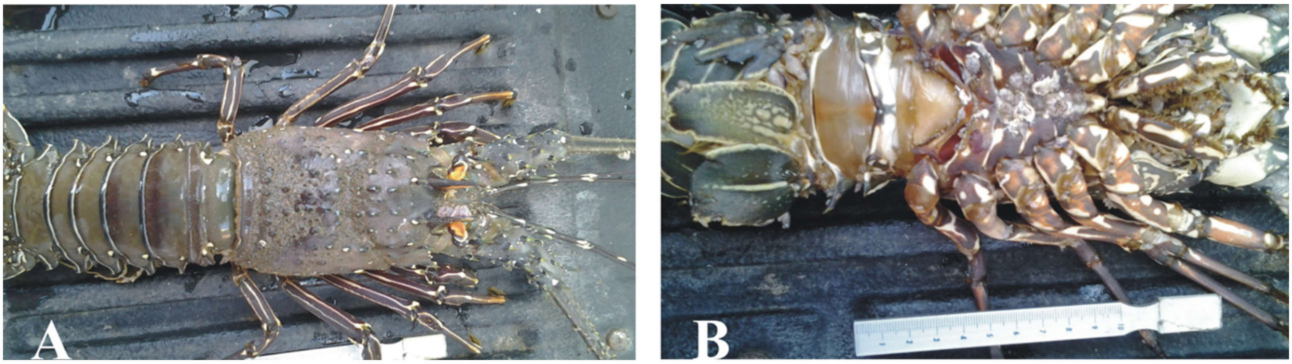

Figure 3. Large specimens of *Balanus trigonus* Darwin, 1854, observed on the spiny lobsters *Panulirus gracilis* Streets, 1871 (CL 74 mm). A. On the right carapace frontal horn. B. On the sternal plates.

Discussion

A dense settlement of barnacles such as the one observed during this study on a single lobster individual is unusual and had not been reported previously in the area.

Balanus trigonus is a cosmopolitan species. In the eastern Pacific it occurs from Monterey, California, to Peru, including the entire Gulf of California (Pitombo and Ross, 2002). Its presence as epizooites on species of spiny-lobsters has apparently not been reported previously. The presence of cypris and of relatively large pre-adults specimens on the same individual of *P. gracilis* indicates a long-term exposure to settlement of this species and the lack of a recent molt.

The presence of Cirripedia on decapod crustaceans have been commonly reported in previous studies. Several species of goose barnacles, or pedunculate cirripeds (*e.g.*, *Lepas* Linnaeus, 1758; *Octolasmis* Gray, 1825), are known to attach to these crustaceans, including spiny lobsters (see Costa *et al.*, 2010). For example, the pedunculate barnacle *Dianajonesia amygdalum* (Aurivillius, 1894) is associated with two species of spiny lobsters, *Panulirus japonicus* (von Siebold, 1824) and *P. penicillatus* (Olivier, 1791) (Bowers, 1968: as *Trilasmis fissum hawaiense* Pilsbry, 1928).

Acorn barnacles have also been observed on many species of decapod crustaceans. Dawson (1957) and Eldred (1962) have reported the presence of encrusting barnacles on several species collected in Florida, Mississippi, and South Carolina (USA): on the shrimps *Litopenaeus setiferus* (Linnaeus, 1767) and *Sicyonia dorsalis* Kingsley, 1878; on two species of crabs, *Menippe mercenaria* (Say, 1818) and *Callinectes sapidus* Rathbun, 1896; and on the lobster *Panulirus argus* (Latreille, 1804). More recently, Giri and Wicksten (2001) found *Amphibalanus improvisus* (Darwin, 1854) attached to the caridean shrimp *Lysmata wurdemanni* (Gibbes, 1850) off Texas, with a rate of colonization of 18% in the sample population. Other records of *Balanus* on decapod crustaceans in the eastern and western Atlantic include the lithodid *Paralithodes camtschaticus* (Tilesius, 1815) with a prevalent infestation rate by *Balanus crenatus* Bruguière, 1789, of 42.9% in the Barents Sea (Dvoretsky and Dvoretsky, 2009).

In the eastern Pacific, information dealing with settlement of true barnacles on decapod crustaceans is scarce. In a review of association and pathology of crustaceans from Colombia, Alvarez-Léon (2009) reported several species of encrusting cirripeds on decapods of the western coast, including: *Balanus* sp. on *Callinectes arcuatus* Ordway, 1863, and *C. toxotes* Ordway, 1863; *Chelonibia* sp. on *C. arcuatus*, *C. toxotes*, and *Euphylax robustus* A. Milne-Ewards, 1874. He also reported *Octolasmis* sp. on *C. arcuatus* and *E. robustus*. Other species of decapod crustaceans from Chile have also been observed with encrusting cirripeds, in this case *Chthamalus cirratus* Darwin, 1854, on *Homalaspis plana* (H. Milne Edwards, 1834) and *Romaleon setosus* (Molina, 1758) (Marco Retamal, pers. comm., September 2017). Also in Chile, encrusting cirripeds have been observed on two other species of brachyuran crabs: *Hepatus chiliensis* H. Milne Edwards, 1837 (*Austromegabalanus psittacus* (Molina, 1788), and *Balanus laevis* Bruguière, 1789) and *Platyxanthus orbignyi* (H. Milne Edwards and Lucas, 1843) (*Notobalanus flosculus* Darwin, 1854 and *B. laevis*) (Guillermo Guzman, pers. comm., September 2017).

The specimen of *P. gracilis* captured during this survey is particularly interesting as it was infested by cirripeds of different sizes, including many cypris. Although a substantial percentage of the fixed barnacles were dead, all these were able to grow up after they settled as cypris larvae, thus finding suitable conditions for metamorphosis into juvenile barnacles, remain alive and grow on the lobster external skeleton for at least some time. There is no clear reason why a substantial percentage of individuals that had successfully settled on the lobster died before reaching maximum size (at least 11 mm as seen from specimens on other lobsters), thus leaving only an empty shell as the proof of their earlier settlement on the animal. In a natural, rocky environment, death of balanids is the result of predation by many groups of invertebrates (*e.g.*, flatworms, snails and chitons, brachyuran crabs, echinoderms) (Murina *et al.*, 1995; Buschbaum, 2002) or by intraspecific crowding in dense populations leading to death, thus providing food for scavengers (Connell, 1970). Although predation by living animals cannot be fully discarded, death of young balanids is probably linked to the habitat in which adult spiny lobsters live and move around. They often seek refuge under rocky ledges and in crevices, and the lateral and ventral portions of the carapace are often in contact with the bottom or with suspended sediments. Superficial erosion and temporal turbidity would not favor survival of young individuals.

The cypris larvae of most species of barnacles are known to be attracted by the presence of attached adults of their own kind (Newman and Abbott, 1980), but in this case it is difficult to assess if large "juveniles" (>2.82 mm in size) played a similar attractive role. Harder *et al.* (2001) concluded that larval settlement of the barnacle *Amphibalanus amphitrite* (Darwin, 1854) (Cirripedia, Balanidae) is influenced by natural biofilms. In laboratory experiments, Thiyagarajan *et al.* (2006) found that settlement of *B. trigonus* cypris is positively influenced by the presence of microbial films. In this study we were not able to determine the presence of a peculiar bio-substrate on the lobster carapace, but we assume that there was some kind of deposit. *Balanus trigonus* is an opportunist, short-lived species that will settle on any free space (Ayling, 1976). During the settlement process, cypris larvae perform what is known as the "exploratory phase" during which they move forwards and backwards searching for a settlement substrate and assessing how much room is available as well as testing the substratum (Lagersson and Høeg, 2002). The settlement pattern observed on the carapace of *P. gracilis*, with cypris larvae forming a regular pattern and leaving a similar distance between individuals, fit with the strategy of being close enough to your neighbors to leave as little room as possible for competing animals and plants to settle and grow, yet still leave enough room so that conditions don't become too crowded (see Carefoot, 2019).

Ayling (1976) analyzed the strategy of orientation in *B. trigonus* and concluded that direction of water flow is the primary factor that influences during the settlement process. In the case of a moving "substrate", however, water flow can be extremely variable over time. Observation of the pedunculate barnacle *D. amygdalum* associated with two species of spiny lobsters, *P. japonicus* and *P. penicillatus* (Bowers, 1968), indicated that this barnacle exhibits weak orientation behavior to water currents. Bowers (1968) suggested that the habitat, the oral region of lobsters, provided the goose barnacles with food and protection from predators. In our study, the distribution of *B. trigonus* do not clearly support the idea of food or protection benefits to the barnacles, although it should be stressed that the majority of encrusting specimens were found on the cephalothorax and on the second pair of antennae, thus close to the mouth. But these areas are also exposed to predators and to environment factors.

Position adopted at settlement by the cyprid larva is crucially important to the survival and growth of the animal and it will determine the location and orientation of the encrusting barnacles. Cypris choice of orientation at settlement is influenced by the direction of the current, thus anticipating optimal conditions for food-gathering of the adult barnacle (Pasternak *et al.*, 2002).

Gaines *et al.* (1985) suggested that nearshore oceanic processes that influence the arrival and concentration of cypris larvae contribute to the control of barnacle benthic community structure. These processes include current, wind patterns, and shoreline topography; larval mortality rate is another factor affecting the ultimate success for benthic communities (Gaines *et al.*, 1985). In this study, there were no data related to arrival of larvae or settlement on other substrates (*e.g.*, on rocky structures). The specimen was fished in March 2017, a period during which average monthly temperature was 24°C (NOAA, 2019). This temperature is suitable for nauplius of *B. trigonus* to be released, to go through a short pelagic life of about 5 to 6.5 days, and for the subsequent settlement of cyprid after 6 days (Thiyagarajan *et al*., 2003).

There is no information on relative growth (mm/day) for *B. trigonus*. García and Moreno (1998) reported a maximum mean size of 6.2 mm (carino-rostral distance) 20 weeks after settlement for a Caribbean population. A much slower growth rate has been reported for a New Zealand population of the same species (8 mm in 3.5 weeks; Ayling, 1976). Growth curve provided by García and Moreno (1998) indicates that it would take about 6.7 weeks for *B. trigonus* to reach a size of 2 mm (the average value of the intermediate size category used in this contribution: 1.99–2.82 mm). When Ayling's (1976) value is used, specimens would reach a 2 mm size in less that one week. Data for other species indicate an average growth of 0.03 mm/day for *Tetraclita squamosa* (Bruguière, 1789), 0.06-0.07 mm/day for *T. stalactifera* (Lamarck, 1818), and up to 0.12 mm/day for *Semibalanus balanoides* (Linnaeus, 1767) (Skinner *et al*., 2007), but growth rate decreases after the first year of development or even earlier (Sanford and Menge, 2001; Skinner *et al*., 2007). Assuming an average growth rate of 0.07 mm/day for the barnacles observed on *P. gracilis* (Ayling, 1976), the largest specimens (*i.e*., >2.82 mm diameter) would be about 40 days old and the smallest (*i.e*., <1.99 mm diameter) about 28 days old.

Balanus trigonus reaches sexual maturity in less than 14 days (between 2-2.5 mm diameter). Its high growth rate and early maturity combined with a high level of predation result in short generation time and high turnover of populations (Ayling, 1976). Settling on organisms that molt (*i.e*., changing their carapace) is not a good survival strategy, unless inter-molt period is long enough to allow the barnacles to reproduce. As in other species of decapod crustaceans, when reaching large size, spiny lobsters intermolt period increases (Hartnoll, 1985; Briones-Fourzan and Lozano-Alvarez, 2003). In *P. gracilis*, Briones-Fourzan and Lozano-Alvarez (2003) calculated a maximum intermolt period of 16.2 weeks for males and 22.6 weeks for females. Depending upon environmental conditions (in summer) and presence of injuries, however, this rate can be shortened to 12.9 weeks. In any case, the series of large barnacles (>2.82 mm) observed on *P. gracilis* in this study were large enough to warrant their reproduction.

Because spiny lobsters are subject to seasonal fishery in western Mexico, a large series of individuals could be available with a view to performing an exhaustive survey of cirriped settlement in the area. This would provide a more complete overview of these associations considering important factors such as season, distribution, size of the hosts, and environmental conditions.

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