

MOVEMENTS OF THE SYMBIOTIC CRAB *LIOPETROLISTHES MITRA* BETWEEN ITS HOST SEA URCHIN *TETRAPYGUS NIGER*

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ABSTRACT

The behavior of symbiotic organisms is strongly affected by host ecology. It has been hypothesized that symbionts that inhabit densely aggregated hosts show little territorial behavior and move frequently between host individuals. Herein we tested this hypothesis for the porcellanid crab *Liopetrolisthes mitra* that occurs in aggregations of several crabs on sea urchins *Tetrapygus niger*. The hosts of these crabs are often in direct physical contact to each other and the structure of symbiont aggregations suggests that these are unstable, possibly due to frequent movements of crabs. Herein, we examined the mobility of crabs both in laboratory and field experiments. Many crabs that were placed at natural densities on one sea urchin moved to crab-free sea urchins within 12 h over night. Both sexes and all sizes of crabs moved between different sea urchin individuals, but adult males moved more frequently than adult females. However, when placed on a sea urchin with a receptive female, male crabs reduced their movements. In the field, the first crabs appeared on experimentally crab-free sea urchins within 1 d, and within 3 d after the start of the experiment these sea urchins had been fully recolonized by crabs. Crabs on experimental sea urchins were significantly smaller than on control sea urchins, but no significant differences in sex-ratio were found after 3 or 5 d. Our results suggest that the mating system of *L. mitra* is similar to that of many free-living crabs in which males roam in search of receptive females. We hypothesize that this behavioral similarity is due to the fact that individual sea urchin hosts are difficult to guard by crustacean associates due to their structural complexity and their aggregation pattern. A comparison with published reports on other urchin-dwelling crabs suggests that host abundance and distribution exert a strong effect on symbiont movements and host-use patterns.

Many organisms form aggregations on resources that are patchily distributed. The composition of these aggregations may be highly organized or unstructured, depending on the species under consideration. Aggregations of many marine invertebrates in resource patches are characterized by a high and rapid turnover (e.g., Taylor, 1998). Fluctuations within aggregations may be particularly strong when resource patches are abundant and costs for moving between patches are low. For example Taylor (1998) concluded that amphipods crawled directly from one alga onto another suggesting that costs and risks of moving between patches are low. In particular, when only specific requirements (e.g., feeding) can be fulfilled in one patch, organisms may switch between patches that allow them to fulfill different essential requirements. Thus, resource characteristics (function, distribution, size, and longevity) have a strong influence on resource utilization behavior and consequently on the intraspecific aggregation pattern of the organisms that utilize these resources.

Organisms with an obligate symbiotic life style are restricted in their distribution and abundance by the availability of suitable hosts. Factors such as host morphology, size, and distribution patterns are likely to affect symbiont abundance per host individual (intensity), percentage of hosts occupied (prevalence), and the partner fidelity of these associations and thereby intraspecific interactions among symbiotic organisms (Tsuchiya and Yonaha, 1992). Crustaceans live on/in a variety of invertebrate organisms of highly di-

verse shapes and sizes. The intensity and prevalence of these crustacean-invertebrate associations is similarly diverse. Many species inhabit their hosts as single individuals (Thiel and Baeza, 2001), while others occur in heterosexual pairs (Hsueh and Huang, 1998) or in groups of variable numbers on their hosts (Patton et al., 1985). The intraspecific association pattern of crustaceans on their hosts is likely to depend on host size, morphology, distribution and abundance (Thiel and Baeza, 2001). In particular, the last two factors may strongly influence movements of symbiont crabs.

Many sea urchin species, some of which harbor endo- or ectosymbiotic crustaceans, show a highly aggregated distribution pattern (e.g., Rodríguez and Ojeda, 1993). Sea urchins may form aggregations consisting of tens of individuals, which are in direct contact with each other (Reese, 1966). In these dense aggregations, ectosymbiotic crustaceans may easily move from one sea urchin to the next under the cover of their spines (Bell, 1984; Stebbins, 1988). The hypothesis that under these conditions symbiotic crabs move without any impediment between different host individuals was also supported by the observation that groups of crabs on individual sea urchins exhibit no distinct demographic structure (Baeza and Thiel, 2000). Herein, we put the hypothesis that porcellanid crabs move frequently between sea urchin hosts to a test, using laboratory and field experiments.

MATERIALS AND METHODS

STUDY SITE AND STUDY ORGANISM.—Sea urchins *Tetrapygus niger* and porcellanid crabs *Liopetrolisthes mitra* occur abundantly in shallow subtidal waters along the coast of Chile. Crabs and sea urchins for the experiments were collected in May and June 2000 at Bahía La Herradura and La Pampilla, Coquimbo (29°58'30" S–71°22'30" W), Chile. All laboratory experiments were conducted in the flowing seawater laboratory of Universidad Católica del Norte. A field experiment was done in Bahía La Herradura at La Pergola, near the University shore.

Following collection in the field, crabs were held together with their natural hosts in trays with flowing seawater. In order to obtain receptive females, adult females were maintained in sexual isolation in holding trays without any male crabs. When an exuvia was found in this tray, the female with the soft exoskeleton was identified and used for the respective experiment. Crabs were maintained in the laboratory for a maximum of 7 d before being used in the experiments. All crabs and sea urchins were only used once in the experiments and then released immediately.

EXPERIMENT 1 – MOVEMENTS OF CRABS OF DIFFERENT SIZE AND SEX.—Four sea urchins of sizes that commonly harbor crabs in the field (55–65 mm test diameter) were placed in the four corners of an aquarium (15.6 l capacity; 26 cm length × 30 cm width × 20 cm height) with flowing seawater. At the start of the experiment, on one of these sea urchins, four crabs were placed while the other three urchins were left without crabs. All sea urchins were individually marked with small pieces of rubberband that were tied to one spine. Ten replicates were started each evening and left for 12 h overnight until the following morning when the experiment was finished. During the experiment, the four sea urchins could move freely within the aquaria, and during the morning control they were often found aggregated in one corner of the aquarium. The location of each crab (on original urchin or on new urchin) was determined. All crabs that were found on the original sea urchin were considered as residents that did not move during the experiment. However, crabs may have moved away from and back to their original hosts, and thus these values represent minimum estimates of crab movements. For these experiments, we distinguished female and male crabs and three different size categories (crabs <4.5 mm carapace width CW, 4.5–7.0 mm CW, and >7.0 mm CW). Herein, all crabs <4.5 mm CW were considered as subadults because the smallest ovigerous female found in a preliminary sample (n = 54 females) had a CW of 5.0 mm. The four crabs in one replicate

always belonged to the same sex and size category; for example all four crabs were females of intermediate size (4.5–7.0 mm CW). For statistical analysis, the effects of crab sex and size on the number of crabs remaining on the original sea urchin were compared using a two-way ANOVA. Before conducting the ANOVA, we tested whether sample variances were homogeneous using Bartlett's test of homogeneity.

EXPERIMENT 2 – MOVEMENTS OF LARGE MALES IN PRESENCE AND ABSENCE OF FEMALES.—The general set-up of this experiment was similar to the previous experiment with the difference that in addition to the four focal crabs either a female or a male crab was fixed to the original sea urchin. A receptive female (with soft carapace) or an adult male was restrained on the original sea urchin with a rubberband that was glued to their carapace. This rubberband was attached to a spine of the sea urchin leaving a length of ~5 cm, thus allowing the crab to move relatively free on the designated sea urchin without the possibility to leave it. Following fixation of this crab onto a sea urchin, four large males (>7 mm carapace width) were placed on the same sea urchin. Crabs were placed in the evening, recovered 12 h later in the morning, and then released. The number of males remaining on the original sea urchin with either a male or a receptive female were compared using the Mann-Whitney U-test because variances of the contrasted data sets were not homogeneous after Bartlett's test (Sokal and Rohlf, 1981).

EXPERIMENT 3 – COLONIZATION OF CRAB-FREE SEA URCHINS IN THE FIELD.—To obtain an estimate of movement rates in the field, we placed crab-free sea urchins in an experimental area, and monitored their recolonization by crabs in the days following their release. Sea urchins were collected from the field, and all symbiotic crabs were carefully removed from these urchins in the laboratory. Crab-free sea urchins were then marked with a small piece of rubberband that was tied to one of their spines and returned to the field. One hundred sea urchins were released in an area of approximately 2 m × 4 m with an original density of ~38 sea urchins m⁻². By bringing out the experimental sea urchins, the density was artificially increased to ~50 sea urchins m⁻². We decided not to spread the experimental sea urchins over a wider area to ensure sufficient recapture rates. Five days after being released, some of the marked sea urchins (5 out of 100 marked sea urchins) were found >5 m from the release area. As a result of the increase in urchin density, the movement rates reported herein may represent a slight overestimate of natural movement rates. Originally, it was planned to recollect the sea urchins on days 1, 3 and 5 after their release but because of stormy weather sampling had to be interrupted on day 1. The few sea urchins that were collected on this occasion had to be discarded since divers could not take reliable samples due to wave action. The first complete set of samples could not be taken before day 3. Experimentally crab-free (= marked) and unmanipulated control (= unmarked) sea urchins were collected within and in the immediate vicinity of the release area. A diver located a sea urchin, placed a cut-off plastic bottle over the sea urchin and then 'scraped' it carefully with all the associated crabs into the bottle. The open end of the bottle was immediately covered with the glove-covered hand, and the bottle was then transported to the water surface, where it was handed to a second person who transferred the urchin with all the crabs into a sealable plastic bag. Occasionally a crab (maximally one crab per sea urchin) escaped during sampling but this was true for both the experimentally crab-free and the control sea urchins. For statistical analysis, the effects of treatment and time (experimentally crab-free and unmanipulated control, day 3 and day 5) on the number and sizes of crabs on sea urchin were compared using a two-way ANOVA. Before conducting the ANOVA, we tested whether sample variances were homogeneous using Bartlett's test of homogeneity. The frequency of male and female crabs on experimental sea urchins was compared to that on control urchins by using an Independence χ^2 test (Sokal and Rohlf, 1981).

RESULTS

During the laboratory experiments all stages of *L. mitra* moved between sea urchins (Fig. 1). Within 12 h many individuals had left their original host. Approximately 40% of small crabs (<4.5 mm CW) remained on the original sea urchin (Fig. 1). Among the

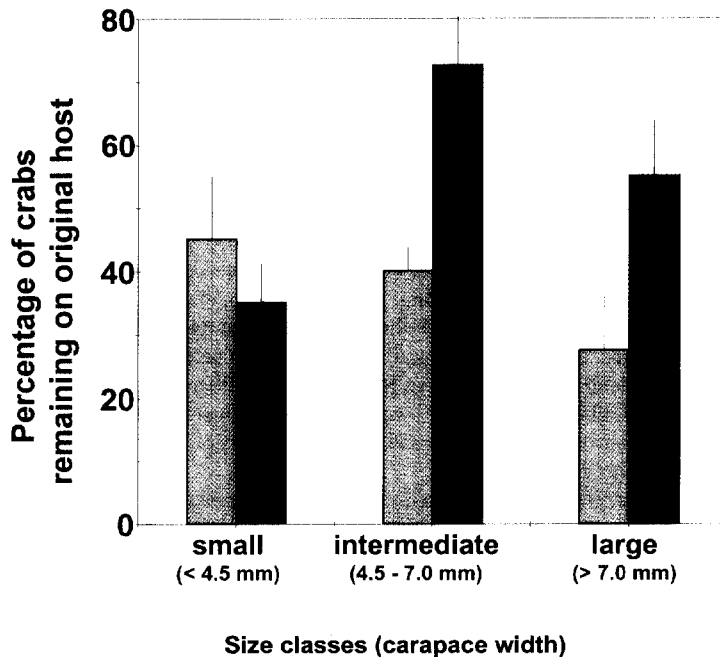


Figure 1. Average percentage (\pm SE) of female (black columns) and male (gray columns) crabs *Liopetrolisthes mitra* remaining on original host individual; three size categories of male and female crabs were distinguished; at the start of the experiment, the crabs were placed on one sea urchin *Tetrapygus niger* in an aquarium together with three other sea urchins that were free of crabs; crabs were recollected 12 h after the start of the experiment; of each treatment 10 replicates with 4 crabs each, all of the same size category and sex, were conducted.

intermediate and large crabs (≥ 4.5 mm CW) many females remained on the original sea urchin, while many males moved between sea urchins (Fig. 1).

The movement of *L. mitra* crabs between hosts depends on their sex, but not on the size of the experimental crabs (Table 1). The interaction term was significant (Table 1), because large males moved more frequently between sea urchins than small males, while large females moved less than small females.

In the second experiment, movements of males differed depending of whether they were on a sea urchin with a fixed receptive female or with a fixed male crab (Fig. 2). Residence of large males that were together with a receptive female was significantly higher than that of large males placed with another male on a sea urchin (Fig. 2) (Mann-Whitney U-test, $P < 0.05$).

Table 1. Residence of the porcellanid crab *Liopetrolisthes mitra* on its host, the sea urchin *Tetrapygus niger*. Results for two-way ANOVA of crab residence on sea urchins based on number of crabs that remained on original sea urchin; $n = 10$ replicates of each variable combination with sex (male, female) and size (small, intermediate, large); * $P < 0.05$.

	Sum of squares	df	F	P
Sex	6.667	1	5.310	0.025*
Size	5.233	2	2.084	0.134
Sex * size	8.633	2	3.438	0.039*
Error	67.800	54		

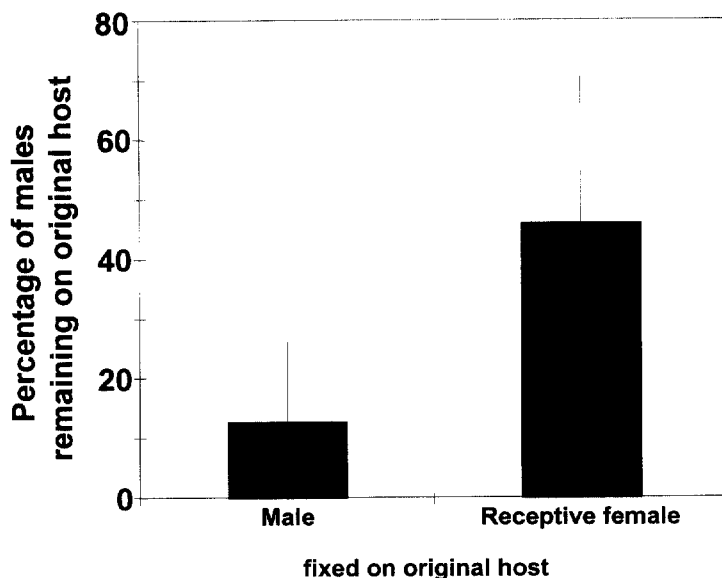


Figure 2. Average percentage (\pm SE) of large (>7.0 mm CL) male crabs *Liopetrolisthes mitra* remaining on a sea urchin with receptive female and male crabs; a female (or male) crab was fixed with a rubberband to one sea urchin, and then four large male crabs were placed on the same sea urchin; the large male crabs were recollected from the sea urchins 12 h after the start of the experiment; of each treatment (female or male crab fixed to sea urchin) 10 replicates were conducted.

In the field, the first crabs were seen on crab-free sea urchins on day 1 after the release of these urchins (no quantitative data available due to sampling problems — see Materials and Methods). Within 3 d large numbers of crabs had recolonized the crab-free sea urchins (Fig. 3A). Neither treatment of sea urchins nor the day of recollection had a significant effect on their numbers (Table 2). However, crabs found on experimental sea urchins were smaller than those on unmanipulated control sea urchins (Fig. 3B, Table 3). Additionally, the sex-ratios were more female-biased on control than on experimental sea urchins, but differences were not significant (Table 4).

Both in the field and in the laboratory, crabs usually hid under the oral side of their sea urchin host. When two urchins were in direct physical contact to each other, crabs moved without any apparent hindrance from one sea urchin to the next. Sometimes, crabs were seen sitting directly between two sea urchins without any apparent tendency towards either of these host individuals. On two occasions, we observed direct interactions between males and receptive (recently molted) females. In the laboratory, we observed a

Table 2. Recolonization of sea urchins *Tetrapygyus niger* by the porcellanid crab *Liopetrolisthes mitra*. Results for two-way ANOVA of crab numbers on experimentally crab-free and unmanipulated control sea urchins; $n = 10$ experimental and 10 control sea urchins were collected on day 3 and day 5 after experimental sea urchins were released; * $P < 0.05$.

	Sum of squares	df	F	P
Treatment	0.625	1	0.152	0.699
Time	4.225	1	1.030	0.317
Treatment * time	1.225	1	0.299	0.588
Error	147.700	36		

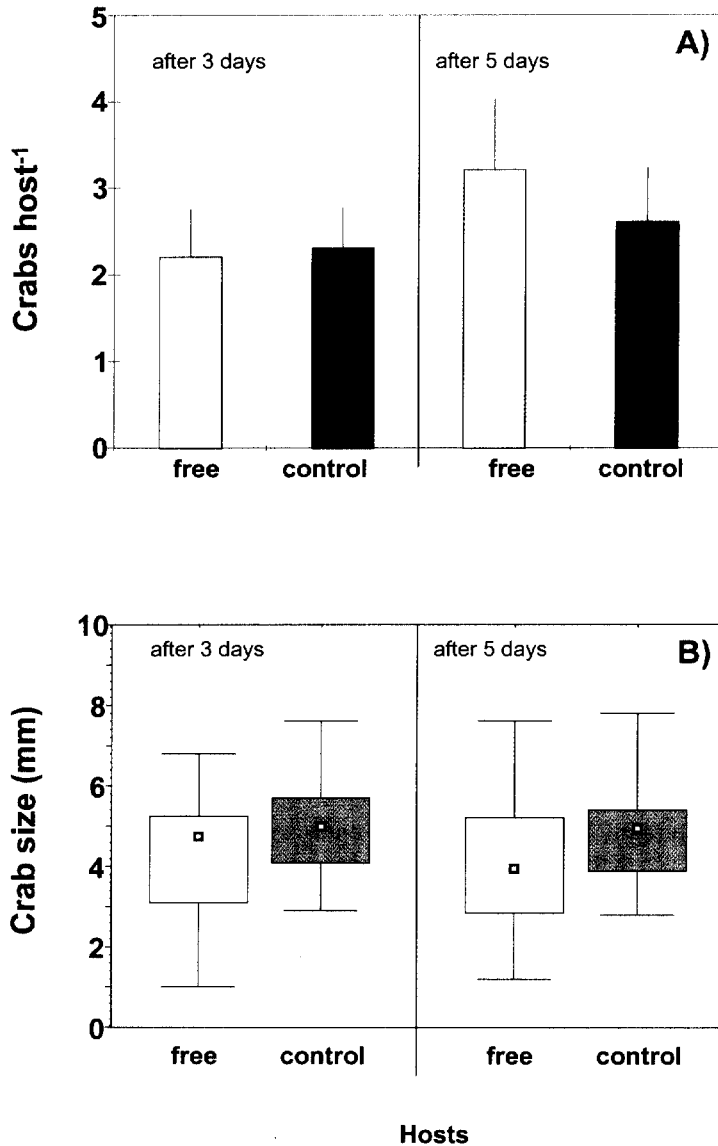


Figure 3. (A) Numbers and (B) sizes (carapace width) of crabs *Liopetrolisthes mitra* on sea urchins *Tetrapygus niger* from which all crabs had been removed (crab-free hosts) and sea urchins that had been left untouched (control hosts); sea urchins were recollected 3 d and 5 d after they had been placed in the natural environment; at each sampling date, 10 crab-free hosts and 10 control hosts were collected.

male approaching a receptive female repeatedly touching it with its antennae. The male then embraced the female for about 5 min with the ventral sides of male and female directed towards each other. Following this short bodily contact, the male and the female separated without any further interactions. In the field, we once found a large male covering a receptive female in a position, which is typical for mate-guarding in brachyuran decapods, both sitting motionless on the substrate at the edge of a sea urchin.

Table 3. Recolonization of sea urchins *Tetrapygus niger* by the porcellanid crab *Liopetrolisthes mitra*. Results for two-way ANOVA of crab sizes on experimentally crab-free and unmanipulated control sea urchins; n = 10 experimental and 10 control sea urchins were collected on day 3 and day 5 after experimental sea urchins were released; * P < 0.05.

	Sum of squares	df	F	P
Treatment	12.456	1	6.166	0.015*
Time	1.674	1	0.829	0.365
Treatment * time	0.521	1	0.258	0.613
Error	200.003	99		

Throughout the laboratory experiments, we often found exuviae in the aquaria indicating that the crabs molted in the laboratory. Exuviae were exclusively found during the morning suggesting that *L. mitra* molts preferentially at night. During a night observation we observed the molting process in a female crab. Shortly before the old exoskeleton was shed, the crab moved away from the sea urchin and sought hold on a nearby stone where it remained motionless for ~1 h. The process of shedding the old exoskeleton lasted approximately one minute, and within 1 h thereafter the crab had moved back to the sea urchin.

Table 4. Numbers of *Liopetrolisthes mitra* found on experimentally crab-free and unmanipulated control sea urchins after (a) 3 d and (b) 5 d; experimental sea urchins were released in a 2 m × 4 m large release area and recollected from this area or its immediate vicinity; n = 10 experimental and 10 control sea urchins were sampled 3 d and 5 d after release of the experimental sea urchins; Independence χ^2 test after Yates' correction; $\chi^2_{0.05,1} = 3.841$.

	Males	Females	Total	χ^2
a) 3 d after release				
Experimentally crab-free	11	9	20	1.516
Control unmanipulated	8	15	23	
b) 5 d after release				
Experimentally crab-free	12	14	26	1.327
Control unmanipulated	7	19	26	

DISCUSSION

Both in the laboratory and in the field *L. mitra* moved rapidly and easily between its sea urchin hosts. The experiments conducted herein indicate that adult males have a high tendency to move between hosts. However, these males reduced their movements when they were placed together with a receptive female. Sexually mature females, many of which were ovigerous, showed the lowest rates of movements between sea urchins. These observations suggest that the mating system in *L. mitra* shows resemblance to that of some free-living crabs. This may be consequence of host abundance and distribution pattern as will be discussed in the following.

MOVEMENTS OF *L. MITRA* BETWEEN HOSTS.—The porcellanid crab *L. mitra* occurs in groups of up to 25 ind comprising crabs of both sexes and all life stages on one sea urchin (Baeza and Thiel, 2000). Similar as other urchin-dwelling crabs (Reeves and Brooks, 2001), *L. mitra* may find protection from predation on its sea urchin host. Because the hosts of *L. mitra* occur in dense aggregations, we had hypothesized that crabs move eas-

ily from one sea urchin to the next. The results presented herein confirmed this, but furthermore sex-related differences were found: adult male crabs moved more than females. The high movement rates revealed in the present study indicate that the groups of *L. mitra* on individual hosts are continuously reshuffled. Males, instead of associating for long time periods with one or more female as is known from other symbiotic crustaceans (Knowlton, 1980; Baeza, 1999) move frequently between hosts, possibly in search of receptive females. This suggests that male crabs follow a mating strategy based on 'search and interception' of females (sensu Christy, 1987), similarly to that observed in other symbiotic crabs in which males search for receptive females on different host individuals (Dales, 1957; Christensen and McDermott, 1958; Knowlton, 1980; Wirtz and Diesel, 1983; Yanagisawa and Hamaishi, 1986). Further support for this interpretation is found in the fact that frequent movements of male *L. mitra* are reduced in presence of a receptive female. After locating a female, males may determine her reproductive state and remain on hosts if females are receptive (Diesel, 1988). Active male mate-searching does not, however, occur in all symbiotic crustaceans because in many species, males cohabit with one or several females in groups or in pairs regardless of the reproductive state of the female (Wickler and Seibt, 1970; Seibt and Wickler, 1979; Knowlton, 1980; Kropp, 1987; Shuster, 1992).

In *L. mitra* not only the males moved between hosts; adult females and subadults were also found to change hosts, albeit at a lower rate than large males. Reduced mobility as shown herein for adult female *L. mitra* has also been reported for reproductive females of other symbiotic crabs (Yanagisawa and Hamaishi, 1986) and for free-living brachyuran crabs (Howard, 1982). Activities related to incubation of developing embryos may cause these reproductive females to assume a more sedentary life-style.

Mobility of *L. mitra* may not only be related to mating (males) or to reproductive stages (females). Sea urchins *T. niger* have been observed to move from day to day in the shallow subtidal zone (see results of field experiment; J.A.B., pers. observ.), and crabs are thus forced to follow these movements. During the movements of the sea urchins crabs may also occasionally switch between sea urchins. Furthermore, *L. mitra* is a passive suspension-feeder (Zander, 2000), and crabs may seek sites or sea urchins in favorable positions for suspension-feeding. Symbiotic crabs that live on the outside of sea urchins may also be susceptible to movements of spines (Bell and Stancyk, 1983), which may be the reason why crabs move away from hosts for molting. Since sea urchin hosts are highly mobile, host changes may occur when freshly molted crabs return to the shelter of sea urchins.

Movements of crustacean symbionts between hosts have also been observed or inferred for many other ectosymbiotic species (Ache, 1974; Castro, 1974; 1978; Tsuchiya and Yonaha, 1992; VandenSpiegel et al., 1998). These movements occur primarily in the shelter of the night, particularly in species that live on spatially separated hosts (Castro, 1974, 1978; Wirtz and Diesel, 1983; Gherardi, 1991). Many of the crustaceans living as ectosymbionts on sea urchins or other megainvertebrates are common prey items for fish predators (for *L. mitra* see, e.g., Vargas et al., 1999). It is thus not surprising that movements between host individuals occur preferentially at night. In the present study, the laboratory experiments were conducted during the night hours but because the sea urchin hosts of *L. mitra* often form dense assemblages, movements between hosts may also occur during daylight hours. Also in other species of symbiotic crustaceans, movements between host individuals are facilitated when hosts are in direct physical contact to each

other (Bell, 1984; Patton et al., 1985; Ng and Lim, 1990; Gherardi, 1991). We hypothesize that in situations where hosts are spatially separated, movements between hosts may occur exclusively at night. In situations, where hosts are in physical contact with many other host individuals, movements between host individuals can occur at any time. In *Zebrida adamsii*, movements between hosts in search of mating partners appear to be entirely restricted to the breeding season (Yanagisawa and Hamaishi, 1986). Since the sea urchin hosts of *Z. adamsii* are rarely in contact with each other, male crabs in search of receptive females need to leave hosts, which may lead to increased male mortality expressed in the strongly female-biased sex-ratio during the breeding season of *Z. adamsii* (see data in Yanagisawa and Hamaishi, 1986).

MOTILITY AND GROUP STRUCTURE IN SYMBIOTIC CRUSTACEANS.—Movements between hosts, similarly as other behavioral decisions of organisms, can be viewed from a cost-benefit perspective (see e.g., Roughgarden, 1975). When costs are high compared to expected benefits, movements will be rare, whereas when costs are low compared to benefits, symbionts may frequently move between hosts. Symbionts may move to find better hosts that provide more nutrition or better protection than the original host. Or they may move in search of conspecifics, such as mating partners (see above). Costs may comprise the risk of predation or uncertainty of finding a suitable new host. Costs of movements will be low when hosts occur in dense aggregations, since symbionts can evaluate new host individuals before leaving their original host. Thus, in symbionts that inhabit hosts with a highly aggregated distribution pattern, movements occur to a much higher degree than in symbionts living on highly dispersed and rare host species (see e.g., Srinivasan et al., 1999). Direct contact between host individuals facilitates symbiont movements between hosts (Telford, 1978; Bell, 1984). A comparison between different crab symbionts of sea urchins appear to confirm this idea. Symbionts that inhabit sea urchin species, which are abundant and frequently in direct contact with other sea urchin individuals, have been shown or suspected to be highly mobile, frequently moving between hosts (Table 5).

Movements will have a strong effect on composition of symbiont groups. Frequent movements between hosts will lead to a continuous reshuffling of group members, and consequently, it will be difficult to identify groups with a particular structure. This appears to be the case in *L. mitra* in which no distinct relationship between host size and symbiont number/size has been found (Baeza and Thiel, 2000). Movements appear to be relatively common in *L. mitra* as was shown herein by the results from both laboratory as well as field experiments. Frequent movements of all life stages have also been reported for small isopods that live in dense aggregations on invertebrate hosts (*Colidotea rostrata* on sea urchins, Stebbins, 1988; *Iais californica* on sphaeromatid isopods, Rotramel, 1975). The shrimp *Gnathophylloides mineri* lives in small aggregations on its sea urchin host, often consisting of a male with several females: it is thought that females aggregate around males, and that movements between hosts occur infrequently since hosts are dispersed over relatively large areas (Patton et al., 1985).

In species, in which symbiont movements between individual hosts are uncommon, structured groups or distinct associations may result. The sea urchin *Echinometra lucunter* often harbors groups consisting of a heterosexual pair and some small subadults of the porcellanid crab *Clastocheilus vanderhorsti* (Werding, 1983). This sea urchin lives in boreholes on wave-exposed shores with no physical contact between neighboring hosts. Thus, movements of *C. vanderhorsti* between host individuals may not occur as common

Table 5. Crustacean ectosymbionts on sea urchins, their host species and host distribution pattern are shown together with symbiont movements, association pattern and stability of symbiont groups.

Symbiont species	Host species	Host distribution	Symbiont movements	Symbiont association (sG?)	Association stability	Reference
<i>Gnathophylloides mineri</i>	<i>Tripneustes ventricosus</i>	D	(+)	S, P, G	(+)	Patton et al., 1985
<i>Athanas kominatoensis</i>	<i>Anthocidaris crassispina</i>	D	+	S, P, G	(+)	Nakashima, 1987
<i>Athanas indicus</i>	<i>Echinometra mathaei</i>	(A, wC)	++	S, P, G	(-)	Gherardi 1991
<i>Tuleariocaris zanzibarica</i>	<i>Diadema setosum</i>	(A, wC)*	++	S, P, uG	(-)	Fricke & Hentschel, 1971
<i>Tuleariocaris neglecta</i>	<i>Diadema antillarum</i>	A, wC	(+)	?	(-)	Castro, 1974
<i>Colidotea rostrata</i>	<i>Strongylocentrotus</i> spp.	A, wC	+++	uG	-	Stebbins, 1988
<i>Zebrida adamsii</i>	<i>Toxopneustes pileolus</i>	D, nC	(-)	S	+	Yanagisawa & Hamaishi, 1986
<i>Percnon gibbesi</i>	<i>Diadema antillarum</i>	A, nC	+++	S	-	Hayes et al., 1998
<i>Stenorhynchus seticornis</i>	<i>Diadema antillarum</i>	A, nC	+++	S	-	Hayes et al., 1998
<i>Dissodactylus mellitae</i>	<i>Mellita quinquesperforata</i>	A, wC	+	S, P, uG	(+)	Telford, 1982; Bell, 1988
<i>Dissodactylus crinitichelis</i>	<i>Mellita sextesperforata</i>	A, wC	+	P, G	(+)	Telford, 1982
<i>Dissodactylus primitivus</i>	<i>Meoma ventricosa</i>	(D, nC)	(+)	S, P, uG	(+)	Telford, 1982
<i>Clastoecochus vanderhorsti</i>	<i>Echinometra lucunter</i>	A, nC	(-)	hP	+	Werding, 1983
<i>Liopetrolisthes mitra</i>	<i>Tetrapygos niger</i>	A, wC	+++	uG	-	this study

A - aggregated, D - dispersed

nC - no body contact, wC - with body contact

S - solitary, P - pair, hP - heterosexual pair, G - group, uG - unstructured group, sG - structured group

* - aggregated during day, dispersed during night (Fricke, pers. comm.)

as in *L. mitra*, *C. rostrata* or *G. mineri*. As a consequence, heterosexual pairs of *C. vanderhorsti* may remain together for relatively long time periods under one sea urchin.

Both, environmental (e.g., predation risk) as well as host-related factors (host abundance and distribution) have a strong effect on movements between hosts. In crustaceans that live on densely aggregated sea urchins, symbionts may easily move between host individuals without ever having to leave the protective cover of the sea urchins (Stebbins, 1988). This also appears to be the case in *L. mitra*, and movements between hosts are frequent and consequently group stability in this symbiont is low. In general, movements of crab symbionts are affected by the abundance and distribution pattern of their hosts (and by predation pressure), similar to fish living symbiotically with sea anemones (Srinivasan et al., 1999). Pair-living or solitary life style is favorable on spatially separated sea anemones while group-living appears to be the best option in dense anemone assemblages (Srinivasan et al., 1999). This corresponds to what has been discussed herein for urchin-dwelling crab symbionts. Host distribution and the resulting probability of symbiont movements between hosts may thus have a strong influence on the life history of their crustacean symbionts.

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