

# Early egg traits in *Cancer setosus* (Decapoda, Brachyura): effects of temperature and female size

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**ABSTRACT:** Previous study on *Cancer setosus* Molina, 1782 showed that latitudinal changes in temperature control the number of annual egg masses. This study focused on the effects of pre-oviposition temperature and female size on egg traits in *C. setosus* from northern (Antofagasta, 23° S) and central-southern (Puerto Montt, 41° S) Chile. Blastula eggs produced in nature ranged in dry mass (DM) from 9.1 to 15.1 µg, in carbon (C) from 4.8 to 8.4 µg, in nitrogen (N) from 1.0 to 1.6 µg, in C:N ratio between 4.7 and 5.4, and in volume (V) between 152 and 276 mm<sup>3</sup> × 10<sup>-4</sup> per female. Blastula eggs from females caught early in the reproductive season in Puerto Montt (September 2006) were significantly higher in DM, C, N, and V than those of females caught 2 mo later, reflecting a seasonal increase in water temperature. In Puerto Montt 'early' and 'late' season blastula eggs were higher in DM, C, N, and V than eggs from Antofagasta by about 32 and 20%, respectively. Subsequent egg masses produced in captivity in Puerto Montt followed this pattern of smaller eggs with lower DM, C, and N content at higher pre-oviposition temperatures. In Antofagasta no significant difference in DM, C, N, and V between eggs produced in nature and subsequent eggs produced in captivity was found and all egg traits were significantly positively affected by maternal size. Reproductive plasticity in *C. setosus* helps to explain the species wide latitudinal distribution range.

**KEY WORDS:** Crustacea · Cancridae · Chile · Latitudinal cline · Reproductive plasticity

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## INTRODUCTION

One of the central questions in the life history of marine invertebrates is whether to invest the limited energy available for reproduction into many small or fewer but larger eggs (Strathmann 1985, Stearns 1992, Levin & Bridges 1995). Large, nutrient-rich eggs develop more slowly (Steele & Steele 1975), but give rise to more advanced and larger larvae (Herring 1974, Clarke 1992). However, the production of large eggs implies an increase in energy allocation to the individual offspring, which occurs at the cost of reduced fecundity and thus lowers offspring numbers (Smith & Fretwell 1974). In general, species with large, nutrient-rich eggs increase in frequency towards high latitudes (for gastropods, Thorson 1936, 1950; decapod crustaceans, Clarke 1979; gammarid amphipods, Sainte-Marie 1991). This poleward cline in egg size and the concomitant decrease in

number of species with planktotrophic larval development, often referred to as 'Thorson's rule' (Mileikovsky 1971), is seen as an evolutionary adaptation to the mismatch between short periods of food availability (= primary production) and prolonged (larval-) development at lower temperatures at higher latitudes (for discussion see Thatje et al. 2005). Differences in egg traits can be substantial even between closely related species. Within the caridean shrimps an increase in egg dry mass and lipid content of up to 3 orders of magnitude occurs from tropical to polar species (Clarke 1979, 1993a). However, egg traits differ not only interspecifically, but can vary also intraspecifically within a certain 'reaction norm', which is a life-history character in itself (Ricklefs & Wikelski 2002). Such phenotypic plasticity presumably allows for the optimization of reproductive effort under different environmental conditions (Hadfield & Strathmann 1996, Thatje & Bacardit 2000, Allen et al. 2008).

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Within the Crustacea, seasonal (Boddeke 1982, Amsler & George 1984, Sheader 1996, Paschke 1998), inter-annual (Kattner et al. 1994) and latitudinal (Crisp 1959, Clarke et al. 1991, Wehrtmann & Kattner 1998, Lardies & Castilla 2001, Lardies & Wehrtmann 2001, Brante et al. 2003, 2004) intraspecific differences in egg traits have been reported. Furthermore, in Crustacea with consecutive ovipositions, egg quality may vary with spawning order, a feature of considerable importance in shrimp aquaculture (e.g. Arcos et al. 2003, Racotta et al. 2003).

However, unless common environment experiments are conducted, it remains speculative if latitudinal differences in reproductive traits are based on genetic differences or represent adaptive phenotypic responses to environmental heterogeneity (e.g. temperature) (see Kokita 2003).

In the brachyuran crab *Cancer setosus* Molina, 1782, which is distributed over more than 40° of latitude along the South American Pacific coast (2° S, 079° W to 46° S, 075° W; Fig. 1) (Rathbun 1930), fecundity per egg mass, egg dry mass, and egg volume increases with increasing latitude (Brante et al. 2003, 2004). At its southern range *C. setosus* incubates one annual egg mass throughout the austral winter until the time of larvae hatching in spring. In central- and northern Chile, reproduction is not restricted to a certain season leading to an annual output of about 2 to 3 egg masses (Fischer & Thatje 2008). So far, it remains unknown whether latitudinal differences in egg traits of *C. setosus* are co-adapted, and if changes in egg dry mass (DM) and volume (V) reflect real differences in egg quality (egg energy content, e.g. measured as carbon (C) and nitrogen (N) content). Answers to these questions and to the underlying factors shaping the life history of *C. setosus* are potentially valuable for developing an adaptive fisheries management scheme for this commercially important species (Thatje et al. 2008) and for our understanding of the evolution of reproductive traits in marine invertebrates. Here, we present the DM, C, N, and V traits of early blastula eggs from ovipositions in nature and in captivity for females from Antofagasta (northern Chile) and Puerto Montt (central-southern Chile) in relation to pre-oviposition temperature (T) as well as female carapace width (CW). The observed patterns provide evidence for physiological plasticity in the reproductive traits of a marine invertebrate in response to environmental heterogeneity.

## MATERIALS AND METHODS

**Sampling and maintenance.** Ovigerous *Cancer setosus* were caught by divers at 5 to 10 m water depth at different sites around Antofagasta, northern Chile (23° 45' S, 70° 27' W; in November 2005 and January 2006) and in Carelmapu, close to Puerto Montt in central

southern Chile (41° 44' S, 73° 41' W, in September and November 2006). These locations were chosen for representing the upper and lower temperature conditions encountered by *C. setosus* throughout its natural range. Puerto Montt is located close to the southern limit of this species. In Antofagasta Bay sea surface temperature (SST) is significantly higher than in the surrounding Humboldt Current upwelling system (+ 2 to 3°C) due to the bay's particular oceanographic conditions (Castilla et al. 2002, Piñones et al. 2007), and thus SST is comparable to the temperature encountered by *C. setosus* at its northern distributional limit off Peru (IMARPE 2008) (Fig. 2). The near bottom temperature at the sampling locations deviates by less than 2°C from SST (pers. obs., see also Escribano et al. 1997).

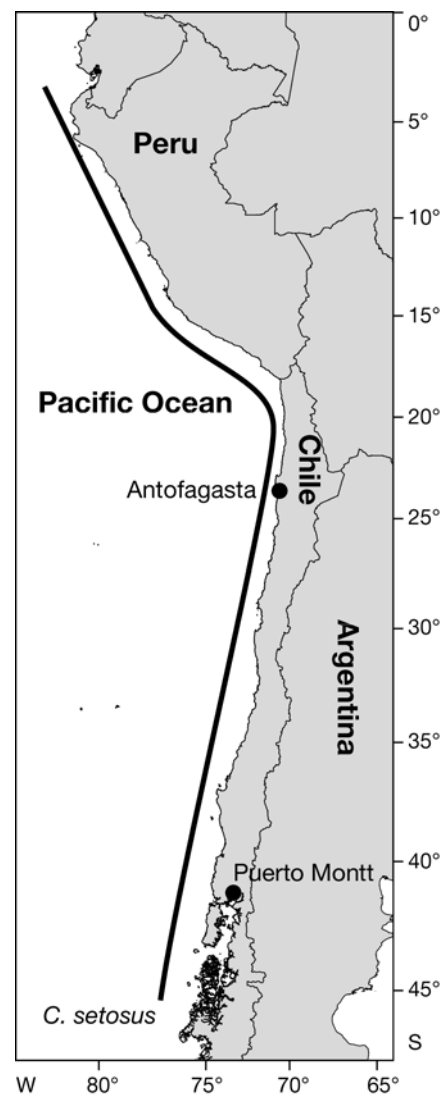


Fig. 1. Distribution of *Cancer setosus* along the Pacific coast of South America (Rathbun 1930) (thick black line) and locations of female collections in this study at Antofagasta and Puerto Montt, Chile

Live females with bright yellow-orange egg masses indicative of early blastula stage were transferred to the laboratory and eggs were taken with fine forceps from the outer part of the egg mass. Only eggs from females with early blastula stage eggs, as identified microscopically by the uniform distribution of yolk and absence of cleavage, were used for the analysis of egg volume and elemental composition. Females sampled for egg traits, including some females with embryos that had already surpassed the early blastula stage (see Table 4, females A3 to A8), were kept in captivity in order to sample subsequently produced egg masses (Captivity 1, Captivity 2; see below).

Lengths ( $D_1$ ) and widths ( $D_2$ ) of 20 unpreserved eggs (Sheader & Chia 1970) per female were measured microscopically with a calibrated eyepiece micrometer. Egg volume was calculated based on the formula for oblate spheroids:  $V = (\pi \cdot D_1^2 \cdot D_2)/6$  (Turner & Lawrence 1979). For elemental analysis (after Anger & Dawirs 1982) 5 aliquot samples of 50 eggs each per female were briefly rinsed in distilled water and subsequently transferred to pre-weighted tin cartridges. Samples were lyophilized overnight at  $<0.01$  mbar and their DM was taken with a microbalance (Sartorius M2P) to the nearest  $\mu\text{g}$ . Subsequently, samples were combusted at  $1020^\circ\text{C}$  in an elemental analyzer (Hekatech Euro EA) for the determination of C and N content using acetanilide as a standard.

After egg sampling the ovigerous crabs were maintained in aquaria. All crabs were individually labelled with a small plastic tag glued onto their carapace, and carapace width (CW) was measured with calipers, including the 10th anterolateral spine. In Antofagasta, crabs were held in two 3200 l flow-through aquaria ( $\leq 12$  ind. per basin) for up to 10 mo under natural seasonal temperature conditions ( $16$  to  $23^\circ\text{C}$ ). In Puerto Montt, crabs were held in two 500 l aquaria ( $\leq 9$  ind. per basin) for up to 6 mo. Temperatures were kept constant at  $16 (\pm 0.5)$  and  $19 (\pm 0.3)^\circ\text{C}$  in order to simulate the temperature conditions at oviposition in northern Chile (Fig. 2). The crabs were acclimatized over 4 to 5 d by gradually increasing the temperature from the natural temperature at the time of crab capture.

In both locations, crabs were fed ad libitum with live mussels *Perumytilus purpuratus*, aquaria were cleaned and water temperature was recorded daily. Subsequent egg masses produced in captivity (Captivity 1, Captivity 2) (Antofagasta:  $n = 24$ ; Puerto Montt:  $n = 8$ ) were sampled for DM, C, N, and V with the same methods as those used for prior egg masses.

**Data analysis.** The effects of location (Antofagasta, Puerto Montt) and oviposition (Antofagasta: Nature, Captivity 1, Captivity 2) on DM, C, N, and V of blastula stage eggs were tested in 2 separate covariance analyses with female CW as a covariate (ANCOVA; based

on the means of DM, C, N and V with 'female' as sampling level). Egg traits were significantly different between females caught 'early' (September 2006) and 'late' (November 2006) in the reproductive season in Puerto Montt (see 'Results') and therefore were treated separately for statistical analysis. In order to enhance data set homogeneity the ANCOVAs were restricted to eggs from females with  $>105$  mm and  $>95$  mm CW for the effects of location and oviposition, respectively. The categorical factors and the covariate were tested for interaction (location  $\times$  CW; oviposition  $\times$  CW). The interactions were not significant (homogeneity of slopes) and therefore the interaction term was removed. Homogeneity of variances was tested with Levene's test and normality of residuals with the Shapiro-Wilk test (Sokal & Rohlf 1995). A post hoc comparison of means was conducted using Tukey's test. For this study, pre-oviposition temperature (T) was calculated as the mean sea surface temperature in the month prior to oviposition. The effects of T ( $^\circ\text{C}$ ), and CW (mm) on blastula egg C content ( $\mu\text{g egg}^{-1}$ ) were analysed for all data combined, independently of location and conditions of oviposition, applying a multiple linear regression model:  $C = a + b_1 \times T + b_2 \times CW$ .

## RESULTS

### Oviposition in nature

Blastula eggs ranged in DM from  $9.1$  to  $15.1 \mu\text{g}$ , in C from  $4.8$  to  $8.4 \mu\text{g}$ , in N from  $1.0$  to  $1.6 \mu\text{g}$ , in C:N ratio

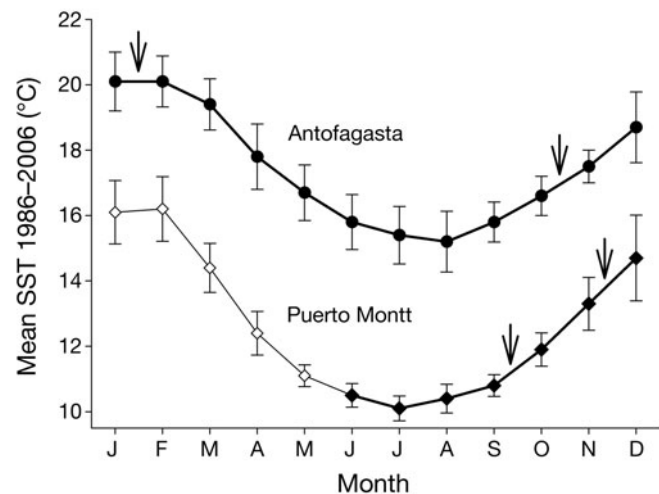


Fig. 2. Mean monthly SST ( $^\circ\text{C}$ ) in Antofagasta and Puerto Montt (based on a 20 yr average  $\pm 1$  SD (CENDHOC 2008)). The main periods during which ovigerous *Cancer setosus* occur at each location (after Gutiérrez & Zúñiga 1976, Pool et al. 1998) and the time of crab capture are indicated by filled symbols and arrows, respectively

between 4.7 and 5.4, and in egg volume between 152 and 276 mm<sup>3</sup> × 10<sup>-4</sup> for individual females. DM, C, N, and V differed significantly between sites (p always <0.0001). DM, C, N, and V from Puerto Montt 'early' and 'late' eggs were about 32 and 20% higher as in Antofagasta, respectively (Tables 1 & 2, Fig. 3). CW had no significant effect on DM, C, N, and V (p ≥ 0.045) in the ANCOVA, which was restricted to females between 105 and 142 mm in CW (Table 1).

**Oviposition in captivity**

In the flow-through aquaria in Antofagasta (16 to 23°C) as well as in the constant temperature aquaria in Puerto Montt (16 and 19°C), females produced up to 2 more egg masses after the one produced in nature (for details on the reproductive cycle, see Fischer & Thatje (2008)).

In Antofagasta, eggs from 2 subsequent ovipositions in captivity (n = 16 and n = 8) (mean pre-oviposition temperatures of 19 and 21°C, respectively) were not significantly different in DM, C, N, and V from eggs previously produced in nature (mean T of 19°C, n = 15; Fig. 4). Maternal size (CW) had a significant positive effect on all egg traits (p < 0.0001; Table 3). Across the whole range of sizes of ovigerous females in Antofagasta (79 to 142 mm CW), DM, C, N, and V increased by about 20% from the smallest to the largest specimen.

In Puerto Montt, DM, C, N were lower by about 17% (n = 2) at 16°C, and by 21% (n = 4) at 19°C, compared to eggs previously produced in nature (T of about 11°C). At 19°C, 2 females produced a second captivity egg mass of eggs 28% lower in DM, C, N, and V as in the initial egg mass (Tables 3 & 4).

Despite the variability in quantitative energy investment per egg, the relative DM-specific values of C and N and also the V-specific DM, C, and N

Table 1. *Cancer setosus*. Results of ANCOVA ( $Y = a + b_1 \times CW + b_2 \times loc$ ) testing for the effects of female size (carapace width [CW]; covariate) and location on dry mass (DM), C, N, and volume (V) of blastula eggs produced in nature in Antofagasta (A) and Puerto Montt (PM 'early', PM 'late') (p-values given in brackets; n = 35). ANCOVA was restricted to females ≥105 mm in CW. DM, C, N, and V, differed significantly between locations (Tukey's HSD test at  $\alpha = 0.05$ )

Y	a	b <sub>1</sub>		Location	b <sub>2</sub>		r <sup>2</sup>
DM	8.138	0.028	(p = 0.0743)	A	0	(p < 0.0001)	0.71
				PM 'early'	1.365		
				PM 'late'	-1.602		
C	4.511	0.014	(p = 0.1146)	A	-0.931	(p < 0.0001)	0.72
				PM 'early'	0.803		
				PM 'late'	0		
N	0.751	0.004	(p = 0.0450)	A	-0.154	(p < 0.0001)	0.67
				PM 'early'	0.141		
				PM 'late'	0		
V	0.0147	5.442×10 <sup>-5</sup>	(p = 0.0865)	A	-0.0037	(p < 0.0001)	0.76
				PM 'early'	0.0031		
				PM 'late'	0		

Table 2. *Cancer setosus*. Traits of early blastula eggs produced in nature and in captivity in Antofagasta and Puerto Montt and mean temperature in the month prior to oviposition (T). Absolute composition: mean DM, C, N and V ± 1 SD. Relative composition: C:N ratio, DM specific C and N content (% of DM) and V-specific DM, C and N concentration (µg mm<sup>-3</sup>)

n	Oviposition	T (~°C)	DM (µg egg <sup>-1</sup> )	C (µg egg <sup>-1</sup> )	N (µg egg <sup>-1</sup> )	C:N	V (mm <sup>3</sup> × 10 <sup>-4</sup> )	C (% of DM)	N (% of DM)	DM (µg mm <sup>-3</sup> )	C (µg mm <sup>-3</sup> )	N (µg mm <sup>-3</sup> )
Antofagasta												
15	Nature	19	9.6 ± 0.7	5.1 ± 0.4	1.02 ± 0.07	5.0	171 ± 10	53.1	10.6	564	299	60
16	Captivity 1	19	10.1 ± 0.4	5.3 ± 0.3	1.03 ± 0.05	5.2	180 ± 8	53.0	10.3	558	296	58
8	Captivity 2	21	9.6 ± 0.9	5.1 ± 0.4	0.98 ± 0.10	5.2	180 ± 16	53.1	10.2	531	282	54
Puerto Montt												
13	Nature 'early'	11	13.1 ± 1.1	7.1 ± 0.6	1.35 ± 0.12	5.3	246 ± 22	54.7	10.3	531	288	55
2	Captivity 1	16	11.0 ± 0.3	5.8 ± 0.2	1.03 ± 0.01	5.2	207 ± 19	52.9	10.2	533	282	55
4	Captivity 1	19	10.7 ± 0.7	5.7 ± 0.4	1.08 ± 0.07	5.3	203 ± 17	53.6	10.1	525	281	53
2	Captivity 2	19	9.6 ± 0.4	5.0 ± 0.2	0.97 ± 0.06	5.1	182 ± 22	52.1	10.1	525	281	53
12	Nature 'late'	14	12.0 ± 0.8	6.4 ± 0.5	1.23 ± 0.09	5.3	222 ± 18	54.3	10.2	539	290	55

remained stable. Blastula eggs consisted of 52 to 55% C and 10 to 11% N. The volume-specific content (concentration) ranged from 525 to 564  $\mu\text{g DM mm}^{-3}$ , 281 to 299  $\mu\text{g C mm}^{-3}$  and 53 to 60  $\mu\text{g N mm}^{-3}$  (Table 2).

### Multiple linear regression analysis

For all data combined (Antofagasta, Puerto Montt 'early' and 'late'; oviposition in nature and captivity) blastula egg DM, C, N, and V were significantly positively influenced by female CW and negatively by T. The effects of the factors T and CW on C were explored by multiple linear regression (Fig. 5).

## DISCUSSION

Temperature dependent plasticity in egg traits is an important life history parameter, which is thought to promote reproductive success for a wider set of environmental conditions and thus extend the spatial (e.g.

latitudinal, bathymetrical) and temporal (seasonal) 'window of opportunity' for reproduction. In the brachyuran crab *Cancer setosus*, blastula eggs from ovipositions in nature at 2 locations, representative for the species' upper and lower temperature range (Antofagasta, about 19°C; Puerto Montt 'early', about 11°C), differed by 32% in DM, confirming a pattern previously described by Brante et al. (2003, 2004). In the present work, egg volume, and consequently egg density, followed the same pattern. However, volumes were about 20% lower in both locations than in the study of Brante et al. (2003, 2004), which was based on combined blastula and more advanced gastrula stage eggs. Crustacean eggs increase in volume with progressing embryo development and thus well defined developmental stages are prerequisites for comparisons within and between species (Crisp 1959). The observed differences in field produced eggs can be directly related to differences in ambient temperatures. In Puerto Montt females that produced large eggs at low temperatures (about 11°C), went on to produce eggs similar in size to those produced in nature by crabs near Antofagasta, when reared at the corresponding higher temperatures (16 and 19°C; Table 4). Eggs produced in captivity in Antofagasta (Captivity 1, at ~19°C; Captivity 2 at ~21°C) did not differ signifi-

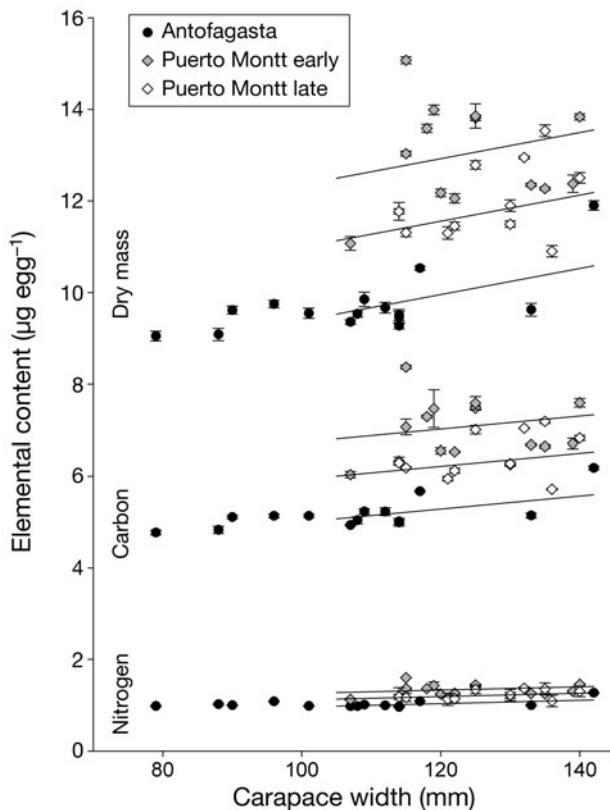


Fig. 3. *Cancer setosus*. Dry mass, carbon, and nitrogen content of blastula stage eggs from Antofagasta and Puerto Montt ('early'; 'late') in relation to female carapace width (CW) (each point represents the mean of 5 replicate measurements  $\pm 1$  SD). Regression lines represent data range of the ANCOVA ( $\geq 105$  mm CW)

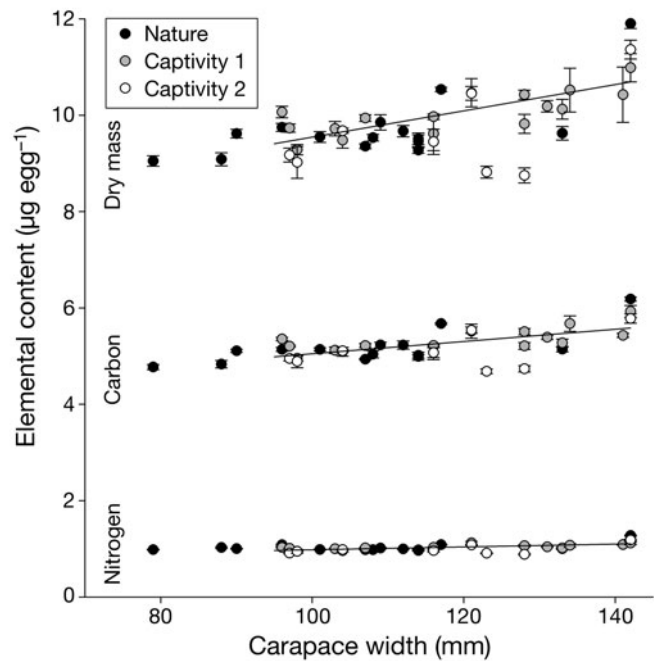


Fig. 4. *Cancer setosus*. Dry mass, carbon, and nitrogen content of blastula stage eggs from Antofagasta from ovipositions in nature and captivity (1 and 2) in relation to female carapace width (CW) (each point represents the mean of 5 replicate measurements  $\pm 1$  SD). ANCOVA (for CW  $\geq 95$  mm) showed no significant difference between treatments. Therefore only the overall regression line is shown



Table 3. *Cancer setosus*. Results of ANCOVA ( $Y = a + b_1 \times CW + b_2 \times \text{ovip.}$ ) testing for the effects of female size (CW, covariate) and oviposition (Nature, Captivity 1, Captivity 2) on blastula egg DM, C, N and V in Antofagasta (p-values given in brackets). ANCOVA was restricted to females  $\geq 95$  mm in CW

Y	a	b <sub>1</sub>	Oviposition	b <sub>2</sub>	r <sup>2</sup>	n		
DM	6.654	0.027	(p < 0.0001)	Nature	0.072	0.42	36	
				Captivity 1	0.162			(p = 0.235)
				Captivity 2	0			
C	3.739	0.013	(p = 0.0002)	Nature	0.040	0.40	36	
				Captivity 1	0.079			(p = 0.220)
				Captivity 2	0			
N	0.673	0.003	(p = 0.0004)	Nature	0.018	0.38	36	
				Captivity 1	0.014			(p = 0.184)
				Captivity 2	0			
V	0.0159	$1.614 \times 10^{-5}$	(p = 0.230)	Nature	-0.000403	0.13	32	
				Captivity 1	0.000176			(p = 0.312)
				Captivity 2	0			

Table 4. *Cancer setosus*. Female size CW (mm), DM, C, N, C:N ratio and V of blastula eggs of females with subsequent ovipositions in Antofagasta and Puerto Montt and mean temperature in the month prior oviposition T (°C). Of females A3 to A8 only captivity egg masses were sampled for egg traits, because their prior eggs produced in nature already surpassed the early blastula stage at crab capture. Paired *t*-tests (or Wilcoxon signed rank test when normality test failed) showed no significant differences in DM, C, N, and V between subsequently produced egg masses in Antofagasta. In Puerto Montt, Captivity 1 eggs were significantly lower in DM, C, N, and V than previous eggs produced in nature (paired *t*-test/Wilcoxon signed rank test)

Location Specimen	CW	T (°C)	Oviposition	DM ( $\mu\text{g egg}^{-1}$ )	C ( $\mu\text{g egg}^{-1}$ )	N ( $\mu\text{g egg}^{-1}$ )	C:N	V ( $\text{mm}^3 \times 10^{-4}$ )
Antofagasta								
A1	142	16.0	Nature	11.9 ± 0.1	6.2 ± 0.0	1.27 ± 0.01	4.9	201 ± 1
		21.8	Captivity 1	11.0 ± 0.3	5.9 ± 0.0	1.12 ± 0.03	5.3	–
A2	96	16.0	Nature	9.8 ± 0.1	5.1 ± 0.1	1.08 ± 0.01	4.7	176 ± 14
		19.7	Captivity 1	10.1 ± 0.1	5.4 ± 0.3	1.03 ± 0.01	5.2	197 ± 16
A3	128	17.7	Captivity 1	9.8 ± 0.2	5.2 ± 0.1	1.06 ± 0.02	4.9	170 ± 6
		21.2	Captivity 2	8.8 ± 0.2	4.7 ± 0.1	0.88 ± 0.02	5.4	–
A4	116	17.8	Captivity 1	9.6 ± 0.4	5.1 ± 0.2	1.00 ± 0.02	5.1	170 ± 14
		21.2	Captivity 2	9.5 ± 0.3	5.1 ± 0.1	0.96 ± 0.01	5.3	169 ± 12
A5	121	17.9	Captivity 1	10.5 ± 0.3	5.5 ± 0.1	1.10 ± 0.01	4.9	187 ± 7
		20.5	Captivity 2	10.5 ± 0.1	5.5 ± 0.1	1.08 ± 0.04	5.1	–
A6	97	19.4	Captivity 1	9.7 ± 0.1	5.2 ± 0.0	0.73 ± 0.00	5.2	173 ± 10
		23.0	Captivity 2	9.2 ± 0.1	5.0 ± 0.1	0.91 ± 0.01	5.4	–
A7	104	19.5	Captivity 1	9.5 ± 0.2	5.1 ± 0.1	0.96 ± 0.02	5.3	180 ± 11
		23.0	Captivity 2	9.7 ± 0.1	5.1 ± 0.0	0.98 ± 0.01	5.2	185 ± 12
A8	98	19.5	Captivity 1	9.3 ± 0.1	5.0 ± 0.1	0.95 ± 0.01	5.2	173 ± 10
		23.0	Captivity 2	9.0 ± 0.3	4.9 ± 0.1	0.95 ± 0.04	5.2	182 ± 14
Puerto Montt 'early'								
P1	118	11.2	Nature	13.6 ± 0.1	7.3 ± 0.0	1.36 ± 0.01	5.4	233 ± 26
		15.9	Captivity 1	11.2 ± 0.1	6.0 ± 0.1	1.14 ± 0.01	5.3	210 ± 16
P2	139	11.2	Nature	12.4 ± 0.2	6.7 ± 0.1	1.30 ± 0.03	5.1	244 ± 21
		15.9	Captivity 1	10.8 ± 0.1	5.7 ± 0.0	1.13 ± 0.01	5.1	205 ± 15
P3	115	11.2	Nature	15.1 ± 0.1	8.4 ± 0.0	1.60 ± 0.00	5.2	276 ± 16
		19.3	Captivity 1	10.7 ± 0.1	5.8 ± 0.0	1.09 ± 0.01	5.3	203 ± 10
P4	119	11.2	Nature	14.0 ± 0.1	7.5 ± 0.4	1.43 ± 0.08	5.2	263 ± 27
		19.3	Captivity 1	11.8 ± 0.1	6.3 ± 0.0	1.18 ± 0.01	5.3	222 ± 16
P5	120	11.2	Nature	12.2 ± 0.1	6.6 ± 0.1	1.25 ± 0.02	5.3	223 ± 19
		19.3	Captivity 1	10.1 ± 0.1	5.3 ± 0.2	1.02 ± 0.02	5.2	194 ± 13
P6	140	19.5	Captivity 2	9.2 ± 0.1	4.8 ± 0.1	0.91 ± 0.01	5.2	171 ± 24
		11.2	Nature	13.8 ± 0.1	7.6 ± 0.0	1.46 ± 0.01	5.2	270 ± 21
		19.4	Captivity 1	10.0 ± 0.1	5.5 ± 0.0	1.04 ± 0.01	5.3	195 ± 14
		19.3	Captivity 2	9.9 ± 0.2	5.2 ± 0.0	1.02 ± 0.00	5.1	192 ± 14

cantly in traits from prior eggs produced in the field at  $\sim 19^{\circ}\text{C}$  (Table 3; Fig. 4). Therefore, aquaria rearing and continuous spawning 'as such', which may affect egg quality in penaeid shrimp (Racotta et al. 2003), can be excluded in *C. setosus* as underlying causes of egg trait variability.

In general, egg size and DM have to be treated with caution in inter- and intraspecific comparisons of female investment in offspring as they do not always relate to egg energy content (for examples on echinoderms see McEdward & Carson 1987, McEdward & Chia 1991, Jaekle 1995). In the estuarine crab *Chasmagnathus granulatus* egg DM did not always correlate to egg C content (Giménez & Anger 2001, Bas et

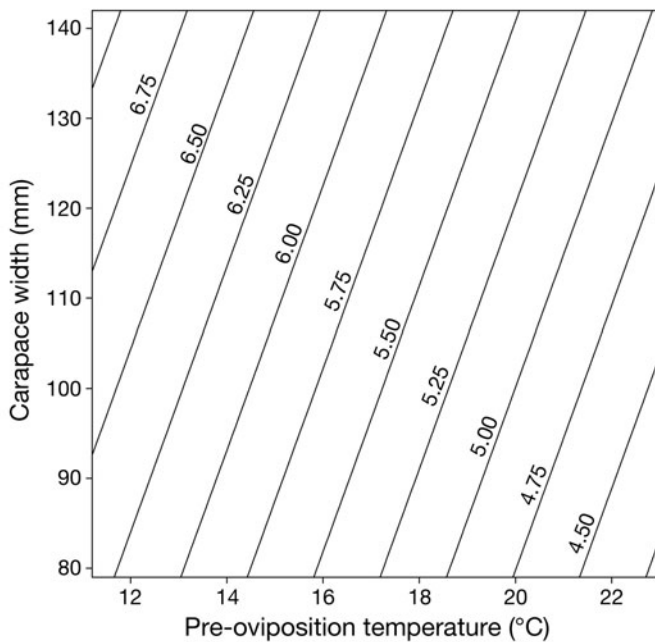


Fig. 5. *Cancer setosus*. Contour plot of blastula stage egg carbon (C) content ( $\mu\text{g egg}^{-1}$ ) in relation to pre-oviposition temperature (T) ( $^{\circ}\text{C}$ ) and female carapace width (CW) (combined for Antofagasta, Puerto Montt 'early' & 'late'; ovipositions in nature and captivity) derived from multiple linear regression:  $C (\mu\text{g}) = 7.388357 - 0.180933 \times T + 0.012288 \times \text{CW}$ ; for T,  $p < 0.0001$ , and for CW,  $p = 0.0023$ ;  $n = 72$ ,  $r^2 = 0.72$

al. 2007) and in the Atlantic blue crab *Callinectes sapidus*, 'winter eggs' had, despite equal size, a 20% higher lipid content than 'summer eggs' (Amsler & George 1984).

For *Cancer setosus*, absolute egg traits (DM, C, N, V) showed high plasticity, but the relative egg composition remained fairly stable (V specific concentration of DM, C and N; DM specific content of C and N). Therefore, differences in DM and V represent real differences in investment per embryo in *C. setosus*. The relative egg composition was comparable to values compiled for a variety of caridean shrimp species (Clarke 1993a, Anger et al. 2002) and also to values of 5 brachyuran crab species which co-occur with *C. setosus* in Antofagasta (Table 5).

Differences in egg energy provision may directly affect later life history stages including their fitness (for review on decapod Crustacea see Giménez 2006). In the brown shrimp *Crangon crangon* (Caridea), a 20% difference in egg V and DM provision found between 'winter' and 'summer' eggs, directly translated to larvae size (Boddeke 1982, Paschke 1998, Paschke et al. 2004). The zoea I larvae hatched from 'winter eggs' were not only larger, but had a shorter development time, higher starvation resistance, and required less larval stages to reach the juvenile stage than larvae from 'summer eggs' (Linck 1995, Paschke et al. 2004). These are all adaptive features, which enhance larval survival under conditions of low or unpredictable food availability at lower (winter) temperatures. However, at warmer (summer) temperatures and likely better feeding conditions for planktotrophic larvae the 'few large offspring strategy' does not necessarily enhance overall larvae fitness, making it more advantageous to maximize fecundity (for details see Yampolsky & Schreiner 1996). An alternative explanation for smaller eggs at higher temperature is the assumption that temperature imposes some physical or physiological constraint on egg size (Yampolsky & Schreiner 1996). For *Cancer setosus*, the mismatch between increased metabolism and thus oxygen demand with lower oxygen solubility at higher temperature has been

Table 5. Blastula egg traits of 5 brachyuran crab species from Antofagasta, northern Chile. Specimens were caught and egg samples were processed as described for *Cancer setosus*. Species are *Cancer porteri*, *Cancer coronatus* (Cancridae), *Platyanthus orbignyi*, *Homalaspis plana* (Xanthidae), and *Taliepus marginatus* (Majidae). Absolute composition: DM, C, N and V  $\pm 1$  SD. Relative composition: C:N ratio, DM-specific C and N content (% of DM) and V-specific DM, C, and N concentration ( $\mu\text{g mm}^{-3}$ )

Species	n	DM ( $\mu\text{g egg}^{-1}$ )	C ( $\mu\text{g egg}^{-1}$ )	N ( $\mu\text{g egg}^{-1}$ )	C:N	V ( $\text{mm}^3 \times 10^{-4}$ )	C (% of DM)	N (% of DM)	DM — ( $\mu\text{g mm}^{-3}$ ) —	C — ( $\mu\text{g mm}^{-3}$ ) —	N — ( $\mu\text{g mm}^{-3}$ ) —
<i>C. porteri</i>	1	11.3 $\pm$ 0.1	6.0 $\pm$ 0.0	1.22 $\pm$ 0.01	4.9	229 $\pm$ 16	52.6	10.8	494	260	53
<i>C. coronatus</i>	1	9.0 $\pm$ 0.2	4.7 $\pm$ 0.1	0.91 $\pm$ 0.01	5.1	222 $\pm$ 15	52.2	10.1	405	211	41
<i>P. orbignyi</i>	2	25.6 $\pm$ 2.7	13.3 $\pm$ 0.2	2.70 $\pm$ 0.03	4.9	458 $\pm$ 33	52.0	10.5	560	291	59
<i>H. plana</i>	2	32.6 $\pm$ 3.4	16.6 $\pm$ 0.3	3.42 $\pm$ 0.02	5.0	635 $\pm$ 58	50.9	10.5	514	261	54
<i>T. marginatus</i>	1	26.6 $\pm$ 0.5	14.7 $\pm$ 0.1	2.59 $\pm$ 0.06	5.7	638 $\pm$ 44	55.3	9.7	417	230	41

proposed to act as limiting factor on large eggs due to their low surface to volume ratio (Brante et al. 2003). This effect might be pronounced for species brooding large egg capsules and for gelatinous egg masses (Strathmann & Strathmann 1995), but oxygen limitation alone may not explain egg size variation in *C. setosus*. Cancrid eggs are fairly small and many brachyuran crabs produce eggs which are significantly larger under comparable conditions of temperature and oxygen availability (e.g. *Homalaspis plana*; see Table 5).

Egg energy provision of *Cancer setosus* was not only negatively affected by temperature but also positively affected by female size (Table 3, Figs. 4 & 5). However, CW was not significant in the latitudinal model (Table 1, Fig. 3), which might be a consequence of the limited size range of ovigerous females sampled in Puerto Montt (105 to 142 mm). The overall pattern of increasing egg size and nutrient content with increasing maternal size resulting in increased offspring fitness has been reported for several marine invertebrates and vertebrates (e.g. Chambers 1997). Consequently, in some species larger females are likely to make a higher contribution to the population than explained by their size specific increase in fecundity alone (Birkeland & Dayton 2005) and in the case of *C. setosus* should be protected by management measures from an excess in fishing pressure.

Within the Crustacea, a positive effect of female size on egg traits has been shown for 3 high latitude caridean shrimp species (Clarke 1993b), the brachyuran crab *Chasmagnathus granulatus* (Giménez & Anger 2001), for American and European lobster (*Homarus americanus* and *H. gammarus*) (Attard & Hudon 1987; Tully et al. 2001) and the spiny lobster *Jasus edwardsii* (Smith & Ritar 2007). However, the reported variation in crustacean egg traits might not directly relate to female size, but may rather reflect differences in the reproductive and moulting cycle of larger females, which tend to moult less frequently and thus might be able to invest more energy into reproduction (Oullet & Plante 2004). In the present study, interbrood periods were comparable between females (see Fischer & Thatje 2008); most likely none of the females sampled were primiparous and no female moulted between consequent ovipositions. However, further studies are needed to understand if maternal size effects are more widespread in Crustacea with a planktivorous larval development (Marshall et al. 2008).

This study documents temperature-dependent plasticity in egg energy provision of *Cancer setosus*, which is postulated to be one of the key factors in explaining the species' broad distributional range and ecological success. Future studies should focus on the nexus of energy investment in eggs to later larval and juvenile

quality ('latent' or 'carry-over' effects) and possible variability with temperature conditions experienced throughout embryonic development.

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