

Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: tolerance of cold and food limitation in a lithodid crab from high latitudes

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ABSTRACT: *Paralomis granulosa* Jacquinot is a commercially fished lithodid crab species living in subantarctic and cold-temperate regions of southern South America. Its larval stages (Zoea I, II, Megalopa) are fully lecithotrophic, developing in the complete absence of food from hatching through metamorphosis; first feeding occurs in the first juvenile crab stage. In laboratory rearing experiments conducted at constant 1, 3, 6, 9, 12, and 15°C, we studied rates of larval and early juvenile survival and development in relation to temperature. At 1°C, many larvae (52%) reached the Megalopa stage almost 2 mo after hatching, but all died subsequently without passing through metamorphosis. Larval development was successfully completed at all other temperatures, with maximum survival at 6 to 9°C. The time of non-feeding larval development from hatching to metamorphosis lasted, on average, from 24 d (at 15°C) to almost 4 mo (117 d, at 3°C). When the experiment was terminated 1 yr after hatching, the 3rd (3°C) to 8th (15°C) juvenile crab instar had been reached. The relationship between the time of development through individual larval or juvenile stages (y) and temperature (T) was described as a power function ($y = a \times T^b$, or $\log[y] = \log[a] + b \cdot \log[T]$); the same regression model was also used to describe the temperature-dependence of cumulative periods of development from hatching. The wide thermal tolerance window for successful larval development (at least 3 to 15°C) and the broad geographic range of this species show that the early life-cycle stages of *P. granulosa* are cold-eurythermal. This physiological trait together with larval independence of food indicate that this lithodid crab species is well adapted to severe conditions of cold in combination with the food-limitation in subantarctic regions. Since similar traits have been also observed in other Lithodidae, we suggest that early life-history adaptations to low temperatures and low planktonic productivity may explain the high number of lithodid species occurring at high latitudes and in the deep sea, i.e. in conditions under which other Decapoda show strongly reduced diversity.

KEY WORDS: Lithodidae · *Paralomis granulosa* · Temperature · Larval development · Juvenile growth · Cold tolerance

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INTRODUCTION

A macroecological pattern in the geographical distribution of higher animal and plant taxa is a decreasing trend in species diversity from low latitudes towards the poles (for recent review of the literature, examples, and discussion of relevant theories see Chown et al.

2000). Among the marine benthic invertebrates, this pattern has been particularly well documented for molluscs and crustaceans (e.g. Knox 1994, Clarke 1997, Crame & Clarke 1997). In a recent review of the distribution and life histories of temperate and antitropical Decapoda of the SW Atlantic Ocean, Spivak (1997) listed a total of 243 species reported from the South

American coasts from 25 to 55° S. Among these, only 37 species (15%) have been found in the southernmost region including Tierra del Fuego, the Falkland Islands (Islas Malvinas) and South Georgia (ca. 50 to 55° S). In another biogeographical review for the entire antiboreal region south of ~42° S (including the southern parts of the Atlantic, Pacific and Indian Oceans) Gorny (1999) listed 132 decapod crustacean species, with only 12 (9%) of these occurring south of the Antarctic Convergence. The impoverishment of the Antarctic decapod fauna during periods of climate cooling, about 20 million yr ago, is well documented in the fossil record also (Clarke 1993, Crame 1999, Stillewell & Feldmann 2000), indicating that declining temperatures and/or associated factors such as low productivity were critical factors in this process.

Besides food limitation in high-latitude environments (Knox 1994), physiological constraints to evolutionary cold adaptation are considered a principal cause of these patterns in biodiversity (Pörtner et al. 2000). In ectothermic animals in particular, their energetic metabolism appears to be affected by both unfavourably high and unfavourably low temperatures. When temperature drops below a species-specific critical level, insufficient aerobic capacity of the mitochondria leads to a shift towards an anaerobic mode of metabolism and, as a consequence, to an insufficient supply of cellular energy (for review of physiological mechanisms see Pörtner 2001, 2002). In most marine decapod taxa, this problem appears to be aggravated by synergistic effects of Mg^{2+} ions, which reduce the scope for activity, especially at low temperatures (Frederich et al. 2000, 2001). Since the Decapoda and other marine invertebrates in high latitudes originated from warm-water ancestors (Arntz et al. 1994), the physiological problems typically faced under cold conditions require special evolutionary adaptations (Pörtner 2002), implying that relatively few, particularly adaptable, species may be successful.

Within the complex life cycles of decapod crustaceans and other marine invertebrates, the early (larval and juvenile) stages represent a physiological bottleneck, as they are generally more vulnerable to thermal, nutritional and other stress than the conspecific adults (for review see Anger 2001). In high latitudes, a mismatch of low water temperatures (causing long development times) and a short season of plankton production (implying lack of food throughout most of their pelagic development) should select against planktonic larvae. This may explain another macroecological pattern, namely a decreasing tendency in the number of species with planktonic larvae in latitudinal clines from warm to cold regions, i.e. 'Thorson's rule' (Thorson 1950; for recent discussion see Gallardo & Penchaszadeh 2001). While many species in high lati-

tudes have evolved an abbreviated, often non-feeding mode of larval development (Gore 1985, Rabalais & Gore 1985, Anger 2001), others have completely suppressed their planktonic larval phase. However, phylogenetic constraints may, in some taxa, prevent the evolution of an abbreviated or direct mode of development, so that the particular vulnerability of larvae may have contributed to the latitudinal gradients in biodiversity.

Despite severe problems associated with cold- and food-limited conditions in high latitudes, however, several decapod taxa have successfully adapted to Arctic or Antarctic biota (Christiansen & Christiansen 1962, Arntz & Gorny 1991, Arntz et al. 1997, 1999, Gorny 1999, Paul et al. 2002). In addition to some caridean shrimps and pagurid hermit crabs, this is most conspicuous in the distribution of stone crabs or king crabs (Lithodidae; for recent review see Zaklan 2002). In Spivak's (1997) species list, only 9 (3.7%) out of 243 decapod species recorded for the SW Atlantic region belong to this family, but 7 of these 9 (i.e. 78%) occur in the southernmost parts of this area, where they contribute about 19% to the regional decapod fauna. Similarly, 18 of 80 crab species recorded for the cold-temperate and subarctic waters of Alaska (22%) are lithodids (Stevens 2002), while warm-temperate and tropical decapod faunas show typically much lower proportions of stone crabs (for references see Dawson 1989). Moreover, recent observations have shown that lithodid crabs occur also in the extremely cold coastal waters of Greenland (Woll & Burmeister 2002) and in the high Antarctic Sea (Klages et al. 1995, Arana & Retamal 1999). It is thus not surprising that lithodids belong also to the most typical inhabitants of another cold- and food-limited environment, the deep sea (Chevaldonné & Olu 1996, Rex & Etter 1997, Gorny 1999, Zaklan 2002).

Since, as far as is known, the Lithodidae have several larval stages (McLaughlin et al. 2001, in press, and earlier papers cited therein), special adaptations to the conditions prevailing in high latitudes or in the deep sea are also required in their early life-history stages. Compared with other Anomura (including the closely related pagurid hermit crabs), lithodid crabs show tendencies towards an abbreviation of the pelagic larval phase and lecithotrophy, i.e. towards a food-independent mode of larval development (Anger 1996, Shirley & Zhou 1997, Lovrich et al. 2003). This holds true also for the subject of the present study, the subantarctic stone crab *Paralomis granulosa* Jacquinet. Recent observations on its larval development (comprising only 2 zoeal stages and a megalopa: Campodonico & Guzman 1981, McLaughlin et al. in press), larval survival and biochemical composition in laboratory cultures with and without food have shown that its

development from hatching to metamorphosis is fully endotrophic, being mainly based on a degradation of internal lipid reserves remaining from the egg yolk (Calcagno et al. in press, Kattner et al. in press).

Complete larval independence of external food sources may be considered a reproductive adaptation of *Paralomis granulosa* to conditions of low or seasonally brief productivity in subantarctic regions. In addition, in this species we would also expect larval adaptations to low temperatures. Since the zoeae hatch during the austral winter (Lovrich & Vinuesa 1999), they should be cold-tolerant, and their endotrophic potential should suffice for extended periods (weeks to months) of non-feeding development in the plankton. However, very little is known about the effects of temperature on the early life-history stages of this species. In a previous experimental study (Vinuesa et al. 1989), most larvae died in the zoeal stages, and metamorphosis from the megalopa to the first juvenile stage was not reached in any of the conditions tested (5 to 14°C).

In the present investigation on *Paralomis granulosa*, we studied the influence of temperature on survival and development of larvae and early juveniles, attempting to identify early life-history adaptations in this subantarctic species. Possible adaptive traits should also enhance our understanding of macroecological patterns such as latitudinal gradients in biodiversity, Thorson's rule, and the exceptional role of the Lithodidae within these patterns.

MATERIALS AND METHODS

The capture and maintenance of *Paralomis granulosa* as well as the rearing of their larvae are described in detail by Lovrich et al. (2003) and Calcagno et al. (in press). Briefly, ovigerous females were collected in April 2001 from the Beagle Channel (Tierra del Fuego, southern Argentina) using commercial fishing boats (for details of local crab fisheries see Lovrich 1997). They were kept in flow-through seawater aquaria at the local research institute (Centro Austral de Investigaciones Científicas), and eventually transported with the German research icebreaker 'Polarstern' to the marine biological laboratory on Helgoland (Biologische Anstalt Helgoland), Germany. Subsequently, the crabs were maintained in flow-through seawater aquaria at a constant 6°C, ca. 32‰, and a 12:12 h light:dark cycle.

Freshly hatched, actively swimming larvae from 3 different females (A, B, C) were randomly selected and subsequently reared in individual 100 ml bowls kept under the same conditions of salinity and light. Since *Paralomis granulosa* releases only low numbers of larvae per night (normally <100, similar to the number

reported for another lithodid species, *Lithodes maja*; see Anger 1996), we had to start 'parallel' experiments with different rearing temperatures using sibling larvae that hatched on different days. As rearing temperatures, we used 1, 3, 6, 9, 12 and 15°C; the lowest and the highest temperature, however, were tested only with larvae from 1 hatch (A). The initial number of larvae per treatment and hatch was $n = 48$, except for the experiment with Hatch B larvae reared at 9°C, where insufficient material allowed an initial number of only 46.

The larvae were reared without addition of food, since previous experiments (McLaughlin et al. 2001, in press, Calcagno et al. in press, Kattner et al. in press) had shown that all larval stages of *Paralomis granulosa* are non-feeding. From the day of metamorphosis onwards, juvenile crabs were fed with *Artemia* sp. nauplii. At 9 to 15°C the culture water (and for juveniles also the food) was changed every other day; at lower temperatures the changes were made every third day. In all treatments, the larvae or juveniles were checked daily for moults or mortality.

The rearing experiments with 1 hatch (A) were continued throughout 1 yr, from August 2001 to August 2002, while all other experiments were terminated as soon as Crab Stage II was reached. Because of accidental loss of data, the experiment with Hatch A larvae reared at 12°C was prematurely terminated at Crab Stage III (instar stage), so no data were obtained for later juvenile stages in this group.

Our statistical analyses followed Sokal & Rohlf (1995). A 1-way ANOVA followed by comparisons between pairs of means was used for comparing survival and time of development at each larval stage. The durations of individual (larval or juvenile) stages as well as cumulative periods of development (e.g. from hatching to metamorphosis) are described as power functions of temperature (i.e. as linear regressions after log-transformation of both variables). Arithmetic mean values for different females rather than individual data were used as replicate values in the regression analyses. Slope parameters of the linearized regressions were compared with a test for heterogeneity of slopes using *F* statistics. Where average values with error estimates are given in the text or in figures and tables, these represent arithmetic mean values ± 1 SD.

RESULTS

Rates of survival

The survival of *Paralomis granulosa* through successive larval and juvenile stages varied greatly among temperatures and, at identical temperatures, among

hatches from different females (Table 1). Since the experiments with Hatches B and C were conducted only at 3 to 12°C and, moreover, terminated at Crab Stage II, the survival rates of different hatches can be compared only in this temperature range and only in the larval stages and in the first juvenile instar. For all larval stages, Hatch C showed lower survival than the other 2 hatches, except at 12°C. In contrast, Hatch A showed high survival of all larval stages, but high mortality at the first crab stage at 12°C and not at the other temperatures.

While the comparison among different hatches did not reveal a clear pattern, temperature was shown to have strong effects on survival. At the lowest temperature (1°C, tested only for Hatch A), 52% of the larvae survived through the 2 zoeal stages, but none of the survivors reached metamorphosis; i.e. complete mortality occurred at the Megalopa stage. The next higher temperature (3°C) allowed for 10 to 31% survival from hatching through metamorphosis in all hatches; however, complete mortality subsequently occurred at the first or second juvenile stage (Table 1). The highest level of survival was observed at 6°C, with a decreasing tendency at higher temperatures (accidental loss of data precluded inclusion of 12°C). When the experiments were terminated 1 yr after hatching, the survivors had maximally reached Juvenile Instars II (3°C), VI (6°C), VII (9°C), and VIII (15°C). Tables 1 to 3 show survival and development data for the latest juvenile instars near the end of the experiments only when all surviving individuals at a given temperature had reached these stages in August 2002. For instance, at 15°C, some crabs were at that time already in Juvenile

Stage VIII, while others were still at Stage VI; in this case, the data for Stages VII and VIII were incomplete and thus not included in our tables or statistical analyses.

Rates of development

The development times of individual larval and juvenile stages are given in Table 2, the cumulative development times from hatching in Table 3. Among larvae originating from different females, statistically significant differences in individual stage durations were observed only in the 2 zoeal stages reared at 3 and 12°C. Variability among hatches often showed opposite tendencies in successive stages; e.g. Zoea I duration was shorter in Hatch A than in Hatch B, but Zoea II was longer in Hatch A than in Hatch B; Table 2). As a corollary, the cumulative durations to successive stages at identical temperatures were generally similar among the 3 hatches (no statistically significant differences: Table 3).

Increasing temperature had a clearly accelerating effect on development, especially in the lower temperature range. While an increase from 1 to 3°C or from 3 to 6°C caused a substantial decrease in moult-cycle duration in all stages, the differences observed between 12 and 15°C were mostly insignificant, the only exception being the Megalopa (Table 2). Within the temperature range tested in this study (1 to 15°C), the Zoea I lasted on average 3 to 17 d and Zoea II 4 to 39 d. The Megalopa stage (data available only for 3 to 15°C) lasted 17 to 84 d. Complete larval development from hatching to

Table 1. *Paralomis granulosa*. Rates of survival of individual developmental stages (% of survivors to a given stage) and cumulative survival from hatching to a given stage (as % of initial number at hatching [cum. %]). n = 46 for Female B at 9°C, n = 48 for all other experiments. Italics and bold-face: cumulative survival

T (°C)	Female	Zoea I %	Zoea II % cum.%	Megalopa % cum.%	Crab I % cum.%	Crab II % cum.%	Crab III % cum.%	Crab IV % cum.%	Crab V % cum.%	Crab VI % cum.%
1	A	90	58	52	0	0				
3	A	94	71	67	47	31	20	6		
	B	92	66	60	38	23	0	0		
	C	79	76	44	17	10	0	0		
6	A	98	89	88	95	83	90	75	100	75
	B	90	86	77	89	69	79	54		
	C	96	70	63	59	38	58	23		
9	A	98	85	83	85	71	85	58	90	54
	B	98	78	72	71	54	100	54		
	C	100	90	90	81	73	89	54		
12	A	98	94	83	86	58	53	4	10	
	B	96	84	77	54	42	70	29		
	C	96	61	58	46	27	92	25		
15	A	98	94	83	82	73	50	38	67	25
									92	23
									91	21
									70	15
									57	8

Table 2. *Paralomis granulosa*. Duration of development (d) of successive larval and juvenile stages from 3 different females (A, B, C) at different temperatures

T (°C)	Female	Zoea I x ±SD	Zoea II x ±SD	Megalopa x ±SD	Crab I x ±SD	Crab II x ±SD	Crab III x ±SD	Crab IV x ±SD	Crab V x ±SD	Crab VI x ±SD
1	A	16.9 (1.1)	39.2 (2.7)							
3	A	7.8 (1.7)	26.9 (2.8)	83.7 (2.4)	102.3 (11.0)					
	B	9.7 (1.5)	25.5 (1.6)	82.0 (3.2)						
	C	9.6 (1.3)	21.6 (1.8)	85.8 (1.9)						
6	A	5.2 (0.5)	10.9 (0.5)	39.2 (2.2)	48.4 (3.0)	55.8 (6.4)	75.5 (15.6)	88.4 (15.4)		
	B	5.3 (0.5)	10.9 (0.5)	37.8 (1.9)	47.4 (3.5)					
	C	5.6 (1.3)	10.3 (1.0)	38.8 (1.8)	45.6 (4.0)					
9	A	3.4 (0.5)	6.3 (0.6)	31.6 (2.3)	33.8 (2.6)	37.0 (3.2)	50.6 (6.2)	53.3 (6.9)	74.8 (12.5)	74.4 (17.7)
	B	3.5 (0.5)	5.8 (0.6)	28.6 (2.8)	35.1 (2.5)					
	C	3.4 (0.5)	6.2 (0.4)	32.0 (2.7)	33.4 (1.9)					
12	A	3.0 (0.0)	4.9 (0.3)	23.0 (2.5)	24.1 (8.8)	29.5 (0.7)				
	B	4.0 (0.0)	3.5 (0.5)	22.2 (1.8)	28.0 (2.9)					
	C	4.0 (0.0)	3.5 (0.5)	24.1 (1.4)	27.4 (1.7)					
15	A	3.0 (0.0)	4.1 (0.5)	17.4 (1.6)	26.4 (2.7)	28.4 (4.8)	32.9 (5.2)	39.9 (8.9)	43.7 (4.3)	53.0 (12.8)

Table 3. *Paralomis granulosa*. Cumulative time of development (days from hatching) to successive larval and juvenile stages from 3 different females (A, B, C) at different temperatures

T (°C)	Female	Megalopa x ±SD	Crab I x ±SD	Crab II x ±SD	Crab III x ±SD	Crab IV x ±SD	Crab V x ±SD	Crab VI x ±SD	Crab VII x ±SD
1	A	56.3 (2.8)							
3	A	34.6 (3.2)	117.4 (2.7)	219.0 (9.5)					
	B	34.8 (1.3)	115.9 (3.8)						
	C	30.5 (1.5)	115.4 (2.0)						
6	A	16.0 (0.4)	55.2 (2.4)	103.7 (4.6)	154.4 (8.4)	218.5 (19.1)	266.3 (11.6)		
	B	16.2 (0.7)	54.0 (2.0)	101.5 (4.5)					
	C	15.8 (0.7)	48.9 (2.0)	99.6 (3.7)					
9	A	9.6 (0.5)	41.2 (2.5)	75.4 (3.7)	112.0 (5.5)	163.0 (8.2)	217.3 (13.1)	291.6 (21.2)	356.7 (16.7)
	B	9.3 (0.5)	37.9 (2.7)	73.0 (4.5)					
	C	9.6 (0.5)	41.5 (2.7)	74.7 (4.0)					
12	A	7.9 (0.3)	30.8 (2.9)	64.0 (5.7)					
	B	7.5 (0.5)	29.8 (1.8)	57.9 (3.9)					
	C	7.5 (0.5)	31.5 (1.2)	58.8 (1.9)					
15	A	7.1 (0.5)	24.3 (1.6)	50.6 (3.3)	78.7 (7.7)	112.0 (9.8)	150.6 (15.4)	188.4 (12.4)	240.5 (20.2)

metamorphosis took from 24 d at 15°C to 117 d at 3°C, i.e. from 3.5 wk to almost 4 mo (Table 3).

The moult-cycle duration of successive juvenile instars also showed a clear decrease with increasing temperature; e.g. the duration of Crab Stage I varied from 26 d at 15°C to 102 d at 3°C. As another consistent trend, the young crab stages showed increasing moult-cycle durations in successively later instars. At 15°C, for example, Crab Stage I lasted on average 26 d, while Crab Stage VI was about twice as long (53 d).

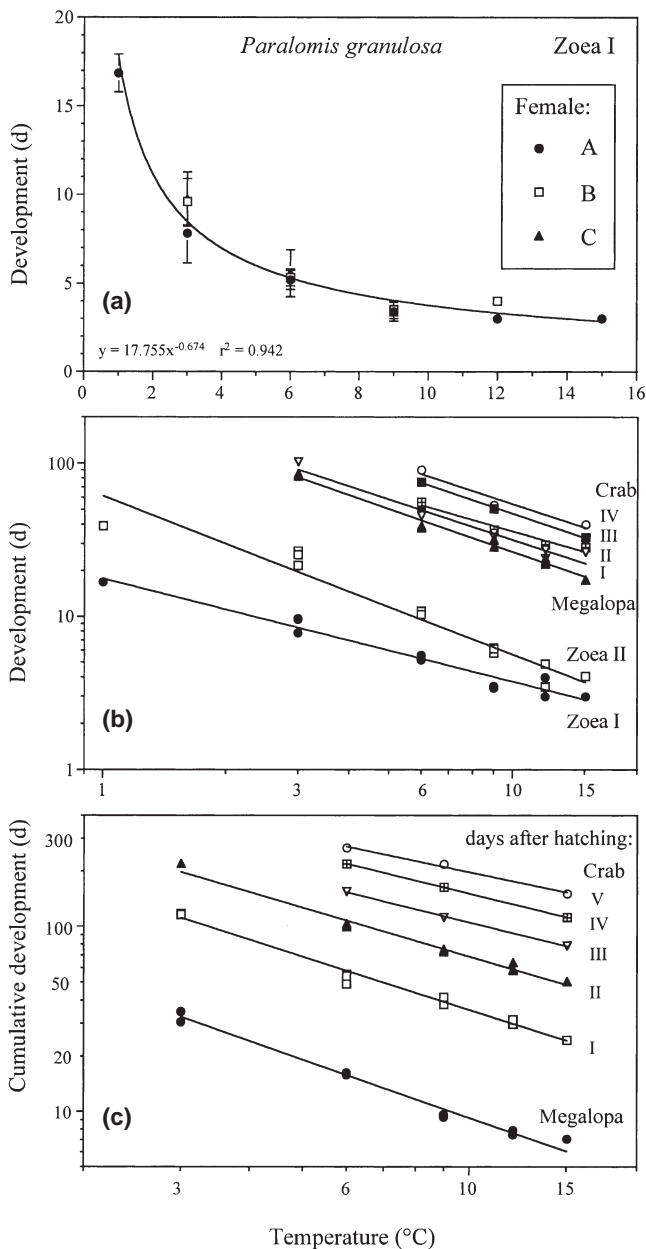
The patterns of development duration (y, days) in relation to temperature (T, °C) could generally be described with a best fit between observed and predicted data when a power function was used as a

model: $y = a \times T^b$, with a and b being fitted constants; all coefficients of determination, $R^2 > 0.9$ (Table 4). Only the data for Zoea Stage II fitted better with a logarithmic function: $y = -33.1 \times \log[T] + 38.9$; $R^2 = 0.959$; the power function yielded in this case $R^2 = 0.929$; however, since this was the only exception, herein we consistently use the power function as a general model of developmental temperature-dependence for individual stages as well as for cumulative development times from hatching to successively later stages. The fitted regression parameters and R^2 coefficients are compiled in Table 4.

These non-linear patterns are illustrated in Fig. 1a using the untransformed Zoea I data as an example.

Table 4. *Paralomis granulosa*. Fitted parameters (a, b) and coefficients of determination (R^2) of non-linear regression equations (power functions, $y = a \times T^b$) describing development time (y, days) as a function of temperature (T, °C). Dev/stage: time of development in individual stages; Cum. dev: cumulative time of development from hatching to later stages

Parameter	Zoea I	Zoea II	Megalopa	Crab I	Crab II	Crab III	Crab IV	Crab V
Dev/stage								
a	17.8	61.3	223.4	237.4	210.0	376.6	386.4	
b	-0.674	-1.036	-0.925	-0.874	-0.765	-0.904	-0.855	
R^2	0.942	0.929	0.983	0.958	0.952	0.998	0.951	
Cum. dev								
a		17.8	103.2	316.5	515.7	569.9	808.6	832.2
b		-0.674	-1.048	-0.950	-0.874	-0.734	-0.730	-0.626
R^2		0.942	0.986	0.986	0.980	0.999	0.999	0.990



The linearized regressions (after log-log transformation) are shown in Fig. 1b for all individual stages for which complete data for a minimum of 3 different temperatures were available (i.e. from Zoea I to the Crab IV; cf. Table 2). The cumulative development duration in relation to temperature is shown in Fig. 1c. The slopes of these regression lines were not significantly different from each other (ANCOVA, $p > 0.05$), indicating a similar degree of temperature-dependence for successive developmental stages.

DISCUSSION

Perhaps the most striking result of this study is the wide range of temperatures tolerated by larval and early juvenile stone *Paralomis granulosa*. At a temperature as low as 1°C, about one-half of the larvae developed successfully to the megalopa stage, and metamorphosis to the first juvenile crab stage was reached within a tolerance window from 3 to 15°C. This suggests that the complete mortality before metamorphosis observed in a previous study (Vinuesa et al. 1989) was not caused by unsuitable temperatures but probably was due to either weakness of the larval material or poor rearing conditions.

In the area of origin of our material, the Beagle Channel, the larvae of *Paralomis granulosa* hatch in winter (July and August: Lovrich & Vinuesa 1999), when the water temperature is near its average annual minimum (5.4°C: Lovrich 1999). Since our experimental data suggest an optimum of about 6 to 9°C, the larvae and juveniles of this species appear to be optimally

Fig. 1. *Paralomis granulosa*. Duration of larval and early juvenile development in relation to temperature. (a) Non-linear relationship (power function), Zoea I stage at 1 to 15°C; (b) development of successive stages (Zoea I to Crab IV); (c) cumulative development duration from hatching to successive stages (Megalopa to Crab V)

adapted to the regional climate near Tierra del Fuego. According to the regional water temperatures in winter and spring, and considering our present results, the larvae should become megalopae 2 to 3 wk after hatching (late July and August), and metamorphosis to the first juvenile crab would be expected to occur throughout September to November. In the following winter, 1 yr after hatching from the egg, the juveniles should approximately reach Crab Instars VI to VII.

At 1°C we observed successful development to the Megalopa and larval survival for about 2 mo, suggesting that this species is well adapted to tolerate more severe conditions of cold than those occurring in the Beagle Channel. Theoretically, this capability might enable *Paralomis granulosa* to occasionally cross the Drake Passage and invade Antarctic waters, although the prevailing current patterns would probably favour an indirect immigration via South Georgia rather than a direct route (see Knox 1994, his Fig. 11.8). With continued global warming, *P. granulosa* may thus be considered a pioneer candidate for a possible recolonization of the Antarctic shelf by reptant decapods. However, earlier invaders may be found among the cold-stenothermal deep-sea lithodids.

The average maximum summer temperature reached in the Beagle Channel is 9.8°C (Lovrich 1999). Again, this shows that the tolerated range for larval development in *Paralomis granulosa* is much wider than would be required within the region of origin of our material. This tolerance of relatively warm conditions (up to at least 15°C) indicates that *P. granulosa* is not really a typical 'cold-adapted', i.e. cold-stenothermal, but actually a cold-eurythermal species (cf. Pörtner et al. 2000, Pörtner 2002). This is consistent with its broad geographic distribution in the subantarctic region and along both sides of southern South America, ranging in the Atlantic north to Santa Catarina, Brazil (Boschi et al. 1992), and in the Pacific to the Island of Chiloé, Chile (Retamal 1981). Likewise, this response pattern is congruent with the observation that *P. granulosa* is the only species of its genus that also inhabits shallow coastal waters where temperatures may be quite variable (Macpherson 1988).

The thermal response pattern of the early life-history stages of *Paralomis granulosa* may be typical of those Lithodidae (or at least of *Paralomis* and *Lithodes* spp.) that live in high latitudes, commonly with wide ranges of geographic and bathymetric distribution (for references see Paul et al. 2002). In contrast, true deep-sea species living in a more stable environment should be cold-stenothermal. Since our observations show that the larvae and juveniles of *P. granulosa* are cold-eurythermal, they should be an interesting object for testing the physiological hypotheses of thermal tolerance recently proposed by Pörtner (2001, 2002). These

hypotheses suggest that this species, including its early life-history stages, should be capable of regulating its mitochondrial densities and/or its energetic capacity in response to seasonal, bathymetric, or regional changes in temperature, or after differential acclimatization in the laboratory.

With regard to extremely long periods of larval development at low temperature (<6°C), it should be stressed that during this time no intake of food occurs, and development depends solely on the utilization of internal energy reserves. Although an extended lecithotrophic period under cold conditions indicates low rates of metabolic consumption, successful non-feeding development over a period of up to 4 mo remains highly remarkable, since metabolic disturbance below a critical temperature leads to insufficient cellular oxygen and energy supplies (Pörtner 2001, 2002), which may eventually prevent effective utilization of internal energy reserves. When larvae of warm-temperate crab species were simultaneously exposed to unfavourably low temperatures and an absence of food, they died sooner than sibling larvae starving at higher temperatures, although metabolic energy demands increase at higher temperatures, and thus one would expect shorter survival times in warmer waters (Anger et al. 1981).

In summary, our study has shown that *Paralomis granulosa* is well adapted to thrive under the conditions of food limitation and cold found in high-latitude marine ecosystems. On the other hand, it is equally well adapted to cool temperate regions, where relatively elevated temperature levels exclude truly cold-adapted stenothermal species. Thus, a remarkable larval eurythermal ability together with an unusually high endotrophic potential allow extended periods of completely food-independent development from hatching through metamorphosis in this species.

Similar patterns were also observed in a stone crab from the North Atlantic, *Lithodes maja* (Anger 1996), as well as in a Pacific congener, *L. aequispinus* (Shirley & Zhou 1997). In the latter species, the maximum period of non-feeding larval development (148 d at 3°C: Paul & Paul 1999) even exceeds, by 1 mo, the maximum time observed in *Paralomis granulosa*. Successful larval development at 9°C as well as a wide geographic distribution (from Japan to the Bering Sea, Canada and Alaska: Zaklan 2002) suggest that, like *P. granulosa*, *L. aequispinus* is a eurythermal rather than a cold-stenothermal species.

The occurrence of ovigerous females of *Lithodes maja* in coastal waters of Greenland, where water temperatures between -1 and 5°C were recorded (Woll & Burmeister 2002) suggests cold resistance in the early life-history stages of this species similar to that in *Paralomis granulosa* and (probably) *L. aequispinus*. Al-

though no data on temperature effects are available for larvae of *L. maja*, a longer development from hatching to metamorphosis (about 50 d at 9°C: Anger 1996) than in *P. granulosa* (38 to 42 d) suggests that *L. maja* also passes through a very long non-feeding larval development at low temperatures. In this species also, the early life-history stages are not cold-stenothermal but eurythermal, as reflected by its wide geographic distribution from the southern North Sea to Spitzbergen, Iceland and Greenland (Zaklan 2002).

These patterns contrast with those of the commercially more important lithodid *Paralithodes camtschatica*. Although this species also occurs at high latitudes (Stevens 2002, Sundet & Hjelset 2002) and its larvae tolerate a wide range of temperatures, from low to moderately high (0 to 15°C: Shirley & Shirley 1989), its zoeae are known to require planktonic food (e.g. Kurata 1960, Paul & Paul 1980); however, its megalopa stage is secondarily lecithotrophic (see Abrunhosa & Kittaka 1997a,b).

While these comparisons of larval tolerance of cold and food limitation show that not all lithodid crabs occurring at high latitudes have reached the same degree of adaptation to thermally and nutritionally harsh conditions, similarities among the various species suggest that a combination of larval eurythermality and lecithotrophy may be a widespread trait in lithodids. Phylogenetic constraints in other reptant Decapoda may not generally allow for an evolution of such special adaptations and may thus have contributed to both gradients of decreasing species diversity and to the tendency towards a reduction of the larval phase with increasing latitude ('Thorson's rule').

Acknowledgements. We greatly appreciate the help of the crew of PFS 'Polarstern' during the transport of live crabs. U. Nettelmann and several students helped in maintaining larval and juvenile cultures. J.C. is grateful to the German Academic Exchange Service (DAAD, Bonn) and the Alfred-Wegener-Institut für Polar- und Meeresforschung (Bremerhaven) for funding his research visits to Helgoland. This project was funded by the International Bureau of the German Ministry of Scientific Research (BMBF, project no. ARG 99/002), and the Argentine Secretaría Nacional para la Tecnología, Ciencia e Innovación Productiva (SETCIP).

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