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ORIGINAL ARTICLE

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Extended hatching periods in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea: Decapoda: Lithodidae)

Abstract Temporal pattern of hatching was studied in the subantarctic lithodid crabs *Lithodes santolla* (Molina) and *Paralomis granulosa* (Jaquinot) from the Argentine Beagle Channel. In both species, larval hatching occurred in low daily numbers over an extended period of up to several weeks, depending on hatch size. Low daily hatching activity and low oxygen-consumption rates in freshly hatched *P. granulosa* larvae are discussed as life history adaptations to, and/or physiological constraints by, the environmental conditions of high latitudes.

Keywords Stone crabs · Hatching mode · Behaviour · Energy investment · Reproduction

Introduction

Hatching is one of the most conspicuous behavioural phenomena in marine and terrestrial decapods (e.g. Saigusa and Hidaka 1978; Anger et al. 1994). Hatching synchrony is principally assumed to be controlled by the combination of internal rhythms and environmental conditions (Forward 1987; DeVries and Forward 1989, 1991; Zeng and Naylor 1996, 1997). Primary abiotic signals for hatching behaviour in decapod females are well studied and known to result in, for example, tidal, lunar or diurnal hatching rhythms (DeCoursey 1983; DeVries et al. 1983; Saigusa and Kawagoye 1997; Zeng and Naylor 1997). They have been most intensively studied in coastal and estuarine species (e.g. Anger et al. 1994). The hatching of larvae is based on chemical and behavioural interactions between late embryos and the brooding female (Naylor 1976; Saigusa and Iwasaki 1999; Saigusa and Terajima 2000), although the hierarchical order of factors involved in hatching is not yet well understood. Hatching rhythms related to abiotic and biotic cycles, including primary production, allow for a synchronisation of reproduction with favourable environmental conditions (Starr et al. 1990, 1994). This may aid larval dispersal, growth and survival. However, little is known of hatching modes in decapod species from high latitudes and the deep sea, where some species have developed a food-independent mode of larval development.

We studied the hatching mode in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* from the Argentine Beagle Channel. Both species follow a completely lecithotrophic larval development (Calcagno et al., 2003; Lovrich et al. 2003). Our results are discussed in relation to environmental and physiological constraints affecting decapod life histories and survival in cold waters.

Methods

Capture and maintenance of ovigerous females

Ovigerous females of *Lithodes santolla* and *Paralomis granulosa* were caught at about 15 to 30 m depth using commercial fishery traps in the Argentine Beagle Channel (54°53.8′S, 68°17.0′W) in April 2001. The crabs were kept in aquaria at 6±0.5°C in the Centro Austral de Investigaciones Científicas (CADIC) in Ushuaia. In May, the lithodids were transported on board the German scientific research vessel R.V. “Polarstern” to Bremerhaven and finally to the

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Table 1 The effect of water temperature on the oxygen consumption of zoea I of *Paralomis granulosa*

Temperature (°C)	Oxygen consumption (μg0$_2$/h×individual)	
	Mean	SD
1	1.38	0.47
3	1.30	0.10
6	1.59	0.55
9	1.94	0.42
12	3.35	0.56
15	3.98	0.96

marine biological laboratory in Helgoland (Germany). During this cruise of about 1 month, water was kept at 6±0.5°C and was changed three times per week. Food (squid) was given twice a week.

In the laboratory, maintenance of females and rearing of larvae took place under constant temperature (6±0.5°C) and salinity (32‰), and a 12:12 h light:dark rhythm. Ovigerous females were kept individually in flow-through tanks of at least 35 l.

Newly hatched larvae were collected from the overflow filters (300-μm mesh size). Since almost all larvae hatched at night, sampling and counting of larvae was done every morning.

Hatching of both species was studied during 7 weeks. Some females were still carrying remains of egg-clutches when this study had to be finished for logistic reasons; therefore, we cannot present complete hatching curves for all females studied. The theoretical number of eggs in each egg mass was calculated after the fecundity–CL (carapace length) relationships available from the literature for *P. granulosa* (Lovrich and Vinuesa 1993) and *L. santolla* (Lovrich 1997).

Oxygen consumption measurements

Freshly hatched larvae of *P. granulosa* taken for measurements of oxygen consumption were reared individually in 100-ml cups with filtered sea water of constant temperature (see Table 1). Oxygen consumption was measured in the middle of the zoea-I moulting cycle. It was measured in a closed system with a 2-ml gas-tight glass syringe used as a respirometer chamber and oxygen micro-optodes (Pre Sens, Neuburg a. d. Donau, Germany). The syringe was filled with aerated sea water (100% oxygen saturation) and the optode (tip size from <30 to 100 μm) was inserted from the side of the cannula. Prior to insertion in the syringe, the optode was calibrated and its drift recorded. Blank measurements in empty syringes revealed no oxygen consumption (due to bacterial contamination) during the measuring period (up to 1 h). The larvae were carefully transferred into the syringe with a pipette and subsequently the volume was reduced to 1 ml. Mixing of the water inside the syringe was achieved by the movement of the larvae. Variation in the position of the sensitive tip of the optode confirmed that no oxygen gradient occurred inside the chamber. Measurements were terminated when the oxygen saturation decreased below 80% (15–60 min). Oxygen consumption of larval *P. granulosa* was measured at temperatures ranging from 1° to 15 °C (*n*=5–8), which roughly represents their range of temperature tolerance (Anger et al. 2003). At the end of the measurements, optodes were removed and recalibrated. All measurements and calibrations were carried out in coolers at temperatures corresponding to the incubation temperature.

Results

Hatching was studied in nine females of *Paralomis granulosa* and three females of *Lithodes santolla* over a period of about 7 weeks (Figs. 1, 2). Total amount of hatched larvae per female varied from 426 to 2,915 and from 204 to 3,821 larvae in *P. granulosa* (Fig. 1) and *L. santolla* (Fig. 2), respectively. The actual numbers, however, are an underestimation, since not all females (except females A, B, E of *P. granulosa*) had finished hatching their larvae when this study was terminated (see Figs. 1, 2). The average daily hatching rates were 52.9±52.3 (range 0–379) and 53.4±88.2 (range 0–366) in *P. granulosa* and *L. santolla*, respectively. In *P.*

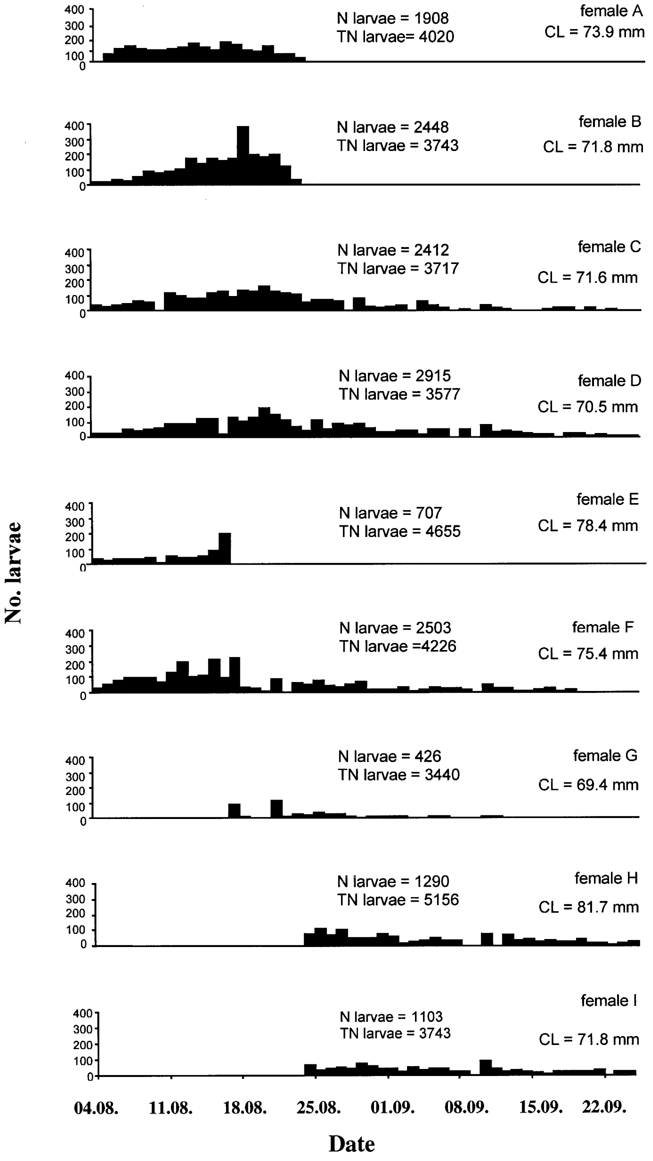

Fig. 1 Daily hatching numbers in *Paralomis granulosa* (Jaquinot) from the subantarctic Beagle Channel in 2001. Only the females A, B and E completed the hatching of all larvae within the study period. *TN larvae* Theoretical egg/larvae number; *CL* carapace length

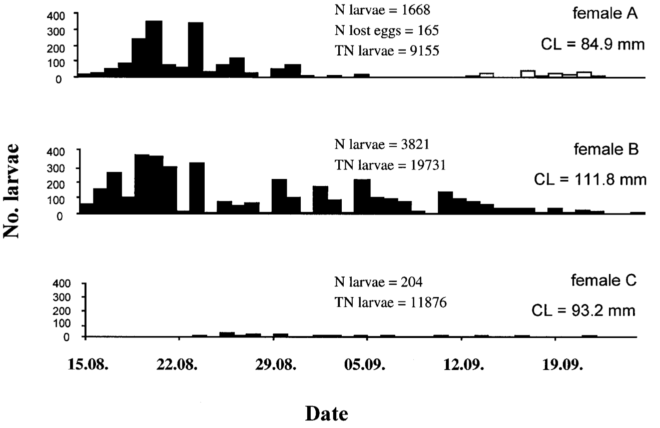

Fig. 2 Daily hatching numbers in *Lithodes santolla* (Molina) from the subantarctic Beagle Channel in 2001. *Open bars* the numbers of lost eggs. *TN larvae* Theoretical egg/larvae number; *CL* carapace length

granulosa and *L. santolla*, the total hatching period lasted between 13 and 61 days and 35 and 41 days, respectively. Again, the maximum values were underestimated, because at the end of the study most females were still carrying remains of their egg masses.

Depending on incubation temperature, the oxygen consumption of the larvae varied between 1.38 (1°C) and 3.98 (15°C) $\mu gO_2/h \times$individual (r=0.94; P=<0.01; Table 1).

Discussion

Larval release in decapods is known to occur frequently in response to abiotic environmental conditions, such as lunar or tidal cycles, leading to synchronised hatching which usually does not exceed a period of a few hours to days (DeCoursey 1983; DeVries et al. 1983; Saigusa and Kawagoye 1997; Zeng and Naylor 1997). Although aquatic invertebrate embryos are usually tolerant of low oxygen concentrations, egg masses are size-limited, owing to oxygen gradients (Strathmann and Strathmann 1995). Decapods, which produce compact egg masses of up to several centimetres in diameter, compensate oxygen deficiency in the centre of their egg-masses mainly by abdominal flapping. This maternal-care behaviour tends to increase during late embryonic development when the oxygen demand of the embryos increases (Nakanishi 1985; Naylor et al. 1999; Fernández et al. 2000; Baeza and Fernández 2002). The energetic cost of brooding depends mainly on the size of the egg mass and on oxygen partial pressure. Since the oxygen partial pressure in sea water is temperature-dependent, these costs should be higher in temperate and warm shallow subtidal zones than in the deep sea and at high latitudes.

In cold environments, such as the Antarctic and adjacent regions, the hatching mode of decapods is little known. Biogeographic limits in decapod distribution, in particular the absence of reptant crabs in polar areas, have been assumed to be due to low temperatures in combination with food limitation, owing to short primary-production periods, both affecting larval survival (for recent review, see Anger 2001). Recently, these distribution patterns were proposed to be due to physiological constraints at low temperatures; namely, the Reptantia are poor Mg^{2+} regulators which may suffer narcotising effects induced by low temperatures in combination with high Mg^{2+} levels in the haemolymph (Frederich et al. 2001). As a consequence, brooding activities such as abdominal flapping should be dramatically reduced at low temperatures.

Limited food availability at high latitudes may be compensated by lecithotrophic larval development, which has been shown in lithodid crabs (Anger 1996; Shirley and Zhou 1997), including the species studied here, *P. granulosa* and *L. santolla* (Calcagno et al., 2003; Lovrich et al. 2003). Embryonic development in these species is known to last between about 1 and 2 years (*L. santolla* 9–10 months, Vinuesa 1984; *P. granulosa* 18–22 months, Lovrich and Vinuesa 1993).

Freshly hatched larvae of *P. granulosa* showed low oxygen-consumption rates at low temperatures in our study (Table 1); the rate, however, increased strongly with increasing temperature. The same tendency has been reported in other lithodid species (Nakanishi 1985; Anger 1996). Low larval oxygen consumption may be a consequence of low-temperature regimes and restricted maternal aid in oxygen supply. Active enhancement of the hatching by means of strong abdominal flapping was not observed in our study. Low daily hatching rates suggest that hatching in lithodids is associated with little activity and low energetic costs for the female. Lecithotrophic development makes larvae independent of food, so that there is no need for hatching to coincide with periods of high primary production in these species. Their larvae show a demersal drifting behaviour and do not occur in the productive upper parts of the water column (for discussion, see Lovrich 1999).

Paralomis granulosa and *L. santolla* are known to carry up to 10,000 and 32,000 eggs per clutch, respectively (Lovrich 1997). Since the females of *L. santolla* used in this study were on average much smaller than in natural populations (cf Lovrich et al. 1999), hatching in nature may last even longer than 7 weeks. This is indicated also by those females in both species which had not completed hatching at the end of the study period. Differences between total hatching numbers obtained during our study period of about 7 weeks and the estimated theoretical amount of larvae in each clutch support this point of view (see Figs. 1, 2), not taking into account the females A, B, and E of *P. granulosa* which apparently hatched most of their larvae before being individualised (Fig. 1). Since in some females the study included both the beginning and end of larval hatching, we probably have not missed conspicuous peaks in hatching. This is also supported by the fact that daily means in hatching numbers were rather similar. The continuous release of demersal larvae may have an adaptive value, since it enhances the dispersal and may reduce the susceptibility to pelagic predation.

If we assume that the duration of embryonic development in decapods is not strictly determined genetically, but is also dependent on temperature and dissolved-oxygen level, oxygen gradients in egg masses of brachyuran crabs could be responsible for the delay in hatching of larvae from the innermost layers of the egg mass (Chaffee and Strathmann 1984), thus explaining the occurrence of extended hatching periods.

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