

Host use pattern and life history of *Liopetrolisthes mitra*, a crab associate of the black sea urchin *Tetrapygus niger*

Baeza, J.A. and M. Thiel*

Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281,
Campus Guayacán, Coquimbo, Chile. *Corresponding author: e-mail: thiel@nevados.cecun.ucn.cl

The porcellanid crab *Liopetrolisthes mitra* is a common associate of the black sea urchin, *Tetrapygus niger* in north central Chile. The host-use pattern, population dynamics and reproductive pattern of *L. mitra* on sea urchins were examined between January 1996 and February 1997. Each month, between 60 and 95 per cent of all collected urchins hosted crabs, with the highest frequency of cohabitation occurring during the austral summer (January to March). Group sizes of crabs on individual urchins ranged from 1 to 25 crabs per host. The average density of crabs on the urchins ranged from 2 to 5.5 crabs per host. Large urchins were inhabited by crabs more frequently than small urchins but urchin size had no effect on the number or size of crabs. The sex ratio of adult crabs was ~1:1 during most months. Reproduction occurred throughout the year but was most intense during the austral spring and summer (October to March), when the highest percentage of ovigerous females were found. Similarly, recruitment of *L. mitra* occurred throughout the year but reached a peak during austral summer and early autumn (January to May). All life stages of *L. mitra* including recently settled megalopae and reproductive adults were found on urchins. Size–frequency analysis indicated that many crabs live >1.5 years. The results of this study confirm that the association between *L. mitra* and *T. niger* is strong and persists throughout the benthic life of the commensal crab.

INTRODUCTION

Among the marine Decapoda, crabs of the family Porcellanidae represent one of the most diverse and abundant groups, living in tropical and temperate waters all around the world (Williams, 1984). Most porcellanid species are free-living, inhabiting crevices and cavities in the rocky intertidal and shallow subtidal (Stevcic, 1986). Some species have developed a relatively strong association with other organisms, living between fronds or inside the adhesive discs of macroalgae (Viviani, 1969), or on sessile colonial invertebrates (Haig, 1955, 1960). Several porcellanid species have adopted a completely commensal life-style (Haig, 1960; Werding, 1983; Baeza & Stotz, 1995), utilizing sponges, corals, sea anemones, sea urchins and tube-worms as hosts. While the general biology and ecology of free-living porcelain crabs have been relatively well studied during the last four decades (Viviani, 1969; Stevcic, 1986; Jensen 1989, 1991; Sampedro et al., 1997; Achituv & Pedrotti, 1999), symbiotic porcellanid crabs have received comparatively little research attention (for exceptions see e.g. Werding, 1983).

Most free-living porcelain crabs inhabit crevices and cavities at exposed rocky shores where they can be found in large aggregations of both males and females (Antezana et al., 1965). Within these aggregations, dominant large individuals may occupy the sheltered parts of refuges, restricting small subordinate conspecifics to less well protected areas. Alternatively, a single dominant male may aggressively monopolize a shelter against any intruder of the same sex, allowing access only to females, with which it copulates when they become receptive

(Molenock, 1975). The few available studies on symbiotic porcelain crabs indicate that they inhabit hosts as single or heterosexual pairs (Gray, 1961; Werding, 1983; Ng & Goh, 1996; Hsueh & Huang, 1998). Most free-living porcelain crabs are suspension-feeders, gathering food from the water column by active or passive feeding activities (Achituv & Pedrotti, 1999). Symbiotic porcelain crabs may gather food from hosts, e.g. flesh, faecal matter, debris, mucus (Viviani, 1969; Werding, 1983; Williams, 1984). The symbiotic lifestyle may have resulted in particular adaptations with respect to social interactions, feeding modes and reproductive patterns.

In Chile, two species of *Liopetrolisthes* are frequently found on sea urchins and occasionally on sea stars (Haig, 1960). The genus *Liopetrolisthes* was formerly believed to be monospecific (Haig, 1960) but morphometric and genetic-biochemical studies demonstrated that it contains at least two sibling species (Weber, 1991; Weber & Galleguillos, 1991). *Liopetrolisthes patagonicus*, of mainly greenish coloration, inhabits the red sea urchin *Loxechinus albus* (Molina, 1782) in shallow waters down to 15 m depth from Peru to Magellan Strait, Chile (Weber, 1991). Its congener, *Liopetrolisthes mitra* (Dana, 1852), of dark brown coloration, has been frequently observed on black sea urchins *Tetrapygus niger* (Molina, 1782) and occasionally on *Arbacia spatuligera* (Valenciennes, 1846) in the intertidal and shallow subtidal zone. It may also be found between arms of sea stars (Weber, 1991). Both species of *Liopetrolisthes* were initially assumed to be associated with macroinvertebrates only during their early life-stages (Haig, 1955, 1960). Based on these observations, Haig (1955) suggested that only immature juvenile crabs of

Liopetrolisthes engage in the commensal association with benthic macroinvertebrates, and that adult crabs were free-living. However, subsequent studies also reported adult porcelain crabs on sea urchins (Weber, 1991) but the general host use pattern of *Liopetrolisthes* still remains unclear.

The aim of the present study is to describe the association between *L. mitra* and one of its most commonly reported hosts, the black sea urchin *T. niger*. The specific objectives were to examine the host-use pattern, population dynamics and reproductive biology of *L. mitra*.

MATERIALS AND METHODS

Black sea urchins *Tetrapygus niger* were collected during 1996–1997 at La Herradura de Guayacán Bay, Coquimbo (29°58'30"S 71°22'30"W), Chile. The shallow subtidal of the north-western part of the bay is characterized by a semi-protected sloping bedrock intermingled with large rocks and boulders to a depth of 0–6 m. The fauna is dominated by black sea urchins and the sea anemone *Phymanthea pluvia* (Drayton, 1846), while the algal flora consists mainly of coralline algae, comprising a barren ground community. The commensal crab *Liopetrolisthes mitra* occurs abundantly 0–3 m below MLW (mean low water) on these barren grounds. Within the bay, water temperatures usually vary between 13°C (winter) and 20°C (summer) (Moraga & Olivares, 1993).

Between January 1996 and February 1997, sea urchins were collected randomly at regular intervals, usually once per month, by SCUBA diving. Urchins were collected within a 50 m long strip parallel to the coast line at a depth of 0–3 m. Preliminary observations had indicated that commensal crabs move between adjacent sea urchins when disturbed. Therefore, sea urchins were collected rapidly in order to prevent crabs from escaping during sampling. Each urchin together with its crab associates was immediately placed in a sealable plastic bag. Samples were discarded when commensal crabs escaped from their hosts and could not be recaptured.

Upon return to the laboratory, the diameter of each sea urchin was measured. Also, the number, sex and size (measured as carapace length, CL) of all crab associates from each host individual was noted. Measurements were taken to the nearest 0.05 mm with a manual calliper. Megalopa larvae collected during the present study were identified according to the rostrum and carpus shape, that are similar to those found in adults. Each female crab was classified according to the presence or absence (ovigerous or non-ovigerous) and the developmental stage (I, II & III) of embryos in the abdominal chamber. The embryo mass of each ovigerous female was examined under the stereomicroscope for classification of the developmental stage according to the following characters: stage I, embryo with uniformly distributed yolk and absence of eyes; stage II, embryo with visible but not well developed eyes, presence of pigments and early development of thoracic appendages; and stage III, embryo with well developed eyes, chromatophores, and appendages.

The fecundity of *L. mitra* was determined by counting all embryos carried by at least 30 ovigerous females (stage I) in July 1996 (austral winter) and January 1997 (austral summer). The relationship between carapace

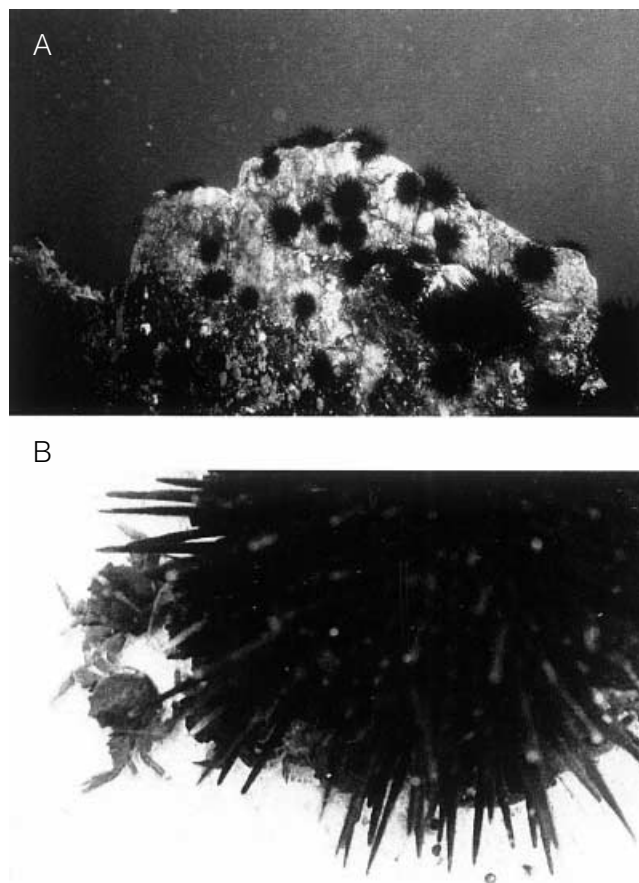


Figure 1. (A) Sea urchins *Tetrapygus niger* in their habitat in the shallow subtidal of Punta Lengua de Vaca, north central Chile; (B) sea urchin with adult and juvenile symbiotic crabs *Liopetrolisthes mitra*.

length and the number of embryos per female was examined, and we tested for differences in fecundity between winter and summer by analysing the data with an ANCOVA (Sokal & Rohlf, 1969). The frequency of occurrence (number of hosts with at least one crab) and density (number of crabs per host individual) of *L. mitra* on sea urchins was examined each month during the sampling period. To determine if *L. mitra* occurs as singles, pairs or aggregations on sea urchins, the frequency of occurrence of hosts with none, one or more crabs per host was analysed for each month. We examined the importance of sea urchin size on the demography of associated crabs by two types of correlation analysis for those urchins that hosted crabs. The first correlation analysis tested for the effect of urchin size on the size of the largest crab associated with its respective urchin host. The second correlation analysis examined the effects of urchin size on the accumulated size of all crabs dwelling on a single host individual.

RESULTS

Host-use pattern and demography of Liopetrolisthes mitra

Black sea urchins occur in dense aggregations in the shallow subtidal along the Chilean coast (Figure 1A). Small crabs *Liopetrolisthes mitra* usually find shelter among the spines of the urchins while larger crabs dwell

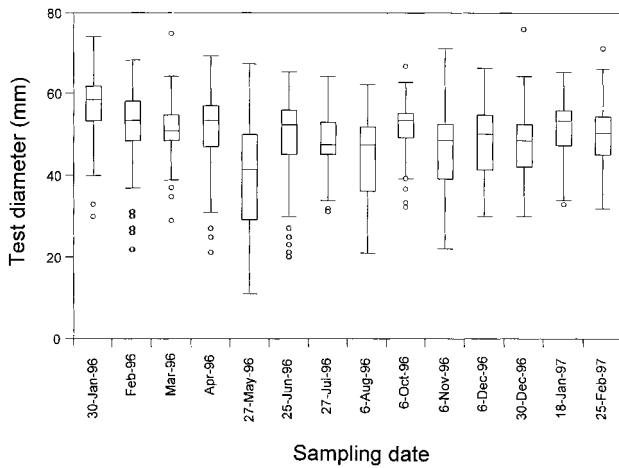


Figure 2. Test diameter of black sea urchins *Tetraphygus niger* collected between January 1996 and February 1997; shown are the median \pm 25-percentiles, the 95% confidence interval and outliers.

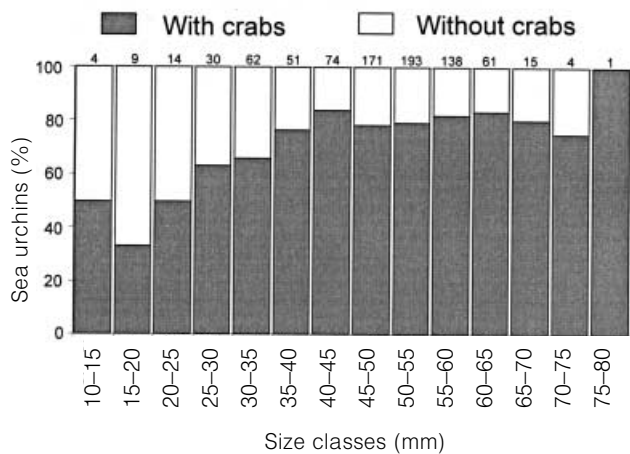


Figure 3. Frequency of occurrence of *Liopetrolisthes mitra* on sea urchin hosts of different size classes. The number above bars indicate the total number of collected hosts measured. Note that N=827 (not=832) since various sea urchins were not measured due to logistic problems.

underneath the urchin between the periphery of the oral surface of the urchins and the substrate (Figure 1B). During the present study, a total of 832 black sea urchins were sampled in the shallow rocky subtidal of La Herradura Bay. The diameter of sea urchins varied between 11 and 76 mm with an average of 48.58 mm (SD=10.72). Despite seasonal differences of mean urchin size during the collection period, urchins of all sizes were observed year round in La Herradura Bay (Figure 2). *Liopetrolisthes mitra* was found on 77.5% (N=645 of 832) of all sea urchins collected during the present study. Sea urchin size slightly affected the occurrence of the association. Crabs occurred less frequently on urchins <25 mm test diameter than on those >25 mm test diameter (Figure 3) (Independence χ^2 -test with Yates correction, $\chi^2=15.24$, df=1, $P<0.001$). The frequency of occurrence of *L. mitra* also varied throughout the year. During the summer months of 1996, the occurrence of the association was relatively high (94.6% during January 1996) whereafter it gradually decreased. The frequency of occurrence was

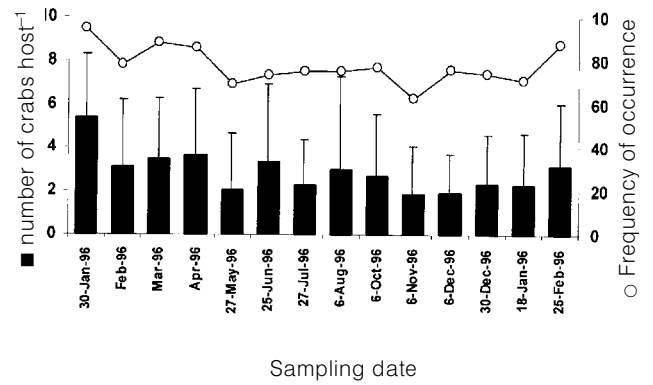


Figure 4. Average number (\pm SD) of crabs *Liopetrolisthes mitra* on sea urchins *Tetraphygus niger* and percentage of urchins that hosted at least one commensal crab between January 1996 and February 1997.

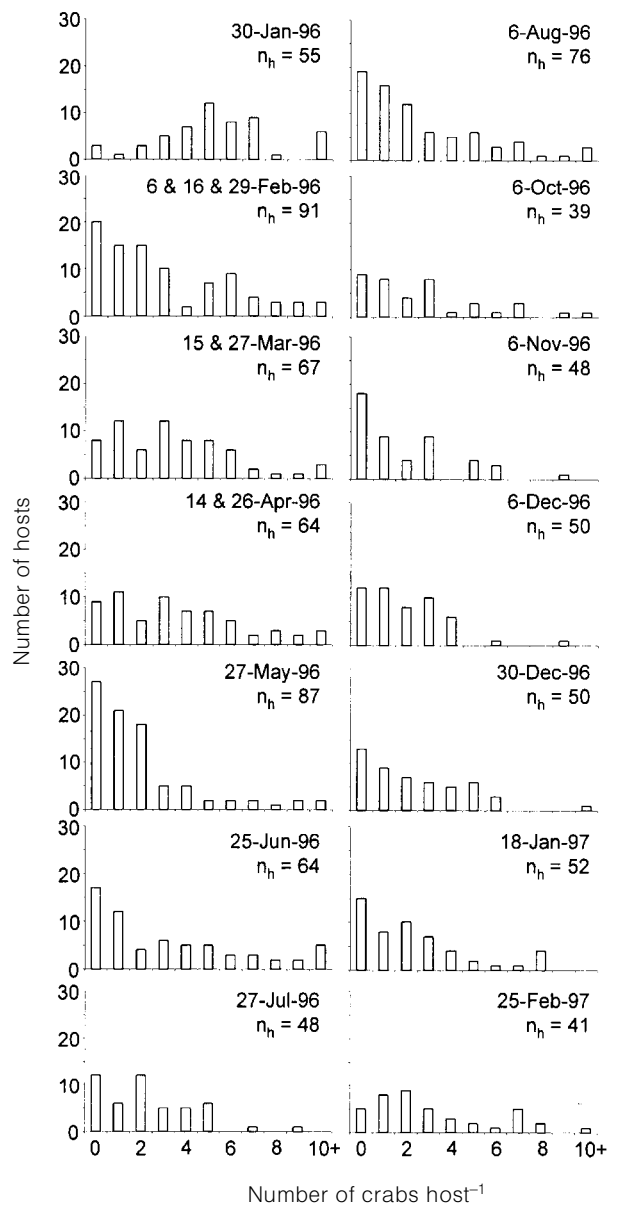


Figure 5. Number of black sea urchins *Tetraphygus niger* hosting aggregations of *Liopetrolisthes mitra* between January 1996 and February 1997; all crabs were pooled for each month; nh, number of sea urchins (hosts) collected per month.

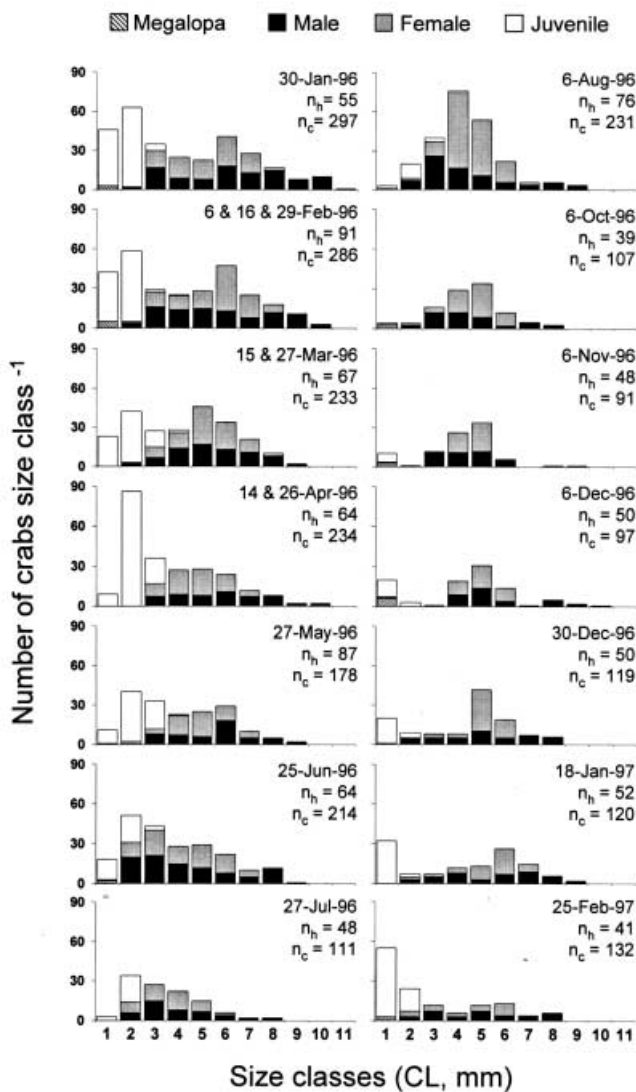


Figure 6. Number of crabs *Liopetrolisthes mitra* in respective size classes found on black sea urchins *Tetrapygus niger* between January 1996 and February 1997; all crabs were pooled for each month; n_h and n_c , number of sea urchins and crabs collected per month, respectively; values at x-axis represent the median for each size class such that for example the first size class includes all values from 0.6 to 1.5 mm, the second size class from 1.6 to 2.5 mm etc.

relatively low during winter and early spring months (62.5% during November 1996), gradually started to increase during late spring and reached relatively high values again during the austral summer of 1997 (Figure 4). The mean number of crabs per host was approximately three ($SD=3$) during the sampling period. As was observed for the occurrence of crabs on hosts, density of *L. mitra* on sea urchins was relatively high during summer months and relatively low during winter months (Figure 4). Up to 25 crabs *L. mitra* were observed on one host individual, but most commonly between one and nine crabs inhabited a single host (Figure 5). In general, *L. mitra* occurred in small aggregations on its host. The number of crabs harboured by a single host individual was not affected by the size of sea urchins. No significant relationship between host size and the number of crabs per host was registered during most months ($r < 0.23$, $P > 0.05$).

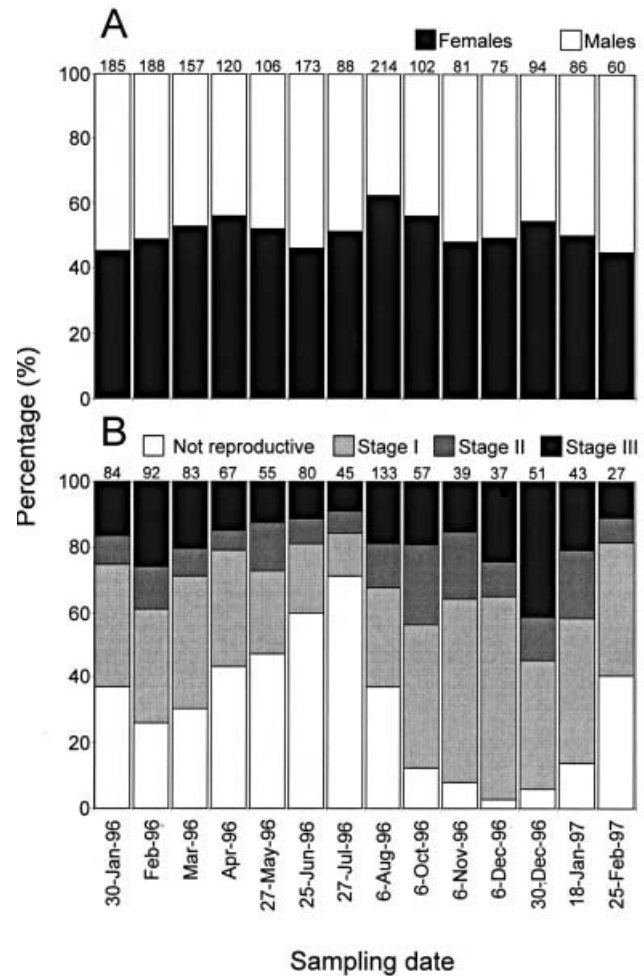


Figure 7. (A) Percentage of male and female crabs *Liopetrolisthes mitra* found on black sea urchins *Tetrapygus niger* between January 1996 and February 1997; (B) of female crabs *L. mitra* without or with embryos of respective developmental stages; all crabs were pooled for each month; the number above the bars represents (A) number of sexed crabs and (B) number of female crabs collected in each month.

Only in May 1996 (host diameter, HD vs no crab per hosts: $r=0.22$, $t_{85}=2.1$, $P=0.044$) and late December 1996 (HD vs no crab per hosts: $r=0.44$, $t_{48}=3.36$, $P=0.002$) a slightly significant correlation between urchin size and the number of crabs per host was found. In general, sea urchins of all sizes could harbour small as well as large aggregations of *L. mitra*.

Host size did not significantly affect the distribution of the different ontogenetic stages of *L. mitra*. No significant relationship was observed between the size of sea urchins and the sizes of crabs inhabiting it during most of the year ($r < 0.24$, $P > 0.05$ for most months). Only in May (HD, vs accumulated size of all crabs on a host, ASC: $r=0.23$, $t_{85}=2.2$, $P=0.03$), July (HD vs ASC: $r=0.29$, $t_{46}=2.03$, $P=0.047$) and early (HD vs largest crab on host, LCH: $r=0.38$, $t_{36}=2.44$, $P=0.019$) and late December 1996 (HD vs LCH: $r=0.47$, $t_{35}=3.12$, $P=0.004$; HD vs ASC: $r=0.44$, $t_{48}=3.41$, $P=0.001$) significant correlations between urchin size and the size of the LCH or the ASC inhabiting a single host were found. In general, when *L. mitra* occurs on sea urchins, crabs of all sizes dwell on hosts of different sizes.

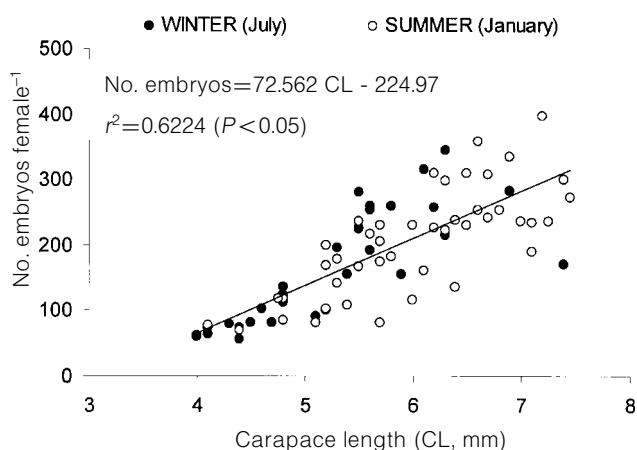


Figure 8. Relationship between carapace length of female crabs *Liopetrolisthes mitra* and number of embryos carried by each female for females collected in austral winter (July 1996) and in austral summer (January 1997).

Crabs ranging in sizes from 0.7 (megalopa) to 10.6 mm CL (male) inhabited the black sea urchins. Many large and mature crabs were found on the urchins, the smallest ovigerous female having a CL of 3.8 mm. Megalopa larvae were collected from several sea urchins. Thus, all life stages of *L. mitra* (including mature crabs) inhabit *T. niger*. Size–frequency distribution analysis for crabs inhabiting black sea urchins showed that adult crabs were found year-round on sea urchins (Figure 6). However, many large adults (>9.0 mm CL) disappeared (probably died) during late autumn (April/May).

Reproductive biology of *Liopetrolisthes mitra*

The sex ratio of *L. mitra* found on the urchins was close to 1:1 throughout most of the year (Figure 7A). At each sampling date, females carrying embryos were found but the percentage of ovigerous females varied substantially during the year. The proportion of females carrying embryos was significantly higher during the spring/summer months (October–March) than during the late autumn/winter months (April–September) (Figure 7B) (Independence χ^2 -test, $\chi^2=64.09$, $df=1$, $P<0.001$). Thus, reproduction in *L. mitra* is continuous throughout the year, but with higher intensity during spring and summer months and lower reproductive activity during winter months (<30% of females found in July were ovigerous). Small immature juvenile crabs were found throughout the year on sea urchins. The abundance of these juveniles varied with a pattern corresponding to that observed for ovigerous females, being relatively abundant between January and June 1996 and relatively rare during the austral winter and early spring (July–November 1996) (see Figure 6). Megalopae were found during the whole year in low numbers. In general, recruitment and reproductive pattern of *L. mitra* inhabiting *T. niger* showed a clear seasonal cycle, with increased reproductive and recruitment activity during spring and summer months and decreased reproduction and recruitment during winter months. At least two distinct generations inhabited sea urchins during any time of the year, one generation consisting of mature, old and reproductive crabs, and

another one comprising immature, young and growing crabs.

Fecundity of *Liopetrolisthes mitra*

Female crabs carried between 70 and 397 eggs (203.18 ± 81.84 , mean \pm SD) during the austral summer and between 57 and 344 eggs (162.97 ± 88.38) during the austral winter. The size range of ovigerous females was similar both in winter (smallest and largest ovigerous female = 4.0 and 7.4 mm CL, respectively) and summer (smallest and largest ovigerous female = 4.1 and 7.45 mm CL, respectively). The fecundity of *L. mitra* significantly increased with female size, both during winter (no. eggs = $80.04CL - 254.25$, $r^2=0.80$, $t_{28}=10.77$, $P<0.005$) and summer samples (no. eggs = $74.36CL - 242.41$, $r^2=0.57$, $t_{43}=7.76$, $P<0.005$) (Figure 8). Fecundity (number of eggs per female) did not differ significantly between summer and winter months (ANCOVA, $F_{1,73}=2.10$, $P=0.1517$).

DISCUSSION

All ontogenetic life stages (megalopa larvae, juveniles and adults) of *Liopetrolisthes mitra* dwell on black sea urchins *Tetrapygus niger*. This indicates that the association between this crab and the urchins is continuous throughout the benthic life of the crab and stronger than previously believed. However, the fact that small as well as large aggregations of *L. mitra* occur on sea urchins of similar sizes, and that crabs of all sizes dwell on hosts of various size suggest that fidelity of each crab to a single host individual is relatively low. The reasons for this association pattern and the consequences for the life history of the crab will be examined herein.

The association between Liopetrolisthes mitra and Tetrapygus niger

During the present study all ontogenetic stages of *L. mitra* were found on sea urchins, and it was observed that commensal crabs reproduce on hosts, indicating a continuous association of crabs with sea urchins during its benthic life. The observation that crabs dwell among spines of sea urchins suggests that one of the main benefits for crabs on these hosts is protection against predation. *Liopetrolisthes mitra* presents a dark brown coloration, similar to that of its host *T. niger*. Homochromy of crabs on sea urchins may improve protection against visual predators, e.g. crabs and fishes, as has been demonstrated for commensal decapods inhabiting algae (Hacker & Madin, 1991). Another probable benefit for the crabs dwelling on sea urchins may be food acquisition. It is considered likely that *L. mitra* feeds on particles released or produced by hosts (e.g. detritus, mucus, epibionts, flesh) as has been previously reported for other commensal porcelain crabs (Werdling, 1983) and other decapods dwelling on macroinvertebrates, including sea urchins (Patton et al., 1985). Previous studies on *L. mitra* had reported sediment ingestion (Weber, 1991). Since large and small crabs live near the mouth of sea urchins, material eroded during host grazing activities may be suspended in the water and

subsequently gathered by crabs, as has been previously suggested to occur in sphaeromatid isopods that live in the mantle cavity of chitons in the Caribbean Sea (Glynn, 1968). Free-living porcelain crabs are mainly filter-feeders (Achituv & Pedrotti, 1999). Thus, it is also possible that the crabs simply find attachment substrate and protection among the sea urchin spines but receive alimentionation from the wave-swept waters in the urchin habitat. Future laboratory studies are required to illuminate the feeding behaviour and food resources of *L. mitra*.

Benefits acquired by sea urchins from associated crabs appear to be less likely to occur. Defence of hosts by symbiotic crabs, shrimps and polychaetes has been demonstrated to occur in tropical seas (Smith, 1977; Glynn, 1980). Hosts may be aggressively defended by claws, chelipeds and mouthparts displayed against intruders. On barren grounds, sea stars are conspicuous predators of sea urchins (Vásquez & Buschmann, 1997). However, host defence as previously observed for other symbiotic decapods appears unlikely to occur in *L. mitra* since its small size and weak armament probably does not permit it to repel large predators. Should future observations reveal that *L. mitra* feeds on host products or host epifauna or -flora, this could be considered positive since parasites or other non-desirable materials may be removed by crab activities (see Stachowicz & Hay, 1996; Bunkley-Williams & Williams, 1998). At present the association between *L. mitra* and *T. niger* can be characterized as a commensal one, with benefits for the crabs but no apparent benefits or costs for sea urchins.

Life history of Liopetrolisthes mitra

The presence of megalopa larvae on several collected sea urchins suggests that settlement occurs on hosts, as has been indicated for other symbiotic decapods (Castro, 1978; Baeza & Stotz, 1998). *Liopetrolisthes mitra* recruits are not found in crevices, between rocks or under boulders used by free-living porcelain crabs (Baeza & Stotz, 1998). Possibly, the symbiotic association is established by an active habitat selection behaviour of the porcelain crab during larval settlement. This behaviour may be mediated by chemical signals produced by the host as has been previously described for *Echinoecus pentagonus* (A. Milne Edwards), a commensal crab of the sea urchin *Echinothrix calamaris* (Pallas) (Castro, 1978). Since *L. mitra* live aggregated on sea urchins, cues from conspecifics may also be important as has been previously reported for free-living porcelain crabs *Petrolisthes eriomerus* Stimpson and *Petrolisthes cinctipes* (Randall) (Jensen, 1989, 1991).

Recruitment to hosts during larval settlement of the crab appears to occur throughout the year as suggested by the presence of megalopae and small immature crabs throughout the study period. However, recruitment was most intense during the austral summer and early autumn. After recruitment, crabs reach sexual maturity during winter months, when a small proportion of the adult population reproduces. Crabs continue to grow during late austral winter, and then reproduce continuously during the next spring, summer and autumn. Most crabs then die (probably by senescence) during their second winter, as suggested by the disappearance of large

crabs from sea urchins during June/July 1996. Thus, *L. mitra* appears to live at least one and a half years and it reproduces continuously after reaching sexual maturity. Nevertheless, although reproductive and recruitment activities occur year round, both recruitment and reproduction decrease during winter months, when the lowest water temperatures occur within the bay (Moraga & Olivares, 1993).

The reproductive cycle of *L. mitra* is similar to that reported for various free-living porcellanids that live in sympatry with this commensal crab. In those species, reproductive activity considerably decreases during some months. Thus, the reproductive pattern of *L. mitra* and sympatric free-living porcelain crabs differs from that of another commensal crab, *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) which reproduces continuously and with similar intensity year round (J.A. Baeza, unpublished data). This observation suggests that the adoption of a commensal life style by *L. mitra* did not have strong effects on its life history and general ecology as has been previously documented for *A. spinifrons*.

The host of *L. mitra*, the black sea urchin *T. niger*, represents an abundant resource and a relatively large refuge for this small porcelain commensal crab. Thus, it has characteristics similar to the microhabitats (cavities and crevices) used as shelter by free-living porcelain crabs. Aggregations of several (up to 25) individuals of *L. mitra* on single urchins *T. niger* suggest that this crab does not monopolize host individuals. During most months no relationship existed between host size and the number of crabs per host individual. Only in May and late December 1996, a significant relationship between host size and number of crab associates was found. What do these results imply for the reproductive biology of *L. mitra*? In December, most crabs are reproductively active (see high percentage of ovigerous females), while during the winter months the proportion of reproductive crabs is low. Assuming female centered competition (see e.g. Christy, 1987), male *L. mitra* may aggregate around receptive females. Given seasonally varying availability of receptive females, this would have the following consequences for the association pattern of *L. mitra* on its host. During time periods when reproductive activity of *L. mitra* is low (few receptive females available), distinct aggregations of reproductive crabs will form, independent of the host size. Reproductive crabs would aggregate on a few hosts resulting in relatively large aggregations on individual hosts—this is supported by the fact that the largest aggregations on individual sea urchins were primarily found during austral autumn and winter. On the other hand, during time periods when many crabs are reproductive (i.e. in December), one may expect many aggregations and host size will gain greater importance in determining the size of these aggregations. The results on the association pattern of *L. mitra* would thus indicate that males and females can move relatively easy between hosts in search of mating partners. In shallow subtidal waters, black sea urchins occur in dense patches (Rodríguez & Ojeda, 1993), and crabs may wander under the protective cover of the urchins without much risk of predation. Within existing aggregations of reproductive crabs, receptive females may be dominated by a large dominant male, which may aggressively exclude other small males as has

been reported for various free-living porcelain crabs (Molenock, 1975). In summary, the life style of *L. mitra* resembles that of free-living porcellanid crabs which is probably due to the fact that availability and relative size of its urchin host is comparable to that of refuges for free-living species.

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REFERENCES

- Achituv, Y. & Pedrotti, L.M., 1999. Costs and gains of porcelain crab suspension feeding in different flow conditions. *Marine Ecology Progress Series*, **184**, 161–169.
- Antezana, T., Fagetti, E. & Lopez, M.T., 1965. Observaciones bioecológicas en decápodos comunes de Valparaíso. *Revista de Biología Marina, Valparaíso*, **12**, 1–60.
- Baeza, J.A. & Stotz, W., 1995. Estructura poblacional del cangrejo comensal *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Porcellanidae) en su hospedador habitual *Phymactis clematis* (Drayton, 1846) y dos nuevos hospedadores. *Revista de Biología Marina, Valparaíso*, **30**, 255–264.
- Baeza, J.A. & Stotz, W., 1998. Selección del hábitat durante el asentamiento larval de *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae), un cangrejo comensal de la anémona *Phymactis clematis* (Drayton, 1798) (Coelenterata: Anthozoa). *Revista de Biología Marina y Oceanografía, Valparaíso*, **33**, 331–343.
- Bunkley-Williams, L. & Williams Jr, E.H., 1998. Ability of Pederson cleaner shrimp to remove juveniles of the parasitic cymothoid isopod, *Anilocra haemuli*, from the host. *Crustaceana*, **71**, 862–869.
- Castro, P., 1978. Settlement and habitat selection in the larvae of *Echinoecus pentagonus* (A. Milne Edwards), a brachyuran crab symbiotic with sea urchins. *Journal of Experimental Marine Biology and Ecology*, **34**, 259–270.
- Christy, J.H., 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bulletin of Marine Science*, **41**, 177–191.
- Glynn, P., 1968. Ecological studies on the associations of chitons in Puerto Rico, with special reference to sphaeromid isopods. *Bulletin of Marine Science*, **18**, 572–626.
- Glynn, P., 1980. Defence by symbiotic Crustacea of host coral elicited by chemical cues from predators. *Oecologia*, **47**, 287–290.
- Gray, I.E., 1961. Changes in abundance of the commensal crabs of *Chaetopterus*. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **120**, 353–359.
- Hacker, S.D. & Madin, L.P., 1991. Why habitat architecture and color are important to shrimp living in pelagic *Sargassum*: use of camouflage and plant-part mimicry. *Marine Ecology Progress Series*, **70**, 143–155.
- Haig, J., 1955. The Crustacea Anomura of Chile. Reports of the Lund University Chile Expedition 1948–49. *Lunds Universitets Arsskrifts*, **51**, 1–68.
- Haig, J., 1960. The Porcellanidae (Crustacea, Anomura) of the eastern pacific. *Allan Hancock Pacific Expeditions*, **24**, 1–440.
- Hsueh, P.-W. & Huang, J.-F., 1998. *Polyonyx bella*, new species (Decapoda: Anomura: Porcellanidae), from Taiwan, with notes on its reproduction and swimming behavior. *Journal of Crustacean Biology*, **18**, 332–336.
- Jensen, G.C., 1989. Gregarious settlement by megalopae of the porcelain crabs *Petrolisthes cinctipes* (Randall) and *P. eriomurus* Stimpson. *Journal of Experimental Marine Biology and Ecology*, **131**, 223–231.
- Jensen, G.C., 1991. Competency, settling behavior, and post-settlement aggregation by the porcelain crab megalopae (Anomura: Porcellanidae). *Journal of Experimental Marine Biology and Ecology*, **153**, 49–61.
- Molenock, J., 1975. Evolutionary aspects of communication in the courtship behavior of four species of anomuran crabs (*Petrolisthes*). *Behaviour*, **53**, 1–30.
- Moraga, J. & Olivares, J., 1993. Variabilidad térmica de la Bahía La Herradura de Guayacán, Coquimbo, Chile. *Estudios Oceanológicos*, **12**, 29–36.
- Ng, P.K.L. & Goh, N.K.C., 1996. Notes on the taxonomy and ecology of *Aliaporcellana telestophila* (Johnson, 1958) (Decapoda, Anomura, Porcellanidae), a crab commensal on the gorgonian *Solenocaulon*. *Crustaceana*, **69**, 652–661.
- Patton, W.K., Patton, R.J. & Barnes, A., 1985. On the biology of *Gnathophylloides mineri*, a shrimp inhabiting the sea urchin *Triploneustes ventricosus*. *Journal of Crustacean Biology*, **5**, 616–626.
- Rodríguez, S.R. & Ojeda, F.P., 1993. Distribution patterns of *Tetrapygyus niger* (Echinodermata: Echinoidea) off the central Chilean coast. *Marine Ecology Progress Series*, **101**, 157–162.
- Sampedro, M.P., Fernández, L., Freire, J. & González-Gurrarián E., 1997. Fecundity and reproductive output of *Pisidia longicornis* (Decapoda: Porcellanidae) in the Ría de Arousa (Galicia, NW Spain). *Crustaceana*, **70**, 95–110.
- Smith, W.L., 1977. Beneficial behaviour of a symbiotic shrimp to its host anemone. *Bulletin of Marine Science*, **27**, 343–346.
- Sokal, R.R. & Rohlf, F.J., 1969. *Biometry*. San Francisco: W.H. Freeman & Co.
- Stachowicz, J.J. & Hay, M.E., 1996. Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. *Oecologia*, **105**, 377–387.
- Stevcic, Z., 1986. Autoecological investigations of the porcelain crab *Porcellana platycheles* (Pennant) (Decapoda: Anomura) in the Rovinj area (northern Adriatic). *Crustaceana*, **50**, 242–252.
- Vásquez, J.A. & Buschmann, A.H., 1997. Herbivore–kelp interactions in the Chilean subtidal communities: a review. *Revista Chilena de Historia Natural*, **70**, 41–52.
- Viviani, C.A., 1969. Los Porcellanidae (Crustacea, Anomura) chilenos. *Beiträge zur Neotropischen Fauna*, **6**, 1–14.
- Weber, L.I., 1991. Sinonimia y caracterización de *Liopetrolisthes mitra* (Dana, 1852) y *Liopetrolisthes patagonicus* (Cunningham, 1871) n. comb. *Gayana, Zoología*, **55**, 13–22.
- Weber, L.I. & Galleguillos, R., 1991. Morphometric and electrophoretic evidences for two species of the genus *Liopetrolisthes* (Crustacea: Decapoda: Porcellanidae) and some aspects of their variability. *Comparative Biochemistry and Physiology*, **100B**, 201–207.
- Werdning, B., 1983. Kommensalische Porzellaniden aus der Karibik (Decapoda, Anomura). *Crustaceana*, **45**, 1–14.
- Williams, A.B., 1984. *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida*, 2nd ed. Washington D.C.: Smithsonian Institution Press.

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