



Temperature-induced oviposition in the brachyuran crab *Cancer setosus* along a latitudinal cline: Aquaria experiments and analysis of field-data

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Abstract

Ovigerous females of *Cancer setosus* are present year-round throughout most of its wide range along the Peruvian/Chilean Pacific coast (2°S–46°S). However, their number of egg-masses produced per year remains speculative and as such has neither been considered in latitudinal comparisons of reproduction, nor for its fisheries management. In order to reveal the effect of temperature on egg-mass production and egg-development, female *C. setosus* were held in through-flow aquaria under natural seasonal temperature conditions (16–23 °C) in Antofagasta (23°S), Northern Chile (05/2005–03/2006; 10 months), and at three constant temperatures (12, 16, 19 °C) in Puerto Montt (41°S), Central Southern Chile (09/2006–02/2007; 5 months). Female crabs uniformly produced up to 3 viable egg-masses within 4 1/2 months in Antofagasta and in Puerto Montt (at 19 °C). The second egg-mass was observed 62.5 days (± 7.6 ; $N=7$) after the oviposition of the first clutch and a third egg-mass followed 73.5 days (± 12.5 ; $N=11$) later in Antofagasta (at 16–23 °C). Comparably, a second oviposition took place 64.4 days (± 9.8 , $N=5$) after the first clutch and a third, 67.0 days (± 2.8 , $N=2$), thereafter, at 19 °C in Puerto Montt. At the two lower temperatures (16 and 12 °C) in Puerto Montt a second egg-mass was extruded after 82.8 days (± 28.9 ; $N=4$) and 137 days ($N=1$), respectively. The duration of egg-development from oviposition until larval hatching decreased from 65 days at 12.5 °C to 22.7 days at the observed upper temperature threshold of 22 °C. Based on the derived relationship between temperature and the duration of egg-development ($y=239.3175e^{-0.107x}$; $N=21$, $r^2=0.83$) and data on monthly percentages of ovigerous females from field studies, the annual number of egg-masses of *C. setosus* was calculated. This analysis revealed an annual output of about one egg-mass close to the species northern and southern distributional limits in Casma (9°S) and Ancud (43°S), respectively, while at Coquimbo (29°S) about two and in Concepción (36°S) more than 3 egg-masses are produced per year. © 2008 Elsevier B.V. All rights reserved.

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1. Introduction

Most of the 24 extant species of cancrinid crabs (Nations, 1975, 1979; Carvacho, 1989) are found in cold temperate and boreal waters of the Pacific and Atlantic Oceans (MacKay, 1943). Their reproductive cycles follow seasonal changes in temperature and food availability in these regions. Typically, one annual egg-mass is produced in autumn, incubated throughout the winter-period, and larvae are released at the time of the spring plankton peak when food and growth

conditions are favourable (Krouse, 1972; Hines, 1991; Shields, 1991; Stone and O'Clair, 2002; Park et al., 2007). Exceptions to this general pattern are *C. antennarius* and *C. anthonyi*, which are able to produce multiple egg-masses per year in the Southern California current at the North American Pacific coast, where they find relatively stable conditions year-round (Carroll, 1982; Shields et al., 1991).

Reproductive parameters vary not only between species, but also latitudinally. The size of maturity in *C. irroratus* and *C. pagurus* (Shields, 1991, and citations therein), larvae size in *C. magister* (Shirley et al., 1987), and egg-size, and fecundity in *C. setosus* follow a latitudinal cline (Brante et al., 2003). Such knowledge on the effects of seasonal and latitudinal changes in

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temperature on reproductive traits is crucial to understanding large-scale distributional patterns of species.

The hairy edible crab *Cancer setosus* (Molina 1782; synonymous *C. polyodon* Poepig 1836) is one of the key predators in a variety of shallow water habitats (<25 m depths) in the Humboldt Current ecosystem (Wolff and Cerda, 1992; Cerda and Wolff, 1993; Ortiz and Wolff, 2002a,b; Jesse and Stotz, 2003; León and Stotz, 2004). This species is caught by an artisanal diving and trapping fishery throughout its wide latitudinal range from Guayaquil in Ecuador (2°S, 079°W) to the Peninsula of Taitao in Southern Chile (46°S, 075°W) (Garth, 1959). A collapse of this fishery has been reported in years that follow strong El Niño events when the upper temperature threshold for survival of *C. setosus* has been exceeded (Arntz et al., 1988; Arntz and Fahrback, 1991; Lang, 2000). Egg-bearing *C. setosus* and females having ripe gonads are found year-round at various locations between Central Chile and Central Peru (Gutiérrez and Zúñiga, 1976; Veaz, 1981; Talledo and Ishiyama, 1988; Wolff and Soto, 1992; Moya, 1995; Jesse, 2001). Nevertheless, it remains speculative if *C. setosus* possesses an extended reproductive period or if individual females actually produce more than a single egg-mass annually.

The aim of this study was to estimate the possible occurrence of multiple annual ovipositions and the duration of interbrood periods for females from Antofagasta (Northern Chile; 23°S, 70°W) and Puerto Montt (Central Southern Chile; 41°S, 73°W; see Fig. 1). Furthermore, the duration of egg-development of *C. setosus* was observed under the natural seasonal temperature regime in Antofagasta (16–23 °C) and for the local ambient temperature in Puerto Montt (~ 12.5 °C). Based on the derived relationship between temperature and the duration of egg-development, the annual number of egg-masses of *C. setosus* was calculated from the literature on the percentage of egg-bearing females and temperature (Giесе, 1959; Wenner et al., 1991) for the locations Casma, Coquimbo (La Herradura Bay and Tongoy Bay), Concepción, and Ancud (see Fig. 1).

2. Material and methods

2.1. Capture and rearing of crabs

Mature female *C. setosus* were caught by divers at 5–10 m water depth at different sites around Antofagasta, Northern Chile (23°S, 70°W; capture between 05/2005 and 10/2005) and in Carelmapu, Central Southern Chile (41°S, 73°W; capture between 09/2006 and 11/2006). The crabs from Northern Chile were held in captivity for up to 10 months in the Aquaculture Institute of the “Universidad de Antofagasta” and the specimen from Central Southern Chile for up to 5 months in the “Universidad Austral de Chile” in Puerto Montt.

2.1.1. Antofagasta

In Antofagasta, ovigerous and non-ovigerous crabs were placed in two 3200-l aquaria in groups of 12 specimens each. These aquaria constantly had a high flow through of fresh seawater, which ensured cleanliness and maintained the water temperature at a comparable level as found in Antofagasta

Bay (Fig. 2). Illumination took place by natural day light. To allow for burying activity of the crabs, the aquaria were equipped with sand-filled boxes and with stones and PVC-tubes to provide additional shelter. Two large males were given to one of the aquaria for 3 months to make observations on mating activity. Females that moulted in the absence of males, where separated from their co-specimen until their new exoskeleton was hardened to avoid cannibalism in the soft-shell state. Dead crabs were replaced by new specimens from the field.

2.1.2. Puerto Montt

In Puerto Montt, solely females with undifferentiated blastula-state eggs were used, which was checked microscopically. Up to nine specimen were held at a time in one of three 500-l aquaria, with constant temperatures of 12 (±0.3), 16 (±0.5) and 19 (±0.3) °C, respectively. Crabs in the 16 and 19 °C aquaria, where acclimatized over 2 to 3 days to this temperatures by gradually raising the temperature from 12 °C. However, for hygienic reasons the closed aquaria did not contain sand-filled boxes, but only large rocks to provide shelter. Light was kept at a 12:12 day–night cycle.

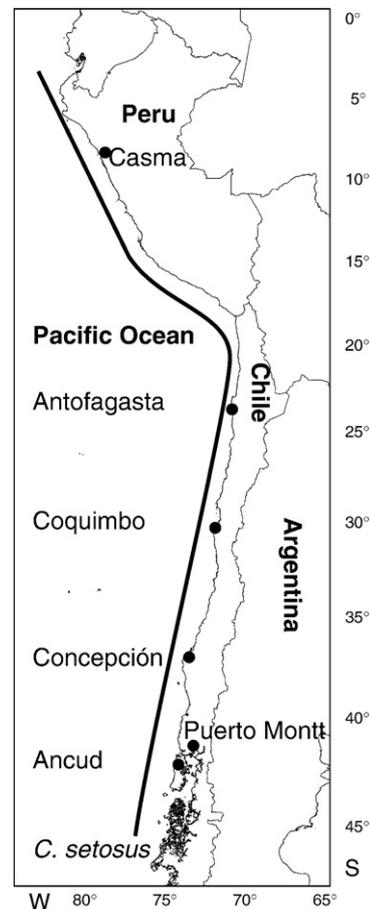


Fig. 1. Distributional range of *C. setosus* along the Latin American Pacific Coast (after Garth, 1959), the experimental sites Antofagasta and Puerto Montt and sites considered for literature review (Casma, Coquimbo, Concepción, Ancud); map modified after PanMap (Diepenbroek et al., 2000).

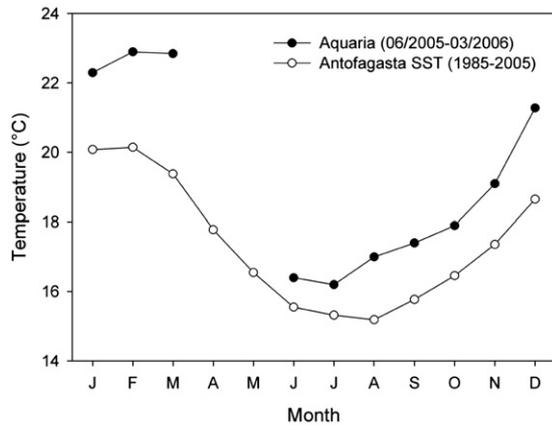


Fig. 2. Antofagasta/Northern Chile: Temperature throughout the experiment (06/2005–03/2006) and mean monthly SST (1985–2005; CENDHOC).

In both locations the crabs were fed *ad libitum* with living mussels *Perumytilus purpuratus*; aquaria were cleaned and water temperature was recorded daily.

2.2. Measurements and observations

Each crab was individually marked with a small plastic tag glued onto the carapace and the width of the carapace (CW) was measured with callipers to the nearest millimetre including the 10th anterolateral spine. The crabs were checked twice daily for the occurrence of moulting, mating, oviposition, and hatching of larvae. After oviposition, the developmental success of the egg-mass was monitored until hatching. Eggs were taken with fine forceps from the border of the egg-mass every 2 to 3 days and were assigned microscopically to one of four successive developmental stages:

- I. Blastula — no yolk used; 1 to 2 days after oviposition
- II. Gastrula — 25% of the yolk used, still no eyes visible
- III. Eye-placode — eyes are visible as a kidney-shaped small dark spot, but still no chromatophores present and no heartbeat
- IV. Pre-hatching — all yolk utilized, eyes completely roundish, chromatophores well developed, heart beats vigorously and embryo moves inside the egg-shell; 1 to 2 days before larvae hatching (stages modified after Baeza and Fernández, 2002).

Eggs were identified as dead by the presence of discolorations in the first three developmental stages and by the lack of a heartbeat in the pre-hatching stage.

2.3. Annual number of egg-masses along latitude

The annual number of egg-masses was calculated for populations from Casma, Coquimbo (La Herradura Bay; Tongoy Bay), Concepción and Ancud (for locations see Fig. 1) based on the literature on the monthly percentage of ovigerous females (N_i), the mean length of a month of 30.4 days and the duration of egg-

development (days) for the mean monthly sea surface temperature at the respective location (d_{ie}):

$$\text{Annual_egg-masses} = \sum_{i=1}^{n \leq 12} \frac{N_i(\%) \times 30.4}{d_{ie}}$$

3. Results

Female *C. setosus* were held in captivity for up to 10 months in Antofagasta, Northern Chile, and for up to 5 months in Puerto Montt, Central Southern Chile. Their reproduction was presented as the sequence of moulting/mating, oviposition, embryo incubation, and interbrood periods. Ovigerous females ranged in carapace width from 79 to 158 mm in Antofagasta and from 107 to 140 mm in Puerto Montt.

3.1. Moulting, oviposition, and interbrood periods

3.1.1. Antofagasta (natural seasonal temperature conditions of 16–23 °C)

Thirteen females moulted successfully in captivity, of which 5 mated with a male crab. Males started the pre-copulatory embrace about a week before the females' ecdysis took place and extended their mate-guarding for 2–3 days post-copula. The average increment in carapace width per moult was 12% (± 5 ; $N=13$).

Oviposition took place 2 months after moulting ($62.1 \text{ days} \pm 10$; $N=9$), when female crabs buried in the sand to form an incubation chamber with their abdomen. Eggs were extruded stepwise over several hours into this incubation chamber, allowing a part of the egg-mass to attach to the pleopod-hairs, before the abdomen was further opened and more eggs were extruded. At the end of oviposition females kneaded the new egg-mass with the dactyli of their pereiopods and showed abdominal flapping. After eclosion of larvae, females produced up to two more viable egg-masses without moulting. The second egg-mass was observed 62.5 days (± 7.6 ; $N=7$) after the oviposition of the first clutch and a third egg-mass was laid another 73.5 days (± 12.5 ; $N=11$) later. The interbrood periods took 29.7 days (± 13.1 ; $N=17$) and 47.8 days (± 18.2 ; $N=6$), calculated as the duration from larvae hatching to the oviposition of the following egg-masses two and three, respectively. Females moulted again about 2 months after larval release (59.3 ± 18.8 ; $N=9$) (Table 1).

3.1.2. Puerto Montt (12, 16, 19 °C)

Two months after the first oviposition a second egg-mass was produced ($64.4 \text{ days} \pm 9.8$, $N=5$) and a third egg-mass followed 67.0 days (± 2.8 ; $N=2$) later at 19 °C (± 0.3) in Puerto Montt (Table 1). The interbrood periods took one month ($30.8 \text{ days} \pm 3.0$; $N=4$) between the first and the second egg-mass. At 16 °C (± 0.5) four females produced a second egg-mass about 82.8 days (± 28.9) after the oviposition of the first one. A single female moulted 66 days after larval hatching. At 12 °C (± 0.3) one female produced a second egg-mass about 137 days after the oviposition of the first and two more showed ripe ovaries when the experiment was ended (81 days after oviposition).

Table 1
Temporal sequence of reproductive events in cancrids: moult, oviposition, interbrood periods and annual number of egg-masses

Species	T (°C)	Moult–oviposition (days)	Oviposition–oviposition (days)		Interbrood period (days)		Larvae hatching–moult (days)	Egg-masses/year
			1–2	2–3	1–2	2–3		
			<i>C. antennarius</i>	12±2 ¹ ;	77 (N=1) ¹			
<i>C. anthonyi</i>	13.5±1.6 ³				41.9±11.5 (N=78) ³			Ovigerous year-round ² ; up to 3 ^{a3}
<i>C. magister</i>		90 ³ ; 163 (81–391; N=14) ⁵						≤1 ⁴
<i>C. pagurus</i>		120 ³						≤1 ³
<i>C. gracilis</i>	6.9–13.4 ⁶							2 ^a (2. very small) ⁶
<i>C. productus</i>	6.9–13.4 ⁶							2 ^a (2. very small) ⁶
<i>C. setosus</i>								0.9–3.6 ^b
Puerto Montt	12±0.3		137 (N=1)					
Puerto Montt	16±0.5		82.8±28.9 (N=4)				66 (N=1)	
Puerto Montt	19±0.3		64.4±9.8 (N=5)	67.0±2.8 (N=2)	30.8±3.0 (N=4)			up to 3 in 124.0 days±2.8 ^a (N=2)
Antofagasta	16–23	62.1±10.0 (N=9)	62.5±7.6 (N=7)	73.5±12.5 (N=11)	29.7±13.1 (N=17)	47.8±18.2 (N=6)	59.3±18.8 (N=9)	up to 3 in 133.6 days±6.6 ^a (N=7)

(1) Caroll (1982); (2) Reilly (1987); (3) Shields et al. (1991) and studies therein; (4) Swiney et al. (2003); (5) Ebert et al. (1983); (6) Knudsen (1964).

^a Laboratory conditions.

^b Analysis of field-data on percentage of ovigerous females.

3.2. Egg-development and survival

Throughout the study period 44 egg-masses were produced in Antofagasta, however not all egg-masses successfully completed development. Within the temperature range of 16–22 °C larvae hatched in 21 out of 34 egg-masses (62%). Egg-mass mortality within this temperature range occurred in advanced developmental stages (eye-placode to pre-hatching) (Fig. 3). Females continued to produce egg-masses in the austral-summer (N=10) when temperatures ranged between 22 and 24 °C. However, at these temperatures, all eggs either failed to connect to the setae on

the pleopods at oviposition, or died within few days afterwards. Egg-development in Antofagasta took 43.2 days from oviposition to hatching of larvae at 16 °C in austral-winter and was shortened to 22.7 days at a mean temperature of 22 °C in summer (Fig. 3). The effect of temperature (x) on the duration of egg incubation until larvae hatching (y) is described by an exponential decay function: $y = 239.3175e^{-0.0107x}$ ($r^2 = 0.83$; $N = 21$). Egg-development at 12.5 °C in Puerto Montt took 65 days (±1.2; N=5), which is similar to the calculated duration of 62.8 days for this temperature (based on the formula from Antofagasta). The relation between temperature and duration of egg-development was then used to calculate the annual number of egg-masses along latitude from field studies (see Section 3.3).

3.3. Seasonal reproductive cycle and annual number of egg-masses along latitude (south to north)

Ovigerous *C. setosus* are found in Ancud (41°S) from austral-winter until early austral-summer (Pool et al., 1998), reaching a maxima from August to October, which coincides with the spring temperature rise (Fig. 4). Based on the percentage of egg-bearing females and the duration of egg incubation at the mean monthly SST (°C) an annual output of 0.9 egg-masses per female was calculated for this location. Five degrees of latitude further north in Concepción (36°S), reproduction takes place year-round (Veaz, 1981) (Fig. 4), which leads to an annual output of 3.6 egg-masses per female. In Tongoy Bay and La Herradura Bay, the former located south and the later north of Coquimbo (29°S), 2.1 and 1.8 annual egg-masses are produced, respectively (Soto, 1990; Jesse, 2001) (Fig. 4). With the exception of the hot summer months, reproduction also takes place round the year in Casma (9°S) (Moya, 1995) (Fig. 4), but due to the low

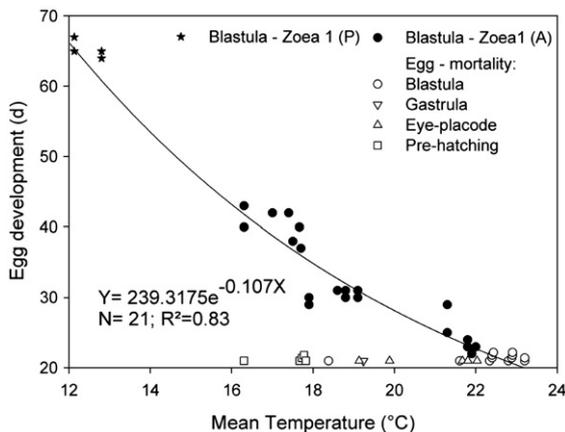


Fig. 3. Duration of egg-development of *C. setosus* from oviposition to larvae hatching in Antofagasta (A) (filled dots). Throughout the experiment in Antofagasta 44 egg-masses were produced of which 23 died, before larvae hatched (unfilled symbols, showing the developmental stage when egg-mass mortality occurred; not scaled to the y-axis). The duration of egg-development of *C. setosus* in Puerto Montt (P) at 12.1–12.8 °C is indicated by asterisks (n=5).

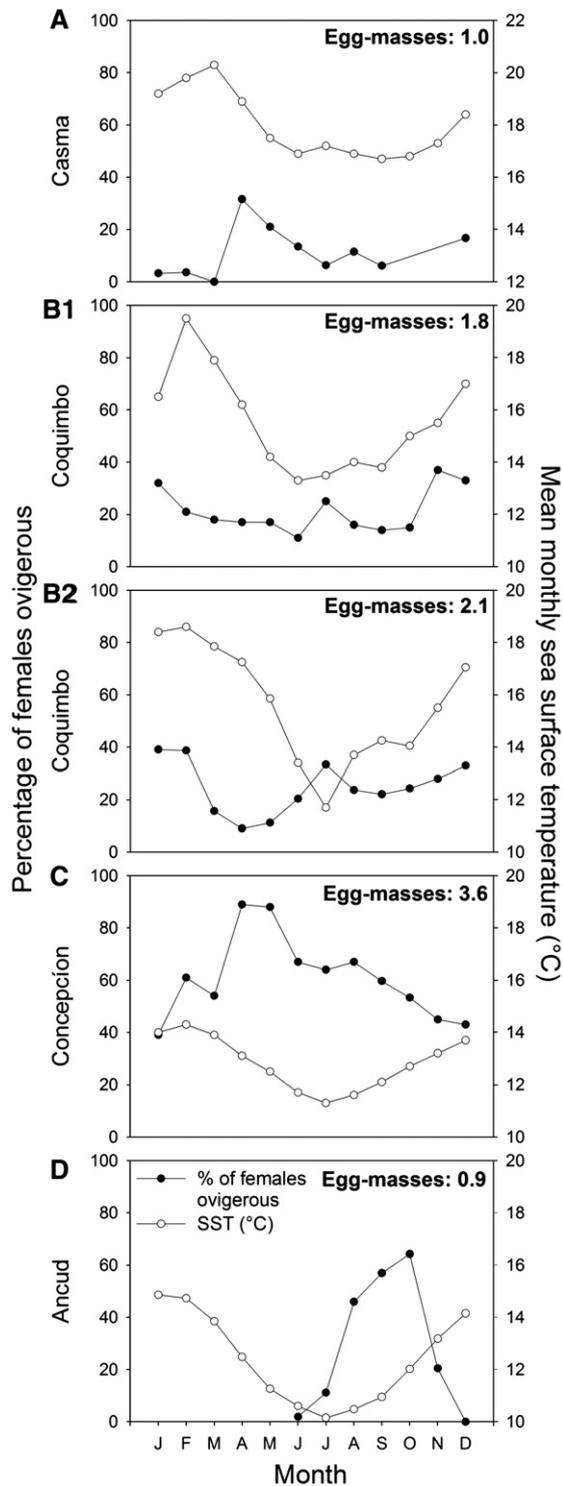


Fig. 4. Monthly percentage of ovigerous female *C. setosus* and SST (°C) along latitude and calculated annual egg-masses: (A) Casma, Guaynuna Bay, 9°S, 12/1994–09/1995 (Moya, 1995); SST 01/2002–09/2006; Acuacultura y Pesca S.A.C. pers. com.; (B) Coquimbo: (1) La Herradura Bay, 29°S, 02/1987–01/1988 (Soto, 1990); SST—same study; (2) Tongoy Bay, 30°S, 06/1996–05/1997 (Jesse, 2001); SST 06/1996–05/1997 (CENDHOC); (C) Concepción, Concepción Bay & San Vincent Bay, 36°S, 11/1980–08/1981 (Veaz, 1981); SST 01/1983–01/2003 (CENDHOC); (D) Ancud, Yuste Bay 41°S, 06/1997–05/1998 (Pool et al., 1998); SST 01/1999–12/2005 (CENDHOC).

overall percentage of egg-bearing females only one annual egg-mass is produced at this location.

4. Discussion

4.1. Reproductive potential — aquaria experiments

Contrary to most other cancrid crabs who have but one annual egg-mass (Shields, 1991), *C. setosus* produced up to 3 egg-masses within 4 1/2 months (at 16–23 °C in Antofagasta and at 19 °C in Puerto Montt), which is the highest known reproductive output within this genus (Table 1). These observations were highly comparable in Antofagasta and Puerto Montt, showing that the potential to have multiple ovipositions is not genetically constrained to crabs from Northern Chile. Interestingly, all crabs in Antofagasta needed about the same time span of 2 months from moult to an initial oviposition, thereafter to a following oviposition and finally from larvae hatching to moult (Table 1). Based on these results, it seems reasonable to argue that the energetic costs of moulting and oviposition are comparable.

Multiple ovipositions were also observed at 12 and 16 °C in Puerto Montt, however due to the slowing down of metabolism at lower temperatures, more time was required to obtain sufficient energy for a second oviposition. To meet the energy demand of egg-production, ovigerous females were not quiescent as reported for *C. pagurus* and *C. magister* (Howard, 1982; Stone and O'Clair, 2002), but active and constantly feeding. Furthermore, this continuous reproduction of *C. setosus* is enabled by the storage of sperm in the spermatheca after mating, which serves to inseminate at least three egg-masses without an intervening moult. Such a reduced moult-frequency of mature females has the advantage that mortality in the soft-shell state is avoided and energy effectively can be directed towards egg-production. The price of this energetic investment in offspring is a reduction of female growth efficiency by half, compared to male crabs (Wolff and Cerda, 1992). Sperm stored in the spermatheca stays viable for at least 2 1/2 years and serves in *C. magister* and *C. pagurus* to inseminate more than one egg-mass, which however are produced over consecutive years (Pearson, 1908; Edwards, 1966; Bennett, 1974; Hankin et al., 1989). In these two species, but not for *C. setosus* (this study), “sperm plugs” protrude after mating for some time from the female gonopores, where they are easy to be recognised and thus help to resolve the mating history of crabs from field studies (Edwards, 1966; Haefner, 1977; Oh and Hankin, 2004). In *C. setosus*, sperm can even be retained via moults as shown by females who moulted in the absence of male crabs and afterwards produced up to two viable egg-masses.

4.2. Duration and success of egg-development

Temperature is the main factor determining the duration and success of (crustacean) egg-development (Wear, 1974). Egg incubation was accelerated by the seasonal temperature rise in Antofagasta until a thermal limit of 22 °C, when larvae hatched three times earlier than at 12 °C in Puerto Montt ($Q_{10} \sim 3$). The overall temperature-related duration of egg-development was comparable to that of *C. antennarius* and *C. anthonyi* (Carroll,

Table 2
Duration of cancrid egg-development and temperature

Species	T (°C)	Egg-development (days)	Reference
<i>C. antennarius</i>	12±2	49–56	Carroll (1982)
<i>C. anthonyi</i>	10	55	Shields and Kuris (1988)
<i>C. magister</i>	15	42	Wild (1980, 1983a,b)
	20 ^a	27	
	9.4	123	
	~13–14	72	
<i>C. pagurus</i>	16.7 ^a	64	Wear (1974)
	12.5	~80 ?	
<i>C. setosus</i>			
Puerto Montt	12.5	65.0	Present study
Antofagasta	16	43.2	
Antofagasta	20	28.2	
Antofagasta	22 ^a	22.7	

^a Upper temperature threshold of egg-development.

1982; Shields and Kuris, 1988), who also have similar-sized eggs (Hines, 1991; Shields et al., 1991; this study), but faster than for the larger eggs of *C. pagurus* and *C. magister* (Wear, 1974; Wild, 1983a) (see Table 2).

Eggs produced at temperatures above 22 °C failed to connect to the female pleopods at oviposition (Fig. 3), which occurred most likely due to a temperature limitation within the complex process of egg-attachment (Saigusa et al., 2002). Such a failure of egg-attachment at high temperatures has also been reported for the American lobster *Homarus americanus* (Waddy and Aiken, 1995). However, at lower temperatures (16–22 °C) about 40% of the egg-masses died before larvae hatching occurred, which might be attributed to an oxygen limitation inside the egg-mass (Brante et al., 2003). Oxygen demand of developing eggs increases with ontogenetic progress and scales with temperature (Naylor et al., 1999; Baeza and Fernández, 2002), which may explain why egg-mass mortality occurred at progressively earlier developmental stages with seasonal temperature rise (Fig. 3).

22 °C presents the highest reported temperature for successful cancrid egg-development and for *C. magister* larvae-hatching success is already greatly reduced at 16–17 °C (Wild, 1983a). A further source of substantial egg mortality of *C. magister* are infestations by nemertean egg-predators *Carcinomertes errans* (Wickham, 1979; Kuris, 1991), which however, were only found infrequently and in low densities in egg-masses of *C. setosus*.

4.3. Annual number of egg-masses along latitude

Favourable temperatures year-round, which are subject solely to moderate seasonal oscillation (Urban, 1994), combined with the high food availability in the shallow water benthic ecosystem (Wolff and Soto, 1992) create ideal conditions for continuous reproduction of *C. setosus* from Central Southern to Northern Chile. This is reflected in an annual output of about 2 egg-masses in Coquimbo (both La Herradura Bay and Tongoy Bay) and more than 3 egg-masses in Concepción (Fig. 4). A comparable reproductive potential within the cancrids is only known for the yellow rock crab *C. anthonyi* from the Southern California Current (Shields et al., 1991).

Nevertheless, *C. setosus* only produces about one annual egg-mass close to its southern and northern extremes of distribution (Ancud, Casma) (Fig. 4), most likely due to the high relative metabolic cost of life nearby the species lower and upper temperature threshold (for reviews see Clarke, 1987, 2003; Pörtner, 2001). Likewise, *C. magister* fails to acquire sufficient energy to produce one egg-mass every year at their northern distributional range in Southern Alaska (Swiney and Shirley, 2001; Swiney et al., 2003), which is the normal reproductive output throughout most of this species range.

5. Conclusions

The annual number of egg-masses produced by *C. setosus* is primarily dependent on temperature when food is not limited, and presents a key reproductive parameter, which has to be considered for comparisons of reproductive output and effort along latitude.

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