Journal of Experimental Marine Biology and Ecology 411 (2012) 52–58

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

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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ARTICLE INFO

Article history:
Received 10 May 2011
Received in revised form 26 October 2011
Accepted 28 October 2011
Available online 26 November 2011

Keywords:
Aquaculture
Diet
Larvae
Paralomis granulosa
Stock-enhancement

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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0022-0981/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2011.10.029

This intraspecific predation represents an important source of mortality in decapod crustaceans such as *Macrobrachium rosembergii*, *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 ZI, 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 cm^2). 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

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