Experimental natural substrate preference of southern king crab *Lithodes santolla* larvae

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ABSTRACT

Notwithstanding the commercial importance of *Lithodes santolla* in the southern tip of South America, little is known about settlement habitat and behavior of their larvae. Such information is relevant for understanding its life history and for management and development of fishery-stock enhancement programs. The aims of this study were to determine the natural substrata that larval stages, zoeae and megalopa select for recruitment, and the effects of megalopa density and diurnal–nocturnal phase on such selection. Different laboratory experiments with durations of 8 h to 4 weeks were performed in 6-L round containers with their bottoms divided in four equal portions, each filled with sand, gravel, cobble and broken shell as substrata. Containers were kept in a cold room at 7.1 ± 0.5 °C and under 12:12 h light and dark photoperiod. Trials began with the release of larvae of different stages in the center of the containers. After different time periods, proportions of larvae swimming or settled on each substrate were determined. Larvae selected and settled on natural substrata immediately after being placed into the containers. Experiments showed that all larval stages (zoeae and megalopa) preferred complex substrata such as broken shell, cobble and gravel over sand which was rejected. The megalopa selects the substrate even during night period. Selection seems to be density-dependent since at the lowest density broken shell was the preferred substrate. Selection of complex substrata (i.e. mussel beds and/or shell fragments in nature) by all larval stages, even as early as the first zoea stage, provides a cryptic habitat which may reduce mortality by predation and/or cannibalism. Knowledge on habitat preference is useful for fishery management and also for assessing the different habitats in a potential stock enhancement program of southern king crab.

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1. Introduction

In many marine decapod crustaceans the transition from planktonic larvae to benthic juveniles plays a key role during recruitment. This transition involves many factors (e.g. current, tide, salinity, temperature, settling behavior, cannibalism, predation, or competition) (Fernández et al., 1993; Forward, 1990; Hasek and Rabalais, 2001; Heck et al., 2001; Moksnes et al., 2003; Phillips et al., 1991; Stevens, 2003; Sulkin and Epifanio, 1984; Van Montfrans et al., 2003) which may affect the recruitment success and reduce significantly the number of individuals surviving to adulthood (Rabalais et al., 1995; Wahle, 2003; Wahle and Steneck, 1991). This demographic bottleneck effect is of special relevance for management in species of fishery and aquaculture interest (Rabalais et al., 1995; Wahle and Steneck, 1991). For example, the density estimation of young juvenile lobsters is a good indicator of interannual variations in settlement and is a good proxy of future harvests (Incze et al., 2003).

Settlement behavior is one of the most important factors affecting recruitment since it involves the selection of an adequate substrate that provides shelter and food during the critical early juvenile stages.

Several studies have demonstrated that megalopae actively select substrate to settle before they metamorphose to the first juvenile crab (Stevens, 2003; Van Montfrans et al., 2003; Wahle and Steneck, 1992). Such selection can be made on the basis of adult conspecific presence (e.g. *Petrolisthes cinctipes* (Randall, 1839); Jensen, 1991, *Petrolisthes laevigatus* (Guérin, 1835); Gebauer et al., 2011 and *Uca pugilator* (Bosc, 1802); O'Connor, 1993), or in response of chemical cues which orientate megalopae towards nursery areas (e.g. *Callinectes sapidus* Rathbun, 1896; Forward et al., 2003). Also, many studies suggest that megalopae do such selection on the basis of settlement habitat complexity. For example, the fourth larval stage of the American lobster *Homarus americanus* Milne Edwards, 1937 selects rapidly sheltered habitat such as macroalgal-covered rocks, and delays settlement when sand substrate are offered (Botero and Atema, 1982). Megalopae of the intertidal Dungeness crab *Cancer magister* Dana, 1852 settle near shore and select shell habitat over mud (Fernández et al., 1993). Particularly, megalopae of the red and blue king crabs (*Paralithodes camtschaticus* (Tilesius, 1815) and *Paralithodes platypus* Brandt, 1850) actively select complex natural substrata (Stevens, 2003; Stevens and Kittaka, 1998; Stevens and Swiney, 2005; Tapella et al., 2009).

The southern king crab (SKC) *Lithodes santolla* Molina (1782) is the most valuable commercial species among the lithodids that

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inhabits the Sub-Antarctic waters of South America. Distribution of SKC is associated with cold-temperate water, between 4 °C and 12 °C, and commonly occurs at shallow waters south to 41°S. Off the Pacific coast, *L. santolla* is distributed south from Chiloé Island (42°S 74°W) to the Cape Horn (55°S 67°W) including the Straits of Magellan (53°S 70°W) and fjords around Tierra del Fuego (Macpherson, 1988). In the Atlantic waters *L. santolla* has a disjoint distribution: mainly in the Golfo San Jorge (46°S 66°W) and the Beagle Channel (54°S 67°W) (Boschi et al., 1992; Lovrich et al., 2002; Retamal, 2000). The SKC fishery around Tierra del Fuego began during 1920s and 1930s in Chilean and Argentinean waters, respectively (Guzmán et al., 2004; Vinuesa, 1991). Maximum yields of the Chilean fisheries were at least one order of magnitude higher than in Argentina: annual landings peaked at 320 t in the Argentinean Beagle Channel and 2756 t in the Chilean fisheries. After a constant reduction in landings from the Beagle Channel, in 1994 the fishery for *L. santolla* was closed due to overfishing (Lovrich, 1997). The decreasing yields of *L. santolla* in both Argentina and Chile also encouraged retaining the sympatric less valuable species, the stone or false southern king crab *Paralomis granulosa* Jacquinot, 1847, which had been considered a bycatch species at early stages of the fishery. Currently, though *P. granulosa* is the main target of the fishery, the catch pressure on the SKC *L. santolla* remains high because of its elevated commercial value in the local and international markets.

L. santolla has an annual reproductive cycle. In late November–early December and immediately after females molt, mating occurs, oocytes are fertilized and eggs develop for approximately 9–10 months before hatching (Lovrich and Vinuesa, 1999; Vinuesa, 1991). Larval hatching extends for 4–6 weeks (Thatje et al., 2003) and larval development is completely nonfeeding (endotrophic) (Lovrich et al., 2003) from hatching to metamorphosis (3 zoea stages followed by a megalopa) (Campodonico, 1971; McLaughlin et al., 2001). Southern king crab larvae are absent from plankton samples (Lovrich, 1999) and in laboratory larval rearing they remain associated with the aquarium bottom (Anger et al., 2004; Calcagno et al., 2004; Vinuesa et al., 1985), suggesting that they have a strong epibenthic habit. There are few studies dealing with distribution of early stages of *L. santolla* and all revealed that they are associated with 3-dimensional habitats, such as the holdfast of the kelp *Macrocystis pyrifera* (L.) C. Agardh, 1820 (Brusca et al., 2000; Cárdenas et al., 2007). Juveniles of 1.5–13.5 mm carapace length (CL) occur at <40 m depth and settle in passive collectors that were also colonized by sea urchins, polychaetes and ophiurids (Tapella and Lovrich, 2006).

Despite the commercial importance of SKC *L. santolla* in the southern South America, little is known about the settlement habitat and behavior of their larvae. Thus, the aims of this study, as a part of a stock enhancement program, were to determine whether SKC larvae (zoea and megalopa stages) exhibit a preference for any of four natural substrata with different complexity level, which are commonly found in the distribution depth range of early stages (Brambatti et al., 1991; Colizza, 1991; Pineda et al., 2002). Two additional experiments were done with megalopae to test whether substrate selection was affected by their density or the schedule (day and night) at which the trials started.

2. Materials and methods

2.1. Animals captured and maintenance

During August 2006, 25 SKC ovigerous females were caught with commercial traps in the Beagle Channel at the proximity of Ushuaia city (54°S 67°W) and were taken to the wet laboratory of the Centro Austral de Investigaciones Científicas (CADIC). Throughout the two-month-hatching period, females were maintained in an increasing temperature regime from 7 to 10 °C, in individual 20-L containers which were set up in a recycling 3000-L seawater system. Water quality was maintained with mechanic (20 μm) and biological filters, and UV-sterilizer. Nitrogen wastes were measured twice a week and ammonia (NH_3/NH_4^+), nitrite (NO^{-2}) and nitrate (NO^{-3}) levels were kept under 0.25, 0.8 and 12.5 mg·l^{-1}, respectively by the replacement of ~1000 l of seawater (commonly every ~10 days). Females were fed ad libitum twice a week with squid (*Illex* spp.) and the leftovers were removed the following day.

2.2. Larval cultivation

During the peak of the hatching period (*ca.* 400–1800 larvae·day^{-1}; Tapella, unpublished results), stage 1 zoeae (Z1) were collected by siphoning with a tube of 10 mm diameter, thus avoiding larval damage. Massive larval cultivation allowed us to obtain a large number of stage zoeae 2 and 3 (Z2 and Z3) and megalopae for substrate preference experiments. Larval cultures were performed in a cold room at 7.1 ± 0.5 °C with 12:12 h dim uniform light (0.5 lx) and dark photoperiod. Larvae were reared at a density of 30 individuals·l^{-1} in round containers of 11.5 l (24×25.5 cm of diameter and height, respectively). Containers were filled with 10 l of seawater previously filtered to 5 μm and UV-sterilized and aerated continuously to maintain oxygen at saturation levels and keep larvae suspended in the water column. Water was changed three times per week (Monday, Wednesday and Friday) and larvae were not fed since they are lecitotrophic (Lovrich et al., 2003). Dead larvae were removed every time that water was changed, and close to each molting stage periods daily observations were made to determine the occurrence of different larval stages. Substrate selection experiments were performed with freshly hatched Z1, with Z2 and Z3 that molted in the previous 24 h, and with megalopae that molted 96 h before the start of the trials.

2.3. Zoea and megalopa substrate preference

In order to determine natural substrate that SKC zoea and megalopa stages prefer to settle and whether they redistribute among substrata over time, two experiments of 24 h and 4 week duration were performed for each zoea stage (Z1, Z2 and Z3) and megalopa, respectively. Experiments were conducted in 6 L-round containers (22×16 cm of diameter and height, respectively) with their bottoms divided in four equal portions by a cross-shaped white plastic sheet of 5 cm height. Each section of the container was filled with one of the following natural substrata: 150 cm^3 of beach sand (<0.1 cm), 220 g of gravel (0.1–0.34 cm), 250 g of cobble (0.96–1.9 cm), and 110 g of broken shells of 0.34–0.96 cm length of several bivalves as mussels *Mytilus chilensis* (Hupé, 1854), *Perumytilus purpuratus* (Lamarck, 1797) and *Aulacomya atra* (Molina, 1782) and clams *Eurhomalea exalbida* (Chemnitz 1795) and *Tawera gayi* (Hupé, 1854). Particle size for each experimental substrate was controlled by sieving. Before setting up the substrata into round containers, they were rinsed three times with fresh water to remove naturally occurring organisms and dried at 50 °C. Substrata were randomly sorted in each portion of the round container to avoid location effect. The surface of each substrate was *ca.* 3–4 cm below the upper lip of the white plastic divider. This design allowed larvae to settle in any substrate and change among them only by an actively swimming over dividers. Experiments utilized a total of 40 round containers (4 for each zoea stages and 28 for megalopa) filled with 5 l of filtered (5 μm) and UV-sterilized seawater. Containers were randomly distributed in a single rack inside the cold room where larvae were cultured. During the course of experiments, all containers were covered with a white plastic sheet in order to avoid any possible external perturbation.

Experiments began with the release of 36 larvae belonging to the corresponding stage in the center of each container at water surface by means of a pipette. During the course of the experiments four replicate containers of each larval stage were analyzed by removing them from the experiments after periods of 24 h, 2, 4, 7, 14, 21 and

28 days (treatments), respectively. Thus, at 24 h period a total of 16 containers were removed (4 of each larval stage), whereas during the rest of the experiment 4 containers with megalopae were analyzed at each date.

In order to determine whether phototaxis or any possible external perturbation but not substrate may affect larval location or settlement behavior, control round containers were set up for all zoea and megalopa stages. Sixteen containers (4 for each zoea stage and megalopae) were arranged under same experimental conditions but without substrata. Thus, during the course of the experiment 4 control containers of each larval stage were removed and analyzed after periods of 24 h and 4 days for zoea stages and megalopae, respectively.

On each treatment date, swimming larvae were counted in each container immediately after removing the white plastic cover. Then water was siphoned down to the divider edge, and live and dead specimens were recorded in each substrate. Individuals that occurred on dividers or container walls were recorder as being on "other" substrata. Water in experimental containers was changed once a week by siphoning down to 1 cm above the divider edge and refilling to 5-L with filtered and UV-sterilized seawater. To minimize the disturbance, water change was performed 6 days before larvae were removed and only in those containers that belonged to 14, 21 and 28 day treatment periods. Finally, proportions of Z1, Z2, Z3 and megalopae stages either swimming or settled on each substrata and portion (for experimental and control containers, respectively) were calculated on the basis of total animals alive in each round container.

2.4. Effect of megalopa density on substrate preference

In order to determine the effect of megalopa abundance on natural substrate selection, a 4-day experiment was designed. A total of 16 round containers were used, with 4 densities (18, 36, 72 and 144 megalopae·container^{-1}) replicated 4 times each. All container bottoms were divided in 4 portions and filled with the same substrata previously described. Containers were filled with seawater and megalopae released in the center of each container by pipetting. After 4 days, proportions of megalopae on each substrate and swimming individuals were calculated in the same way as in the previous experiment. Data used for the density of 36 megalopae·container^{-1} were those obtained at 4 day period from the previously described experiment.

2.5. Effect of diurnal and nocturnal periods on megalopa substrate selection

To determine whether megalopa selection occurs during day or night periods, two experiments of 8 h duration each were performed under light and darkness conditions, respectively. Each experiment was conducted in 12 experimental round containers which were prepared identically as those used for the previous experiments and kept in the cold room. Experiments started when releasing with a pippette 36 megalopae in the center of each container at 10:00 h and 22:00 h for diurnal and nocturnal conditions, respectively. Therefore, the schedule of the experiment intended not to influence the circadian rhythm of megalopae. Containers were removed by 4 (replicates) at 2, 4 and 8 h periods after larval release and the proportion of megalopae either swimming or settled on each substrate were calculated as in previously described experiments.

2.6. Data analysis

Proportions of larvae on natural substrata, swimming and settled on "other" substrate are presented as means ± standard errors (SE). Categories of swimming and settled on "other" substrate were excluded from the statistic analysis since they produced statistical differences without a biological meaning. However, they were used as

qualitative variables and are presented in all figures. Similarly, every time that larval proportion on a specific substrate was zero in all replicates, statistic analyses were performed excluding these data since there was no SE to calculate.

Data were arcsine-transformed and assessed for normality and homogeneity of variances by Kolmogorov–Smirnov and Cochran tests, respectively (Sokal and Rohlf, 1995). Analyses of variance (one-way ANOVAs) were performed to determine natural mortality among larval stages and over time, the preference of larvae for the different natural substrata and the effect of megalopa density and, nocturnal and diurnal period conditions on such preference. All analyses were performed separately for each sampling period and larval density. Significant differences ($P<0.05$) were compared using Tukey post-hoc test (Sokal and Rohlf, 1995).

3. Results

Natural mortality of SKC larvae during the course of experiments was low and similar between larval stages and sampling periods. At 24 h sampling period, mortality was statistically similar (ANOVA, $F=0.444$, $P=0.726$) among Z1, Z2, Z3 and megalopa stages, and it was in average $4.86 \pm 3.99\%$. Likewise, non statistical differences were observed in the proportion of dead megalopae among sampling periods of 4 week experiment (ANOVA, $F=1.209$, $P=0.340$) or density treatments (ANOVA, $F=1.953$, $P=0.175$). On average, megalopa mortality was $1.49 \pm 2.33\%$ and $1.39 \pm 1.88\%$ in the 4 week and density experiments, respectively. Since the number of dead larvae in all larval stages was low and constant over time, we assumed that habitat selection experiments were not affected by natural mortality. Moreover, control treatments showed that larval locations among the four separated portions were not affected by light or any external perturbation factors. During all larval stages, proportions of individuals in the four portions without substrata were statistically similar (Table 1), and swimming animals and larvae settled on "other" substrate were scarce and only present in some larval stages. Larvae settled on "other" substrate were present in all but Z3 stage at 2.1–4.9%, whereas swimming larvae were only found in Z2 and Z3 stages at 1.4% and 10.4%, respectively.

3.1. Zoea and megalopa substrata preference

Southern king crab larvae selected and settled on natural substrata immediately (within 24 h) after being placed into the experimental containers. During the course of substrate selection experiments, the proportions of swimming and settled larvae on "other" substrate were low. Particularly, swimming larvae were only found at 24 h in Z2 and megalopa experiments in a proportion of $4.48 \pm 5.27\%$ and $0.71 \pm 1.43\%$, respectively (Figs. 1 and 2). Likewise, larvae settled on "other" substrata occurred at 0.69–3.38% in Z2 and Z3 trials and in all megalopa sampling periods (except in 21 days) (Figs. 1 and 2).

Table 1

Lithodes santolla. Results of one-way analyses of variance (ANOVAs) conducted to test the effect of any possible disturbance on the proportions of settled southern king crab zoea and megalopa stages at 24 h and 4 days, respectively in containers without natural bottom. References: *F*, F-statistic; df, degree of freedom and MS, mean square. For details on controls treatments see Materials and methods.

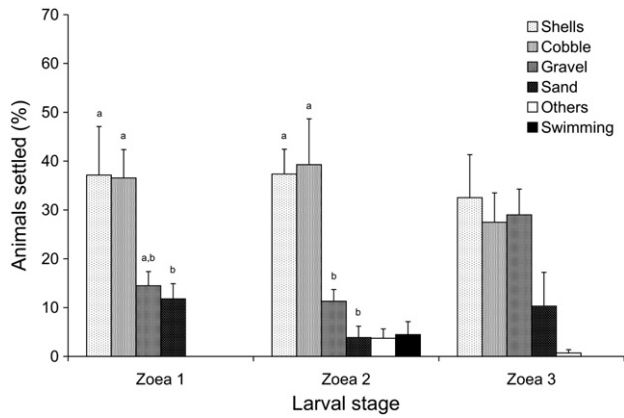| Stage	Source	df	MS	F	P
Zoea 1	*24 h*	3	67.41	0.599	0.628
	Error	12	112.52		
Zoea 2	*24 h*	3	91.45	3.224	0.061
	Error	12	28.36		
Zoea 3	*24 h*	3	23.96	0.431	0.735
	Error	12	55.60		
Megalopa	*4 days*	3	24.25	1.046	0.408
	Error	12	23.19		

Fig. 1. *Lithodes santolla*. Proportions of southern king crab zoea stages on natural substrata after 24 h of being released into the experimental containers. Vertical lines are standard errors and different letters above bars indicate significant differences at $P<0.05$. Note that swimming individuals and larvae settled on "other" substrate were excluded from the statistic analyses. For details on substrata see Materials and methods.

Although slight differences were observed between zoea stages and megalopae, our experiments showed that all larval stages preferred complex substrata such as broken shell, cobble and gravel instead of sand (Figs. 1 and 2). During all but early Z3 stages, larvae settled differentially on natural substrata (Table 2). In Z1 and Z2 experiments, the proportion of larvae on broken shell and cobble were higher than those observed on gravel and sand (Fig. 1). Particularly in Z3 proportions of larvae were statistically similar in the four substrata (Table 2), although larvae occurred less frequently in sand (Fig. 1). In contrast to zoea stages, megalopae were virtually absent on sand during all but at days 7 and 28, when they occurred at 0.71% and 3.72%, respectively (Fig. 2). Although there were general non statistic differences on the proportion of megalopae on complex substrata, broken shell was the most selected substrate compared to cobble and gravel (Table 2, Fig. 2). According to the proportion of megalopae on cobble and gravel, both substrata were equally selected during all observation periods (Table 2, Fig. 2).

3.2. Effect of megalopa density on substrate preference

The substrate preference of *L. santolla* megalopae was affected by larval density since a relocation of larvae among substrata was observed
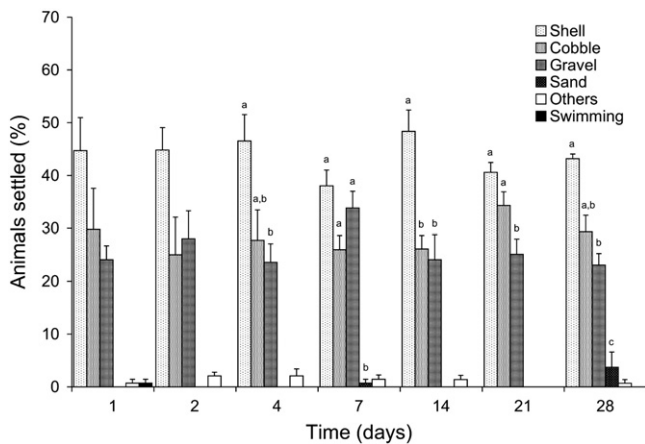

Fig. 2. *Lithodes santolla*. Proportion of southern king crab megalopae on natural substrata at different time-periods after being released into the experimental containers. Vertical lines are standard errors and different letters above bars indicate significant differences at $P<0.05$. Note that swimming and settled larvae on "other" substrate were excluded from the statistic analyses. For details on substrata and sampling periods see Materials and methods.

Table 2

Lithodes santolla. Results of one-way analyses of variance (ANOVAs) conducted to test the preference of southern king crab larval stages for natural substrata at different time-periods. References: F, F-statistic; df, degree of freedom and MS, mean square. For details on treatments see Materials and methods.

Stage	Source	df	MS	F	P
Zoea 1	*24 h*	3	358.39	5.250	0.015
	Error	12	68.27		
Zoea 2	*24 h*	3	869.68	12.323	0.001
	Error	12	70.58		
Zoea 3	*24 h*	3	382.34	3.180	0.063
	Error	12	120.23		
Megalopa	*24 h*	2	175.02	2.865	0.109
	Error	9	61.09		
	2 days	2	187.37	3.097	0.095
	Error	9	60.49		
	4 days	2	223.56	6.403	0.019
	Error	9	34.91		
	7 days	3	1079.90	68.476	<0.001
	Error	12	15.77		
	14 days	2	271.93	10.343	0.005
	Error	9	26.29		
	21 days	2	93.59	9.301	0.006
	Error	9	10.06		
	28 days	3	816.96	27.100	<0.001
	Error	12	30.15		

according to the increase of density. At all densities, megalopae located differentially on natural substrata (Table 3). Proportion of megalopae on broken shell was significantly higher than those on cobble, gravel and sand (Fig. 3). The latter substrate was mostly rejected and megalopae only occurred on sand at low proportions in the two higher densities (Fig. 3) where swimming larvae were also found at *ca.* 2–4%. At the lowest density, broken shell was significantly preferred over cobble and in turn cobble was significantly preferred over gravel (Table 3), this being the less preferred substrate before sand, which was virtually rejected (Fig. 3). In contrast, at the highest density this pattern changed and gravel and broken shell were significantly preferred over cobble and sand (Fig. 3).

3.3. Effect of diurnal and nocturnal periods on megalopae substrata preference

Substrate selection of *L. santolla* megalopae was not affected by the time (diurnal or nocturnal) at which the experiment started. During the course of both light and dark experiments, proportions of megalopae were significantly different among substrata at all observation periods (Table 4 and Fig. 4). However, even though substrate selection was not affected by the light condition, results suggest that selection of complex substrata was slightly more evident under light than in darkness. Under light, broken shell cobble and gravel were always significantly preferred over sand (Fig. 4). In contrast, in darkness sand substrate was equally preferred to at least one of the complex substrata in all periods (Fig. 4).

Table 3

Lithodes santolla. Results of one-way analyses of variance (ANOVAs) conducted to test the effect of larval density on the preference of different natural substrata during megalopa stage. References: F, F-statistic; df, degree of freedom and MS, mean square. For details on treatments see Materials and methods.

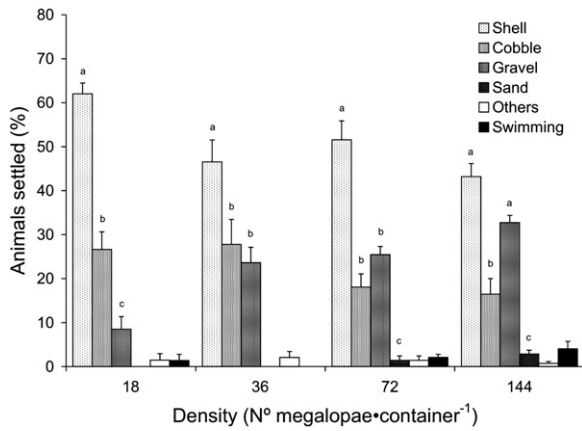| Source	df	MS	F	P
18 larvae·container^{-1}	2	1394.00	31.562	<0.001
Error	9	44.16		
36 larvae·container^{-1}	2	223.56	6.403	0.019
Error	9	34.91		
72 larvae·container^{-1}	3	1159.50	53.556	<0.001
Error	12	21.65		
144 larvae·container^{-1}	3	782.40	51.970	<0.001
Error	12	15.05		

Fig. 3. *Lithodes santolla*. Proportion of southern king crab megalopae on natural substrata at different densities after 4 days of being released into the experimental containers. Vertical lines are standard errors and different letters above bars indicate significant differences at *P*<0.05. Note that swimming and settled larvae on "other" substrate were excluded from the statistic analyses. For details on substrates and sampling periods see Materials and methods.

Fig. 4. *Lithodes santolla*. Proportion of southern king crab megalopae on natural substrata under diurnal and nocturnal conditions at three different time-periods after being released into the experimental containers. Vertical lines are standard errors and different letters above bars indicate significant differences at *P*<0.05 within each sampling and light condition group. Note that swimming and settled larvae on "other" substrate were excluded from the statistic analyses. For details on substrata, light conditions and sampling periods see Materials and methods.

4. Discussion

Experiments conducted in this study showed that all larval stages of the southern king crab *L. santolla* select natural substrata on the basis of their complexity. Our results suggest that both zoea and megalopa stages prefer substrata with a high number of interstitial spaces such as broken shell, cobble and gravel, instead of flat and open substrata such as sand. Selection of complex substrata may provide a cryptic habitat to larvae and first juveniles, and reduces predation and/or cannibalistic interactions during the early life and critical stages (e.g. Moksnes et al., 1998; Stevens and Swiney, 2005). This selection pattern has also been reported for the red and blue king crab *P. camtschaticus* and *P. platypus*, respectively. In these species zoeae are typically planktonic, and megalopae and first juveniles exhibit a strong association with complex substrata. Megalopae of *P. camtschaticus* select either artificial (mesh) (Stevens and Kittaka, 1998) or biological substrata as hydroids and red algae (Stevens, 2003), where larvae are able to grip and hide among small interstitial spaces. Likewise, megalopae and juveniles of *P. platypus* prefer shell, cobble, or gravel substrata (Tapella et al., 2009) covered with diatoms, bryozoans and algae (Armstrong et al., 1985), and avoid sandy habitats (Tapella et al., 2009).

The preference of megalopae for natural complex substrata such as broken shell gravel and cobble during the 4 weeks of the experiment (Fig. 2), supports the hypothesis that in channels and fjords of southern South America the recruitment to the early juvenile phase (2.5 mm CL) occurs at shallow waters. The morphological and sedimentological surveys performed in the Beagle Channel, Magellan Strait and surrounding fjords suggest that bottom complexity decreases as depth increases. Mud and sandy-mud sediments are usually found at greater depths (>60–70 m), whereas bottoms dominated by sandy-
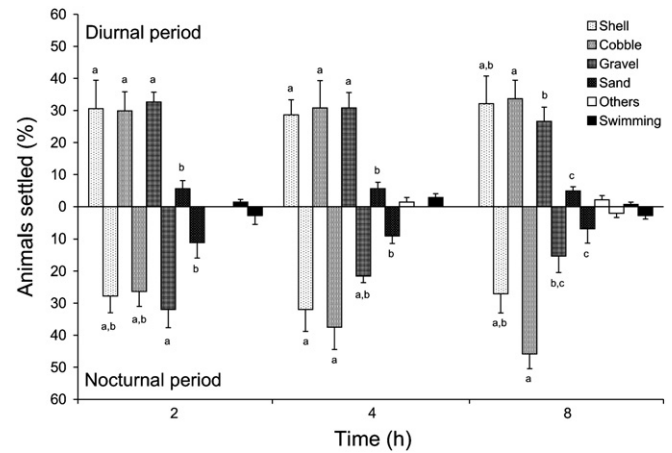
Table 4

Lithodes santolla. Results of one-way analyses of variance (ANOVAs) conducted to test the effect of diurnal and nocturnal periods on the selection of natural substrata of megalopa stage. References: *F*, F-statistic; df, degree of freedom and MS, mean square. For details on treatments see Materials and methods.

Source	df	Diurnal			Nocturnal		
		MS	F	P	MS	F	P
2 h period	3	490.06	7.383	0.005	210.19	3.717	0.042
Error	12	66.37			56.76		
4 h period	3	445.29	7.107	0.005	326.94	7.036	0.005
Error	12	62.66			46.47		
8 h period	3	448.99	8.212	0.003	667.19	9.250	0.002
Error	12	54.68			72.13		

rock and gravel with shell debris are more frequent in shallow waters (<40 m) (Brambatti et al., 1991; Colizza, 1991; Pineda et al., 2002). In the Beagle Channel, SKC juveniles of an average size of *ca.* 6 mm CL occur in passive collectors located at depths of 10 to 40 m and next to *M. pyrifera* kelp forests (Tapella and Lovrich, 2006). Particularly in the Magellan strait, pod aggregations of advanced SKC juvenile stages (ranging in size from 34 to 75 mm CL) have been found at shallow waters in the holdfasts and stipes/sporophylls of *M. pyrifera* which were distributed in a sandy–rocky embayment at <5 m depth (Cárdenas et al., 2007).

Our unexpected finding of zoeae selecting complex substrate as early as in the first stage right after hatching is the first experimental evidence supporting the hypothesis of benthic and cryptic habitat of *L. santolla* larvae (Lovrich, 1999; Vinuesa et al., 1985). The only few decapod species that have benthic zoea stages are freshwater shrimps, which also have short larval development and non-feeding larvae, e.g. *Macrobrachium nattereri* (Heller, 1862), *Macrobrachium ferreirai* Kensley and Walker, 1982, *Pseudopalaemon chryseus* Kensley and Walker, 1982, and *Palaemonetes ivonicus* Holthuis, 1950 (Magalhães and Walker, 1988). All larval stages of *L. santolla* are lecithotrophic and can complete their development without ingestion of external food (Lovrich et al., 2003). Other lithodids that have lecithotrophic larval development as *Lithodes aequispinus* Benedict, 1895, *Lithodes maja* (Linnaeus, 1758), and *P. granulosa* were also reported to be associated to the bottom in experimental trials (Anger, 1996; Calcagno et al., 2004; Shirley and Zhou, 1997). Although lecithotrophy in lithodids is considered as a main adaptation to the deep ocean realm where the food source is unpredictable (Hall and Thatje, 2009), it may confer an extra advantage since larvae save energy by avoiding to actively swim in order to remain in the water column for feeding. In SKC, larval survival cultured in darkness is higher compared to that under a photoperiod regime, since larval swimming towards a light source implies an extra use of energy reserves (yolk) (Paschke et al., 2006). Consequently, the faster zoeae select substrata for hiding and protecting from predators, therefore avoiding the excessive consumption of energetic reserves when swimming, the higher their probability to survive to the juvenile phase will be.

Additional evidence that supports the strong relationship of *L. santolla* larvae with the benthic habitat was the ability of megalopae to quickly select natural complex substrata during either diurnal or nocturnal periods. Our data show that megalopae were able to select complex substrata within 2 h after being released into containers either during darkness

or light periods (Fig. 4), suggesting that in nature habitat selection behavior of SKC larvae is a continuous process which does not depend on daylight. This may be relevant for the success of megalopa recruitment since it allows larvae to hide and protect in sheltered substrata as soon as they find a suitable habitat regardless of light conditions. Moreover, our findings of zoeae selecting complex substrata rather than sand within 24 h, along with the their benthic habits and the reported positive geotaxis of megalopae (Paschke et al., 2006) allow us to speculate that zoeae could also select appropriate substrata under darkness, as it occurs in the megalopae. Thus, since SKC hatching occurs during night (Thatje et al., 2003), the ability of Z1 to select complex substrata right after hatching would be important to avoid demersal predators (e.g. Vanella et al., 2007). In *P. camtschaticus*, planktonic zoeae ascend in the water column during daylight for feeding and descend during the night (Shirley and Shirley, 1988, 1989) as a behavior to avoid nocturnal predators (Stevens and Kittaka, 1998). Therefore, we hypothesize that the main strategy for predator avoidance in *L. santolla* larvae is choosing an adequate sheltered substrate for protection.

The present study suggests that habitat selection of *L. santolla* megalopae is a density-dependent process, and in nature mussel beds and/or shell fragments would be the most suitable nursery habitats. Nevertheless, other complex habitats such as rocky-gravel bottoms may also play an important role in settlement, especially when the shelly habitats become saturated because of high larval arrival. Mussel beds may be advantageous over rocky-gravel bottoms since the organic matter associated to bivalves, which accumulates in the interstices between their bodies (Jones et al., 1994; Ragnarsson and Raffaelli, 1999), may also provide a food source to the first juvenile stages. We hypothesize that if this type of habitat is detected early during the larval development – rather for its protective conditions since larvae do not ingest food – animals could remain until their metamorphosis to the first crab stage, when they start feeding (Anger et al., 2004). Our results show that broken shell is the most preferred substrate, and megalopae do not relocate between substrata at least during the 28 day experiment (Fig. 2) when swimming behavior is more frequent (Gonor and Gonor, 1973; Sotelano et al., in press; Stevens and Swiney, 2005). Likewise, preference for broken shell and avoidance of sand is even evident at the lowest megalopa density (Fig. 3). As density increases larvae relocate among substrata, suggesting that the interference competition for space in the nursery habitat may result in density-dependent movements of megalopae outside the most preferred habitat. Density-dependent emigration from nursery habitats has been described as a common and important behavior that regulates recruitment (Moksnes, 2004 and references therein). For example, an increment in the natural density of juvenile *Carcinus maenas* crabs results in a higher emigration from mussel substrate, which is the most preferred habitat (Moksnes, 2004).

The larval choice for adequate bottoms that provide shelter will also be an adaptive behavior to reduce mortality by cannibalism inflicted by older conspecifics, either crabs in the first juvenile stages recently settled or older juveniles (Sotelano et al., in press). Although intra-specific predation in decapods has been described as a common behavior among early stages (Daly et al., 2009; Luppi et al., 2001; Stevens and Swiney, 2005), it seems to be of particular importance for recruitment to the adulthood phase in *L. santolla* for several reasons. Laboratory experiments conducted during the intermolt period of early *L. santolla* stages have shown high levels of cannibalism, e.g., a single young-of-the-year crab can consume 5 conspecific larvae in less than 4 days (Sotelano et al., in press). Different to other king crab species (*P. camtschaticus* and *P. platypus*) whose zoea and megalopa stages are planktonic or demersal/benthic, all larval stages of *L. santolla* are benthic. Due to both the extended hatching period of SKC, (longer than the reported 6 weeks; Thatje et al., 2003; Tapella, unpublished results) and the 60-day duration of larval development (Calcagno et al., 2004; Tapella, unpublished results), larvae and juveniles of

the same cohort likely share the same habitat and cannibalism can occur (Sotelano et al., in press). Therefore, the selection of shelter performed by zoeae as soon as hatching occurs may play an important role to avoid potential cannibals.

Since all *L. santolla* larval stages prefer complex substrata, we hypothesize that ovigerous females may play a key role in the dispersion and habitat localization for larval recruitment. Dispersion of different deep-sea lithodids of the genus *Lithodes* and *Paralomis* with lecithotrophic larvae has been attributed to adult migrations rather than to currents (Thatje et al., 2005). Planktonic larval transportation to the recruitment areas depends on the combination of larval behavior (time of occurrence and depth distribution) and current intensity, which is significantly lower at the bottom layer by friction (Queiroga and Blanton, 2005 and references therein). During the course of the present study, swimming larvae were exceptional in all trials, even in the control containers devoid of substrate and in the density experiment. At high densities, megalopae were expected to be actively swimming due to the lack of shelters or competition for vacant spaces. Hence, since swimming behavior of *L. santolla* larvae is limited and currents are weak at the bottom, it is unlikely that at mid to large geographical scales (>100s meters) they can localize by their own the appropriate recruitment areas. In contrast, adult SKC females perform vertical migrations associated with the reproductive cycle (Hernández, 1985). During the first part of austral spring (September–October) just before larval hatching occurs (Lovrich and Vinuesa, 1999; Vinuesa, 1991) females migrate to shallow waters where complex substrata are more widespread, and they return to deeper waters in December–January after mating (Hernández, 1985). Ovigerous females of other decapods aggregate in particular bottom types and this was described as a behavior for larval dispersal, among several other factors (e.g. Aguilar et al., 2005; Campbell, 1990; Carr et al., 2004; Darnell et al., 2010; Hill, 1994). Therefore, the larval substrate selection presented in this work seems to be the end of a complex habitat selection behavior that probably begins with the migration of ovigerous females to locate a suitable habitat before hatching.

Our experimental results presented herein can help to orientate the search for the early stages of lithodid species in the field. Several studies that used conventional sampling devices such as nets or trawls failed in finding larvae or first juvenile stages as occurred with *L. santolla* (e.g. Lovrich, 1999). With the knowledge on substrate preference and the use of the adequate sampling gear as e.g. airlift samplers (Loher and Armstrong, 2000), future studies should evaluate the distribution of *L. santolla* early stages and their natural mortality. Thus, a restocking program (provisioning the natural habitats with a massive number of early juvenile stages) would be a feasible initiative in order to improve the population numbers of overfished populations.

Acknowledgments

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