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ORIGINAL PAPER

Egg development, hatching rhythm and moult patterns in *Paralomis spinosissima* (Decapoda: Anomura: Paguroidea: Lithodidae) from South Georgia waters (Southern Ocean)

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Abstract Larval release, hatching rhythms and moult patterns were examined in a captive population of the subantarctic lithodid, *Paralomis spinosissima* from the South Georgia and Shag Rocks region. Larvae hatched throughout the year with the majority of females starting to release larvae at the end of the austral summer and beginning of autumn. Larval release continued over a period of up to 9 weeks with high variability in the numbers that hatched each day. A similar seasonal pattern to hatching was evident in the moulting of females. Intermoult period for two adult females (CL = 63 and 85 mm) ranged from 894 to 1,120 days while an intermoult period for males was estimated to be in excess of 832 days. The results are consistent with other species of *Paralomis* and are discussed in relation to physiological and environmental adaptations to the cold-water conditions south of the Antarctic Convergence.

Keywords Antarctica · Crustacea · Cold adaptation · Stone crab · King crab

Introduction

The Antarctic reptant decapod fauna consists of about a dozen known species of crabs belonging to the family Lithodidae (Thatje and Arntz 2004). Lithodid crabs commonly known as "king crabs" or "stone crabs" are typical representatives of high latitudes (Zaklan 2002) and are of great importance to fisheries in both hemispheres (Dawson 1989). They are slow maturing crabs (Lovrich 1997) and have a high diversity in Subantarctic waters (Zaklan 2002). Five species of lithodid crabs are caught as bycatch in the commercial fisheries operating around the sub-Antarctic island of South Georgia (Morley et al. 2006). *Paralomis spinosissima* and *Paralomis formosa* are regularly caught as bycatch in the longline fishery for Patagonian toothfish (*Dissostichus eleginoides*) and attempts have been made to target them commercially (Purves et al. 2003).

Since the early 1990s there has been interest in exploiting stone crabs in South Georgia waters, and in 1993 a precautionary catch limit was set by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for this species (Collins et al. 2002). An exploratory pot fishery was undertaken in 1992 mainly targeting *Paralomis spinosissima* (Otto and MacIntosh 1996). The results of the exploratory fishery suggested that crab resources in South Georgia waters (CCAMLR subarea 48.3) are large enough to provide a viable fishery (Otto and MacIntosh 1996). Although no commercial fishery has operated since 2001/2002 the crab fishery around South Georgia remains an exploratory fishery regulated by CCAMLR and subject to an exploratory fishing plan (Agnew 2004), with a catch limit of 1,600 tonnes per annum and minimum size limits of 102 mm carapace length (CL) for *Paralomis formosa*, and 90 mm CL for *P. spinosissima*.

This study presents the first data on the moult, egg extrusion and larval hatching patterns in adult *Paralomis spinosissima* collected from waters around South Georgia, and maintained under controlled laboratory conditions.

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Such knowledge is an important contribution to assessing the resilience potential of cold-water crab stocks to exploitation and to implement adequate management tools.

Materials and methods

Adult specimens of *Paralomis spinosissima* were obtained as by-catch by scientific observers working in the commercial longline fishery for Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia from June 2001 to July 2006. Further specimens were collected during the annual bottom trawl research survey on the FPV "Dorada" undertaken each January around South Georgia and the Shag Rocks. On capture carapace length (CL), carapace width, chela height, chela length, and specimen weight were recorded. Crabs were held in tanks in the controlled temperature facility at the King Edward Point applied fisheries research station (British Antarctic Survey). They were kept in re-circulating seawater at 1.8–3.0°C and a salinity of 33–35 ppt, with an artificial light/dark cycle run by an outside photocell to match seasonal day length. Crabs were fed fish and squid weekly, and monitored daily. Crabs were kept in tanks of 4–10 individuals of mixed genders. Timing and duration of moulting was recorded as it occurred. Due to the small numbers of crabs surviving a full intermoult period, minimum premoult periods are given as an indication of length of time between moults; i.e. period from time of capture to the first moult, and are denoted * in the results. Every month, crabs were examined in detail and egg development of the females was noted. When present, egg development was recorded as non-ovigerous, uneyed, eyed, dead eggs or empty egg cases. A simple index of abdominal cavity fullness was recorded; no eggs to trace, <¼ full, ¼ to ½ full, ½ to ¾ and ¾ to full. Further anecdotal information on condition of the carapace and egg mass was documented. When a crab started releasing eggs it was isolated from the main tanks in a separate flow-through system, and the number of live larvae released was recorded daily.

Results

Rearing history of *Paralomis spinosissima*

A total of 51 female (range CL 47–90 mm), 41 male (range CL 40–100 mm) and three juvenile (range CL 20–36 mm) *P. spinosissima* were maintained in captivity over the period 2001–2006. Mean survival time in the facility was 485.9 ± 328.5 days for females, 379 ± 330.7 days for males, and 167.0 ± 48.1 days for juveniles.

Moult cycle

Moulting occurred throughout the year in females and males (Fig. 1). No males survived a full intermoult period of two consecutive moults. In males, time from capture to death without a moult ranged from 14 to 1,307 days ($n = 34$, CL = 40–100 mm) while time from capture to moult ranged from 306 to 639 days ($n = 7$, CL = 40–92 mm). Time from capture to death without a moult in females ranged from 18 to 632 days ($n = 23$, CL = 62–89 mm) while time from capture to moult ranged from 126 to 1,001 days ($n = 28$, CL = 47–90 mm). Two female crabs (CL = 67 and 85 mm) survived a full intermoult period to moult twice. Intermoult period for these two crabs were 894 and 1,120 days, respectively. Neither of these females successfully hatched larvae whilst in the holding facility. High mortality was associated with moulting. Three of the seven males and 13 of the 28 female that moulted died during the moult or within 2 weeks afterwards.

Egg development and larval release

Egg development, hatch period and post hatch period are shown in Fig. 2. Thirteen out of 14 crabs that hatched larvae were captured with uneyed embryos therefore it was not possible to ascertain total time taken for the embryos to become eyed. Mean length of time taken for larvae to hatch after eyespots developed was 238.7 days S.D. 41.1 (range 141–290 days).

The majority of hatch events occurred through mid to late summer except crab 13 and 14, which hatched larvae in winter. Larval release was continuous but numbers released per day fluctuated widely, between 0 and 307 larvae (Fig. 3). No relationship was observed between size of indi-

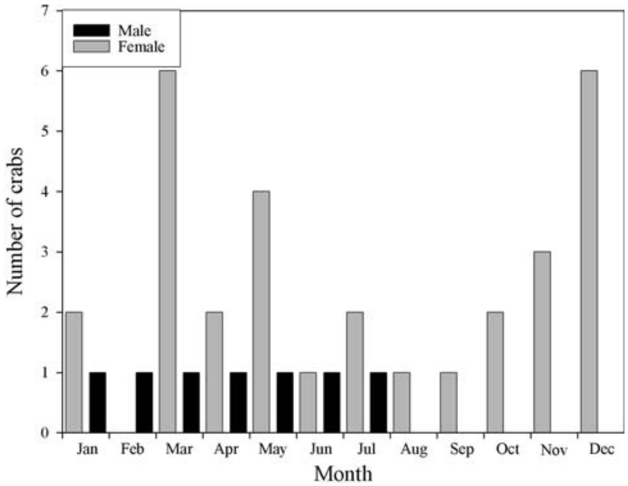

Fig. 1 Number of *Paralomis spinosissima* moulting per month in the temperature controlled facility at King Edward Point, South Georgia, from specimens collected between 2001 and 2006 around South Georgia

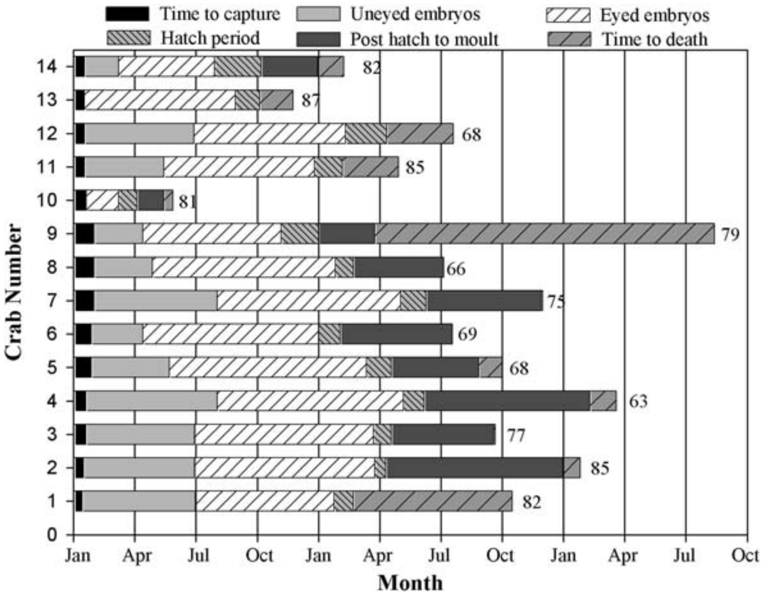

Fig. 2 *Paralomis spinosissima* egg cycle starting of individuals caught around South Georgia and the Shag Rocks in January, between 2001 and 2006, with the carapace length (mm) at the end of the *bars*

vidual and the number of larvae released (Table 1). According to the fecundity estimates calculated after Morley et al. (2006) in most females 1/4 to 1/2 of the clutch size remained with the female following hatching (Table 1). Crabs 6 and 14 were the only crabs to hatch nearly a full clutch of eggs (Table 1). In all other crabs, eggs turned brown and were released by the females after the hatch period.

Discussion

Egg development

Large eggs as seen in *P. spinosissima* (Morley et al. 2006) have the potential to store high-energy reserves facilitating endotrophic larval development (Anger et al. 2003, 2004). The lack of feeding appendages and observed food independent development in the larvae of *P. spinosissima* suggests lecithotrophic development (Watts et al. 2006), which coincides with patterns so far found in sub-Antarctic lithodids (Thatje et al. 2005). Similarity in the development mode of the larvae suggests that brood time in *Paralomis* species could be similar. *P. granulosa* broods eggs for 18–22 months at much higher temperatures (6–12°C) than found at South Georgia (Lovrich and Vinuesa 1999) and brood time in *P. spinosissima* is clearly greater than 12 months. Estimating an accurate length of brood time is difficult. It was not possible to determine duration of the uneyed stage from field-collected specimens as eggs were already present in the incubation chamber of females.

In *P. granulosa* the eyed period in embryos contributes 45–55% of the whole embryogenesis (Lovrich and Vinuesa 1993). Applying this relationship to *P. spinosissima* with a tentative estimation of 9–12 months uneyed and 5–11 months for eyed stage, suggests that the whole embryogenesis in this species may last between 432 and 528 days (=14–18 months). Although this is only a tentative estimation, it suggests that low water temperatures at South Georgia do prolong embryogenesis in *P. spinosissima*.

Hatching and larval release

The hatching mode in *P. spinosissima* is consistent with other species of southern hemisphere lithodids as low numbers of larvae released daily over a long continuous period. This has been observed in *P. granulosa* and *L. santolla* (Thatje et al. 2003) as well as in *Paralithodes platypus* from the northern hemisphere (Stevens 2006). *P. spinosissima* larvae hatched for up to 9 weeks before the cessation of release. This is likely to be an underestimation of the hatching period in the wild, as eleven out of thirteen females had half to three-quarters of the their clutch present at the end of their releasing event, assuming that the majority of the clutch is released. In the wild, hatching could be as long as 12 weeks when release numbers are compared with an estimation of fecundity, calculated using equations by Morley et al. (2006).

Females showed no signs of abdominal flapping during larval release, as found in temperate crab species (Baeza and Fernandez 2002). From a physiological perspective, it had been suggested that brooding activities should be reduced at lower temperatures as a result of reptant decapods being poor Mg^{2+} regulators and the possible narcotising effect at low temperatures and high Mg^{2+} in the haemolymph (Frederich et al. 2001). Thatje (2004) has hypothesised that embryonic development may not only be completely genetically constrained but could also depend

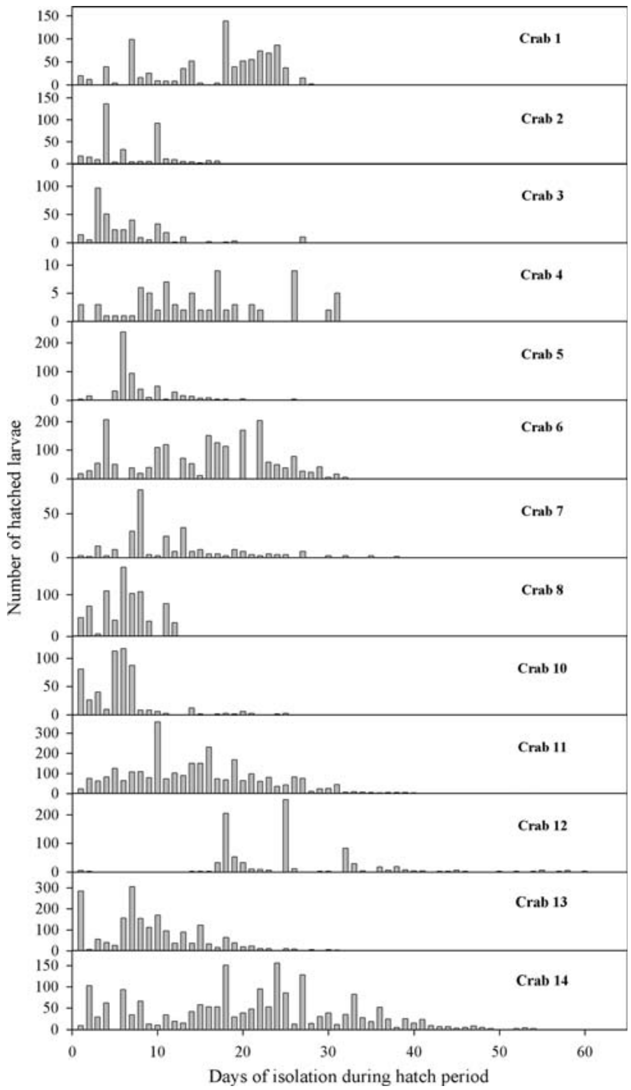

Fig. 3 Daily number of larvae hatched by *Paralomis spinosissima* from specimens caught around South Georgia and the Shag Rocks between 2001 and 2006

on a combination of temperature and oxygen concentration. Oxygen demand by developing larvae increases near to hatching (Thatje 2004). Low abdominal flapping and a decrease in oxygen concentration into the brood (Baeza and Fernandez 2002) may result in a lag in development close to the centre of the clutch increasing the duration of the releasing event. Aborted hatching rhythms in our experiments could indeed be an indication of physiological limits to brooding in the cold, which needs further investigation.

P. spinosissima has a lower fecundity than both *P. granulosa* and *L. santolla* (Lovrich and Vinuesa 1999; Morley et al. 2006) but larvae are released over a similar time frame and longer. Lecithotrophic development in lithodid species has been described as an adaptation to cold environments with short or variable seasonal primary productivity (Thatje 2004). This overcomes the need for food during larval development to crab I stage and buffers against the possible mismatch of food supply with hatching time. Shallow-water lithodids do show signs of seasonality in hatching. *P. granulosa* and *L. santolla* larvae hatch in winter and early spring between June and October (Hoggarth 1993; Lovrich and Vinuesa 1999). This coincides with development to crab stage I in spring and early summer in time for increased primary productivity and food availability. Larval release in *P. spinosissima* is year round. Start of hatching is highly skewed towards summer and decreases into autumn. It is not clear whether this is a result of a low sample size ($n = 14$) or if it is true for the whole population, which shows a much wider bathymetric distribution than species from Subantarctic Tierra del Fuego (Thatje et al. 2005). In July 1992, Otto and MacIntosh (1996) found a considerable variability in the development stage of wild *P. spinosissima* embryos during the experimental fishery around South Georgia and the Shag Rocks. Embryos were a mixture of uneyed to fully formed zoea, which suggested a great deal of variation in hatching time.

Intermoult periods

The intermoult periods of immature and mature male and female *P. spinosissima* (Table 1) were difficult to measure. The information collected on juvenile crabs is low and more data is needed. First year growth of a single crab between crab stage I and II was successfully achieved at 5°C in conjunction with morphological and biochemical larval studies (Watts et al. 2006) and first year growth in lithodids has been shown to be strongly scaling with temperature (Calcagno et al. 2005). The time between crab I and crab II in *P. spinosissima* was approximately 180 days (BAS, unpublished data), which is longer than in other species of lithodids (Calcagno et al. 2005). The time between intermoults is affected by temperature with increased intermoult duration with a decrease in temperature (Anger et al. 2003, 2004). Bottom temperatures around South Georgia are lower than 5°C. Collins et al. (2002) found temperatures around South Georgia to vary between 1.4 and 2.2°C. Lower temperatures in the wild would be expected to cause an increase in the intermoult duration of stone crabs in their first year (Calcagno et al. 2005). In *P. granulosa* the intermoult period doubles in time between 3 and 6°C. If this holds true for *P. spinosissima* then the intermoult period in the wild could be as long one year in the first year of life.

Moulting in sexually mature lithodids is believed to tie in with its reproductive cycle. In the majority of species this process is seasonal (Lovrich and Vinuesa 1999). Mating occurs between a newly moulted male with a hard shell and a female with a soft shell. Eggs must be fertilised immediately as lithodids have no way of storing sperm (Zaklan

Table 1 Carapace length (mm), total number of larvae released, total days in isolation, average daily hatch rates and theoretical fecundity as calculate based on CL using equations by Morley et al. (2006) for *Paralomis spinosissima* caught around South Georgia and the Shag Rocks. *n/a* no data

Crab	CL (mm)	Number hatched	Theoretical fecundity	Hatch period	Clutch size before hatch	Clutch size after hatch
1	78	903	4,748	18.01.05 to 15.02.05	3/4 to full	1/2 to 3/4
2	83	362	5,797	19.03.05 to 04.04.05	3/4 to full	3/4 to full
3	76	345	4,328	17.03.05 to 12.04.05	3/4 to full	1/2 to 3/4
4	63	79	1,600	30.04.05 to 30.05.05	3/4 to full	1/2 to 3/4
5	68	573	2,650	07.03.05 to 12.04.05	3/4 to full	1/4 to 1/2
6	69	1,912	2,859	26.12.04 to 27.01.05	3/4 to full	<1/4
7	75	275	4,118	26.04.05 to 02.06.05	3/4 to full	3/4 to full
8	65	796	2,020	20.01.05 to 15.02.05	3/4 to full	1/4 to 1/2
9	79	n/a	n/a	01.11.04 to 15.12.04	3/4 to full	1/2 to 3/4
10	81	523	5,378	07.03.05 to 03.04.05	1/2 to 3/4	1/4 to 1/2
11	85	2,869	6,217	20.12.05 to 30.01.05	3/4 to full	1/4 to 1/2
12	68	843	2,650	04.02.05 to 05.04.06	3/4 to full	1/2 to 3/4
13	85	1,941	6,217	07.05.06 to 12.06.06	3/4 to full	1/2 to 3/4
14	82	1,940	5,587	11.08.05 to 03.11.05	3/4 to full	<1/4

2002). Moulting in female and male *P. spinosissima* was observed all year round but female moults were highly skewed towards the summer months. With the low sample size of males it is not possible to say whether they are moulting slightly earlier than females or whether the population as a whole is aseasonal. In other species of deep-water lithodids, *Lithodes aequispina* and *Lithodes couesi*, it has been suggested that life history patterns are less tied to surface productivity, temperature and food availability (Somerton 1981; Sloan 1985; Hoggarth 1993). The presence of moulting males and females in deep water lithodids throughout the year could be a consequence of movement away from a cycle linked to seasonal productivity or temperature.

Hoggarth (1993) suggested an intermoult period of 24 months for mature female and up to 36 months for mature male *P. granulosa*. These long intermoult periods were hypothesised to be a result of adaptations to harsh and energetically restricted conditions. A similar estimation of time between moults would be plausible for female *P. spinosissima* as the small number of females that survived for more than 2 years, within this study, did not undergo a moult. Further evidence for a long intermoult period was published by Otto and MacIntosh (1996) who observed biological fouling on the carapace of sexually mature crabs that indicated moult periods of 12 months and longer.

Captive studies for life history investigations

Keeping animals in an artificial environment can ultimately affect their growth and maturity resulting in misleading interpretations (Wenner et al. 1974). Stone crabs are relatively active decapods and are known to migrate large distances (Watters 1997). Low growth increments may be the result of muscle wastage from confined movement in tanks or low nutrition of food. Inappropriate or low energy food may have an effect on other aspects of the lithodid biology and could be a reason why post-moult females discharged uneyed eggs from their brood soon after they were extruded or did not release eggs at all after the moult.

Conclusions

The examination into the life cycle of *P. spinosissima* has given more insight into the biology of these crabs. *P. spinosissima* life history patterns appear to be similar to other species of *Paralomis* and very similar to its South American congener *P. granulosa*. There are however, some specific differences between the two species. *P. spinosissima* has a lower fecundity (Lovrich and Vinuesa 1999; Morley et al. 2006), larger size at sexual maturity (Otto and MacIntosh 1996) and potentially slower growth. There are still large gaps in our knowledge from a resource management perspective, especially for the early life stages. Knowledge of larval development rates at temperatures experienced in the natural environment, juvenile growth rates, time taken to sexual maturity as well as potential environmental effects on recruitment are all important in order to manage any fishery.

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