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Energetic changes throughout lecithotrophic larval development in the deep-sea lithodid crab *Paralomis spinosissima* from the Southern Ocean

Sven Thatje *, Nélia C. Mestre

National Oceanography Centre, Southampton, School of Ocean and Earth Science, University of Southampton, European Way, SO14 3ZH, Southampton, UK

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ABSTRACT

Adult populations of the lithodid crab *Paralomis spinosissima* thrive at the lower temperature boundary of about 1 °C for the Lithodidae, and are endemic to deep waters off South Georgia, Southern Ocean. Here, we present evidence for lecithotrophic development throughout the early ontogeny of this species over a period of 14 months. At constant 5 °C (±0.5), development of the Zoea I and II, the megalopa, and the crab I instar lasted about 12, 24, 108, and 290 days, respectively. Successful development and moult at lower temperatures could not be observed. Changes in biomass and elemental composition (*W*, C, and N) were studied throughout larval and early megalopa development. Initial biomass was about twice as high as in lecithotrophic larval developments previously reported for subantarctic lithodids, and only a minimal shift (9.2 to 8.9) in C:N mass ratio was observed from the Zoea I to the megalopa stage; at the same time an even decrease of both C and N indicated no bias toward the depletion of lipids. Very thin exuviae cast at moult support the view of energy-saving adaptations throughout larval development. The cost of higher maternal investment into single offspring and the lack of evidence for successful larval development at temperatures typical of Southern Ocean deep waters, pose questions with regard to the frequency of successful recruitment events of lithodid crabs at their lower physiological temperature tolerance. Significant intraspecific variability in larval energetic fitness at hatching between females, suggesting variability in offspring fitness, may additionally constrain on offspring survival.

1. Introduction

Lithodid crabs are cold-adapted benthic top predators that are found globally in the deep sea as well as in shallow waters of subpolar latitudes, where some species sustain large fisheries (Zaklan, 2002, and references therein). Research into this decapod family in recent years has been driven by a steep increase in the discovery rate of new species (Macpherson, 2004; Spiridonov et al., 2006; Hall and Thatje, 2009a,b), the potential for opening new fisheries (López-Abellán and Balguerías, 1994; Watters, 1997; Collins et al., 2002; Purves et al., 2003), as well as biogeographic range shifts, either as introduced species and/or in response to climate warming (Orlov and Ivanov, 1978; Jorgensen et al., 2005; Thatje et al., 2005a; Aronson et al., 2007).

From an evolutionary perspective, lithodids present an intriguing case for the study of the effects of temperature on the global radiation of marine invertebrates. Temperature constraints are thought to have restricted most extant shallow water genera to the North Pacific; only deep-water lineages uncoupled from seasonal temperature fluctuations in shallow waters and radiated globally through the deep oceans (Zaklan, 2002; Hall and Thatje, 2009a,b). This radiation through a food limited and cold-water environment has selected for a predominantly lecithotrophic feeding mode in lithodid crabs currently inhabiting the Southern Ocean; to date no exception from this pattern has been reported (Thatje et al., 2005a; Watts et al., 2006). Larval lecithotrophy is discussed to be among the key features that enabled lithodid crabs to colonise deep-sea and polar environments by uncoupling from the mismatch of prolonged larval developments at low temperatures and limited or strongly seasonal food supply (Thatje et al., 2003a,b, 2005b).

The loss of actively feeding larvae is still apparent in those lithodid species that secondarily emerged from the deep to colonising the shallow-waters of the subantarctic Magellan region, where larval lecithotrophy may be regarded as an indicator of deep-sea ancestry (Strathmann, 1978; Hall and Thatje, 2009b).

Here, we present evidence for larval and early juvenile lecithotrophy in the lithodid crab *Paralomis spinosissima* from deep waters off South Georgia, south of the Polar Front. Adult populations of this species are known to thrive at the lower thermal limit for the family of approximately 1 °C (Collins et al., 2002; Thatje et al., 2005a). Different levels of endotrophy throughout early ontogenetic stages within the Lithodidae are discussed with regard to the concept of evolutionary temperature adaptation (for review see Clarke, 2003), and the potential of lithodids to radiate through low-temperature water bodies (Zaklan, 2002; Hall and Thatje, 2009b).

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* Corresponding author. Tel.: +44 2380 596449; fax: +44 2380 593059.
E-mail address: svth@noc.soton.ac.uk (S. Thatje).

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2. Materials and methods

2.1. Capture and maintenance of ovigerous females

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 to December 2004. Crabs were held in tanks in the controlled temperature facility at the King Edward Point applied fisheries research station. They were kept in re-circulating seawater at 1.8–3.0 °C matching in situ temperature (1.4 to 2.2 °C, Collins et al., 2002) 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. Ovigerous females were taken into individual flow-through tanks of approximately 20 L water content when first hatching of larvae was observed (Reid et al., 2007).

2.2. Rearing of larvae

Freshly hatched larvae were collected from the bottom of the tanks every morning, since most larvae hatched at night. Tanks were checked and cleaned every evening for single day hatchers in order to ensure that larval age did not vary by more than 12 h.

Actively moving larvae were randomly selected and kept in individual bowls with about 100 mL seawater. Larvae were cultured at constant 5 °C (±0.5), as preliminary studies had not achieved any successful moult of larvae at lower temperatures (2–3 °C). All larval stages were cultured in absence of food, based on previous study (Watts et al., 2006) indicating that larvae of *P. spinosissima* are lecithotrophic (for discussion see Lovrich et al., 2003; Calcagno et al., 2004).

The larvae were checked daily for deaths or moults, and shed exuviae were sampled for later analyses of biomass loss (see below). Water was changed every two days. Larvae of *P. spinosissima* passed invariably through two zoeal stages and one megalopa stage. The separation of the different stages was done on the basis of an appearing exuvia and morphological changes in the larvae (Watts et al., 2006). Upon reaching the benthic megalopa, a piece of nylon mesh was placed in each bowl as an artificial substrate, which facilitated the settlement and metamorphosis of the megalopa.

2.3. Sampling for elemental analyses

Samples for determinations of dry weight (*W*) and elemental composition (C, N; with $n=5$ replicates each; one individual per replicate) were taken immediately after hatching and in variable intervals during later development (see Table 2); all larvae resulted from the same female. A comparison of intraspecific variability of egg energy contents at hatching was done using freshly hatched larvae from 6 females. Exuviae were sampled from each larval stage in order to quantify biomass losses during successive moults. Since a minimum of 0.2 mg dry mass is needed for each elemental analysis, up to 10 exuviae (originating from various females) per replicate sample were pooled (Lovrich et al., 2003).

Weight measurements were carried out to the nearest of 1 µg with a Micro Balance (Sartorius ME5). Techniques and equipment used for obtaining C, and N content of larvae and megalopae were the same as described by Anger and Harms (1990): short rinsing in distilled water, blotting on fluff-free Kleenex paper for optical use, freezing at −80 °C, vacuum drying at $<10^{-2}$ mbar, weighing and combusting at 1020 °C in a Fison (Carlo Erba) 1108 Elemental Analyser.

2.4. Statistical analysis

The number of larvae per female ($n=5$) and the result from the analysis of homogeneity of variances did not allow the use of the one-way ANOVA to test for significant differences in hatched larvae from different females; consequently the non-parametric Kruskal–Wallis test was applied. Where average values with error estimates are given in the text or in figures and tables, these represent arithmetic mean values ± standard deviation (SD).

Table 1
Paralomis spinosissima. Developmental time for larval and early juvenile stages reared at 5 °C (±0.5); larvae obtained from female A.

	Developmental time (days)		
	n	$\bar{x}$	±SD
Zoea I	24	12.3	1.8
Zoea II	20	24.4	0.9
Megalopa	3	107.0	22.9
Crab I	3	290.7	34.4

3. Results

3.1. Larval and early juvenile development

The early ontogenetic development was followed throughout the larval stages and up to the moult to the crab II juvenile stage. *Paralomis spinosissima* larval development consisted of two zoeal and one megalopa stage, which at the incubation temperature of 5 °C (±0.5) lasted 12, 24, and 107 days in duration, respectively (Table 1). The crab I instar took 290 days for completion. The entire development up to the moult to the crab II instar took place in absence of food. Because of limited incubator space, no separate culture for the study of larval developmental times and mortality was possible. Thus, developmental times derived from specimens tracked up to a certain stage within the cultures for elemental analyses. Morphological descriptions of the larval instars are published elsewhere (Watts et al., 2006).

3.2. Dry weight, percentage C, N, and C:N mass ratio

A continuous decrease of *W* from hatching to reaching the megalopa stage was observed (Table 2, Fig. 1). Upon reaching the megalopa stage (about 30 days after hatching), the average W had decreased to 83% of the initial value measured at hatching (Table 2). The losses of C and N were in the same range throughout that period, and consequently the C:N mass ratio remained stable until the early phase of the megalopa stage, when sampling ended because of lack of material available.

The C:N mass ratio pattern suggests that the lipid:protein ratio remained rather unchanged as well, but with a slight decrease from 9.2 to 8.9 from the Zoea II–megalopa transition (Table 2, Fig. 1). Regardless of the absence of food, a minimal shift in the lipid–protein ratio indicates a rather moderate bias towards use of lipids for development, but a balanced depletion of both lipids and proteins throughout larval and early megalopa development.

A comparison of elemental composition of larvae at hatching from six different females presents significantly different energy contents of larvae as a result of differences of maternal investment into offspring (Tables 4 and 5). For the six females tested, mean initial larval W, C, and N contents varied by about 17, 7, and 7%, respectively, which is reflected in the C:N mass ratio as well (Tables 4 and 5, Fig. 2).

3.3. Exuvial losses

No complete exuvia of the megalopa stage could be retrieved and thus only data for the larval stages are presented (Table 3). Total dry weight (*W*) and contents of C and N per exuvia were low in the zoeal stages and comparable with that of congener from the Subantarctic (Calcagno et al., 2003). The percentage C and N (in % of *W*) in exuviae

Table 2
Paralomis spinosissima. Changes in dry weight (*W*), content of carbon (C), and nitrogen (N) (all in µg/individual and in % of *W*), and C:N mass ratio during lecithotrophic zoeal and megalopa development; age given in days (a) within each stage and (b) after hatching (larvae from female A).

Stage	Age (days)			*W*		C		N		C:N mass ratio	
	(a)	(b)		$\overline{x}$	± SD	$\overline{x}$	± SD	$\overline{x}$	± SD	$\overline{x}$	± SD
Zoea I	0	0	µg/ind	2259.9	112.8	1192.1	68.0	129.5	6.1	9.2	0.2
			% of *W*			53.0	5.5	5.8	0.6		
	5	5	µg/ind	2077.1	98.8	1158.8	62.4	122.1	7.9	9.5	0.3
			% of *W*			55.8	0.4	5.9	0.2		
	9	9	µg/ind	2025.0	72.8	1127.0	37.5	122.0	5.2	9.2	0.3
			% of *W*			55.7	0.3	6.0	0.2		
Zoea II	5	19	µg/ind	1906.2	113.8	1047.9	62.8	114.0	7.1	9.2	0.3
			% of *W*			55.0	0.4	6.0	0.2		
	10	24	µg/ind	2013.5	46.1	1094.1	30.0	119.1	5.0	9.2	0.2
			% of *W*			54.3	0.7	5.9	0.1		
Megalopa	5	30	µg/ind	1881.4	172.3	983.9	75.2	110.9	6.1	8.9	0.4
			% of *W*			52.4	1.5	5.9	0.3		

was in general far below that of the whole body, while exuvial C:N mass ratio was much lower than in total *W* of larvae (Table 3).

The zoeal stage produced very thin exuviae, with low contents of C and N. Upon reaching the megalopa stage, the cumulative exuvial loss accounted for only 6.4% of larval premoult *W*, and about 2.2 and 7.4% of premoult C and N, respectively.

4. Discussion

4.1. Larval development at temperature limits

Lithodid crabs in the Southern Ocean live close to the lower temperature tolerance threshold (Thatje et al., 2005a; Hall and Thatje, 2009b). Most species recorded from waters south of the polar front inhabit the deep sea or seamounts, at measured in situ temperatures as low as 1 to 2.2 °C (Klages et al., 1995; Collins et al., 2002; Thatje et al., 2008). This lower threshold of lithodid temperature tolerance may also explain the absence of species from this decapod family from the high-Antarctic continental shelves, where sub-zero water temperatures are prevailing (for review see Aronson et al., 2007).

In *P. spinosissima*, larval development surprisingly failed at temperatures lower than 5 °C, although multiple, systematic attempts had been made. Initial cultures maintained at 2–3 °C failed to develop and most larvae died during ecdysis. If larvae do not tolerate temperatures typically found *in situ* this poses a major question as to where larval development takes place in the field. Lithodid larvae

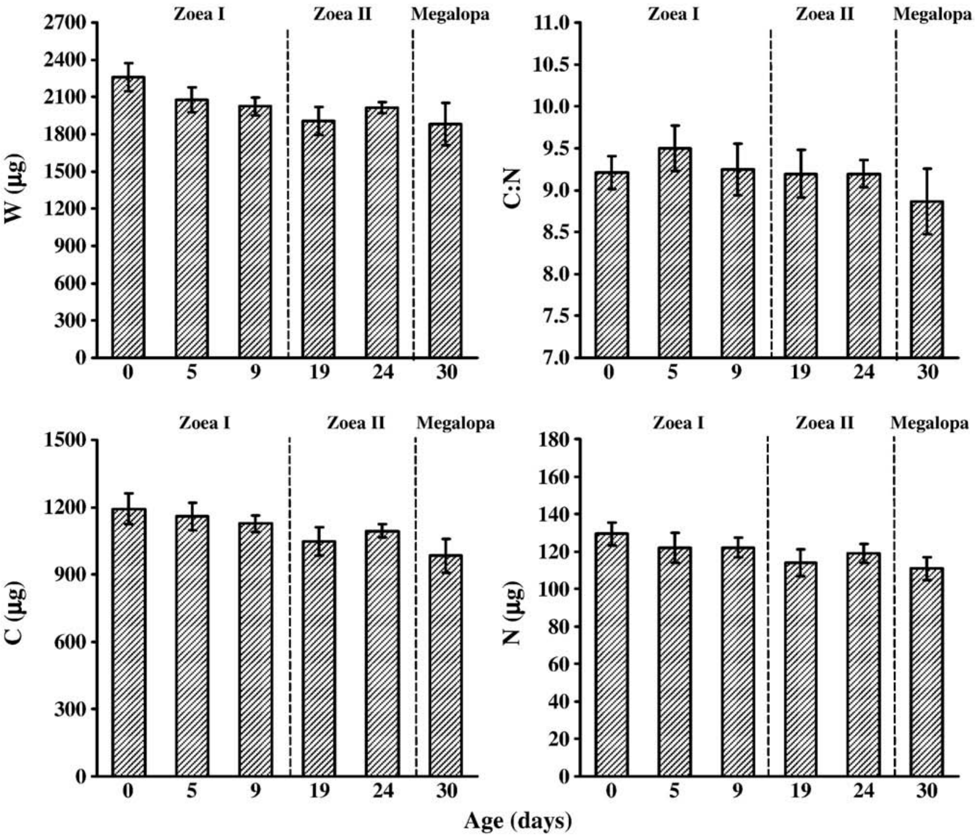

Fig. 1. *Paralomis spinosissima*. Changes in dry weight (*W*), content of carbon (C), and nitrogen (N) (all in µg/individual of *W*), and C:N mass ratio during lecithotrophic zoeal and megalopa development; age given in days after hatching. Sample size, *n* = 5 for each stage; larvae from female A.

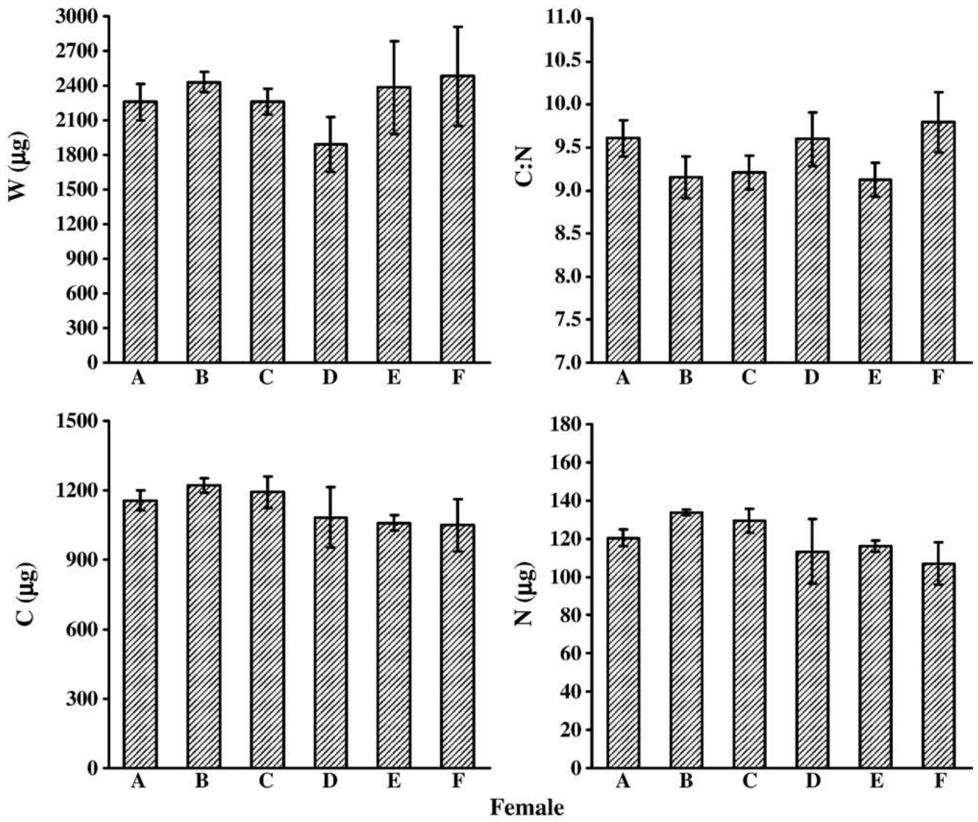

Fig. 2. *Paralomis spinosissima*. Dry weight (*W*), contents of carbon (C), and nitrogen (N) (all in µg/individual of *W*), and C:N mass ratio of larvae from different females at hatching; (for number of larvae per female see Table 4).

did not exhibit any swimming activity in our experiments and are generally assumed to occur as demersal drifters only (Lovrich, 1999; Thatje et al., 2003a). There is no record of lithodid larvae collected from Southern Ocean waters to date and the record of premature juveniles is limited to a single find from the continental slope of the Bellingshausen Sea (Thatje et al., 2008). Data presented in this study support the view that the cold tolerance of lithodid larvae is among the key features for their survival as the only anomuran crab family in Antarctic deep-waters, but at the same time also their potential weakness to the colonisation of high-polar seas (Thatje et al., 2005a).

Ovigerous females used in the present study were obtained from longline by-catch (usually from about 900 to 1100 m water depth). Adult specimens in some cases have been maintained at King Edward Point labs for periods of over 2 years (Reid et al., 2007). It is possible that the embryos suffered from some effect of depressurisation, which may have affected the cold tolerance of later larvae; this however remains entire speculation and requires further investigation.

Lithodid crabs are slowly maturing species and the subantarctic *Paralomis granulosa* and *Lithodes santolla*, living in waters with a seasonal temperature variation between approximately 6 and 10 °C (Anger et al., 2004), are known to mature at an approximate age of 12 and 6 years, respectively (Lovrich and Vinuesa, 1999). At considerably lower temperatures of the Southern Ocean, maturity may delay significantly, possibly by many years if not decades (for discussion see also Clarke, 2003; Reid et al., 2007). At the same time successful reproduction and recruitment into adult populations is likely not following an annual cycle (Reid et al., 2007), which would also explain the missing of small size classes of lithodids from most studies (Collins et al., 2002; Thatje et al., 2008). Because lithodid larval development in the Southern Ocean is taking place at a lower thermal limit, we hypothesise that successful development may depend on other extrinsic factors such as a slight increase in water temperature, which could be the cause of interdecadal climate variability (ENSO),

Table 3

Paralomis spinosissima. Dry weight (*W*), contents of carbon (C), and nitrogen (N) (all in µg/individual and in % of *W*), and C:N mass ratio of the exuviae of all larval stages; *n* = number of exuviae.

Stage	*n*		*W*		C		N		C:N mass ratio	
			$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD
Zoea I	37	µg/ind	63.2	2.6	13.0	0.7	2.5	0.1	5.2	0.1
		% of *W*			20.5	1.3	3.9	0.2		
Zoea II	7	µg/ind	80.2		13.3		2.5		5.4	
		% of *W*			16.5		3.1			

Table 4

Paralomis spinosissima. Dry weight (*W*), contents of carbon (C), and nitrogen (N) (all in µg/individual and in % of *W*), and C:N mass ratio of larvae from different females at hatching; *n* = number of replicates.

Female	*n*		*W*		C		N		C:N mass ratio	
			$\bar{x}$	±S.D.	$\bar{x}$	±S.D.	$\bar{x}$	±S.D.	$\bar{x}$	±S.D.
A	5	µg/ind	2258.7	155.5	1156.6	42.7	120.4	4.3	9.6	0.2
		% of *W*			51.4	4.4	5.3	0.4		
B	5	µg/ind	2430.9	89.1	1223.0	31.3	133.7	1.5	9.2	0.2
		% of *W*			50.3	1.5	5.5	0.2		
C	5	µg/ind	2259.9	112.8	1192.1	68.0	129.5	6.1	9.2	0.2
		% of *W*			53.0	5.5	5.8	0.6		
D	5	µg/ind	1891.5	239.0	1083.7	129.4	113.3	16.8	9.6	0.3
		% of *W*			57.3	0.8	6.0	0.2		
E	5	µg/ind	2383.1	400.8	1059.0	34.0	116.0	3.0	9.1	0.2
		% of *W*			45.3	6.7	5.0	0.8		
F	4	µg/ind	2480.3	427.0	1049.4	113.3	107.1	10.9	9.8	0.3
		% of *W*			42.7	3.1	4.4	0.4		

Fig. 3. *Paralomis spinosissima.* Live image of megalopa stage with notably high amount of lipids visible in the carapace; carapace length (measured from the base of the rostral spine to the posterolateral margin of the carapace) = 3.05 mm.

known to affect the Antarctic circum-polar wave and local temperature regimes of the Southern Ocean (Verdy et al., 2006).

4.2. More energy into eggs, and energy efficiency

The level of endotrophy observed up to the crab II instar of *P. spinosissima* after about 14 months of development, is exceeding any previous records for lithodid lecithotrophic larval developments (Thatje et al., 2005a, and references therein). Previous studies on subpolar lithodids had demonstrated larval and megalopa lecithotrophy, with the need for feeding on reaching the crab I instar (Anger, 1996; Calcagno et al., 2003; Lovrich et al., 2003). In the subantarctic *P. granulosa* and *L. santolla*, distinct levels of lipid depletion of maternal origin by the end of the megalopa stage had been reported, but despite remaining energy reserves at this stage, crab I instars had to feed (Kattner et al., 2003; Saborowski et al., 2006). The C:N mass ratio in *P. spinosissima* is higher than in the subantarctic species but similar to that of the sub-Arctic *L. maja* (Fig. 4). Percentage depletion of C, N from hatching to the megalopa stage is comparable between all species studied to date, despite differences in the experienced environmental temperature (Fig. 4). For *P. spinosissima*, the much higher investment of total energy into the single offspring with dry mass being more than twice as high as in the other species is rather surprising (Fig. 4). The total energy available to the individual larva is thus higher than in any other subpolar lithodid species studied to date, and allows for lecithotrophic development over exceptionally long period (Fig. 3), making the early ontogeny of this species independent from any variability in food supply. However, it remains uncertain whether facultative feeding is possible from the crab I instar, as feeding occurs in the crab I stage of subpolar species (Anger, 1996; Calcagno et al., 2003; Saborowski et al., 2006).

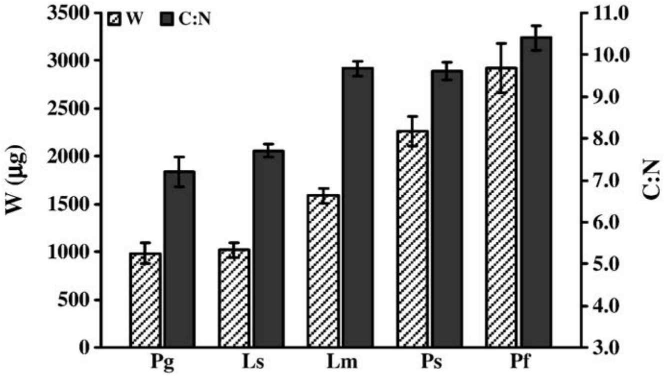

Fig. 4. Comparison of C:N ratios and *W* in freshly hatched Zoea I larvae of lithodid species of the genera *Paralomis* and *Lithodes*; *P. granulosa* (Pg); *P. spinosissima* (Ps); *P. formosa* (Pf); *L. santolla* (Ls); *L. maja* (Lm); data derived from Calcagno et al. (2003), this study (female A), Thatje (unpublished), Lovrich et al. (2003), Anger (1996), respectively. Sample procedure and analyses are as in present work. Sample sizes: $n = 5$ larvae from single female in Lm, Ls, Pg, and Ps; $n = 4$ larvae from each of 2 females in Pf.

Table 5
Paralomis spinosissima. Kruskal–Wallis analysis of variance testing the differences between female larvae at hatching for each biomass parameter analysed (*H* statistic (degrees of freedom, n = number of replicates)).

Biomass parameter	*H* (5, n = 29)	*p*-value
W	12.066	0.034
C	15.699	0.008
N	18.132	0.003
C:N	16.834	0.005

Larval lecithotrophy in lithodids is likely the result of their global radiation through the deep sea (Hall and Thatje, 2009b) and different levels in energy allocation into offspring may represent a response to changes in local ambient temperature (for discussion see also Fischer et al., 2009). Decapod crustaceans are among the best-studied taxa that indicate to follow a latitudinal cline in eggs size (as a measure of energy content) with temperature across latitude (Clarke, 1987; Lovrich et al., 2005; Wehrtmann and Kattner, 1998; Thatje et al., 2005b). Recent studies furthermore demonstrated that an increased energy allocation into eggs in populations of the brachyuran crab *Cancer setosus* is triggered by temperature alone and including increased energy efficiency in embryos developing at lower temperatures (Fischer and Thatje, 2008; Fischer et al., 2009). In addition, Morley et al. (2006) demonstrated a size related cline in egg size with increasing female size in lithodid species from South Georgia, as well as an increase of eggs size with water depth, with *P. spinosissima* presenting the overall smallest eggs in all South Georgia species. Variability in egg size is supported by the findings of intraspecific variability in egg energy contents between females of the present study (Fig. 2), although the observed variability cannot be assigned to exact sampling depth. In addition, different levels of egg energy contents may potentially translate into later-life juvenile fitness and survival (for discussion see Giménez, 2006).

Despite the highest known level of energetic adaptation in any lithodid larval development reported so far for *P. spinosissima*, an even higher level of endotrophy is to be expected in the truly abyssal Neolithodidae, with *Neolithodes diomedeae* from waters off South Georgia having eggs almost twice as big as that of *P. spinosissima* (Morley et al., 2006).

In conclusion, slow larval and early juvenile developments, a high maternal energy investment into the single offspring, an embryonic development lasting at least 2 years in duration (Reid et al., 2007), and overall slow growth in adults (Reid et al., 2007) make the lithodid stocks off South Georgia (Collins et al., 2002; Purves et al., 2003) potentially vulnerable to any fisheries impact of commercial scale. In addition to the early life history data presented here, it is important to assess adult growth rate and age at maturity in order to fully understand the extent of lithodid life history adaptation in response to polar temperatures.

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