



Cannibalism during intermolt period in early stages of the Southern King Crab *Lithodes santolla* (Molina 1872): Effect of stage and predator–prey proportions

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ABSTRACT

The anomuran crab *Lithodes santolla* represents an important fishery resource in the southernmost part of the American continent, where populations are endangered by overexploitation. During first attempts of rearing, intraspecific predation was observed in early stages of *L. santolla* and may stand as a main source of mortality in cultures. Cannibalism (defined as the sum of injured and dead crabs) between larvae and juveniles of *L. santolla* was tested in five Predator–prey (P–p) stage combinations and three P–p proportions during the intermolt period. Intra-stage predation in Megalopae (M), crab stage 1 (C1) and crab stage 2 (C2) was similar between stages (~15%) and lower than inter-stage cannibalism. Difference in size of conspecifics was the main cause of cannibalism. Total consumption of prey after 3–5 days was observed when 1-year-old crabs (C_{1yo}) encountered either zoeae 1 (Z1), M or C1. Cannibalism in the combination C2–C1 occurred immediately after experiments began. Contrastingly, in the combination C1–M cannibalism started after day 9 of the experiment, suggesting that the swimming ability of M is a key factor for predator avoidance. At the end of intermolt period cannibalism was higher in C2–C1 than in C1–M stage combination and reached 75% and 60% respectively. Directionality of attacks among crabs showed that bigger animals can cause severe damage to smaller ones and not vice versa. Injured predators were only observed in C1–M stage combination and are likely the result of intra-stage cannibalism among C1 when M remain unreachable. P–p proportions had an impact on cannibalism since the more unequal the P–p proportions, the higher the cannibalism in both C1–M and C2–C1 stage combinations. Differential limb loss occurred in *L. santolla* since walking legs appeared more vulnerable than chelipeds. Although *L. santolla* showed high predation among conspecifics, cannibalism in early juvenile stages under natural conditions should be lower than in the present study, as density of cultures was high (~950 ind m⁻²) and our experimental design provides no refuge/shelter to animals. Hence, the future challenge for massive culturing crabs will be the mitigation of cannibalism.

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1. Introduction

King Crabs (Crustacea: Decapoda: Anomura) are typical inhabitants of cold water regions (Zaklan, 2002). In coastal waters and continental shelves they represent a valuable resource in both hemispheres and are commercially harvested around the world. In particular, the Southern King Crab, *Lithodes santolla* is one of the commercially most important species in southern South America. Its fishery began during the 1920s and 1930s in Chilean and Argentinean waters, respectively (Guzmán et al., 2004; Vinuesa, 1991). After experimenting one of its maximum yields in 1983, *L. santolla* landings declined constantly through the years, particularly in the Beagle Channel, located at the southern tip of Argentina. Consequently, the fishery was declared as collapsed in 1994 and some areas were banned from fishing (Lovrich, 1997). Despite of the implementation of a number of management

rules to protect the Southern King Crab fishery, there have not been reliable evidences of *L. santolla* population recovery (Iorio et al., 2008; Lovrich and Tapella, in press).

The collapse of certain crab fisheries, as for example that for the Red King Crab *Paralithodes camtschaticus* in Alaska or the reduction of yields in the Blue Crab *Callinectes sapidus* in the NW Atlantic, has stimulated the research on stock enhancement (Bell et al., 2005, 2008; Davis et al., 2004a, 2005; Stevens, 2006). Such initiatives have concentrated on the massive production of juveniles for restocking the natural populations. Most of the research has focused on early stages of commercially important decapods by investigating culturing (Daly et al., 2009; Zmora et al., 2005), tagging (Davis et al., 2004b), substrate preference (Tapella et al., 2009), cannibalism (Borisov et al., 2007; Marshall et al., 2005) and predation (Luppi et al., 2001; Ochwada-Doyle et al., 2010), as the knowledge needed to design enhancement strategies for depressed populations.

Cannibalism, especially at megalopa and juvenile stages, is one of the main reasons for failures in the development of culturing methods for a variety of crab species (Ventura et al., 2008; Zmora et al., 2005).

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This intraspecific predation represents an important source of mortality in decapod crustaceans such as *Macrobrachium rosenbergii*, *Homarus americanus*, *Cancer magister*, *Chionoecetes opilio*, *Cancer pagurus*, *Porcellana platycheles* and *Paralithodes camtschaticus* (Amaral et al., 2009; Daly et al., 2009; Fernandez, 1999; Lovrich and Sainte-Marie, 1997; Mortensen and Damsgard, 1995; Nair et al., 1999; Sainte-Marie and Lafrance, 2002; Sastry and Zeitlin-Hale, 1977; Wahle, 2003). Many studies suggest that recently post-molted animals are especially vulnerable to predation and/or cannibalism and that the probability of mortality increases during the ecdysis (Daly et al., 2009; Kovatcheva et al., 2006; Marshall et al., 2005; Nair et al., 1999; Ryer et al., 1997). Yet, only few studies specifically addressed cannibalism during the intermolt period of early stages of development. (Sainte-Marie and Lafrance, 2002; Stevens and Swiney, 2005).

Southern King Crab *L. santolla* has an annual reproductive cycle and larval hatching occurs each September–October (Boschi et al., 1984; Vinuesa, 1984). Larvae pass through four larval stages (three zoeae and one megalopa) before attaining the first juvenile instar (Campodonico, 1971; McLaughlin et al., 2001). Due to the extended hatching period (i.e. a female takes 35–41 days to release all larvae, Thatje et al., 2003) and the duration of larval and juvenile stages, it is feasible that both first juvenile and larval stages co-exist in their natural environment (Calcagno et al., 2005). Moreover, each year recently hatched larvae and new settlers probably encounter older juveniles in the same habitat.

The knowledge about how long term agonistic interactions and cannibalism affect the survival of *L. santolla* juveniles is important, as both density of juvenile release in nature and stocking density in massive laboratory cultures could constitute the main mortality source in sights of a population subsidy. The aim of this study was to analyse cannibalistic interactions among larval stages (Zoea 1 stage and Megalopa) and juveniles (crabs stage 1 and 2; one-year-old crabs) of Southern King Crab during the intermolt period, with special emphasis on the potential effect of crab stage combinations and proportions of predators and prey.

2. Methods

2.1. Larval and crab rearing

Twenty-one ovigerous *L. santolla* females carrying eggs in advanced stage of development were caught in the Beagle Channel (54° 51' S 67° 30' W) in August 2008 and taken to the wet laboratory of the CADIC. Females were individually held in 30-l containers that were set up in an indoor chilled seawater recirculation system at 6.5 ± 1.1 °C. Water quality was maintained with mechanical (20 µm) and biological filters, and a UV-sterilizer. Water quality was checked every 3 days and pH, salinity, nitrite and nitrate levels were kept at 8.4 ± 0.3, 31 ± 1‰, <0.3 mg/l and <12.5 mg/l respectively. Females were fed *ad libitum* three times a week with squid (*Ilex* spp. or *Loligo* spp.).

Containers were cleaned and checked daily for larval hatching. Since the total hatching period in each female lasts between 35 and 41 days (Thatje et al., 2003), Zoea 1 stage (Z1) was selected for rearing at different time-intervals. Thus, we were able to obtain simultaneously Megalopae (M) and the first crab stages (C1 and C2) for cannibalism experiments. Larval cultivations were performed in a recirculation system at a maximum of 600 larvae container⁻¹. Since *L. santolla* larval development is lecithotrophic (Calcagno et al., 2005; Lovrich et al., 2003), larvae were not fed until metamorphosis to C1. Once C1 stage was attained, crabs were transferred to a cold room at 7 ± 1 °C and maintained individually in 100-ml glasses to avoid injuries due to potential cannibalistic behavior. Crabs were fed *ad libitum* with *Artemia salina* nauplii after water changing three times a week. This type of food was previously tested as effective, since in similar conditions *L. santolla* juveniles survived up to C7

stage (Calcagno et al., 2005). Crabs remained isolated until molting to C2 and/or until they were used in the experiments.

This procedure was also followed during 2007 to obtain 1-year-old crabs (C_{1yo}) that were used along with Z1, M and C1 in the cannibalism experiments performed in 2008.

2.2. Experimental design

In order to describe the cannibalistic behavior dynamics of early stages of *L. santolla*, three experiments were designed (Table 1). In all experiments, each treatment consisted in 10 replicates.

Experiment 1: intra-stage cannibalism was tested in M, C1 and C2.

Experiment 2: cannibalism was evaluated in five different predator–prey (P–p) stage combinations: C_{1yo}–Z1, C_{1yo}–M, C_{1yo}–C1, C1–M and C2–C1. Each stage combination was assessed by combining 1 predator and 5 prey (1–5 proportion).

Experiment 3: cannibalism was tested in three different P–p proportions: 1–5 (from Experiment 2), 2–4 and 3–3. Each proportion was assessed in both C1–M and C2–C1 stage combinations.

Animals used in the experiments were classified into the categories “predator” and “prey” only according to their developmental stage. Thus, in each experimental trial older (=larger) animals were referred to as predators (P) and younger animals as prey (p). Since interactions could be in both directions, in all experiments cannibalism was estimated over the total number of crabs in each replicate, so that both attacks and defences were possible to evaluate. Experimental animals used in this study had an average size of carapace length of 2.0 ± 0.05; 2.4 ± 0.08 and 6.5 ± 0.61 mm for C1, C2 and C_{1yo} respectively.

All experiments were performed in cylindrical PVC tubes (9 cm diameter and 11 cm height) with a bottom of 1-mm polyethylene mesh (64 cm²). Each tube was immersed in a 1.5-l flask filled with 1-l filtered and sterilized sea water. Mesh allowed crabs to grab and move freely over the tube-bottom. Moreover, the PVC tube also minimized the disturbance during water change since crabs were not directly manipulated. Flasks were randomly sorted in a cold room at 7.5 ± 0.5 °C with 12:12 h dim light (0.5 lx) and dark photoperiod, respectively. During the course of experiments, water of each flask was changed three times a week by transferring the PVC tube with crabs inside to a clean flask filled with fresh seawater. Immediately after the water change was performed, crabs were fed *ad libitum* with *Artemia salina* nauplii in order to minimize

Table 1

Summary of cannibalism experiments carried out in early Southern King Crab (*Lithodes santolla*) stages. Numbers and stages of predator (P) and prey (p) involved in each treatment are shown. Reference: Z1 = zoea stage 1; M = Megalopae; C1 and C2 = crabs stage 1 and 2, respectively; and C_{1yo} = one year old crab. 10 replicates per combination were performed.

| Experiments | P stage | P stage | P–p proportion | |
|---------------------------|------------------|---------|----------------|-------------|
| | | | Number of P | Number of p |
| 1 “intra-stage” | M | | 6 | |
| | C1 | | 6 | |
| | C2 | | 6 | |
| 2 “P–p stage combination” | C _{1yo} | Z1 | 1 | 5 |
| | C _{1yo} | M | 1 | 5 |
| | C _{1yo} | C1 | 1 | 5 |
| | C2 | C1 | 1 | 5 |
| | C1 | M | 1 | 5 |
| 3 “P–p proportion” | C2 | C1 | 1 | 5 |
| | C2 | C1 | 2 | 4 |
| | C2 | C1 | 3 | 3 |
| | C1 | M | 1 | 5 |
| | C1 | M | 2 | 4 |
| | C1 | M | 3 | 3 |

the effect of animal starvation on cannibalistic behavior (Luppi et al., 2001).

Experiments started by placing in each flask a total of 6 crabs at different proportions of predator–prey and stages according with treatments (Table 1). Experiments lasted a maximum of 25 days to ensure they were performed during intermolt period or until prey were totally consumed. Only undamaged crabs (with all their limbs), similar in size by stage and within 72–96 h of molting were used in the experiences.

Each day, injured and dead crabs (live and dead animals with at least one missing limb, respectively) and the number and type of lost limbs (chelipeds and/or walking legs) per injured crab were enumerated in each trial. Crabs that disappeared from the flask were judged as cannibalized, and intact dead crabs were considered as natural deaths. Dead crabs were removed from the flask and those recorded as natural deaths were replaced by new live and intact crabs at the same developmental stage.

Cannibalism was evaluated in terms of both dead and injured. Thus, the sum of injured plus dead crabs will be hereafter referred as cannibalism. Both injured and dead were analysed to estimate its relevance in cannibalism. The daily cumulative proportion of cannibalism, injured and dead crabs, was calculated over the 6 animals in each trial. Moreover, the number of lost limbs per injured prey at the end of the trials and the type of appendage that crabs lost first were also recorded.

2.3. Statistical procedures

Cannibalism, injured and dead crabs and the number of lost limbs per injured prey are presented as cumulative means \pm standard errors. Data were arcsine transformed and tested for normality and homogeneity of variances by Kolmogorov–Smirnov and Levene tests, respectively (Sokal and Rohlf, 1995). As data deviated significantly from normality, nonparametric tests were used to analyse differences between treatments at the end of each experiment.

Kruskal–Wallis tests were performed to determine differences in cannibalism, injured, dead and number of limb lost per injured prey between M, C1 and C2 stages (Experiment 1) and also to test the effect of P–p proportions over the fourth variables previously mentioned in both C1–M and C2–C1 stage combinations (Experiment 3). Particularly, in the later stage combination a Mann–Whitney U-test was performed only in limb lost variable since none injured prey remained alive at the end of the experiment in 3P–3p proportion. Mann–Whitney tests were also assessed in order to evaluate the effect of stage combination in cannibalism, injured, dead and the number of limb lost per injured prey (Experiment 2). Treatments with C_{1yo} as predators were excluded from the statistical analysis since all prey were consumed in all replicates within the first 5 days and consequently there was no standard deviation at day 25. Significant differences between treatments ($p < 0.05$) were compared using the Multiple-comparison post-hoc test (Sokal and Rohlf, 1995).

3. Results

During the course of all experiments no crab molted and evidences of cannibalistic interactions between conspecifics were observed in all experiments and replicates. Natural mortality was low, less than 2% of the total animals used in the experiments ($n = 840$). During the experiments crab stomachs were always full as they appeared dark by transparency, indicating that the provided *A. salina* nauplii were consumed. Therefore, starvation cannot be the direct cause of cannibalism in our study.

3.1. Intra-stage cannibalism – Experiment 1

Cannibalism, injured, dead crabs and number of limb loss per injured prey were similar between stages. At the end of the experiment,

the cannibalized crabs reached on average $15\% \pm 3.8$; $15\% \pm 5.8$ and $15\% \pm 4.6$ in M, C1, and C2 stages respectively (Kruskal Wallis; $H = 0.07$; $p > 0.05$; Fig. 1). Likewise, both dead and injured crabs were similar between stages (Kruskal Wallis $H = 0.03$; $p > 0.05$ and $H = 0.19$; $p > 0.05$). Mortality reached $5\% \pm 2.55$ in M and C1 and $6.67\% \pm 2.72$ in C2, whereas injured crabs raised up to $10\% \pm 3.68$ in both M and C1, and $8.33\% \pm 3.73$ in C2 (Fig. 1). At the end of the experience, injured prey remained in similar conditions since they lost on average 0.8 ± 0.36 ; 0.6 ± 0.22 and 0.5 ± 1.05 limbs in M, C1 and C2 (Kruskal–Wallis, $H = 0.20$; $p > 0.05$).

Even though deaths and cannibalism were similar in the three studied stages, cannibalistic patterns were different through time between treatments. In all stages, interactions started as soon as crabs were released into the flasks (within 24 h). However, at the beginning of the experiment (~5–6 days) injuries increased faster in C2 crabs than in C1 and, in turn, than in M (Fig. 1).

3.2. Inter-stage cannibalism

3.2.1. Effect of predator–prey stage combination – Experiment 2

During the experiment and in all stage combination treatments, cannibalized animals were always those defined as prey and no predator was found either injured or dead by conspecifics.

According to the P–p stage combination, cannibalistic interactions described three different patterns (Fig. 2). In all stage combinations with C_{1yo} as predators, cannibalism started as soon as animals were placed together in the flasks, and regardless the stage of prey (Z1, M or C1) all of them were killed and consumed by day 5 (Fig. 2A). These treatments showed the maximum proportion of cannibalism (83.3%), as the predator was never even hurt. Since only missing prey were registered and no injured prey occurred, cannibalistic patterns of C_{1yo} treatments were identical to those of mortality (Fig. 2A and B). At day 5, the experiment was finished and the predator (C_{1yo}) was alive and intact. Megalopae appeared to be more vulnerable than C1 and Z1 stages, because all of them were predated within almost the first 24 h of the experiment.

Cannibalistic interactions between C2–C1 also started immediately after they were in contact and gradually increased over the time until day 16, when cannibalism reached a maximum of $75\% \pm 3.7$, and

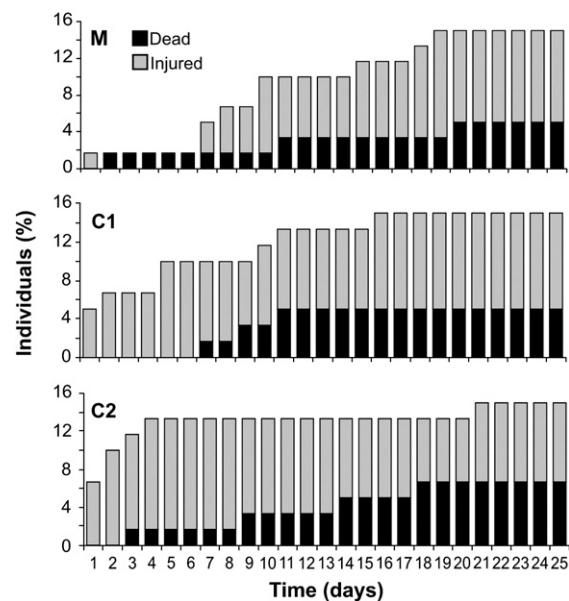


Fig. 1. *Lithodes santolla*. Intra-stage interactions in Megalopae (M), crab 1 (C1) and crab 2 (C2) stages. Mean cumulative proportion of dead (black) and injured (gray) individuals is shown. Cannibalism is the sum of injured plus dead crabs over the total animals of each flask ($n = 6$ crabs). All values are means of ten replicates.

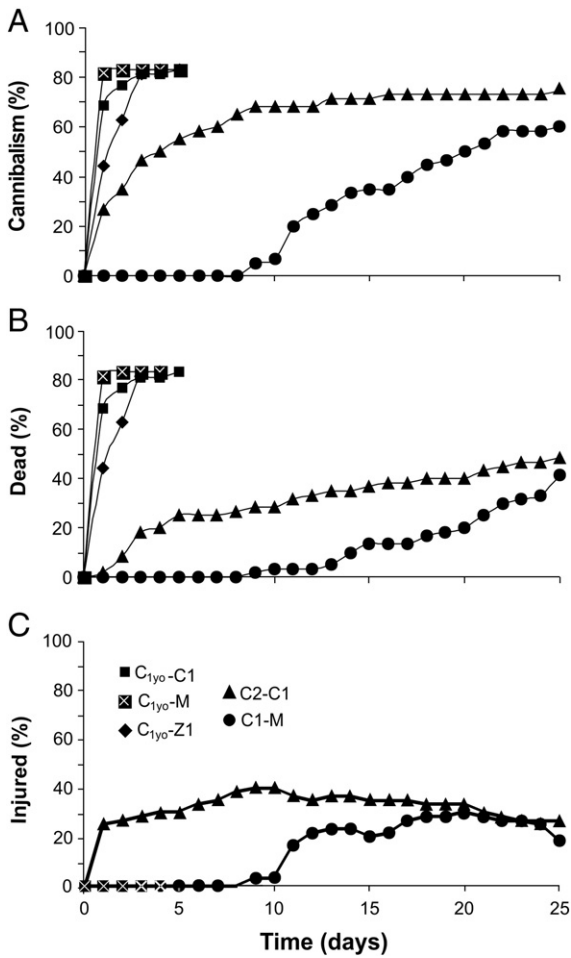


Fig. 2. *Lithodes santolla*. Inter-stage interactions under different predator-prey stage combinations. A) Mean cumulative proportion of cannibalism (injured + dead animals), B) Mean cumulative proportion of dead animals and C) Mean cumulative proportion of injured animals. All points are means of ten replicates of 1 predator and 5 prey. C_{1y0}: 1-year-old-crab, C1, C2: Crab 1 and 2 stages, M: Megalopa, Z1: Zoea 1 stage.

remained practically constant until the end of the experiment (Fig. 2A). In contrast, in C1-M treatment, interactions began 9 days after the start of the experience and incremented slowly over the time until day 22, when maximum values ($60 \pm 5.7\%$) were reached (Fig. 2A). Differences in cannibalism persisted until the end (day 25) of experience as cannibalism in C2-C1 was significantly higher than in C1-M treatment (Mann-Whitney *U*-test; $Z = 2.00$; $p < 0.05$).

Dead animals occurred in all treatments and showed different temporal patterns (Fig. 2B). As previously described, the highest possible values of mortality in C_{1y0} treatments were reached by day 5, when there were no further alive prey. Although dead animals in C2-C1 and in C1-M occurred at day 1 and 9 respectively, no difference was found at day 25 when treatments reached $48.3\% \pm 6.3$ and $41.7\% \pm 6.2$ respectively (Mann-Whitney *U*-test; $Z = 0.62$; $p > 0.05$) (Fig. 2B). The number of injured crabs peaked at days 10 and 20 in C2-C1 and C1-M respectively (Fig. 2C), but no differences in injured crabs were found between the 2 treatments at day 25 when attained $26.67\% \pm 5.66$ and $18.33\% \pm 5.80$ (Mann-Whitney *U*-test; $Z = 0.98$; $p > 0.05$). Final condition of injured crabs at the end of experiment was similar between both stage combinations (Mann-Whitney *U*-test; $Z = -1.05$; $p > 0.05$ respectively) (Table 2).

3.2.2. Effect of predator-prey proportions – Experiment 3

Regardless P-p stage combinations (C1-M or C2-C1), the experiment showed that the more unequal P-p proportion, the more intense cannibalistic interactions occurred (Fig. 3). Cannibalism was

Table 2

Lithodes santolla. Mean number of limb lost per injured prey \pm SE at day 25. Data is presented according to the different predator (P) – prey (p) proportion (1P–5p, 2P–4p and 3P–3p) and stage combinations (C1–M and C2–C1). C1, C2: Crab 1 and 2 stages, M: Megalopa. N is the number of replicates with injured crabs at day 25.

| P-p stage combination | | P-p proportion | | |
|-----------------------|---|----------------|---------------|---------------|
| | | 1P–5p | 2P–4p | 3P–3p |
| C1–M | n | 7 | 6 | 3 |
| | | 1.9 ± 0.4 | 1.8 ± 0.4 | 1.2 ± 0.2 |
| C2–C1 | n | 9 | 3 | 0 |
| | | 2.7 ± 0.5 | 1.7 ± 0.7 | – |

significantly different between P-p proportions in both C1-M and C2-C1 stage combinations (Kruskal-Wallis $H = 7.28$; $p < 0.05$ and $H = 17.04$, $p < 0.01$, respectively). At day 25, total cannibalism in P-p proportions 1–5, 2–4 and 3–3 was $60\% \pm 5.7$, $43.3\% \pm 6.2$ and $31.1\% \pm 6.3$ for C1-M and $75\% \pm 3.8$, $58.3\% \pm 5.1$ and $48.3\% \pm 1.7$ for C2-C1 (Fig. 3). In both C2-C1 and C1-M stage combinations total cannibalism was significantly higher in P-p proportion 1–5 than in 3–3 (Multiple comparisons; $p < 0.01$ and $p < 0.05$, respectively; Fig. 3). Moreover, when more than a single predator was placed in flasks, predators were also damaged. Nevertheless, predators were only observed as injured crabs (no dead predators were found) only in C1-M treatments, both in P-p proportions 2–4 and 3–3 (Fig. 3). In these treatments, injured predators occurred as soon as animals were released inside the flasks and the number of injured predators increased until day 9 and remained constant during the rest of the experiment. During these first 9 days no Megalopae (prey) was observed with signs of cannibalism (injured or dead) (Fig. 3). After day 9, both injured and dead prey appeared and their proportion increased over the time until the end of the experiment (Fig. 3).

In C1-M and C2-C1 stage combinations, the number of deaths described different patterns: in C1-M mortality increased as the more unequal predator and prey proportions ($1-5 > 2-4 > 3-3$; Kruskal-Wallis; $H = 8.92$; $p < 0.05$). The difference in mortality was only found between 1–5 and 3–3 P-p proportions (41% and 15%, respectively; Multiple comparisons $p < 0.05$). In C2-C1 dead crabs were similar between proportions (Kruskal-Wallis; $H = 1.42$; $p > 0.05$; Fig. 3).

Proportion of injured crabs was different among P-p proportions in C2-C1 stage combinations (Kruskal-Wallis $H = 15.46$; $p < 0.01$), but not in C1-M (Kruskal-Wallis; $H = 0.34$; $p > 0.05$). In C2-C1, the proportion of injured crabs ($26\% \pm 5.66$) in 1–5 P-p proportion was significantly higher (Multiple comparisons; $p < 0.01$) than in the 3–3 proportion, in which no prey remained alive by the end of the experiment (Fig. 3). Contrarily, the number of appendages lost per prey at the end of trials was not affected by P-p proportions (Kruskal-Wallis $H = 1.53$, $p > 0.05$ and Mann-Whitney *U*-test; $Z = 1.20$; $p > 0.05$). The number of appendages lost per injured prey ranged between 1.2–1.9 and 1.7–2.7 limbs in C1-M and C2-C1 respectively (Table 2). Particularly in 3–3 P-p proportion trials for the C2-C1 stage combination, no injured prey remained alive at the end of the experiment.

Differential limb loss occurred in *L. santolla* since walking legs appeared more vulnerable than chelipeds to be lost during intra-specific interactions. Although animals in the flasks were not individualized, each crab that suffered a first limb loss was unmistakably recorded. Thus, walking legs were the first lost appendage in more than 84% and 55% of the cannibalized crabs in C1-M and C2-C1, respectively (Fig. 4). Limbs were lost entirely, since appendage sections were lost in $< 1\%$ of the total limb losses.

4. Discussion

The present work provides evidence that cannibalism is a common behavior in early stages of *L. santolla* and occurs intensely during intermolt periods. Our data prove that intra-stage and especially

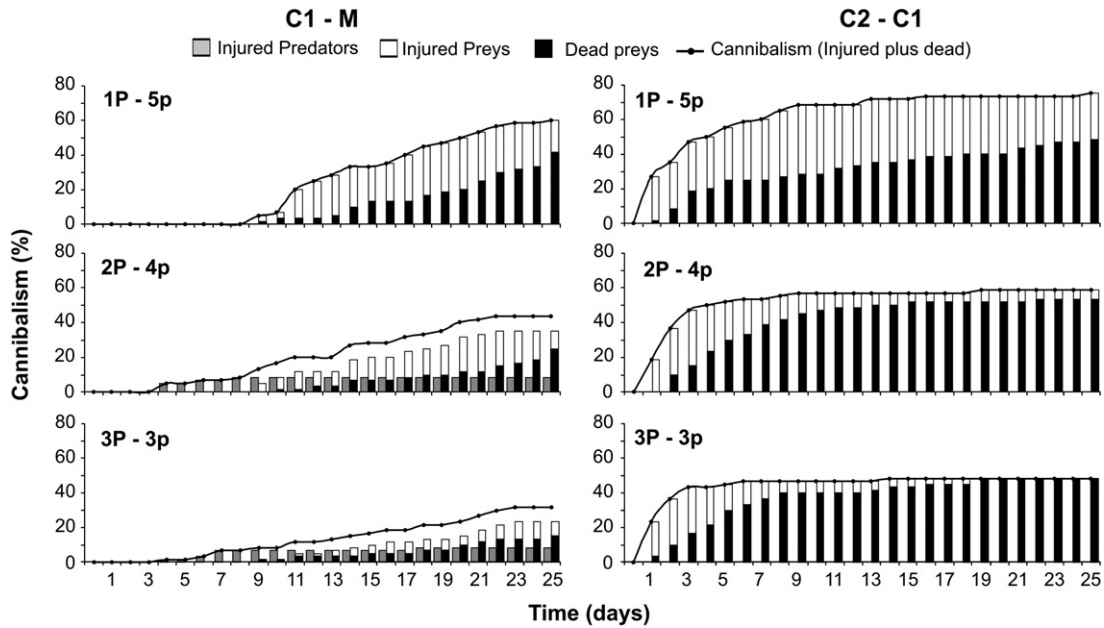


Fig. 3. *Lithodes santolla*. Inter-stage interactions of early stages under different predator (P) – prey (p) proportions (1P–5p, 2P–4p and 3P–3p) and stage combinations (C1–M and C2–C1). Mean cumulative proportion of injured (white bars) and dead (black bars) prey, respectively, and injured predators (gray bars). Cumulative proportion of cannibalism (dead + injured either predators or prey) is represented with a continuous black line. All values are means of ten replicates. C1, C2: Crab stages 1 and 2, M: Megalopa.

inter-stage cannibalism result in high proportion of injured and dead Southern King Crab juveniles, even if they are in a hard-carapace molt-stage. Cannibalism presented here can be considered as maximum levels of this behavior to be expected in early stages of *L. santolla* when rearing animals together, since the design of the experiments did not provide any kind of protection for crabs, as refuge in a complex substrate can offer.

Intraspecific predation in M, C1 and C2 was similar between stages and lower than inter-stage cannibalism. Nevertheless, cannibalism between Megalopae was an unexpected finding since *L. santolla* can reach the first crab stage independently of external food (Kattner

et al., 2003; Lovrich et al., 2003). We hypothesize that limb losses in trials with Megalopae only are likely the result of agonistic behavior rather than facultative lecithotrophy as follows. *L. santolla* larvae lack of endopeptidases that hinder the digestion of external food (Saborowski et al., 2006), have higher initial energetic stores compared with the sympatric *Paralomis granulosa* (Kattner et al., 2003) and have low survival in presence of food (Paschke et al., 2006). It is worthy to note that in Megalopa, intra-stage cannibalism increased after day 7 (Fig. 1A), coincidentally with the time that this stage begins to be more sedentary. Hence, once Megalopae settle onto the bottom more permanently, they are prone to interact with conspecifics searching for space (e.g. Tapella et al., 2009) and consequently begin losing limbs (Fig. 4). Swimming ability of Megalopae represents a key factor influencing cannibalism by allowing both the avoidance of predators, especially if they are restricted to the benthic zone (this study) and the megalopal dispersal for selecting suitable settlement habitats in nature. The ability of lithodid Megalopae to locate complex habitats has been recognised as an adaptive response to high predation levels (Stevens and Kittaka, 1998; Tapella et al., 2009).

In our experiments, difference in size of conspecifics was the main cause of cannibalism. It is generally known that smaller animals are more often eaten by larger ones (Polis, 1981). The present study reinforce this idea as differences were found between intra- and inter-stage cannibalism in Southern King Crab: whereas predation among animals of the same stage (and consequently similar in size) only reached 15% after 25 days during the intermolt period (Experiment 1), cannibalism caused over 58% of animal damage when different stages were involved (Experiment 2). A difference of 18% in crab body size was enough to cause high levels of cannibalism. Moreover, maximum cannibalism was found when animals of different hatching seasons were together. When predators had at least 1 year old, massive mortality of prey occurred within 5 days (regardless they were Z, M or C1).

Directionality of attacks between crabs was clear, indicating that bigger animals can cause sub-lethal and lethal injuries to smaller ones but not vice versa. When only a single larger crab was placed together with five others of a smaller size (Experiment 2), the large crab was always alive and undamaged, suggesting that Megalopae cannot hurt C1, in turn C1 is not able to injure C2, and no Z1, M or C1 can

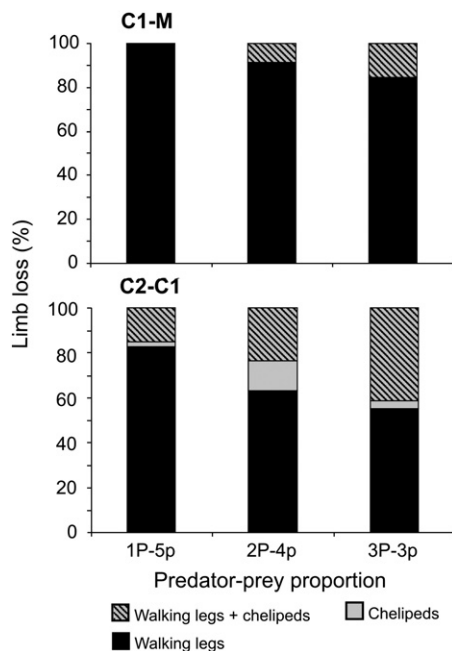


Fig. 4. *Lithodes santolla*. Proportion of injured prey discriminated by the type of appendages that each crab lost first (walking legs, chelipeds or both) (N = 50, 40 or 30 for 1–5, 2–4 or 3–3 proportion respectively). C1, C2: Crab 1 and 2 stages, M: Megalopa.

damage a 1-year-old crab. This fact confirms the role of predators and prey to large and small stages respectively, providing additional evidence that cannibalism is a size dependent behavior (Claessen et al., 2004). Moreover, in trials with more than one predator (Experiment 3), they appeared injured only in the C1–M treatment. Injured predators are likely to be the result of intra-stage interactions when prey remain unreachable, and this is supported by the findings of no injured or dead predator in trials with P–p proportion of 1–5. The megalopal changing behavior through the stage, from swimming to sedentary (Gonor and Gonor, 1973; Stevens and Swiney, 2005), makes interactions between C1 more frequent at the beginning of the experiment. Megalopae escape from their potential predator by actively swimming in the water column and remaining out of reach. Later, when Megalopae sedentary behavior prevails, they become accessible for C1 and consequently vulnerable to predation.

In contrast to adults, our results suggest that juvenile *L. santolla* autotomize their limbs as a strategy of escape from their predators. Adult *L. santolla* are not prone to loose appendages neither in captivity with other conspecifics, as it also occurs with other lithodids as *Paralithodes camtschaticus* (Dvoretzky and Dvoretzky, 2009; Juanes and Smith, 1995), nor during fishing operations (Lovrich pers. obs). Predator attacks in our study were evidenced as an appendage entirely lost whereas a partial appendage loss rarely was seen. The capacity to shed a pereopod in an agonistic situation has an immediate advantage of predation avoidance. However, costs associated with autotomy vary significantly depending on which appendage is lost, the function of the appendage, and the relative significance of habitat, age class, sex, and/or animal condition (Maginnis, 2006). The autotomy of walking legs in *L. santolla* will not affect foraging, but a reduction in growth will make the individual smaller than its conspecifics, increasing its predation risk by cannibalism.

Our findings allow us to hypothesize that cannibalism in *L. santolla* juveniles may cause considerable differences in size among juveniles of the same age. Although massive rearing attempts usually begin with a pool of animals of a particular age or stage, with time molting turns asynchronous causing size variability (Daly et al., 2009). After 8–9 months of massive stocking of juvenile of the same age, intact crabs can double in size others injured conspecific (personal observation). Thus, growth rate in cannibal crabs would be higher since they get an extra energetic source from prey (Møller et al., 2008), whereas injured ones would reduce the size-increment because they prioritize the energy into limb regeneration (Barría and González, 2008).

High predation rates were also observed in other decapod species. In the *Brachyura Neohelice granulata* one juvenile eats 6 new settlers within 48 h (Luppi et al., 2001), whereas in *P. camtschaticus* two C_{1yo} consume 20 Megalopae in 24 h of experiment (Stevens and Swiney, 2005). These figures compare with a single C_{1yo} *L. santolla* that preys upon 5 Megalopae in 48–72 h (Fig. 2). Differences between the two lithodids may be due to the starvation of the predator *P. camtschaticus*, which remained out of food before and during the experiment. The similarity in size between predator and prey leads to a decrease in mortality and cannibalism rates during successive stages. For example in *P. camtschaticus* mortality between C1 and C2 stages was up to ~27% after 25 days (Borisov et al., 2007), which is ca. the half of the ~48% of cannibalism in *L. santolla*. Hence, first instar crabs of *P. camtschaticus* would be less voracious than *L. santolla* of the same stages, as the latter reaches higher rates of cannibalism at lower density (950 ind m⁻² in *L. santolla* vs 1111 ind m⁻² in *P. camtschaticus*). Even at low rearing densities of 100 ind m⁻², cannibalism can attain 50% as reported for the blue-swimmer crab *Portunus pelagicus* (Marshall et al., 2005). Nevertheless, although highly cannibalistic, progress in culturing and rearing *Callinectes sapidus* made possible a 10.5% of survival up to Crab 6 (Zmora et al., 2005).

Cannibalism in early juvenile stages under natural conditions should be considerably less intense than in the present study, as rearing density in experiments was higher (~950 ind m⁻²) than in the

natural habitat. Larvae of *L. santolla* are absent from plankton samples (Lovrich, 1999). Juvenile crabs seem to have initially a cryptic and solitary behavior (Loher and Armstrong, 2000; Lovrich and Vinuesa, 1995). In the Beagle Channel individuals <5 mm CL settle on artificial collectors at a density of 1.5 individuals collector⁻¹ at depths <40 m and near the holdfasts of the kelp *Macrocystis pyrifera* (Tapella and Lovrich, 2006). Afterwards, juveniles of 34–75 mm CL occur in “pods”, ranging from 2 to 58 ind m⁻², around the kelp *M. pyrifera* (Cárdenas et al., 2007) and also may wander in open waters without refuge (Lovrich, 1997). Similar abundance of early stages was observed for *P. camtschaticus* in Alaskan waters where maximum density of juveniles reaches 2 individuals m⁻² (Loher and Armstrong, 2000).

Our results show the simplest possible scenario: predators and prey with food supply interacting during the intermolt. This information is essential for further advances in crab culturing and allows us to describe variations in *L. santolla* cannibalistic behavior throughout the intermolt period. Hereafter, the challenge will be the mitigation of cannibalism to let the coexistence of crabs of different sizes, and therefore to optimize massive rearing conditions.

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