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Temperature effects on reproduction and early life-history traits in the brachyuran crab *Cancer setosus* in the Humboldt Current System

Doctoral thesis
by

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Climate variability and El Niño Southern Oscillation:
Implications for Natural Coastal Resources and Management

"It is evident that the various processes which are characteristic of the life-history of the edible crab [Cancer pagurus] are subject to considerable variation, and it is necessary that further investigations should be made before the numerous problems can be regarded as being solved" (Pearson, 1908).

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SUMMARY

The cold Humboldt Current (HC) allows for a wide distribution range of the crab *Cancer setosus* MOLINA, 1782 along the Pacific Coast of Peru and Chile (~2°S to 46°S). Life of this cold-water adapted brachyuran crab in the HC is challenged by high interannual temperature variability influenced by El Niño Southern Oscillation (ENSO). Early life-history stages may be particularly sensitive to abrupt changes in temperature and may thus represent physiological bottlenecks in species distribution. The present study aims at identifying the effects and limits of latitudinal and ENSO temperature variation on reproduction and early life history traits of *C. setosus*. The number of annual ovipositions was calculated from monthly frequencies of ovigerous females and the temperature dependent duration of egg development (65 days at 12°C to 23 days at 22°C). In Ancud, Chile (41°S) one annual clutch is laid in late winter, while in Concepción (36°S), slightly higher winter temperatures (12°C vs. 10°C in Ancud) enable for reproduction throughout the year (~3.6 clutches per year). However, towards the species´ northern range the annual number of clutches decreases to ~2 in Coquimbo (29°S) and ~1 in Casma (9°S), which is attributed to an increase in metabolic costs of life under warmer conditions. Temperature dependent changes in the reproductive cycle were confirmed by observations on crabs reared in aquaria in Antofagasta (23°S, 16-22°C) and in Puerto Montt (41°S, 12, 16 and 19°C) for up to 10 and 5 months, respectively. The decreasing interbrood periods at higher temperatures are accompanied by a decrease in the energetic investment per offspring. Eggs laid at low temperatures in Puerto Montt (~11°C) contained 32% more energy, measured as dry mass, carbon, nitrogen, and fatty acid content and volume, than eggs of equal sized females produced at ~19°C in Antofagasta. However, when exposed to warmer temperatures, seasonally in the field and under aquaria conditions, females in Puerto Montt went on to produce smaller eggs in subsequent egg masses. The larger investment per offspring at lower pre-oviposition temperature is discussed to be adaptive by providing the hatching larvae with a higher amount of energy needed for their prolonged development at lower temperatures. Female investment in egg traits is not carried over 1:1 into larval traits. Throughout egg development almost twice as much of the total of fatty acids was used for metabolism in eggs incubated at 12°C compared to 19°C (-1.12 and -0.62 µg/egg, respectively). The observed high degree of reproductive plasticity is discussed as a key to the species’ wide distributional range and to sustaining exploitable populations under conditions of high and unpredictable environmental stochasticity. However, the current level of uncontrolled fishing pressure and the low enforcement of the minimum legal size of 120 mm carapace width (CW) have caused Chilean *C. setosus* catches to decline for more than a decade. Next to a strict enforcement of the minimum CW, the creation of no-fishing areas is recommended, for (i) allowing recovery of the stock and maintaining larval supply, (ii) studying population dynamics and the ecological role of this benthic predator in the absence of fisheries mortality, and (iii) preventing likely long-term effects of size selective extraction of large, fast-growing specimens on the populations´ gene-pool (“fisheries-induced evolution”).

ZUSAMMENFASSUNG

Der kalte Humboldtstrom ermöglicht dem Taschenkrebs *Cancer setosus* MOLINA, 1782 eine weite Verbreitung entlang der Pazifikküste von Chile und Peru (~2°S bis 46°S). Die vorherrschende hohe zwischenjährliche Variabilität in den Temperaturbedingungen, verursacht von El Niño und der südlichen Oszillation (ENSO), stellt allerdings diesen an Kaltwasser angepaßten brachyuren Krebs vor Herausforderungen. Frühe Lebensstadien reagieren oft besonders sensibel auf Temperaturveränderungen und bilden somit Engpässe für die Verbreitung der Art. Die vorliegende Arbeit erfaßt die Auswirkungen und Grenzen von Temperaturveränderungen (latitudinal und im Zuge von ENSO) auf die Fortpflanzung und frühen Lebensstadien von *C. setosus*. Die Anzahl an jährlichen Eiablagen wurde anhand der monatlichen Häufigkeit eiertragender Weibchen und der temperaturabhängigen Entwicklungsdauer der Eier berechnet (zwischen 65 Tagen bei 12°C und 23 Tagen bei 22°C). In Ancud, Chile (41°S) wird eine Eimasse jährlich im Winter produziert, wohingegen bereits leicht erhöhte Wintertemperaturen in Concepción (36°S) (12°C vs. 10°C in Ancud) eine ganzjährige Fortpflanzung ermöglichen (~3.6 Eimassen im Jahr). Allerdings nimmt die jährliche Anzahl an Eimassen in Richtung der nördlichen Verbreitungsgrenze wieder auf rund zwei in Coquimbo (29°S) und eine in Casma (9°S) ab, was auf den zunehmenden energetischen Aufwand des Stoffwechsels unter wärmeren Bedingungen zurückgeführt wird. Temperaturabhängige Veränderungen im Fortpflanzungszyklus wurden durch Beobachtungen an *C. setosus,* die für 10 Monate in Aquarien bei 16-22°C in Antofagasta (23°S) und für 5 Monate bei 12, 16 sowie 19°C in Puerto Montt (41°S) gehalten wurden, bestätigt. Mit der Verkürzung des Abstandes zwischen Folgebruten bei höheren Temperaturen ist eine Abnahme der Menge an Energie verbunden, die pro Ei investiert wird. Die unter kalten Bedingungen in Puerto Montt (~11°C) produzierten Eier waren 32% energiereicher, gemessen an ihrer Trockenmasse, ihrem Volumen und Gehalt an Kohlenstoff, Stickstoff und Fettsäuren im Vergleich zu den Eiern, die bei rund 19°C in Antofagasta produziert wurden. Allerdings haben Weibchen in Puerto Montt Folgeeimassen mit kleineren Eiern produziert, wenn sie höheren Temperaturen ausgesetzt waren, sowohl saisonal in der Natur als auch unter Aquarienbedingungen. Dieser höhere Aufwand pro Ei bei niedrigeren Temperaturen wird als Anpassung angesehen, da die schlüpfenden Larven mit mehr Energie für ihre verlängerte Entwicklung bei kalten Temperaturen ausgestattet werden. Der mütterliche Aufwand in die Eier wird allerdings nicht 1:1 an die Larven weitergegeben. Für die Eientwicklung bei 12°C wurde im Vergleich zu 19°C nahezu doppelt soviel an Fettsäuren verbraucht (jeweils -1.12 und -0.62 µg/Ei). Die beobachtete hohe Plastizität in der Fortpflanzungsbiologie von *C. setosus* wird als Schlüsselelement für die weite Verbreitung von befischbaren Populationen dieser Art unter variablen Umweltbedingungen angesehen. Der bisherige unkontrollierte Fischereiaufwand in Chile führte jedoch in Verbindung mit der Nichteinhaltung der gesetzlichen Mindestcarapaxbreite von 120 mm zu einem Rückgang der chilenischen Anlandungen über das vergangene Jahrzehnt. Neben der strikten Einhaltung der Mindestgröße wird die Einrichtung von fischereifreien Gebieten vorgeschlagen, um (i) eine Erholung des Bestandes zu ermöglichen und die Larvenproduktion zu gewährleisten, (ii) die Populationsdynamik und die ökologische Rolle dieses benthischen Räubers in Abwesenheit von Fischereidruck zu untersuchen, und (iii) um den möglichen Auswirkungen einer größenspezifischen Entnahme der schnellwachsenden Individuen auf den Genpool der Art entgegen zu wirken („fischereilich induzierte Evolution“).

RESUMEN

Las condiciones frías de la Corriente de Humboldt (CH) permiten una ámplia distribución del cangrejo *Cancer setosus* MOLINA, 1782 a lo largo de la costa pacífica de Perú y Chile (~2°S hasta 46°S). La existencia de este crustáceo braquiuro en la CH depende de su capacidad para tolerar la gran variabilidad térmica interanual, infuenciada por El Niño-Oscilación del Sur (ENOS). Las etapas tempranas en la historia de vida suelen ser particularmente sensibles a cambios abruptos de temperatura y pueden, por lo tanto, representar "cuellos de botella" para la distribución de las especies. Este estudio pretende identificar los efectos y los límites impuestos por la variación térmica relacionada con la latitud y ENOS sobre la reproducción y las características de las primeras fases en la historia de vida de *C. setosus*. A partir de datos mensuales de frecuencia de hembras ovígeras y la duración termo-dependiente del desarrollo de los huevos (65 días a 12°C hasta 23 días a 22°C) se calculó el número de oviposiciones por año. En Ancud, Chile (41°S) se observó una puesta anual a finales de invierno, mientras en Concepción (36°S) la temperatura invernal ligeramente mayor (12°C vs. 10°C en Ancud) permite la reproducción durante todo el año (~3.6 puestas por año). Sin embargo, hacia el límite norte de la distribución el número anual de puestas disminuye de nuevo hasta ~2 en Coquimbo (29°S) y ~1 en Casma (9°S), lo cual es atribuible al incremento en el costo metabólico de vivir en condiciones más cálidas. Los cambios termo-dependientes en el ciclo reproductivo fueron confirmados al estudiar cangrejos mantenidos en acuarios en Antofagasta (23°S, 16-22°C) durante 10 meses y en Puerto Montt (41°S, 12, 16 y 19°C) durante 5 meses. La reducción del período entre puestas en altas temperaturas coincide con una reducción en la inversión energética por descendiente. El contenido energético, medido como masa seca, contenido de carbono, nitrógeno, ácidos grasos y volumen, de los huevos puestos en bajas temperaturas en Puerto Montt (~11°C) fue 32% mayor que el de los huevos de igual talla producidos por hembras a ~19°C en Antofagasta. Sin embargo, expuestas a temperaturas más altas, ya sea por la estacionalidad en el medio natural o en condiciones de laboratorio, en Puerto Montt las hembras empezaron a producir huevos más pequeños en masas ovígeras subsecuentes. Se discute el valor adaptativo de la mayor inversión por descendiente en temperaturas más bajas antes de la oviposición, lo cual proveería a las larvas de una mayor cantidad de energía requerida para un desarrollo prolongado en condiciones más frías. La inversión energética de las hembras en los huevos no se refleja directamente en las características de las larvas. A través del desarrollo de los huevos, casi el doble del total de los ácidos grasos se usaron en procesos metabólicos en huevos incubados a 12°C comparados con huevos incubados a 19°C (-1.12 y -0.62 µg/egg, respectivamente). El alto grado de plasticidad reproductiva podría ser un factor clave que permite un amplio rango de distribución y el sostenimiento de poblaciones explotables bajo condiciones de gran, e impredecible, estocasticidad ambiental. Sin embargo, el nivel actual de presión pesquera incontrolada y el poco control en el cumplimiento de la talla mínima legal de 12 cm de longitud de caparazón (LC) han causado el declive de las capturas de *C. setosus* en Chile por más de una década. Además de un estricto control de la talla mínima legal LC, se recomienda la creación de áreas de no extracción, para (i) permitir la recuperación de los stocks y el mantenimiento del suministro larval, (ii) estudiar la dinámica poblacional y el rol ecológico de este predador bentónico en ausencia de mortalidad pesquera, y (iii) evitar probables efectos de largo plazo de la extracción selectiva de especímenes grandes, de rápido crecimiento sobre la evolución del pool genético de las poblaciones inducida por las pesquerías.

1 INTRODUCTION

1.1 Macroecology and reproductive traits of marine invertebrates

Ambient temperature is one of the most prominent abiotic factors in the life of ectotherms, basically affecting every aspect of their physiology (Hochachka and Somero, 2002; Pörtner et al., 2006). Over evolutionary timescales ectotherms have developed different ranges of thermal tolerance, setting the limits to their distribution (Hutchins, 1947; Pörtner, 2001). Within this species dependent “thermal tolerance window” the actual temperature endured by a specimen depends on its thermal acclimatization, which may change seasonally and geographically throughout the species’ distributional range (Clarke, 1993b). Furthermore, survival and normal activity may take place under a wider range of temperatures than energetically demanding processes such as reproduction (Fry and Hochachka, 1970). Early life history stages such as eggs and larvae are often found to have narrower thermal tolerance windows and a lesser tolerance to adverse temperature conditions in comparison to adult stages (Hutchins, 1947; Aiken and Waddy, 1986; Urban, 1994; Hoegh-Guldberg and Pearse, 1995; Anger, 2001; Thatje, 2005). Consequently, reproductive processes and the development of early life history stages may represent bottlenecks in temperature dependent species distribution.

1.1.1 Invertebrate reproductive cycles

Temperature has been identified as the main factor controlling the breeding activities of marine invertebrates (Orton, 1920); referred to as “Orton’s Rule” (Thorson, 1946; Patel and Crisp, 1960; Helmuth et al., 2006). Orton suggested that the seasonal reproductive activity is switched on when spring temperature crosses a certain threshold (Clarke, 1993b). However, Orton’s deterministic view of temperature has been criticised for being too sweeping, not taking into account that further exo- and endogenous factors also influence marine invertebrate reproductive cycles (see Giese 1959) and nowadays “our view of the role of temperature has shifted from driving force to environmental cue” (Clarke, 1993b). The timing of reproduction represents a crucial life-history trait, which influences both, the future prospect of offspring and the parental fitness (Varpe et al., 2007). Despite many exceptions, on a global scale, the duration of the reproductive season in marine invertebrates principally increases in length from the Poles towards the Tropics (Giese, 1959;

Bauer, 1992). In high Antarctic regions, reproduction of many invertebrates is thought to be synchronized by seasonal changes in photoperiod and brief periods of phytoplankton production and probably less by the seasonal temperature fluctuation, which seems too slight to act as environmental cue (<1°C in McMurdo Sound, Antarctica) (Clarke, 1988). However, this paradigm of "reproduction being highly seasonalized in Antarctica and tied to the plankton blooms" is fading due to a growing number of reports on invertebrates reproducing aseasonally or even year round (Arntz and Gili, 2001; Pearse and Lockhart, 2004). In temperate regions, the reproductive season in many species extends in length with a decrease in latitude. These geographic shifts in breeding season are frequently associated with the spring temperature rise and either gonad production or larval development are timed to coincide with peak primary production (Bosselmann, 1991). Shifting breeding seasons in temperate species may have pervasive effects on other life-history traits, such as size of maturity, reproductive output, and life span (Hemmi, 1993). In the tropics usually little seasonality in temperature and food availability is found, and due to this predictability in environmental conditions, many tropical invertebrates reproduce year round (Giese, 1959).

Summary:

- Temperature represents an important cue in invertebrate reproductive cycles.
- Intraspecific geographical shifts in breeding season are postulated to affect other life-history traits.

1.1.2 Inter- and intraspecific variability in egg energy provision

Maternal investment in offspring is one of the most central life-history traits, affecting both the fitness of the mother and of the offspring (Stearns, 1992; Fox and Czesak, 2000). The answer to the question, whether it is advantageous to produce many but small or fewer better equipped large eggs, may depend on the environmental conditions experienced by the hatching larvae (Smith and Fretwell, 1974). The Danish ecologist Gunnar Thorson was the first to notice an inverse relationship in egg size and temperature for a wide range of invertebrate taxa (Thorson, 1936; 1946; 1950). Larger eggs in higher latitude species are accompanied by a tendency towards non-planktonic, non-feeding larval development, nowadays referred to as

“Thorson’s rule” (Mileikovsky, 1971; Laptikhovsky, 2006). Later studies confirmed Thorson’s rule for prosobranch gastropods and crustaceans, but not for echinoderms and bivalves (Clarke, 1992; Levin and Bridges, 1995; Poulin and Féral, 1996; Pearse and Lockhart, 2004).

Large, yolky eggs at high latitudes are seen as evolutionary adaptations to the mismatch between short periods of pulsed primary production and prolonged (lecithotrophic-) larval development at lower temperatures (Clarke, 1992; Thatje et al., 2005b). These interspecific differences in egg traits were acquired over evolutionary time-scales. However, egg traits may vary also intraspecifically, within a certain “reaction norm”, which is a life-history trait in itself (Ricklefs and Wikelski, 2002). Such phenotypic plasticity allows for the optimization of reproductive effort towards different environmental conditions (Via et al., 1995; Hadfield and Strathmann, 1996; Allen et al., 2008). Again, in most cases, more energy is invested in the single egg under colder conditions, either compared over gradients in temperature along latitude, depth, between seasons or years (for finfish Rass, 1936; Chambers, 1997; Johnston and Leggett, 2002; Llanos-Rivera and Castro, 2006; Green, 2008); (for Crustacea Crisp, 1959; Patel and Crisp, 1960; Barnes and Barnes, 1965; Efford, 1969; Kerfoot, 1974; Nishino, 1980; Amsler and George, 1984b; Skadsheim, 1989; Gorny et al., 1992; Kattner et al., 1994; Sheader, 1996; Oh and Hartnoll, 2004; Rosa et al., 2007); (for terrestrial arthropods Fox and Czesak, 2000; Fischer et al., 2003).

The Chilean/Peruvian coast presents a very suitable setting for studying latitudinal intraspecific variability in reproductive traits, due to its north-south orientation and the wide distribution ranges of many species. An increase in egg energy provision with higher latitude along this coastline has been reported for decapod Crustacea (Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Brante et al., 2003; 2004; Lardies et al., 2008), for the muricid gastropod *Concholepas concholepas* (higher embryo number per egg capsule) (Fernández et al., 2007) and for the anchovy *Engraulis ringens* (Llanos-Rivera and Castro, 2006). However, the majority of these studies are solely based on field observations, which do not allow for the control of the factors which may affect egg traits (Chambers, 1997) and, in the case of latitudinal comparisons, may be influenced by genetic differentiation (Kokita, 2003). Energetic investment in offspring may vary with the females’ feeding condition, reproductive history, and also with its size (Buckley et al., 1991; Clarke, 1993c). Field observations on variability in reproductive traits should preferably be accompanied by experiments under controlled laboratory conditions, which would allow for the quantification of female plasticity in reproductive traits in response to varying environmental factors and in relation to the individual life-history of females.

Summary:

- Within closely related Crustacea from different latitudes, egg size tends to increase polewards.
- Egg size may change also intraspecifically – the degree of variability is an important life-history trait in itself.
- Intraspecific plasticity in egg energy provision is postulated to extend the reproductive season and the species range.

1.1.3 Carry over effects – “metamorphosis is not a new beginning“

In order to assess the importance or “adaptiveness” of intraspecific variation in egg energy provision one has to know to which degree these initial differences are carried over to later life history stages (Beckermann et al., 2002). Fitness of hatching larvae is affected by the female investment in eggs, also referred to as “maternal effects” (Bernardo, 1996a, b), but as well by the conditions experienced throughout egg development. In the spider crab *Hyas araneus*, eggs incubated at 12°C, instead of naturally 3-6°C, gave rise to larvae, which were hampered in growth throughout larval and early juvenile development (Kunisch and Anger, 1984). Temperature does thus not only affect the duration of egg development (Wear, 1974), but may alter the metabolic efficiency of embryo differentiation. However, higher temperature does not universally have a negative impact on metabolic efficiency of egg development (Heming, 1982). In the snow crab *Chionoecetes opilio* larval size (spine lengths) decreased with an increase in egg incubation temperature, while caloric content of the hatching zoea 1 larvae remained stable (Webb et al., 2006). In gadoid fish, larvae were significantly larger when hatching from eggs incubated at intermediate temperatures and reduced in size at lower and higher temperatures (Chambers, 1997). Small differences in size at hatching may have pronounced effects on larval survival, due to differences in prey spectrum and starvation resistance (Hart, 1995).

The energy available after egg development in some species determines or at least influences the pathways of larval development. In the caridean shrimp *Crangon crangon*, less larval stages are required to reach the juvenile stage for larvae hatching from larger winter eggs, compared to those hatching from smaller summer eggs (Criales and Anger, 1986; Linck, 1995). In the estuarine crab *Chasmagnathus granulata,* the biomass of the hatching larvae was affected by the salinity experienced throughout egg development affecting later growth and number of larval stages (Giménez, 2002, 2006). These "links" between different life-history stages may be of high importance for recruitment and population dynamics, especially in variable environments such as the Humboldt Current System. Consequently, research on development and ecology of invertebrates with a complex life cycle has to consider that "metamorphosis is not a new beginning" (Pechenik, 2006).

Summary:

- Environmental conditions experienced in one life-history stage may have pervasive effects on fitness and development of later life-history stages.

1.1.4 Invertebrate reproduction in the Humboldt Current System

The Eastern Boundary Current of South America, the Humboldt Current (HC), extending from Southern Chile (~42°S) to Ecuador and the Galapagos Islands, is one of the most productive marine ecosystems on Earth (Arntz and Fahrbach, 1991; Castilla and Camus, 1992). Equatorward trade wind forcing, in combination with Ekman transport, causes an offshore transport of coastal surface water. The resulting lowering of the coastal sea level (basin wide east/west slope of ~50 cm) leads to a lowering of the thermocline making nutrient rich water available to upwelling to the euphotic zone, where it boosts extraordinary high primary production, forming the basis to the world's largest industrial fisheries in Peru and Chile (Barber and Chavez, 1986). Due to the equatorward flow of cold water in the HC, mean temperature conditions along Pacific South America are considerably lower than would be expected from their latitudinal position. Furthermore, seasonal temperature oscillation, which is a typical feature of temperate seas, is reduced due to the levelling influence of the cold HC (Brattström and Johanssen, 1983; Urban, 1994). However, an inherent feature of the HC is its high spatial and temporal variability in temperature conditions and nutrient supply (Kaplan et al., 2003; Thiel et al., 2007; Camus, 2008). The latitudinal temperature gradient along the coast of Chile and Peru is not continuous, but interrupted by differences in the local upwelling regime. Upwelling is concentrated within certain regions of the coast, (e.g. 8-18°S in Peru, and 20-22°S, 32-34°S, 36-38°S in Chile (Thiel et al., 2007)). In other stretches of the coastline, upwelling is less intense, follows a seasonal pattern, or may change sporadically. Particularly in regions of less intense upwelling, the extent of daily temperature changes may approach in magnitude the extent of seasonal temperature change (Kaplan et al., 2003; Cantillanez et al., 2005). Superimposed upon this high spatiotemporal heterogeneity in temperature and nutrient supply, is the large scale climate phenomenon of the El Niño Southern Oscillation (ENSO), consisting of cold and warm phases termed "La Niña" and "El Niño", respectively (Arntz and Fahrbach, 1991). La Niña is characterized by a strengthening of the trade winds, resulting in more cold water upwelling, while El Niño conditions occur during a relaxation of the trade winds, resulting in a deepening of the thermocline. As a result, upwelling under El Niño conditions no longer transports the nutrient rich bottom waters to the euphotic zone and primary production is drastically reduced.

Following Trenberth (1997), El Niño and La Niña are identified by positive and negative deviations of 0.4°C, respectively, from the 5-months running-average of the Niño 3.4 area (5°S to 5°N, 170 to 120°W) from the long-term mean SST and for a duration of at least 6 months. On average El Niño occurs every 4 years (2 to 10 years) (see Figure 1). However, each El Niño may develop in a different way, which hampers its prediction. During both, the development and relaxation of El Niño conditions, temperature changes can be extremely sudden (Arntz, 1986; McPhaden, 1999).

During summer to autumn of 1983, SSTs in the northern Peruvian upwelling system surpassed 30°C and were thus more than 10°C above the long-term annual mean (Arntz, 1986), leading to a "tropicalization" of the predominantly cold-water adapted fauna of Peru and Northern Chile. Tropical swimming crabs and penaeid prawns, among many other species, extended their range towards southern Peru were they successfully reproduced (Arntz et al., 1988). A few autochthonous species, such as the scallop *Argopecten purpuratus* (present range ~5°S to 30°S), benefitted from El Niño by tremendously increasing in reproductive output, recruitment and growth in a "scallop-boom" for the artisanal diving fishery (Arntz et al., 1988). The success of *A. purpuratus* during El Niño has been attributed to the species´ evolutionary (sub-) tropical origin (Wolff, 1987; 1988). Under warm El Niño conditions *A. purpuratus* may establish or recolonize more southerly populations (extinct beds found at 37°S) (Wolff and Mendo, 2000). The opposite is the case in the surf clam

Mesodesma donacium, which died off in Peru and Northern Chile in the last major El Niño events, and is thought to depend on cold La Niña conditions to regain its former northern range (Arntz et al., 1987; Riascos, 2008). However, for the majority of the commercially exploited marine invertebrates in the HC (and even more for non-commercial species), very limited information is presently available regarding their reproductive response (i) to latitudinal and local temperature differences, and (ii) to high temperature variability as influenced by ENSO.

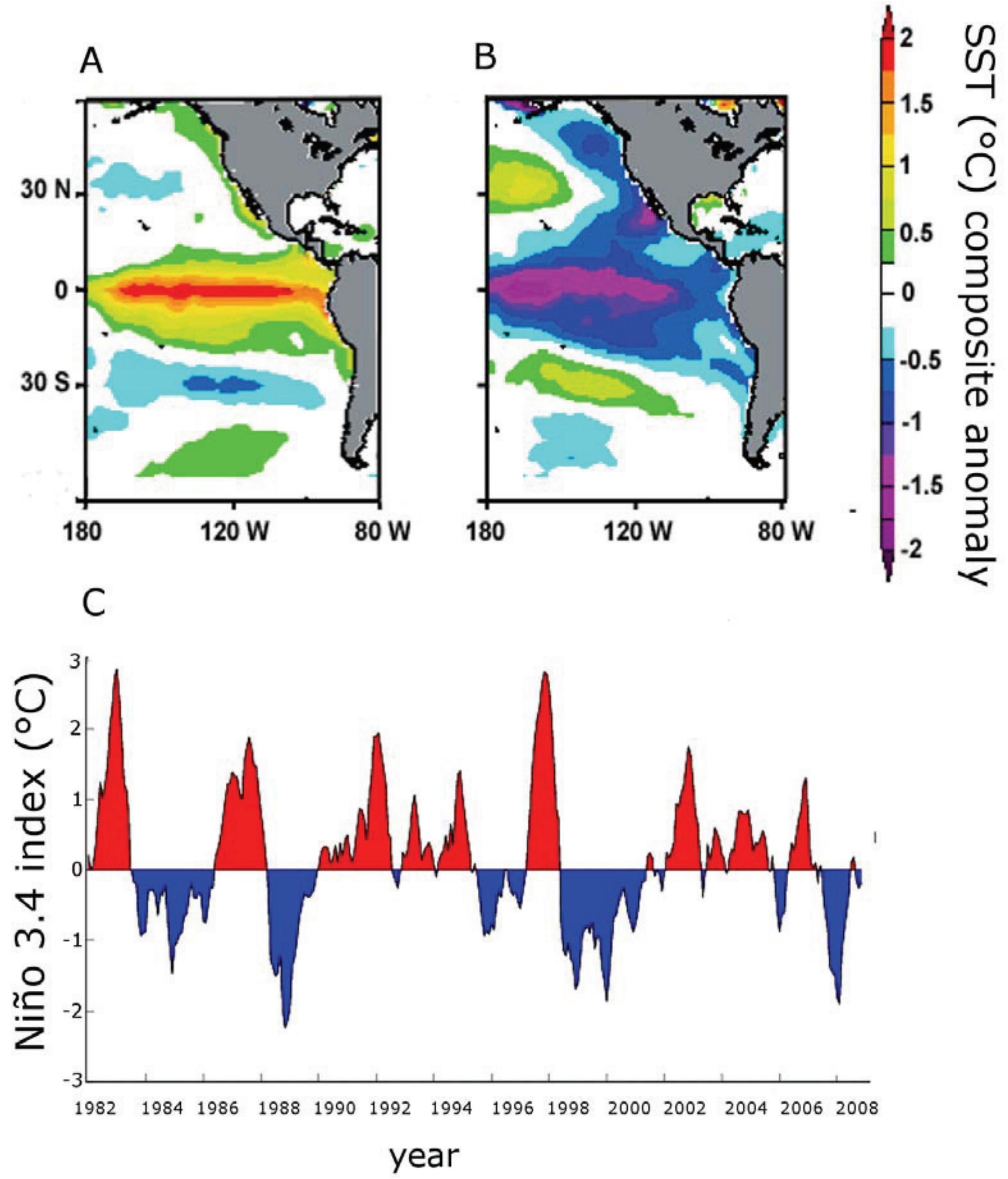

Figure 1. El Niño Southern Oscillation **A & B** Eastern Pacific November-March SST composite anomaly. **A)** El Niño condition (based on mean SST of 1958, 1966, 1969, 1973, 1983, 1987, 1992 and 1997). **B)** La Niña condition (based on mean SST of 1955, 1956, 1965, 1971, 1974, 1976, 1989 and 1999). **C)** ENSO index showing the departure from the long-term annual mean SST in the Niño 3.4 area (5°S to 5°N, 170 to 120°W); based on NOAA-CIRES Climate Diagnostics Center 2009.

In temperate Crustacea, the timing of spawning and moulting may be closely determined by seasonal temperature oscillation. These two processes are antagonistic, the one only occurring at the expense of the other (Sastry, 1983). For example, in the cold-temperate American lobster *Homarus americanus*, slight delays in the usual seasonal temperature rise from 2 to 3°C in winter to over 5°C in spring at the northern range of the species lead to a delay of finale oocyte maturation and thus to spawning failure. However, at the southern end of their biogeographic range, high winter temperatures above 8 to 10°C may lead to a displacement of oviposition by oocyte reabsorption and moulting (Aiken and Waddy, 1986; Waddy and Aiken, 1995). Such knowledge on the responses and limits towards temperature fluctuations is presently lacking for commercial crabs from the HC.

Summary:

- Unpredictable spatial and temporal variability in temperature provide challenges to invertebrate life and their reproduction in the Humboldt Current.
- In many Crustacea, the timing of the antagonistic processes, moulting and reproduction is regulated by seasonal changes in temperature.

1.2 The distribution of Cancer crabs in space and time

Brachyuran crabs of the genus *Cancer* are represented by 24 living species worldwide, which are found in the Pacific and the North Atlantic Ocean (MacKay, 1943; Nations, 1975; 1979; Carvacho, 1989). Evidence from the fossil record and phylogenetics indicate that the genus most likely arose in the early Miocene in the North East Pacific, where the highest diversity of cancrids is found today with nine species (Nations, 1975; Harrison and Crespi, 1999a; although disputed by Schweitzer and Feldmann, 2000, and Brösing 2008). The process of speciation into the South Pacific and North Atlantic is not fully resolved. Principally, *Cancer* crabs have an “antitropical” or “bipolar” distributional pattern (Lindberg, 1991). They are restricted to regions with annual mean sea surface temperatures lower than 24°C (MacKay, 1943) (Figure 2). Species found in the tropics, such as *C. borealis* of Florida and *C. johngarthi* at the Panamanian Pacific coast (the latter was formerly and incorrectly identified as *C. porteri* (Carvacho, 1989)), live at depths of considerably lowered temperatures than the surface waters and thus remain within the temperature limits described for *Cancer* (MacKay, 1943; Garth, 1957). Distribution into the Atlantic either occurred via the pan-Arctic interchange following the submergence of the Bering Strait land ridge approximately 5.2 - 3.4 mya (Vermeij, 1991), or before the closure of the Panamanian Isthmus approximately 3.1 mya (Keigwin, 1978). The later is discussed to be unlikely due to the high water temperatures in Central America and the lacking of *Cancer* fossils in this region (Harrison and Crespi, 1999a). However, genetic divergence based on a cytochrome oxidase I “molecular clock” of living cancrids places the invasion of the Atlantic at approximately 6 to 12 mya and thus prior to most estimates of the initial opening of the Bering Strait (Harrison and Crespi, 1999a).

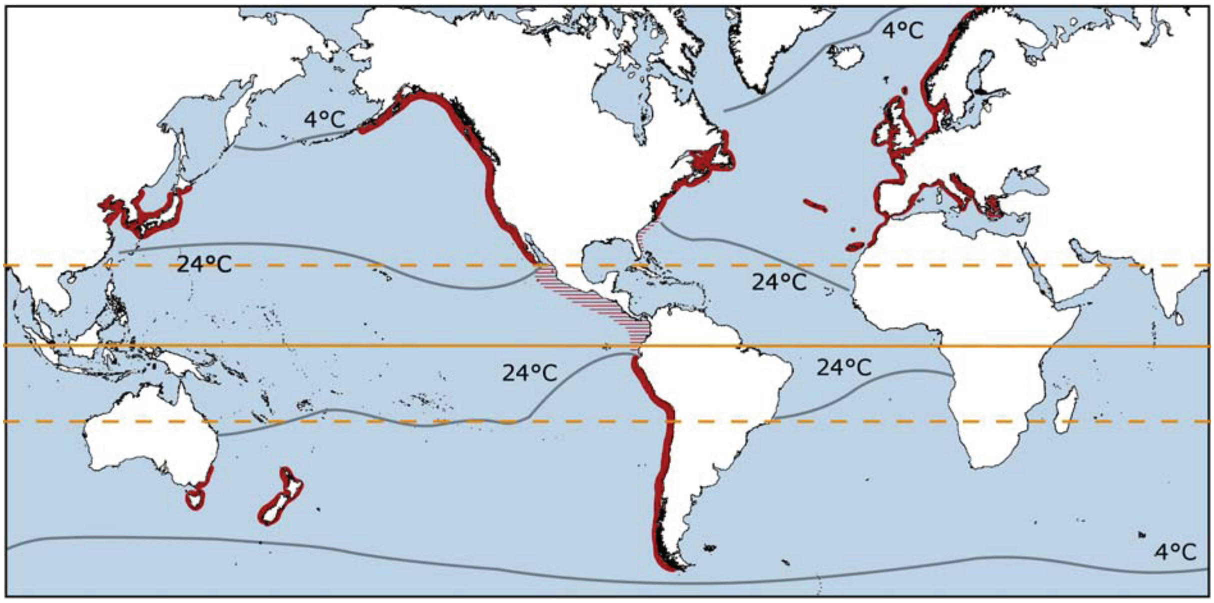

Figure 2. World-distribution of the genus *Cancer* (red areas). *Cancer* crabs are principally restricted to mid-latitudes where mean annual SST is between 4 and 24°C. Along the Chilean/Peruvian Pacific Coast *Cancer* crabs reach into tropical latitudes due to the cooling influence of the Humboldt Current. *C. johngarthi* and *C. borealis* (represented by hatched areas) live at depth in Pacific Central America and Florida, respectively, where water temperature is substantially lower than at the sea surface and thus within the limits of *Cancer* (modified based on MacKay 1943; Nations 1975, 1979; Carvacho 1989; Pinho et al. 2001; Quiles et al. 2001).

Invasion of the South American Pacific, where four living *Cancer* species are found, namely *C. coronatus* MOLINA, 1782 (syn. *C. plebejus*, POEPPIG 1836), *C. edwardsii* BELL 1835, *C. porteri* RATHBUN 1930 and *C. setosus* MOLINA, 1782 (syn. *C. polyodon,* POEPPIG 1836) is discussed to have happened via equatorial submergence to the deep sea, thus avoiding high SST of the tropics (Garth, 1957).

Similar antitropical distributional patterns were recognized by early taxonomists for a wide range of plant and animal species (for review refer to Lindeberg 1991).

Colonization of New Zealand and Tasmania by *C. novaezelandiae,* which closely resembles C. *edwardsii,* ranging to the southern cone of South America until the Beagle Channel (Vinuesa et al., 1999), possibly occurred from South America via Antarctica during the warmer period of the Miocene or Early Pliocene (Nations, 1975). The invasion of Japan, which at present is inhabited by five *Cancer* crabs, most likely occurred from North America, as these species are quite different in morphology from their South American congeners (Nations, 1975). Two regions not inhabited by *Cancer* crabs, although temperature conditions would seem suitable, are the Atlantic Coasts of Southern South America and of South-West Africa.

The high diversity of *Cancer* crabs within certain geographical ranges (e.g. 9 species in the North-East Pacific) was explained by habitat dependent speciation processes. In general, cancrids that are relatively small in body size tend to inhabit more structurally complex habitats like rocky shores, which provide more refuges and shelter from predation (Orensanz and Gallucci, 1988; Harrison and Crespi, 1999b). In open habitats, species appear to have evolved larger sizes to avoid predation – e.g. in 3 lineages of cancrids an increase in maximum species size has been reported with decreasing habitat complexity (Harrison and Crespi, 1999b).

Summary:

- Accordingly to some authors, the origin of diversification of the genus *Cancer* most likely lies in the North-East Pacific.
- *Cancer* crabs are principally restricted to regions with mean annual SST between 4 and 24°C.
- The speciation process was habitat dependent – maximum species size increases towards less structured habitats.

1.3 Species profile: Cancer setosus

1.3.1 Distribution and life-history parameters

The brachyuran crab *C. setosus* is one of the key predators across heterogeneous near-shore benthic habitats (<25 m depth) in the HC (Wolff and Cerda, 1992; Wolff and Soto, 1992; Cerda and Wolff, 1993; Jesse, 2001; Ortiz and Wolff, 2002b, a;

Jesse and Stotz, 2003; Ortiz, 2007). Owing to the influence of the HC, this “hairy crab”, locally known as “jaiba peluda” in Chile and “cangrejo peludo” in Peru, is distributed from the Península de Taitao in central-southern Chile to southern Ecuador (46°S, 75°W to 2°S, 79°W) (Rathbun, 1930); (Figure 3).

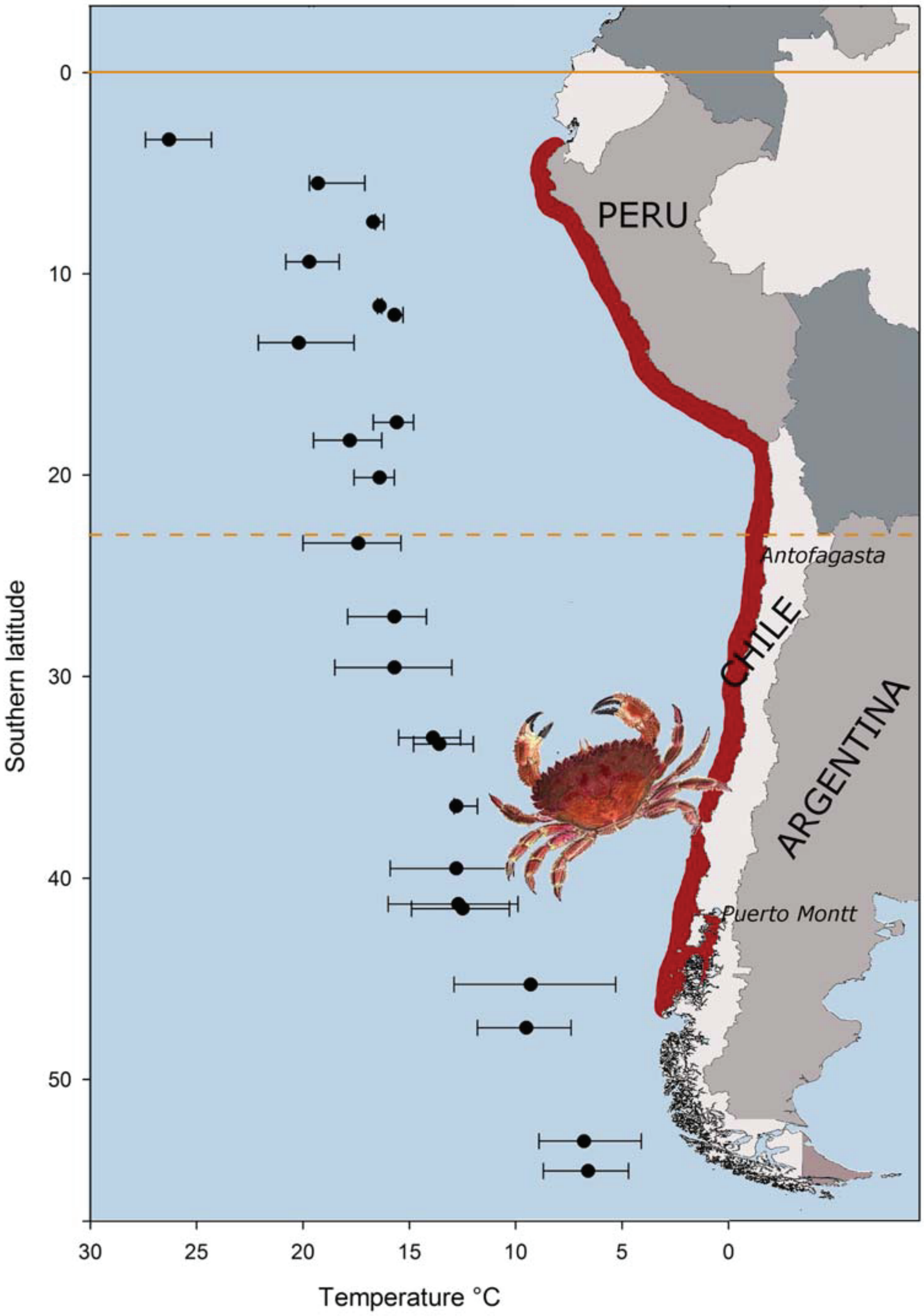

Figure 3. *Cancer setosus.* Distributional range along the coast of Peru and Chile (Rathbun, 1930); crab drawing from Olguín (2006). The long-term mean SST (1996-2006) is shown for various coastal locations. The degree of seasonal temperature oscillation is indicated by the “error bars”: the left hand side being the mean SST in January (austral summer) and the right hand side the mean SST in July (austral winter) (CENDHOC, 2008; IMARPE, 2008).

Genetic studies using allozyme and AFLP analysis (Amplified Fragment Length Polymorphism) show no indication of *C. setosus* stock separation along the Chilean coast (Gomez-Uchida et al., 2003). The HC and the Peru-Chile Counter Current, the former flowing north- and the later southward, combined with the absence of pronounced geographical barriers and the prolonged pelagic larval development of *C. setosus,* seem to promote high genetic exchange over large distances.

Cancer setosus is a very fecund species; large females of ~140 to 150 mm carapace width (CW) produce clutches of ≥2.5 million eggs, which are carried and ventilated under the female abdomen until hatching of a pre-zoea larva (see Figure 4). The pre-zoea stage, lasting only a few minutes, is followed by 5 pelagic zoea stages and a megalopa stage which settles to the benthic habitat after about 2 months of larval development at 14 ± 0.5°C (Quintana, 1981, 1984; Quintana and Saelzer, 1986). Egg size and reproductive output (per clutch) are found to be lower in northern Chile (~20°S) than in central (~30°S) and central-southern Chile (~40°S) (Brante et al., 2003; 2004). The lower reproductive output per clutch in northern Chile was attributed to the increasing energetic costs of egg oxygen provision by abdominal flapping under warm conditions (Fernández et al., 2000; 2002; 2003).

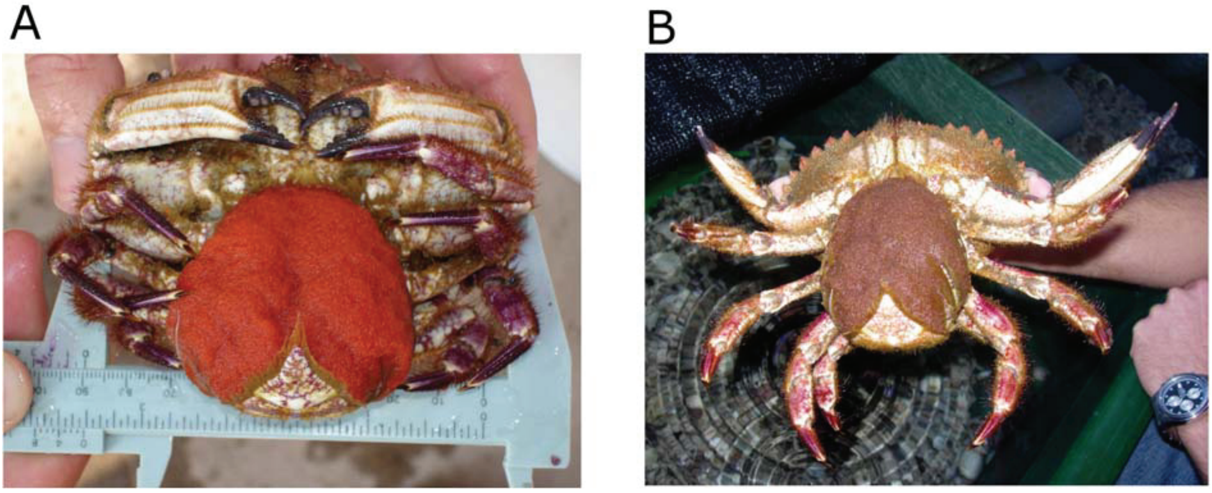

Figure 4. Ovigerous *Cancer setosus* **A**) Small female (89 mm CW) with blastula stage eggs. **B**) Large female (140 mm CW) with eye-placode stage eggs.

Throughout the species´ 4500 km latitudinal extension, mean annual SST ranges roughly from 10 to 20°C (CENDHOC, 2008; IMARPE, 2008); (Figure 3). It is postulated that the colonization of such a vast range has required adaptations and plasticity in physiology and life history traits. However, during El Niño, the maximum temperature threshold for survival of adult crabs can be exceeded (Arntz et al., 1988; Arntz and Fahrbach, 1991; Lang, 2000). Consequently, the artisanal fishery on *C. setosus* has been observed to collapse after strong El Niño events in Peru. So far, the critical temperatures for the different life-history stages of *C. setosus*, egg, larvae (but see Weiss et al. under revision), juvenile and adult, remain largely unknown.

Summary:

- *Cancer setosus* spans in distribution >40 degrees of latitude.
- The strong 1982/83 El Niño has caused mass mortalities of adult *C. setosus* in Peru.
- Effects of temperature variation on the reproductive cycle and on traits of early life history stages remain widely unknown.

1.3.2 Fisheries

Throughout the reach of the HC at least eight species of brachyuran crabs are regularly commercially exploited by artisanal diving and trapping fishery; the most important being *C. edwardsii*, *C. setosus* and *Homalaspis plana* (Xanthidae) in Chile and *C. setosus*, *C. porteri* and *Platyxanthus orbignyi* (Xanthidae) in Peru (SERNAPESCA 2008, IMARPE 2008). All these species are reported to have wide distributional ranges (Rathbun, 1930). However, only *C. setosus* supports a fishery throughout most of its distributional range. In Peru, no management measures on crab fisheries are given. In Chile, the management includes a minimum carapace width of 120 mm and the prohibition to land egg bearing females uniformly for all brachyuran crabs (DCTO. N°9/90). Landings in Chile and Peru are registered by the "Servício Nacional de Pesca" (SERNAPESCA) and the "Instituto del Mar del Peru" (IMARPE), however they are not always distinguished to the species level (i.e. only "crabs" is designated). Among these brachyurans, information on population dynamics is solely available for *C. setosus* in the peer-reviewed literature. The time to reach a size of massive maturity is estimated at 98 mm and 124 mm carapace width

(CW), for females and males, respectively, has been determined to take about two years in Coquimbo (29°S) (Wolff and Soto, 1992). Males and females may reach maximum CWs of 199 mm and 164 mm, respectively (Pool et al., 1998; Olguín et al., 2006). Life history parameters such as growth rate, size of maturity and maximum size are found to vary in many crustaceans spanning wide latitudinal ranges (Hines, 1989; Hemmi, 1993; Cardoso and Defeo, 2003), yet no comparable data from different latitudes have been presented for *C. setosus*.

Summary:

- In Chile, the capture of crabs smaller 120 mm in CW and of ovigerous females is prohibited.
- In Peru, no management measures are given for brachyuran crab fisheries.
- For most commercial crab species in the HC, information on parameters of population dynamics remains scarce.

1.4 Aims of this study

Cancer crabs are of evolutionary cold-temperate faunal origin and consequently are adapted in their reproduction and in early life history traits to the conditions prevailing in temperate waters. The cold Humboldt Current allows four species of *Cancer* crabs to extend their range along the South American Pacific coast into tropical latitudes. While seasonal temperature oscillation is suppressed by the Humboldt Current, both the warm and cold phases of the ENSO cycle cause rapid and drastic changes in the temperate regime. The present study aims at understanding better the degree and limits of plasticity in reproductive traits towards temperature variation, both latitudinally and influenced by ENSO, in the widely distributed and commercially exploited crab *Cancer setosus*.

Hypotheses

(**i**) Plasticity in reproductive traits is the key to the vast range and life under fluctuating environmental conditions of *C. setosus* in the HC.

The major aims of this study are -

(**i**) to assess the reproductive potential (number of annual ovipositions) of *C. setosus* under temperature conditions covering the species' natural range.

(**ii**) to investigate the degree of intraspecific plasticity in egg energy provision (and its causes).

(**iii**) to describe the effects of temperature on duration and nutrient depletion during embryonic development.

(**iv**) to elucidate the importance and limits of reproductive plasticity for the distribution of *C. setosus* and its fisheries in the context of El Niño Southern Oscillation.

2 MATERIALS AND METHODS

2.1 Study areas and sampling

2.1.1 Antofagasta and Puerto Montt

Antofagasta (23°S, 70°W) and Puerto Montt (41°S, 73°W) were chosen as sampling and experimental locations for roughly representing the upper and lower temperature conditions encountered by *C. setosus* throughout its natural range. In Antofagasta Bay SST is significantly higher than in the surrounding HC (+ 2 – 3°C) due to the bay's particular oceanographic conditions (Castilla et al., 2002; Piñones et al., 2007), and thus is comparable to the SST encountered by *C. setosus* at its northern distributional limit off Peru (IMARPE, 2008). Close to the southern species limit, ovigerous *C. setosus* were obtained in Carelmapu located east of Puerto Montt at the open Pacific. *C. setosus* was not found directly in the semi closed bay of Puerto Montt, the "Seño de Reloncaví", despite extensive diving effort, which may be due to the particularly low sea surface salinities in this bay in summertime (>24‰). Long-term annual average SSTs in Antofagasta and Puerto Montt differ by about 6 to 7°C. However, interannual variability in SST may be much more pronounced in Antofagasta, which is under a stronger influence of ENSO, due to its lower latitude.

2.1.2 Capture and maintenance of crabs

Mature females of *C. setosus* were caught by divers at 5 – 10 m water depth at different sites around Antofagasta, northern Chile (capture between May and October 2005) and in Carelmapu, central southern Chile (capture between September and November 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 specimens from central southern Chile for up to 5 months in the Universidad Austral de Chile, Puerto Montt.

Antofagasta

In Antofagasta, ovigerous and non-ovigerous crabs were placed in two 3200-l aquaria in groups of 12 specimens each. These aquaria maintained a high flow through of fresh seawater, ensuring cleanliness and a water temperature at a comparable level to Antofagasta Bay. 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 and thus were without “mate-guarding” were separated from their co-specimens until their new exoskeleton was hardened to avoid cannibalism in the soft-shell state. New specimens from the field replaced dead crabs. A group of three females were held in a 300-l recirculation system at constantly 16 (±0.5)°C.

Puerto Montt

In Puerto Montt, crabs bearing undifferentiated blastula eggs were placed in groups of nine specimens each 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 were acclimatized over 2 to 3 days to this temperatures through a gradual temperature increase. In both locations, the crabs were fed *ad libitum* with living mussels *Perumytilus purpuratus*. Aquaria were cleaned; water temperature and salinity were recorded daily. Salinity was maintained at 30-34‰.

2.1.3 Measurements and observations

Each crab was individually labelled with a small plastic tag glued onto its carapace and its width (CW) was measured to the nearest millimetre, including the 10th anterolateral spine, using callipers. The crabs were checked twice daily for the occurrence of moulting, mating, oviposition, and hatching of larvae. The developmental progress of the egg masses 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 (stages modified after Baeza and Fernández (2002)) (Figure 5):

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 kidney-shaped small dark spots, 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; 1 to 2 days before larvae hatching.

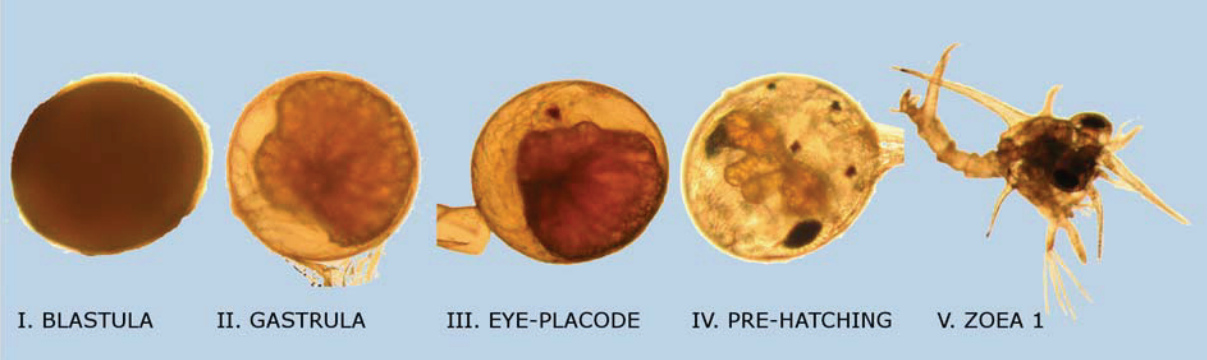

Figure 5. *Cancer setosus*. Early life-history stages sampled for biochemical composition and size (for size, only egg stages were sampled) (publication II & III).

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. Recently hatched zoea 1 larvae were collected in a fine sieve, which was connected to the overflow of the aquaria.

2.2 Sample treatment

2.2.1 Reproductive cycle and parameters

The (grey-) literature on reproductive traits of *Cancer setosus* has been critically reviewed. The annual number of egg-masses was calculated for populations from Casma, Coquimbo (La Herradura Bay and Tongoy Bay), Concepción and Ancud 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), which was derived from the aquaria experiments, for the mean monthly SSTs at the respective location (d_{ie}):

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

2.2.2 Elemental analysis and egg volume

Elemental analysis was conducted following Anger and Dawirs (1982). Five aliquot samples of 50 eggs/zoea 1 larvae per female were counted under a stereomicroscope, then briefly rinsed with distilled water and subsequently transferred to pre-weighted tin cartridges. Samples were freeze dried overnight at <0.01 mbar using a lyophilizer (Lyovac) and their dry mass (DM) was measured with a microbalance (Sartorius M2P) to the nearest µg. Subsequently, samples were combusted at 1020°C in an elemental analyzer (Hekatech Euro EA) for the determination of their carbon (C) and nitrogen (N) content using acetanilide as a standard. Lengths (D_1) and widths (D_2) of 20 unpreserved eggs per female were measured with a microscope which was equipped with a calibrated eye-piece micrometer and their volume was calculated based on the formula for oblate spheroids: $V = (\pi * D_1^2 * D_2) /6$ (Turner and Lawrence, 1979).

2.2.3 Analysis of fatty acid composition

Fatty acid analysis was based on 200 eggs per sample (egg stages I and IV). As an internal standard 19:0 methyl ester was added and the samples were crushed by ultrasonification in dichloromethane:methanol (2:1, v:v). Samples were transesterified with 3% concentrated sulphuric acid in methanol for 4h at 80°C. After extraction of fatty acid methyl esters with hexane, the fatty acid composition was analyzed with a gas-liquid chromatograph (HP GC6890) equipped with a capillary column (30 m x 0.25 mm (i.d.); liquid phase DB-FAB; film thickness: 0.25 µm) using temperature programming following Kattner and Fricke (1986).

2.3 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 two separate covariance analyses with female CW as a covariate (ANCOVA). Interaction terms of the categorical factors and the covariate were not significant (location x CW; oviposition x CW) and therefore covariance analyses with parallel slopes were conducted. The net changes in egg traits throughout development, meaning the respective differences in DM, C, N, and FA between stage I and IV eggs of the same female, were tested for significant differences between treatments with ANOVA. The assumptions of ANCOVA and ANOVA, namely homogeneity of variances and normality of residuals, were tested with Levene´s test and with the Shapiro-Wilk test, respectively (Sokal and Rohlf, 1995). When ANCOVA or ANOVA were significant post-hoc comparisons of means were conducted using Tukey´s test. Consecutive egg stages of females were tested for differences with a paired Student’s t-test, or when normality was not given, with a Wilcoxon signed rank test.

3 RESULTS AND DISCUSSION

3.1 Reproductive cycle

Despite their wide distribution and high ecological and economic importance, relatively little is known on the degree of temperature-dependent reproductive plasticity in *Cancer* crabs. Analysis of the frequency of ovigerous *Cancer setosus* in relation to the duration of egg development along the Chilean-Peruvian coast revealed that slight differences in temperature may lead to pronounced changes in the reproductive schedule and the number of annual egg masses produced (publication I). Only in central-southern Chile (Ancud, 43°S), where winter SST is about 10°C (see Figure 3), did the reproduction of *C. setosus* follow an annual cycle (publication I). One egg mass is produced in winter and larvae hatch in spring as representative for most of its boreal and cold-temperate congeners (Hines, 1991; Shields, 1991). A slightly higher winter SST of 12°C in Concepción (36°S) allows for continuous reproduction leading to the production of on average 3.6 annual clutches per female (publication I). Conditions in Concepción seem to be very suitable for *C. setosus*, where strong upwelling reduces seasonal temperature oscillation (see Figure 3). The winter SST in Concepción roughly represents the lower temperature threshold to continuous reproduction in this species. One female produced a second clutch and several females had ripening gonads in aquaria four months after the oviposition of the first clutch at 12°C. Under increasingly warmer conditions in Coquimbo (29° S) and Casma (9° S), two and one annual egg masses are produced, respectively, which is attributed to the rising energetic cost of metabolism at higher temperatures (publication I).

The assessment of the annual number of clutches from field-data as in the present study is based on the following assumptions: the proportion of ovigerous females caught must be representative for the population and only mature females must be considered. These requirements are met as *C. setosus*, unlike *C. pagurus* (Pearson, 1908; Edwards, 1979) and *C. magister* (Stone and O´Clair, 2002), neither is known to undergo pronounced migrations nor forms aggregations when spawning. Frequencies of ovigerous females were almost identical at sand, seagrass, and cobble gravel grounds, which form the principal habitats of this species (Jesse, 2001). Sampling was mainly conducted by diving, so that selectivity effects of traps could be avoided (Fischer and Wolff, 2006).

Females held in aquaria in Antofagasta and Puerto Montt responded very similarly in their reproductive cycle to different temperature conditions, confirming the results derived from the analysis of field data from the (grey) literature and showing that continuous reproduction is not genetically restricted to northern populations (publication I). This is in line with allozyme and AFLP analysis indicating a genetically homogenous population structure (Gomez-Uchida et al., 2003). Nevertheless, analysis of microsatellite loci as developed for the Dungeness crab *C. magister* and the edible crab *C. pagurus* may show a higher power to resolve genetically separated populations in *C. setosus* than AFLP analysis (Jensen and Bentzen, 2004; Toonen et al., 2004; Beacham et al., 2008; McKeown and Shaw, 2008a, b).

While the majority of *Cancer* crabs are tied to a seasonal moulting and reproductive cycle owing to their cold-temperate to boreal distribution (Haefner and Engel, 1975; Hines, 1991), continuous reproduction is known for *C. antennarius* and *C. anthonyi* (Shields, 1991)*,* thriving under environmental conditions in the southern reach of the California Current similar to those encountered by *C. setosus* in the HC (for review on Eastern Boundary Currents see Arntz et al. 2006). Recruitment success in benthic invertebrates with a long larval persistence time in the water column, such as the muricid gastropod *Concholepas concholepa*s and the Dungeness crab *C. magister,* were found to be modulated by differences in upwelling and current regime influenced by local conditions and by the large scale ENSO (Hadfield and Strathmann, 1996; Moreno et al., 1998; Botsford, 2001). Continuous reproduction seems to be a good strategy under unpredictable conditions of larval growth in an environment characterized by strong spatiotemporal variability in temperature and primary production such as the HC ("match-mismatch", Cushing, 1990).

Thus far, it remains speculative if the co-occuring congeners *C. edwardsii*, *C. porteri* and *C. coronatus* respond in a similar way to temperature in their reproductive schedule as *C. setosus*. Ovigerous *C. edwardsii* occur year-round in Concepción (Quintana, 1981), while around Chiloé, a single annual brood occurs, which is also earlier in season than in *C. setosus* at the same location (Pool et al., 1998). In La Herradura Bay, Coquimbo, ovigerous *C. coronatus* are predominantly found in winter, while ovigerous *C. porteri* are present throughout the year (Jesse, 2001). The number of annual ovipositions in these species remains unknown. For these commercial Crustacea, our understanding of the factors that determine egg production is of uttermost importance for fisheries management (Botsford, 1991).

Continuous reproduction in *C. setosus* is enabled by the ability to produce at least three viable clutches after a single mating event (publication I). The production of subsequent egg masses may occur within one instar in contrast to prior assumptions (see Shields 1991) or be interrupted by moulting without mating, which does not lead to the loss of stored sperm allowing for continuation of egg production in the absence of males (Elner and Beninger, 1995) (publication I).

Conclusions:

- Under conditions of continuous food supply, the mean annual number of egg masses of *C. setosus*, ranging from 0.9 to 3.6, is primarily determined by temperature.
- Very little is known about the reproductive cycles of the economically relevant *C. edwardsii*, *C. porteri,* and *C. coronatus,* which co-occur with *C. setosus*.

3.2 Reproductive output

Clutch size of brachyurans is limited morphometrically by the space available for yolk accumulation in their rigid cephalothorax (Hines, 1982; 1992). In *C. setosus*, clutch dry mass ranged within 9 to 20% of total female dry mass (Brante et al., 2004) in accordance with results found for 9 other *Cancer* species (Hines, 1991). Small *C. setosus* (80 mm CW) produced clutches of 18 to 20% of their body dry mass, irrespectively of location. However, clutches were 9, 15, and 18% of large female dry mass (CW 140 mm) in northern, central and central-southern Chile, respectively (calculation based on Brante et al. 2004). Assuming annual reproduction, the relatively lower clutch dry mass of large females in northern Chile was attributed to the energetic cost of the female ventilating their eggs by abdominal flapping (Brante et al., 2003). At higher temperatures, especially in the final phase of development (eye-placode to pre-hatching stage), embryo metabolism and thus oxygen demand increases (Amsler and George, 1984a; Naylor et al., 1997, 1999; Fernández et al., 2000; 2002; 2003; 2006). *C. setosus* females, and particularly those with large egg masses, thus have to invest more energy in egg ventilation at higher temperatures. However, for calculating reproductive output, defined as the annual investment in weight specific gonad production (Clarke, 1987) and reproductive effort, which is the overall annual energy directed towards reproduction including the energy demand of reproductive behaviour (e.g. abdominal flapping), the mean annual number of ovipositions, ranging in *C. setosus* from 0.9 to 3.6, represents a key reproductive parameter to be considered.

Conclusion:

- Latitudinal differences in one life-history trait (here clutch dry mass) should be analysed taking into account co-variation of other life-history traits (like annual clutch number).

3.3 Growth and size at first maturity

Reproduction and moulting are major metabolic events in Crustacea, which are coupled through endocrine function involving cyclic mobilization of organic reserves (Adiyodi and Adiyodi, 1970; Chang, 1993). In La Herradura Bay, Coquimbo, the growth efficiency of mature female *C. setosus* was lowered by ~50% compared to males because of higher energetic investment into two annual ovipositions (Wolff and Cerda, 1992). Therefore, females of *C. setosus* are slower in post-puberty growth and remain significantly smaller than males, which is true for most brachyuran crabs (Table 1) (Bennett, 1974, 1995; Wolff and Soto, 1992). As for reproduction, moulting in *C. setosus* is not restricted to a certain season throughout most of the species range (Jesse, 2001). However, it remains to be studied in further detail how the two components of the stepwise crustacean growth, moulting frequency, and moult-increment, are affected by temperature related latitudinal differences in clutch production.

The reported size dimorphism is important for mate guarding at moulting, when the larger male shelters the soft-shelled smaller female (Butler, 1960; Hartnoll, 1969; Haefner Jr., 1985). Females are more abundant in most *C. setosus* populations, which indicates a polygynous mating system (see Table 1). However, differences in growth and size-selective fishing pressure on larger males may also have caused shifts in the expected 1:1 male-to-female ratio (Haefner Jr., 1985). Literature-analysis indicates an increase of the size at massive maturity (CW_{mass}) towards higher latitudes in *C. setosus* (see Table 1), as reported for *C. irroratus*, *C. magister*, *C. pagurus* and other Brachyura (Jones and Simons, 1983; Hines, 1989; Methot, 1989; Shields, 1991). CW_{mass} was calculated based on the frequencies of ovigerous females in different size classes as 75 mm in Casma (9°S) and 100 mm in Chiloé (42°S). For males, CW_{mass} defined as the size where relative chela height increases (allometric growth, Mariappan et al., 2000), was 99 mm in Casma and 123 mm in Chiloé (see Table 1). The maximum carapace widths (CW$_{max}$) reported for the different locations as well show considerable variation (for females 119 to 164 and for males 131 to 199 mm CW, respectively). The significance of these differences in CW$_{max}$ remains obscure given a lack of data from unfished populations.

Table 1. *Cancer setosus*. Review of reproductive traits. Male/female ratio (M/F), carapace widths at first massive maturity (CW$_{mass}$), defined as size were 50% are ovigerous at peak-spawning and as inflection point of allometric chela growth for females and males, respectively, and maximum observed carapace widths (CW$_{max}$). Clutch size is given for females of 120 mm CW.

Location	Lat.	M/F ratio	CW$_{mass}$	CW$_{max}$	Clutch size*10³	
Casma	9°S	1:1.3	F 75 (smallest 54)	119	2 166	(1)
			M 99	131		
Lima	12°S	1:2.4				(2)
Bahía Independencia	13°S	1:1.5	M 100	151		(3)
Iquique	20°S	1:2.3	F		1 653	(4)
			F		1 523	(5)
Bahía Mejillones	23°S	1:1.0	F (smallest 79)	158	1 479	(6)
			F		1 619	own. obs.
			M	163		(6)
Bahía La Herradura	30°S	1:2.3	F 98 (smallest 67)	150	1 404	(7)
			F		1 602	(5)
			M 124	197		(7)
Bahía Tongoy	30°S	1:1.7				(8)
Bahía Concepción	36°S	1:1.0	F 104 (smallest 84)	136	1 799	(9)
			M	151		
Chiloé	42°S		F 100 (smallest 70)	164	2 199$^{(5)}$	(10)(5)
			M 123	194		
			M	199		(11)

(1) Moya (1995), (2) Talledo and Ishyama (1988), (3) Lang (2000), (4) Soto (2001), (5) Brante el al. (2004), (6) Gutiérrez and Zúñiga (1976), (7) Soto (1990), Wolff and Soto (1992), (8) Jesse and Stotz (2003), (9) Veaz (1981), (10) Pool et al. (1998), (11) Olguín et al. (2006).

Individual growth in Crustacea may vary considerably (Miller and Smith, 2003). This missing age/size relationship and the absence of calcified hard structures for aging purposes (like otoliths) have challenged crustacean fisheries managers for decades (Hartnoll, 1978, 2001; Botsford, 1985; Smith and Addison, 2003; Wahle, 2003). Age and growth determination by length-frequency analysis is hampered by the discontinuous growth of Crustacea, especially in long-living species with low moulting frequencies (Cobb and Caddy, 1989), and even further in species with continuous reproduction such as *C. setosus,* by the lack of (annual) cohorts. Recently, analysis of the pigment lipofuscin, which accumulates with time in post mitotic tissues (e.g. the brain and eye-stalks) allowed to separate age classes in the edible crab *C. pagurus* (Sheehy and Prior, 2008). Such analysis would be highly valuable to assess the age structure of the *C. setosus* populations with latitude as basis for management, and a requirement for the calculation of lifetime reproductive output.

3.4 Factors determining egg energy provision

3.4.1 Temperature

In crustaceans, as in most marine invertebrates, the major component of egg yolk is lipovitellin, which is comprised of proteins and lipids (Lee, 1991; Walker et al., 2006). The carbon content (C) integrates these two major organic fractions, while the carbon to nitrogen ratio (C:N) is a measure of the relative lipid to protein content (proteins being rich in N) (Gnaiger and Bitterlich, 1984).

In *C. setosus,* blastula egg size and organic content were significantly negatively correlated to the temperature conditions prior to oviposition, both observed over a latitudinal (Antofagasta and Puerto Montt) and a seasonal temperature gradient (Puerto Montt “early” and “late” reproductive season). Females produced eggs 32% lower in DM, C, N, and V reared at ~19°C in Antofagasta than equal sized crabs at ~11°C in Puerto Montt (publication II). These differences were not inherited, but represent real plasticity, as shown by females transferred to aquaria at 19°C in Puerto Montt, which proceeded to produce Antofagasta sized eggs (see Figure 6). In Puerto Montt, eggs from ovipositions in the early reproductive season (Puerto Montt “early”) were 12% higher in DM, C, N, and V than blastula stage eggs produced two months later under warmer spring conditions (Puerto Montt “late”) (publication II). While not observed in the present study, in the blue crab *Callinectes sapidus*, eggs produced at lower temperature were not only bigger, but also differed in their chemical composition, containing proportionally more lipids (Amsler and George, 1984a). The C:N ratio of *C. setosus* ranging from 4.8 to 5.3 in blastula eggs is typical for crustaceans with planktivorous larval development. Considerably higher C:N ratios are found in terrestrial Brachyura and high latitude Crustacea, which provide their eggs with relatively more lipid compared to protein (Anger, 1995). These energetic reserves, lipid containing on a mass basis 40% more energy than protein, enable for “lecithotrophic” larval development in extreme environments, partly or fully independent of external food sources (Anger, 2001).

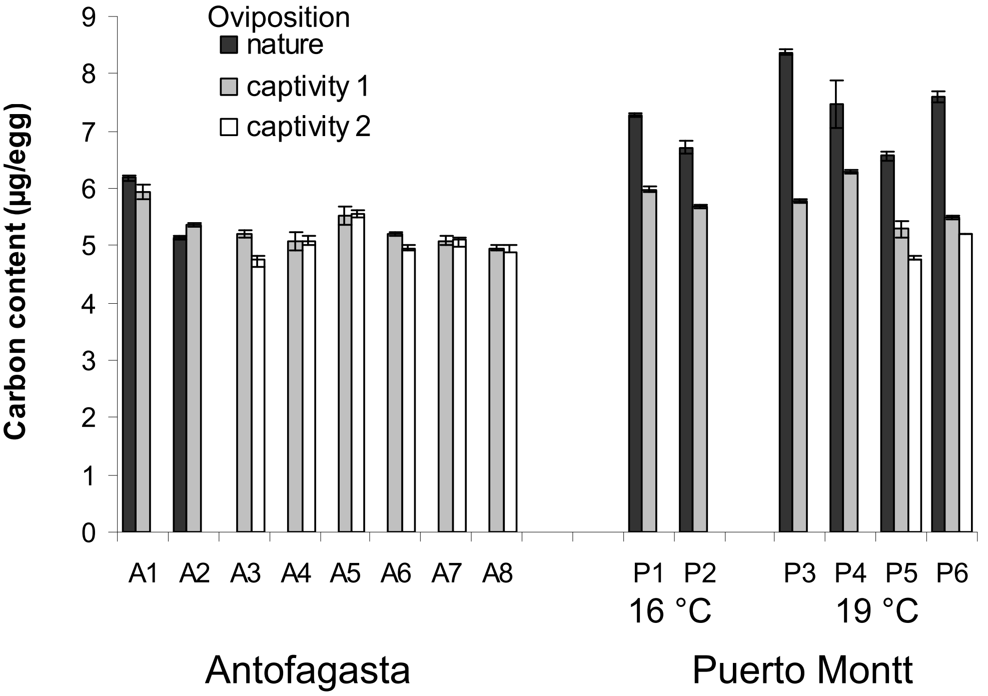

Figure 6. Carbon content of blastula eggs of individual females from consecutive ovipositions in Antofagasta (A) and Puerto Montt (P) (each bar represents the mean of 5 replicate measurements ± 1 SD); see publication II.

Larger energetic investment in the single egg at lower temperature has been observed for a wide range of marine species (Crisp, 1959; Efford, 1969; Chambers, 1997; Green, 2008). Larger eggs may give rise to larger larvae, which are better prepared for conditions of slow development under unpredictable feeding conditions at lower temperature (Efford, 1969). These initial differences in fitness may prevail throughout development. The underlying process leading to egg size variability is seen in the non-proportional slow-down of oogenesis with lower temperatures (Chambers, 1997; Laptikhovsky, 2006).

Within the genus *Cancer*, an interspecific trend towards larger egg size at lower temperature species can be identified (Cobb et al., 1997). *C. setosus* in the HC has fairly small eggs, again most similar to *C. anthonyi* and *C. antennarius,* which are adapted to comparable environmental conditions in the southern California Current (Orensanz and Gallucci, 1988; Hines, 1991; Shields, 1991; Cobb et al., 1997). To my knowledge, intraspecific variability in egg traits has within the *Cancer* crabs solely been studied in *C. setosus* (Brante et al., 2003; 2004; publications II & III). Many published accounts do not narrowly define the egg stage sampled and thus remain difficult to interpret, due to the high ontogenetic changes in egg volume occurring throughout egg development. *C. setosus* eggs increased in volume by 58-100% from the blastula to the pre-hatching stage due to osmotic water uptake and retention of metabolic water (publication III).

Further factors discussed to affect egg traits are the females´ reproductive history and feeding conditions (Racotta et al., 2003). In this study, characteristics of *C. setosus´* eggs produced in captivity in Antofagasta did not differ significantly from eggs produced prior to capture (i.e. under natural conditions). In barnacles, used as model organisms to study intraspecific reproductive variability, the number, but not the size of eggs, depended on feeding conditions (Patel and Crisp, 1960).

Conclusions:

- Egg size and energy content are affected by the temperature conditions prior to oviposition.
- Inter- and intraspecific comparisons of egg traits require a narrow definition of the egg stage.

3.4.2 Female size

In *C. setosus,* female size had a significantly positive effect on DM, C, N and V of eggs produced in Antofagasta in nature and captivity (ANCOVA for females 95 to 142 mm CW) (publication II). However, between locations (Antofagasta, Puerto Montt “early” & “late”) female CW had no significant effect on blastula egg-traits, which might be related to the smaller size range of ovigerous females covered by the ANCOVA (105 to 142 mm CW). For many invertebrates and vertebrates, egg size has been found to be positively related to female size (for Crustacea e.g. Attard and Hudon, 1986; Clarke 1993b, c; for finfish e.g. Chambers, 1997; Tully et al., 2001). Consequently, larger females are shown to make a higher contribution to the population as explained by their size specific fecundity alone, which should be considered in fishery regulation (Birkeland and Dayton, 2005). The reasons why larger females produce larger eggs instead of further increasing fecundity remain unclear (Clarke, 1993c; Johnston and Leggett, 2002).

Conclusion:

- Large females were often found to produce larger eggs, possibly giving rise to an increased fitness of offspring.

3.5 Energetics of egg development

Eggs of individual females held at different temperatures in Antofagasta and Puerto Montt were sampled for their size and biochemical composition throughout embryogenesis until larvae hatching. The duration of egg development decreases from ~65 days at 12°C to 22 days at the upper temperature limit of egg development of 22°C in *C. setosus*. At higher temperatures embryos are quickly killed, but females showed no enhanced mortality (publication I), illustrating that critical temperatures can vary with life-history stage (Aiken and Waddy, 1986). Under El Niño conditions, temperatures may surpass 22°C in Peru and northern Chile (Arntz and Fahrbach, 1991), likely leading to recruitment failure. However, 22°C is the highest reported temperature of successful egg development in the genus *Cancer,* showing that this species is adapted to relatively warm conditions. In the commercially important Dungeness crab, significant egg mortality begins at temperatures of 16 to 17°C. This egg mortality, caused by El Niño conditions in the North Pacific, was identified as one of the major factors for cyclic population decline in the Dungeness crab (Wild, 1980, 1983a; Hankin, 1985).

Conclusions:

- 22°C represents the upper temperature threshold for successful egg development in *C. setosus.*
- El Niño conditions are likely to cause egg mortality of *C. setosus* in Peru and northern Chile.

Egg-energy utilization increased with proceeding embryo differentiation and was fastest after the beginning of the heartbeat. Finally, zoea 1 larvae hatched with 60 ± 3% of their initial blastula egg carbon content independently of location and temperature condition (publication III). Because of initial differences in maternal egg energy provision (see 3.4.1) zoea 1 in Puerto Montt were about 23-31% higher in C than in Antofagasta. However, the decrease in C:N ratio was more pronounced at 12°C than at 16 and 19°C in Puerto Montt, indicating that at lower temperatures comparatively more lipid and less protein was used for embryo metabolism (publication III). Analysis of the composition of fatty acids, which form the major part of the lipid fraction, showed that at 12°C almost the double amount of fatty acids was lost throughout egg development compared to 19°C (-1.12 µg FA/egg and -0.62 µg FA/egg, respectively). Interestingly, pre-hatching eggs in Puerto Montt incubated at

12°C were very comparable in their absolute fatty acid content to pre-hatching eggs in Antofagasta, which developed from smaller blastula eggs at 19°C. It seems thus reasonable to conclude, that the production of larger eggs at lower temperatures might be a necessity to make up the higher metabolic energy losses throughout the prolonged egg development (publication III).

Considering these findings in the context of temperature oscillation in the HC, a rapid temperature rise as simulated experimentally (from 12 to 19°C) in southern Chile, where normally large eggs are produced, will leave the hatching larvae with comparably more lipid based energy. The opposite may be the case in the species northern range. Small eggs produced under warm conditions, might not contain sufficient energy for prolonged development caused by a pronounced temperature decrease, e.g. due to stronger cold-water upwelling under La Niña conditions. Larval energy content thus is affected by maternal investment per egg and also by the conditions experienced throughout egg development (for review refer to Giménez, 2006).

Conclusions:

- At lower temperatures, more lipid-based energy is required for egg development of *C. setosus*.

3.6 Crab fisheries in murky waters

Cancer setosus supports artisanal fisheries throughout its >40° latitudinal range, which is attributed to the species high plasticity in feeding, habitat utilization and reproduction (Wolff and Cerda, 1992; Cerda and Wolff, 1993; Jesse and Stotz, 2003) (publications I - IV). In Peru, landings of brachyuran crabs (~1600 t in 2007), consisting principally of *C. setosus*, *C. porteri* and *Platyxanthus orbignyi*, are not distinguished to the species level, which hampers the analysis of the development of their fisheries. Declining crab catches in Peru are observed for all major El Niño events since 1982/83 (ENSO index >2), but relatively quick recovery of populations occurred thereafter (publication IV) (IMARPE, 2008). In Chile, brachyuran populations are less affected by El Niño. Overall catches increased from around 1000 t per year in the early 1980s to 5000 to 6000 t in recent years (SERNAPESCA, 2008). This increase is completely based on the rapidly developing trapping fishery on *C. edwardsii* in Chilean southern regions (X-XII), while landings of *C. setosus*, caught principally in regions I to IX, have been decreasing since the early 1990s (publication IV) (Figure 7). Fisheries parameters such as catch per unit of effort (CPUE) or the size frequency composition of *C. setosus* catches are not available, but given the high unit value of *C. setosus* on domestic and international markets and the ever growing number of artisanal fishermen in Chile (presently ~70 000), it seems justified to assume that declining catches are representative of the state of its population. Decreasing catches are attributed to the low enforcement of the official Chilean management measures, of the minimum CW of 120 mm, and of the prohibition to land ovigerous females, leading ultimately to recruitment overfishing. Due to the scarcity of large specimens in recent years, fishermen even argued to lower the minimum legal size of brachyuran crabs to 100 mm CW (Olguín et al., 2006). Fishing on sub-legal sized crabs, below the size at first massive maturity, has dramatic effects on the state of the stock and on the economy of the fishery, given that large specimens (preferably >130 mm CW) are demanded for the effective processing of crabmeat (see Figure 8 for pictures of the Chilean crab fishery).

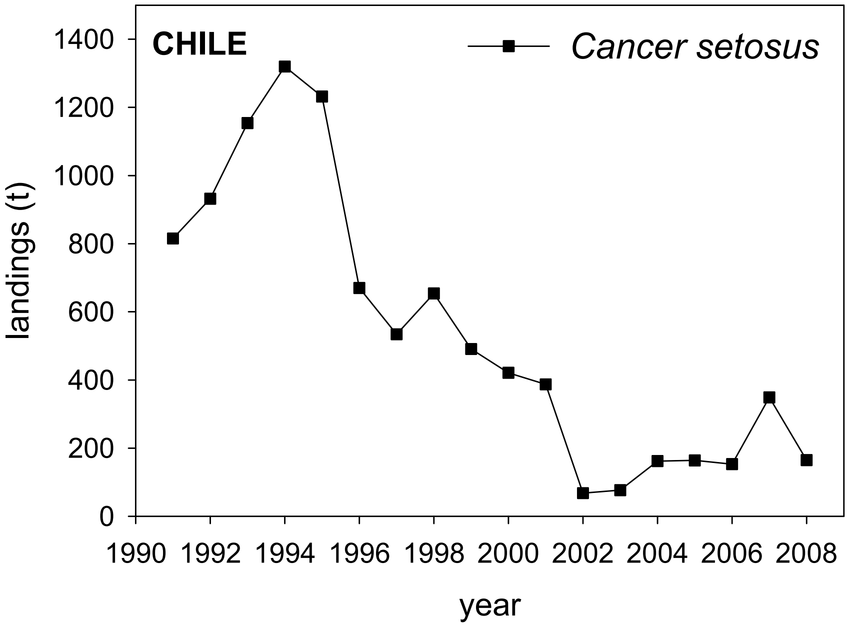

Figure 7. *Cancer setosus.* Development of Chilean landings for the period from 1991 to 2008 (SERNAPESCA, 2008).

Figure 8. Aspects of the brachyuran crab fishery in Chile **A**) Crab fishing boat with traps on board, Ancud, Chiloé **B**) *Cancer setosus* and *Homalaspis plana*, Talcahuano **C**) *C. setosus* and *Cancer porteri*, Valparaíso. Some crabs have been opened to show their ripe orange gonads considered a delicacy **D**) Boiled *Cancer edwardsii*, Puerto Montt. **E**) *H. plana* – ovigerous females illegally sold in the market. **F**) “Paila marina” – in the restaurant “La Olla”, Puerto Varas.

Fisheries management of temperate, slow growing Crustacea such as *C. setosus* have to follow a precautionary approach, given the uncertainty involved in assessing their growth rate, age structure, and natural mortality. For *C. setosu*s, the designation of no capture areas is highly recommended, (i) to study the development of the population in the absence of fishery, (ii) to assess the effect of the continuous removal of these abundant large benthic predators on the ecosystem structure (Cobb and Caddy, 1982; explored by ecosystem modelling by Ortiz and Wolff, 2002a, b), and (iii) to counteract the likely effects of size selective fishing on the genetic structure of the population (Taggart et al., 2004). Size selective fishing pressure selects for early maturation and against those genotypes with the fastest growth rate. “Fisheries-induced evolution” is seen as one of the causes to the low recovery of several depleted finfish species (Jørgensen et al., 2007; Kuparinen and Merilä, 2007), but so far found little attention in (invertebrate-) fisheries management.

3.7 Future perspectives

Cancer setosus has certainly become one of the most frequently studied brachyuran crab species of Chile and Peru. The present study reveals high plasticity in its reproductive traits in response to environmental temperature, which are discussed as the key to the species wide distributional range. It remains unknown, if this plasticity is unique to *C. setosus,* warranting further studies on temperature effects on life-history traits of widespread benthic invertebrates in the Humboldt Current. However, as for its northern hemisphere congeners *C. magister* and *C. pagurus*, which were studied by marine biologists for more than a century, many life history traits, and among them particularly growth rate, life expectancy and natural mortality, remain obscure.

(i) Ecological studies on, and fisheries management of Crustacea, are seriously hampered by the obstacles in determining their age. Recently, this limitation has been overcome by the analysis of the age pigment lipofuscin, which accumulates with time in post-mitotic tissue. Assessing the age/size structure in relation to latitudinal changes in habitat temperature of commercial crabs would be a hallmark in South American crustacean research.

(ii) *C. setosus* shows high variability in the annual number of clutches produced in relation to environmental conditions. In the frame of this thesis, it has been possible to assess the annual clutch number per size class. It would be worthwhile to know, if larger females, which moult less frequently, next to the production of larger clutches (and often larger eggs) also reproduce with a higher frequency compared to smaller crabs.

(iii) A regular monitoring of distributional patterns and reproductive parameters of *C. setosus* would be of high interest given a predicted increase in El Niño frequency with ongoing greenhouse warming.

4 PUBLICATIONS

This cumulative thesis is based on four publications as listed below. My contribution to each study is explained.

PUBLICATION I Fischer, S., Thatje, S, 2008.
Temperature-induced oviposition in the brachyuran crab *Cancer setosus* along a latitudinal cline: Aquaria experiments and analysis of field data.
Journal of Experimental Marine Biology and Ecology 357:157-164; DOI:10.1016/j.jembe.2008.01.007; submitted 26.07.2007 and accepted 19.01.2008.

I did the experimental work, the sampling and wrote the manuscript. The final version of the manuscript was achieved considering the revision by the co-author.

PUBLICATION II Fischer, S., Thatje, S., Brey, T, 2009.
Early egg-traits in *Cancer setosus* (Decapoda: Brachyura): effects of temperature and female size.
Marine Ecology Progress Series 377:193-202; DOI: 10.3354/meps07845; submitted 02.04.2008 and accepted 24.11.2008

I did the experimental work, the sampling and wrote the manuscript. The final version of the manuscript was achieved considering the revision of both co-authors.

PUBLICATION III Fischer, S., Thatje, S., Graeve, M., Paschke, K., Kattner, G, 2009.
Bioenergetics of early life-history stages of the brachyuran crab *Cancer setosus* in response to changes in temperature.
Journal of Experimental Marine Biology and Ecology. In press. Submitted 26.01.2009 and accepted 26.02.2009.

I did the experimental work, the sampling and wrote the manuscript. Fatty acid analysis was done in cooperation with the third author. The final version of the manuscript was achieved considering the revision by all co-authors.

PUBLICATION IV Fischer, S., Thatje, S. 2009.
Brachyuran crabs in the Humboldt Current System: temperature effects on life-history traits cause challenges to fisheries management.
Fisheries Research. Submitted 22.02.2009.

I compiled the information and wrote the manuscript. The final version of the manuscript was achieved considering the revision by the co-author.

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

Sönke Fischer and Sven Thatje

Author's posting. This is the author's version of the work. Please cite the final version published by *Journal of Experimental Marine Biology and Ecology* 357:157-164. Doi:10.1016/j.jembe.2008.01.007

Article submitted on 27 July 2007 and accepted on 19 January 2008.

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 fixed 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 ½ months in Antofagasta and in Puerto Montt (at 19°C). The second egg mass was observed 62.5 d (± 7.6; N = 7) after the oviposition of the first clutch and a third egg-mass followed 73.5 d (± 12.5; N = 11) later in Antofagasta (at 16 – 23°C). Comparably, a second oviposition took place 64.4 d (± 9.8, N = 5) after the first clutch and a third, 67.0 d (± 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 d (± 28.9; N = 4) and 137 d (N = 1), respectively. The duration of egg development from oviposition until larval hatching decreased from 65 d at 12.5 °C to 22.7 d 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.

Key words

C. magister, C. pagurus, El Niño, Humboldt Current, temperature adaptation

1 Introduction

Most of the 24 extant species of cancrid crabs (Nations, 1975; Nations, 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 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* Poeppig 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, 1957). 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; 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 (Giese, 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 *Cancer 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 three 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 where 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 two to three 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. 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 two to three days and were assigned microscopically to one of four successive developmental stages:

I. Blastula - no yolk used; one to two 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 spots, 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 eggshell; one

to two 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}):

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

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 Moult, 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 two months after moulting (62 d ± 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 d (± 7.6; N = 7) after the oviposition of the first clutch and a third egg-mass was laid another 73.5 d (± 12.5; N = 11) later. The interbrood periods took 29.7 d (± 13.1; N = 17) and 47.8 d (± 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 (62.5 d ± 7.6, N = 5) and a third egg-mass followed 67.0 d (± 2.8; N = 2) later at 19°C (± 0.3) in Puerto Montt (Table 1). The interbrood periods took one month (30.8 d ± 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 d (± 28.9) after the oviposition of the first one. A single female moulted 66 d after larval hatching. At 12°C (± 0.3) one female produced a second egg-mass about 137 d after the oviposition of the first and two more showed ripe ovaries when the experiment was ended (81 d after oviposition).

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 - 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 d from oviposition to hatching of larvae at 16°C in austral-winter and was shortened to 22.7 d 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 d (± 1.2; N = 5), which is similar to the calculated duration of 62.8 d 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 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 ½ 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 two 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 ½ 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). 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 Jr., 1977; Oh and Hankin, 2001). In *C. setosus*, sperm can even be retained via moults as shown by females who moulted in 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, 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 Concepcíon (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, 2001; 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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Table 1. Temporal sequence of reproductive events in cancrids: moult, oviposition, interbrood periods and annual number of egg masses

Species	T (°C)	Moult - oviposition (d)	Oviposition - oviposition (d)		Interbrood period (d)		Larvae	Egg masses/year
			1-2	2-3	1-2	2-3	hatching - moult (d)	
C. antennarius	12 ± 2[1]	77 (N=1)[1]						Ovigerous year-round[2]
C. anthonyi	13.5 ± 1.6[3]				41.9 ± 11.5 (N=78)[3]			Ovigerous year-round[2] up to 3*[3]
C. magister		90[3]; 163 (81-391; N=14)[5]						≤ 1[4]
C. pagurus		120[3]						≤ 1[3]
C. gracilis	6.9-13.4[6]							2* (2. very small)[6]
C. productus	6.9-13.4[6]							2* (2. very small)[6]
C. setosus								0.9 - 3.6**
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 d ± 2.8* (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 d ± 6.6*(N=7)

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

*laboratory conditions

**analysis of field data on percentage of ovigerous females

Table 2. Duration of cancrid egg development and temperature

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

*upper temperature threshold of egg development

Figures

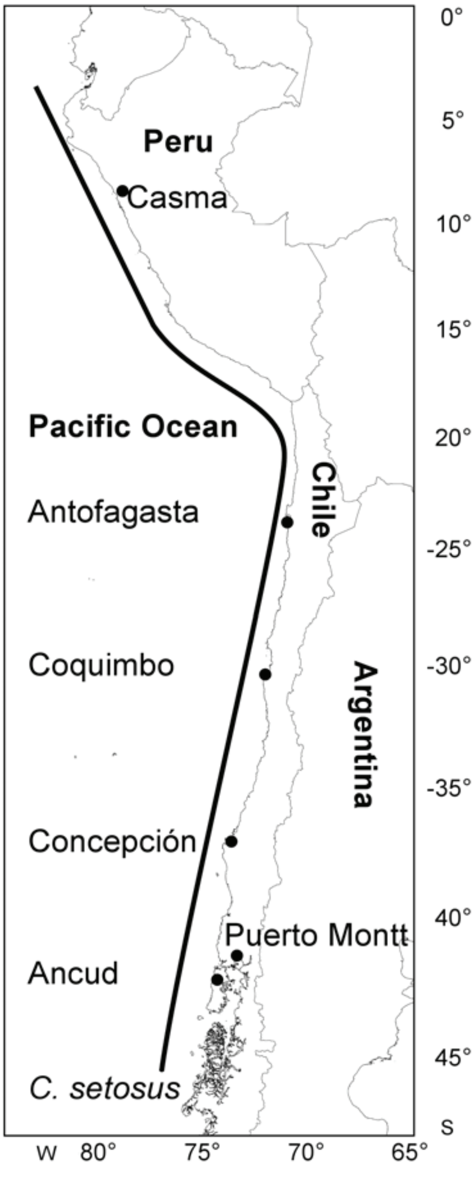


Figure 1. Distributional range of *C. setosus* along the Latin-American Pacific Coast (after Garth, 1957), the experimental sites Antofagasta and Puerto Montt and sites considered for literature review (Casma, Coquimbo, Concepción, Ancud); map modified after PanMap (Diepenbroek et al., 2000).

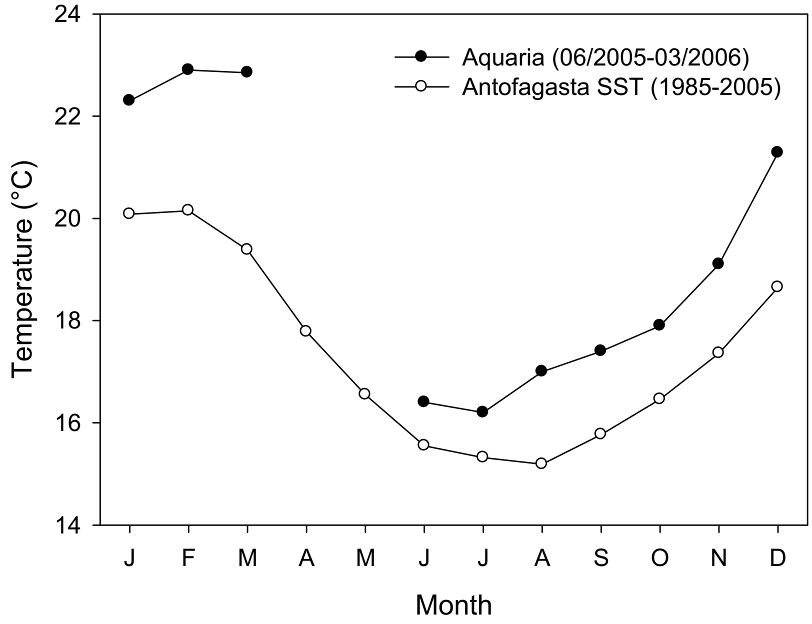


Figure 2. Antofagasta/Northern Chile: Temperature throughout the experiment (06/2005-03/2006) and mean monthly SST (1985-2005; CENDHOC).

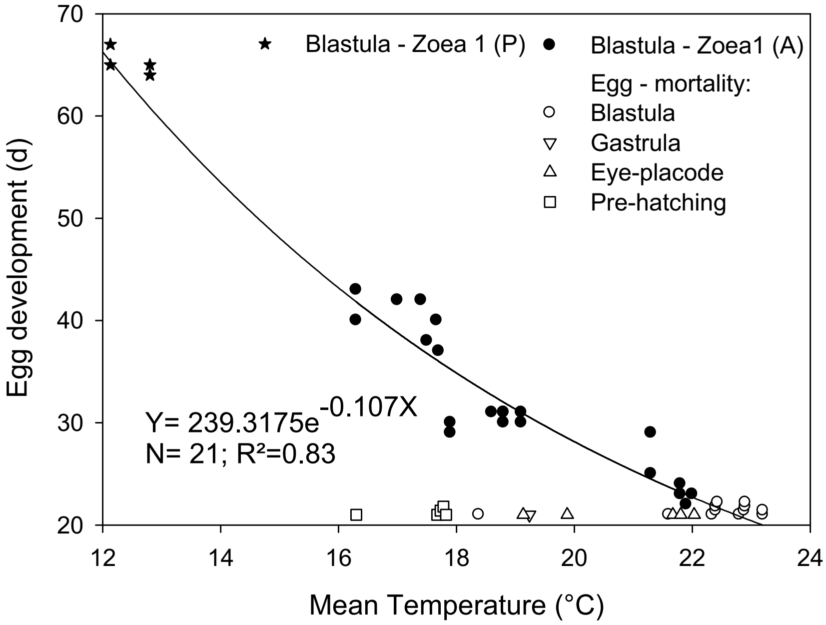
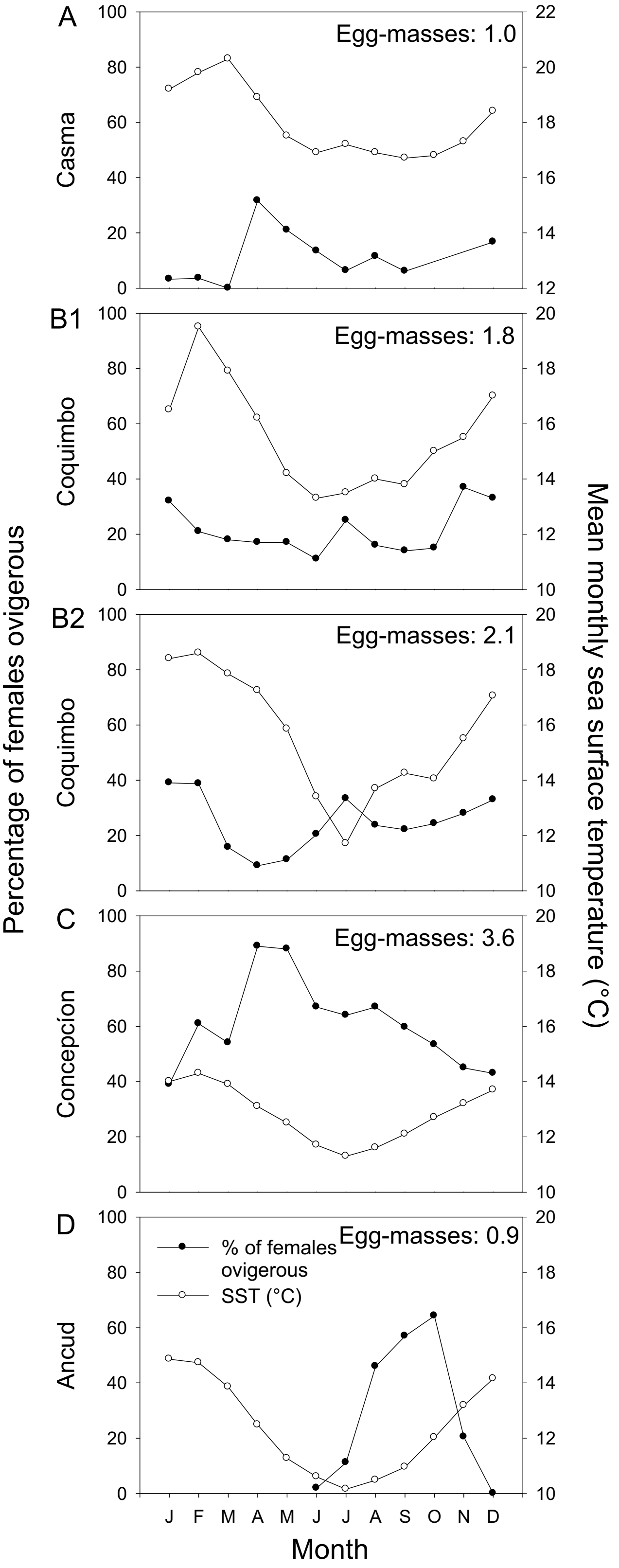


Figure 3. Duration of egg development of *C. setosus* from oviposition to larvae hatching in Antofagasta (A) (filled dots). Throughout the experiment in Antofagasta 44 egg-masses were produced of which 23 died, before larvae hatched (unfilled symbols, showing the developmental stage when egg mass mortality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

Figure 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).



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

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Key words

Crustacea, Cancridae, Latitudinal cline, Reproductive plasticity

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 23ºS) and Central-Southern (Puerto Montt 41ºS) 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 $\text{mm}^3 \times 10^{-4}$ 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.

1 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 and Bridges, 1995). Large, nutrient-rich eggs develop more slowly (Steele and 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 a reduced fecundity and thus lowers offspring numbers (Smith and 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. 2005b. 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 and Wikelski, 2002). Such phenotypic plasticity presumably allows for the optimization of reproductive effort under different environmental conditions (Hadfield and Strathmann, 1996; Thatje and Bacardit, 2000; Allen et al., 2008). Within the Crustacea, seasonal (Boddeke, 1982; Amsler and George, 1984b; Sheader, 1996; Paschke, 1998), inter-annual (Kattner et al., 1994) and latitudinal (Crisp, 1959; Clarke et al., 1991; Wehrtmann and Kattner, 1998; Lardies and Castilla, 2001; Lardies and 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 Southern American Pacific Coast (2°S, 079°W to 46°S, 075°W; see Fig. 1) (Rathbun, 1930), fecundity per egg mass, egg dry mass, and egg volume increase 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 and 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.

2 Materials and methods

2.1 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 2006 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) .

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 (see below).

Lengths (D_1) and widths (D_2) of 20 unpreserved eggs (Sheader and Chia, 1970) per female were measured microscopically with a calibrated eye-piece micrometer. Egg volume was calculated based on the formula for oblate spheroids: $V = (\pi * D_1^2 * D_2) / 6$ (Turner and Lawrence, 1979). For elemental analysis (after Anger and 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 µg. Subsequently, samples were combusted at 1020°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 (≤12 ind. per basin) for up to 10 mo under natural seasonal temperature conditions (16 to 23°C). In Puerto Montt, crabs where held in two 500-l aquaria (≤9 ind. per basin) for up to 6 mo. Temperatures were kept constant at 16 (±0.5) and 19 (±0.3)°C in order to simulate the temperature conditions at oviposition from Northern Chile (Fig. 2). The crabs were acclimatized over 4 to 5 days 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 (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.

2.2 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 x CW; oviposition x 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 and 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 (°C), and CW (mm) on blastula egg C content (µg/egg) were analysed for all data combined, independently of location and conditions of oviposition, applying a multiple linear regression model: $C = a + b_1 * T + b_2 * CW$.

3 Results

3.1 Oviposition in nature

Blastula eggs ranged in DM from 9.1 to 15.1 µg DM, in C from 4.8 to 8.4 µg, in N from 1.0 to 1.6 N µg, in C:N ratio between 4.7 and 5.4, and in egg volume between 152 and 276 mm^3 x 10^{-4} 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 ($p \geq 0.045$) in the ANCOVA, which was restricted to females between 105 and 142 mm in CW (Table 1).

3.2 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 and 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; see Fig. 4). Maternal size (CW) had a significant positive effect on all egg traits (p <0.0001; see 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% at 19°C (n = 4) 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 (see 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 remained stable. Blastula eggs consisted of 52 to 55% C and 10 to 11% N. The volume-specific content (concentration) ranged between 525 and 564 µg DM/mm^3, 281 - 299 µg C/mm^3 and 53 to 60 µg N/mm^3 (Table 2).

3.3 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).

4 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 extends 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 as 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 significantly in traits from prior eggs produced in the field at ~19°C (Table 3; Fig. 4). Therefore, aquarium rearing and continuous spawning “as such” can be excluded as underlying causes of egg trait variability, which have been observed in other studies (see Racotta et al. 2003).

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 (McEdward and Carson, 1987; McEdward and Chia, 1991; Jaeckle, 1995). In the estuarine crab *Chasmagnathus granulata* egg DM did not always correlate to egg C content (Giménez and Anger, 2001; Bas et 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 and George, 1984b).

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 resistence, 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 (Yampolsky and 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 and Schreiner, 1996). For *Cancer setosus,* the mismatch between increased metabolism and thus oxygen demand with lower oxygen solubility at higher temperature has been 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 and 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 and 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 three high latitude caridean shrimp species (Clarke 1993b), the brachyuran crab *Chasmagnathus granulata* (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 (Oulet & 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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Figures

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

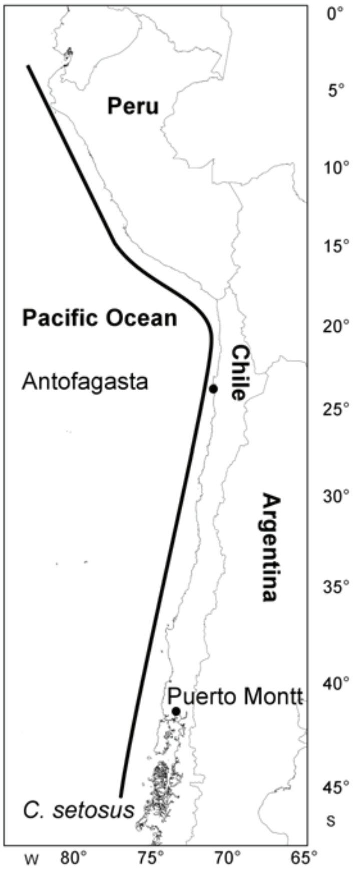
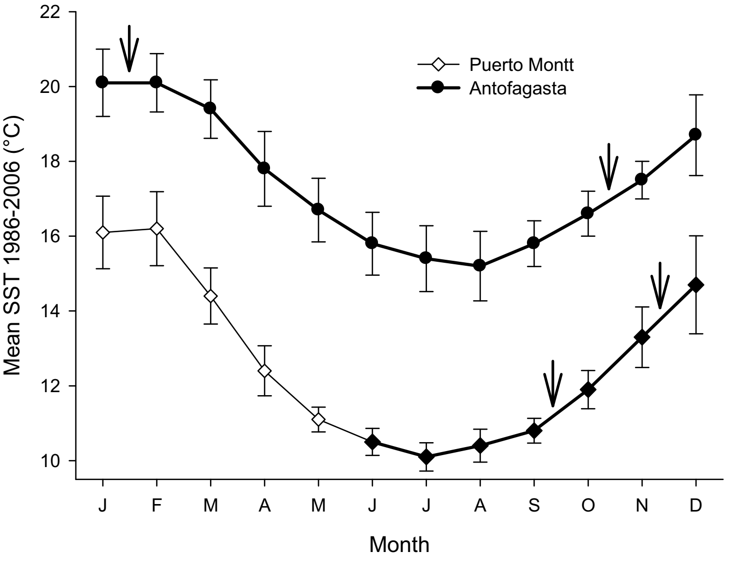


Figure 2. Mean monthly SST (°C) in Antofagasta and Puerto Montt (based on a 20 yr average ± 1 SD (CENDHOC)). The main periods during which ovigerous *C. setosus* occur at each location (after Gutiérrez and Zúñiga 1976, Pool et al. 1998) and the time of crab capture are indicated by filled symbols and arrows, respectively.



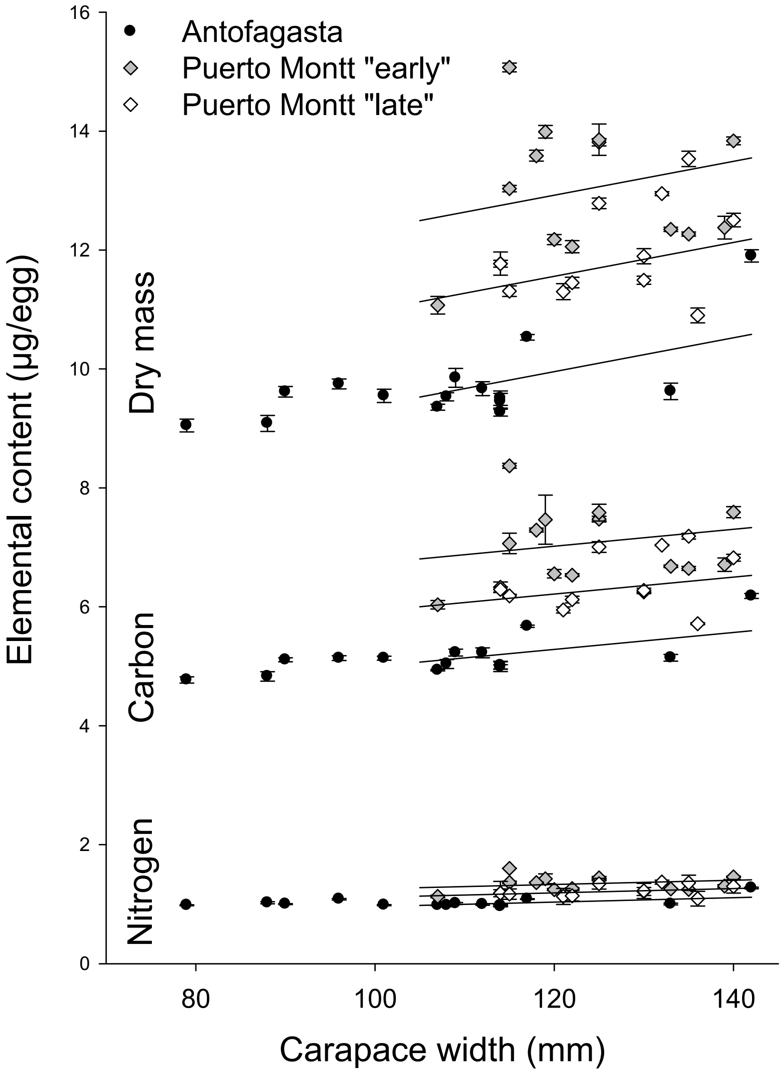


Figure 3. *Cancer setosus.* Dry mass, carbon, and nitrogen content of blastula stage eggs from Antofagasta and Puerto Montt (“early”; “late”) in relation to female carapace width CW (each point represents the mean of 5 replicate measurements ± 1 SD). Regression lines represent data range of the ANCOVA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

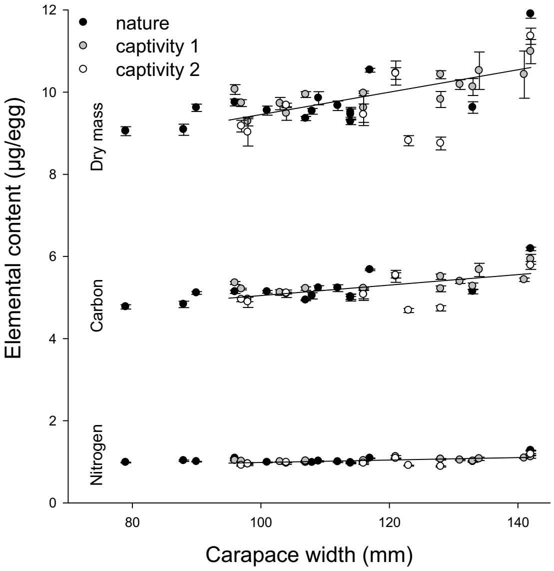


Figure 4. *Cancer setosus.* Dry mass, carbon, and nitrogen content of blastula stage eggs from Antofagasta from ovipositions in nature and captivity (1 and 2) in relation to female carapace width CW (each point represents the mean of 5 replicate measurements ± 1 SD). ANCOVA (for CW ≥ 95 mm) showed no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

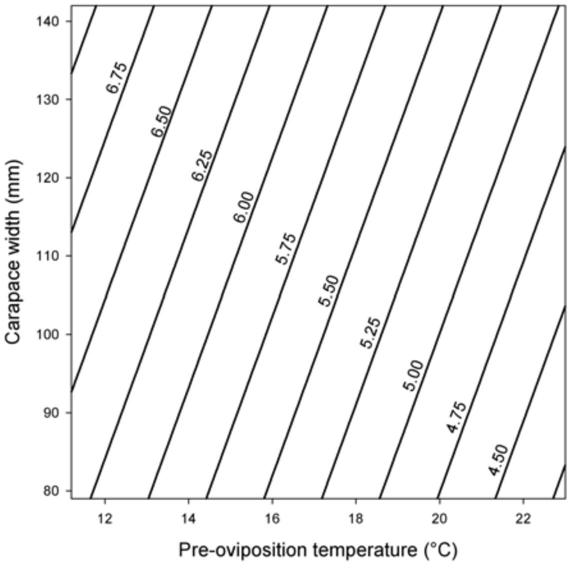


Figure 5. Cancer *setosus*. Contour plot of blastula stage egg carbon content (C) (µg/egg) in relation to pre-oviposition temperature (T) (°C) and female carapace width (CW) (combined for Antofagasta, Puerto Montt “early” & “late”; ovipositions in nature and captivity) derived from multiple linear regression: C (µg) = 7.388357 - 0.180933 * T + 0.012288 * CW; for T $p < 0.0001$ and for CW $p = 0.0023$; $n = 72$, $r^2 = 0.72$.

Table 1. *Cancer setosus.* Results of ANCOVA ($Y=a+b_1*CW+b_2*loc$) testing for the effects of female size (CW; covariate) and location on DM, C, N, and 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 α = 0.05).

Y	a	b_1	Location	b_2		r^2
			A	0		
DM	8.138	0.028	PM “early”	1.365	($p<0.0001$)	0.71
		($p=0.0743$)	PM “late”	-1.602		
			A	-0.931		
C	4.511	0.014	PM “early”	0.803	($p<0.0001$)	0.72
		($p=0.1146$)	PM “late”	0		
			A	-0.154		
N	0.751	0.004	PM “early”	0.141	($p<0.0001$)	0.67
		($p=0.0450$)	PM “late”	0		
			A	-0.0037		
V	0.0147	$5.442*10^{-5}$	PM “early”	0.0031	($p<0.0001$)	0.76
		($p=0.0865$)	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: 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^3).

n	Oviposition	T	DM (µg/egg)		C (µg/egg)		N (µg/egg)		C:N	V (mm^3 x10^{-4})		C	N	DM	C	N
		(~°C)	X	± SD	X	± SD	X	± SD	X	X	± SD	% of DM		µg/mm^3		
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	capt. 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	capt. 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	capt. 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	capt. 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	capt. 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

Table 3. *Cancer setosus*. Results of ANCOVA (Y=a+b1*CW+b2*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 ≥95 mm in CW.

Y	a	b_1	Oviposition	b_2		r^2	n
			nature	0.072			
DM	6.654	0.027	captivity 1	0.162	(p=0.235)	0.42	36
		(p<0.0001)	captivity 2	0			
			nature	0.040			
C	3.739	0.013	captivity 1	0.079	(p=0.220)	0.40	36
		(p=0.0002)	captivity 2	0			
			nature	0.018			
N	0.673	0.003	captivity 1	0.014	(p=0.184)	0.38	36
		(p=0.0004)	captivity 2	0			
			nature	-0.000403			
V	0.0159	$1.614*10^{-5}$	captivity 1	0.000176	(p=0.312)	0.13	32
		(p=0.230)	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-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 subsequent produced egg masses in Antofagasta. In Puerto Montt, capitivity 1 eggs were significantly lower in DM, C, N and V as previous eggs produced in nature (paired t-test/Wilcoxon signed rank test).

Loc/	CW	T	Ovip.	DM		C		N		C:N	V	
Specimen		(°C)		(μg/egg)		(μg/egg)		(μg/egg)			(mm^3 x 10^{-4})	
				X	± SD	X	± SD	X	± SD	X	X	± SD
Antofagasta												
A1	142	16.0	nature	11.9	0.1	6.2	0.0	1.27	0.01	4.9	201	1
		21.8	capt. 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	capt. 1	10.1	0.1	5.4	0.3	1.03	0.01	5.2	197	16
A3	128	17.7	capt. 1	9.8	0.2	5.2	0.1	1.06	0.02	4.9	170	6
		21.2	capt. 2	8.8	0.2	4.7	0.1	0.88	0.02	5.4		
A4	116	17.8	capt. 1	9.6	0.4	5.1	0.2	1.00	0.02	5.1	170	14
		21.2	capt. 2	9.5	0.3	5.1	0.1	0.96	0.01	5.3	169	12
A5	121	17.9	capt. 1	10.5	0.3	5.5	0.1	1.10	0.01	4.9	187	7
		20.5	capt. 2	10.5	0.1	5.5	0.1	1.08	0.04	5.1		
A6	97	19.4	capt. 1	9.7	0.1	5.2	0.0	0.73	0.00	5.2	173	10
		23.0	capt. 2	9.2	0.1	5.0	0.1	0.91	0.01	5.4		
A7	104	19.5	capt. 1	9.5	0.2	5.1	0.1	0.96	0.02	5.3	180	11
		23.0	capt. 2	9.7	0.1	5.1	0.0	0.98	0.01	5.2	185	12
A8	98	19.5	capt. 1	9.3	0.1	5.0	0.1	0.95	0.01	5.2	173	10
		23.0	capt. 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	capt. 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	capt. 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	capt. 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	capt. 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	capt. 1	10.1	0.1	5.3	0.2	1.02	0.02	5.2	194	13
		19.5	capt. 2	9.2	0.1	4.8	0.1	0.91	0.01	5.2	171	24
P6	140	11.2	nature	13.8	0.1	7.6	0.0	1.46	0.01	5.2	270	21
		19.4	capt. 1	10.0	0.1	5.5	0.0	1.04	0.01	5.3	195	14
		19.3	capt. 2	9.9	0.2	5.2	0.0	1.02	0.00	5.1	192	14

Table 5. Blastula egg traits of five brachyuran crab species from Antofagasta, northern Chile. Specimen were caught and egg samples were processed as described for *C. setosus*. *Cancer porteri*, *Cancer coronatus* (Cancridae), *Platyxanthus orbignyi*, *Homalaspis plana* (Xanthidae), and *Taliepus marginatus* (Majidae). Absolute composition: 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^3).

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

Bioenergetics of early life-history stages of the brachyuran crab *Cancer setosus* in response to changes in temperature

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Key words

Crustacea, eggs, larvae, elemental analysis, fatty acids, latitudinal gradient, Chile

Abstract

In many marine invertebrates, a latitudinal cline in egg size is considered an adaptive response to a decrease in temperature, and enhances the energetic fitness of their larvae at hatching. However, the amount of energy carried over from the egg to the larval stage depends on the metabolic efficiency of egg-development. In the present study, eggs of the brachyuran crab *C. setosus* were sampled for their dry-mass (DM), carbon (C), nitrogen (N), and fatty acid (FA) content throughout development from blastula stage until hatching of zoea 1-larvae at Antofagasta (23°S) and Puerto Montt 41°S (Chile) under different temperature treatments (12, 16 and 19°C). Hatching zoea 1 larvae contained 60 ± 3% of the initial blastula egg C content, regardless of site or temperature. However, the ontogenetic decrease in egg C content was to a significantly higher extend based on the utilization of energy-rich FA at 12°C (-1.16 µg/egg) compared to the 19°C treatments in Antofagasta and Puerto Montt (-0.63 to -0.73 µg FA per egg). At 19°C egg-metabolism was based to a substantial extend on protein, which allowed for the saving of energy-richer lipids. We conclude that the production of larger eggs with high FA content appears to be adaptive not only to fuel the larval development, but is also a response to the prolonged egg developmental times at lower temperatures.

1 Introduction

Intraspecific variability in egg energy provision along (latitudinal) temperature clines has been reported for a broad variety of marine invertebrates (Clarke, 1992; Hadfield and Strathmann, 1996). The prevalent pattern, namely the production of larger eggs at higher latitudes (Pandian, 1994; Yampolsky and Schreiner, 1996), is discussed to be an adaptive response to the mismatch of unpredictable food availability and pro-longed development faced by the emerging larvae at lower temperatures (Thatje et al., 2005a). In the brachyuran crab *Cancer setosus* (Molina, 1782), which spans in distribution from Southern Ecuador to Central Southern Chile (2°S, 079°W – 46°S, 075°W) (Rathbun, 1930) energetic investment per egg (measured as dry mass (DM), carbon (C) and nitrogen content (N), volume (V)) is negatively correlated to the temperature experienced by the female crab in the time prior egg-laying (Fischer et al., 2009). Eggs produced close to the species lower temperature limit at ~11°C in Puerto Montt (Central Southern Chile, 41°S), were about one third higher in DM, C, N, and V than eggs produced by equal sized females under conditions representative for the species upper temperature range at ~ 19°C in Antofagasta (Northern Chile, 23°S) (Fischer et al., 2009). In support of these patterns, *C. setosus* larvae from Antofagasta were successfully reared until their fifth zoea stage at 16 and 20°C, but failed to successfully complete development at lower temperatures representative for Puerto Montt (12°C) (Weiss et al., under revision). However, to assess the adaptive significance of both latitudinal and intraspecific differences in egg energy provision one has to define to which extend these differences are carried over into later life-history stages. With regard to this, traits of emerging larvae are not exclusively determined by maternal egg energy provision, but can furthermore be constrained by the physico-chemical environment (e.g. salinity, oxygen, temperature) experienced throughout egg incubation period (Kunisch and Anger, 1984; Pandian, 1994; Giménez, 2002, 2006). Egg development is hastened with temperature rise, but often at the cost of an altered metabolic efficiency (Heming, 1982; Pandian, 1994). This energetic cost may lead to a size reduction of the zoea 1 larvae, as shown for the spider crab *Hyas araneus*, the Dungeness crab *Cancer magister*, the caridean shrimps *Nauticaris magellanica, Betaeus emarginatus,* and *Pandalus borealis*, which in laboratory cultures hatched significantly smaller at higher temperatures of egg development (Kunisch and

Anger, 1984; Shirley *et al.*, 1987; Wehrtmann and Kattner, 1998; Wehrtmann and Lopez, 2003; Brillon *et al.*, 2005). Such pattern has also been supported by field collected larvae of *Nauticaris magellanica* (Thatje and Bacardit, 2000). In the spiny lobster *Jasus edwardsii* and the crayfish *Cherax quadricarinatus* an increase in egg incubation temperature led to a higher consumption of lipids and certain fatty acids (mainly 20:5(n-3)) (Smith et al., 2002; García-Guerrero et al., 2003). On the other hand, in the American lobster *Homarus americanus* less lipids were utilized with higher egg incubation temperature (Sasaki *et al.*, 1986). Lipids and fatty acids contribute about 20-30% to egg-composition (protein 15-25%, salts 2-5%, remainder water), and frequently form the most important source of metabolic energy in decapod crustacean eggs (Pandian, 1994). Fat oxidization contributes 67, 75, and 88% of the metabolic energy in *Eupagurus bernhardus*, *Crangon crangon* and *Homarus gammarus* eggs, respectively (Pandian, 1967; Pandian and Schumann, 1967; 1970). However, in the egg development of two boreo-arctic cirripede species (*Balanus balanoides* and *B. balanus*) and the deepwater giant crab *Pseudocarcinus gigas* protein was utilized in preference over lipid (Barnes, 1965; Gardner, 2001).

The aims of the present study are to

(i) compare fatty acid (FA) content of blastula eggs produced in the field at conditions close to the species upper and lower temperature limit (Antofagasta and Puerto Montt, respectively) and in captivity in Antofagasta

(ii) assess changes in egg traits (DM, C, N, V, FA) throughout embryogenesis until larvae hatching at both locations

(iii) elucidate the adaptive importance of latitudinal variation in egg traits in biogeography and evolution of marine invertebrates.

2 Materials and methods

2.1 Sampling and maintenance

Ovigerous *Cancer setosus* were caught by divers at 5 – 10 m water depth at different sites around Antofagasta, Northern Chile (23°S, 70°W; 11/2005 & 01/2006) and in Carelmapu, close to Puerto Montt in Central Southern Chile (41°S, 73°W, 09/2006 & 11/2006). Females bearing early blastula stage eggs, as identified microscopically by their uniform distribution of yolk and absence of cleavage, were transferred to aquaria at both locations.

Incubation temperatures were chosen to represent the lower and upper range of egg development in normal “non-El Niño” years at both locations: Ovigerous females were held in a recirculation system at 16°C and in a flow through system at 19°C in Antofagasta and in recirculation systems at temperatures of 12 and 16°C in Puerto Montt. In Puerto Montt, a third group of ovigerous crabs was transferred to a recirculation aquaria system at 19°C in order to represent Antofagasta conditions. Salinity ranged between 30 and 34‰. Crabs were individually labelled with a small plastic tag glued onto their carapace and were fed *ad libitum* with living mussels *Perumytilus purpuratus*. Every two days eggs were taken with fine forceps from the border of the egg masses to assess their developmental stage. As described by Fischer and Thatje (2008), *C. setosus* produced several subsequent egg masses in captivity. Three females with eggs laid in captivity in Antofagasta in the flow through aquaria were sampled as ovigerous crabs from the field. Eggs in four successive developmental stages and recently hatched zoea 1 larvae were sampled for elemental analysis (DM, C, N) and eggs in stages I and IV for fatty acid composition (fatty acids were also sampled for stages II & III for eggs produced in captivity in Antofagasta). Samples were kept frozen at -80°C. Egg and zoea stages were defined as:

I. Blastula – no yolk used; approximately 1 to 2 days after oviposition
II. Gastrula – 25% of the yolk used, still no eyes visible (not sampled in Puerto Montt)
III. Eye-placode – eyes are visible as kidney-shaped small dark spots, 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 eggshell, 1 to 2 days before larvae hatching
V. Zoea 1, collected immediately after hatching in a fine sieve which was connected to the overflow of the aquaria.

To assess if aquaria had an effect on the bioenergetic traits of hatching larvae independent of temperature at both locations 3 females caught in the field with advanced stage IV eggs were transferred to the laboratory and their larvae sampled after a brief incubation period.

2.2 *Elemental analysis and egg volume*

For elemental analysis after Anger and Dawirs (1982) five aliquot samples of 50 eggs/zoea 1 larvae per female were counted under a stereomicroscope, then briefly rinsed in distilled water and subsequently transferred to pre-weighted tin cartridges. Samples were freeze dried overnight at <0.01 mbar using a lyophilizer (Lyovac) and their dry mass (DM) was measured with a microbalance (Sartorius M2P) to the nearest µg. Subsequently, samples were combusted at 1020°C in an elemental analyzer (Hekatech Euro EA) for the determination of C and N content using acetanilide as a standard. Lengths (D_1) and widths (D_2) of 20 eggs per female were measured with a microscope which was equipped with a calibrated eye-piece micrometer and their volume was calculated based on the formula for oblate spheroids: $V = (\pi * D_1^2 * D_2) /6$ (Turner and Lawrence, 1979).

2.3 Fatty acid analysis

Fatty acid analysis was based on 200 eggs per sample (stages I and IV) to reach necessary sample size. As internal standard 19:0 methyl ester was added and the samples were crushed by ultrasonification in dichloromethane:methanol (2:1, v:v). Samples were transesterified with 3% concentrated sulphuric acid in methanol for 4h at 80°C. After extraction of fatty acid methyl esters with hexane, the fatty acid composition was analyzed with a gas-liquid chromatograph (HP GC6890) equipped with a capillary column (30 m x 0.25 mm (i.d.); liquid phase DB-FAB; film thickness: 0.25 µm) using temperature programming following Kattner and Fricke (1986) (for overview of samples taken see Table 1).

2.4 Data analysis

The net changes in egg traits throughout development, meaning the respective differences in DM, C, N, and FA between stage I and IV eggs of the same female, were tested for significant differences between treatments with ANOVA (based on the means of the five parallel DM, C, and N measurements with “female” as sampling level). Homogeneity of variances was tested with Levene´s test and normality of residuals with the Shapiro-Wilk test (Sokal and Rohlf, 1995). Differences among treatments after a significant ANOVA were tested with the Tukey HSD test. Consecutive egg stages of females were tested for differences with a paired Student's t-test, or when normality was not given, with a Wilcoxon signed rank test.

3 Results

3.1 Elemental composition and volume

Within the first two developmental stages from blastula (I) to gastrula (II), covering about two weeks of development, no significant changes in dry mass (DM), carbon (C), and nitrogen content (N) were observed in eggs in Antofagasta (Table 2, data combined for all treatments, paired Student's t-test, $\alpha = 0.01$). Therefore, the gastrula stage was not sampled in following experiments in Puerto Montt.

In general, ontogenetic changes in egg DM, C, and N followed a similar temporal pattern between locations and temperature treatments (except for Antofagasta 19°C "captivity") (Table 2). From the blastula stage (I) to the eye-placode stage (III) only minor changes in DM and C, and insignificant changes in N occurred (combined for all treatments, Wilcoxon signed rank test, $p=0.812$)(Table 2). Until pre-hatching (IV), DM decreased by 0.3 – 1.1 µg/ind^{-1}, C decreased by about 20%, while N remained quite stable. The net changes in DM and C from stage I to IV did not differ significantly for the three temperature treatments in Puerto Montt (ANOVA) (Table 3). From pre-hatching to the zoea 1 larvae, C again decreased by about 20% and N decreased by 20-30% (Table 3, Figure 1).

The pattern was different for Antofagasta "captivity" produced eggs, where a pronounced decrease in DM, C, and N occurred as early as the eye-placode stage (III). Nevertheless, the hatching zoea 1 larvae were comparable in their quantitative DM, C, and N content to zoea 1 larvae from eggs produced in nature in Antofagasta (incubated at 16 and 19°C) (Table 2). Throughout development, eggs increased by 60 - 100% in volume.

3.2 Fatty acid composition

The quantitatively most important fatty acids in the blastula stage were the saturate (SAT) 16:0, the monounsaturates (MUFA) 16:1(n-7) and 18:1(n-9), and the polyunsaturates (PUFA) 20:5(n-3) and 22:6(n-3) contributing to about 2/3 of the total of fatty acids (Tables 4 and 5). Despite for palmitic acid (16:0), which was the most abundant fatty acid in all treatments, small differences between fatty acids at both locations were found. In descending order, in Puerto Montt 18:1(n-9), 20:5(n-3), 16:1(n-7) and 22:6(n-3) were the quantitatively most prominent fatty acids following 16:0. In “field-produced” eggs in Antofagasta the order was identical with the exception of 20:5(n-3) showing higher quantities than 18:1(n-9) and for the “captivity eggs” 22:6(n-3) was quantitatively the second most important fatty acid. Overall, PUFA were the most abundant fatty acids in blastula eggs (37-40%), followed by MUFA (32-37%) and SAT (25-28%) (Table 5). As indicated by the C content, little ontogenetic changes in fatty acid content occurred until the eye-placode stage (III) (see Antofagasta “captivity; Tables 3 and 4).

From blastula to pre-hatching SAT changed little on the percentage basis, MUFA decreased over-proportionally, and the percentage share of polyunsaturated fatty acids increased. The marked decrease in MUFA is largely explained by a pronounced utilization of 16:1(n-7) (decrease of 58-84%), and to a lesser extend of 18:1(n-9) and 18:1(n-7) (Table 4). Within PUFA, especially 20:5 (n-3) and 22:6 (n-3) were less utilized than other fatty acids, and thus showed an increase in their relative contribution in the pre-hatching stage (IV) (Table 5).

Fatty acids made up between 13.3 and 15.5% of the blastula egg DM and 25.0 to 28.9 % of blastula C content (Table 6). In the pre-hatching stage (IV) the percentage share of fatty acids dropped to 14.6-15.7% of C, except for Puerto Montt (19°C incubation), where fatty acids still contributed 20.3% to the C content. Overall, 60% of the initial fatty acid was consumed throughout development at Puerto Montt at 12°C, 55 and 48% for “field” and “captivity eggs” in Antofagasta at ~19°C, respectively, and no more than 35% in Puerto Montt at 19°C. The absolute decrease in FA was significantly larger in Puerto Montt at 12°C than at 19°C in Puerto Montt and 19°C in Antofagasta “captivity” (ANOVA).

4 Discussion

4.1 Elemental composition and volume

The temporal sequence of egg energy utilization by the early life stages of *C. setosus* followed the pattern of low losses in carbon until the beginning of the heartbeat (transition stage III – IV) and an accelerated utilization of egg-nutrients thereafter (Gardner, 2001). The observed increase in egg volume (+ 58-100%) throughout embryogenesis is a consequence of osmotic water uptake and, to a lesser extend of the retention of metabolic water (Pandian, 1970; Amsler and

George, 1984b; Rosa et al., 2007). Egg DM is negatively affected by utilization of energy reserves through respiration and positively, at least for marine Crustacea, by the uptake of salts and minerals (Green, 1965; Pandian, 1967). Because of these two antagonistic processes, which accelerate with development, egg DM and energy measures based on DM (e.g. fatty acid content/DM), are not the most suitable measures of energy content of late stage eggs (Jaeckle, 1995). In this respect, DM of recently hatched zoea 1 larvae varied between 75% and 104% of that of early blastula stage eggs, while the C content of the zoea 1 larvae was 60 ± 3% of the blastula stage, irrespective of location and incubation temperature (Table 3). Comparably, the zoea 1 of the estuarine crab *Chasmagnathus granulata* hatches with 60-66% percent of their initial blastula C content depending on the salinity conditions encountered throughout embryogenesis (Giménez and Anger, 2001). The decreasing C:N ratio during egg development indicates that lipids, as in most other Crustacea, were preferably used as energy source over proteins (which are rich in N) (Holland, 1978; Clarke et al., 1990; Petersen and Anger, 1997; Giménez and Anger, 2001).

The reason why eggs produced in captivity in Antofagasta showed an earlier and more pronounced decrease in C and N than eggs of females produced in nature, both incubated parallel under the same conditions, is by no means clear and needs further investigation. Strikingly, larvae hatched with similar DM, C and N content after the same duration of development (Table 2). Furthermore, zoea 1 larvae that were hatched from advanced stage IV eggs obtained from the field were highly comparable in their DM, C and N content to larvae from aquaria incubated eggs (Antofagasta: DM 9.1 ± 1.2 µg, C 3.1 ± 0.1 µg and N 0.77 ± 0.03 µg; Puerto Montt: DM 11.7 ± 0.8 µg, C 4.3 ± 0.3 µg; and N 1.05 ± 0.03 µg) (see Table 2).

4.2 Fatty acid composition

MUFA were utilized at a higher rate in *C. setosus* than SAT and PUFA, confirming the previous described pattern for the hippolytidid shrimp *Lysmata seticaudata*, the European lobster *Homarus gammarus*, and the grapsid crab *Armases cinereum* (Morais et al., 2002; Rosa et al., 2005; Calado et al., 2005 ; Figueiredo et al., 2008b). The 16:1(n-7) fatty acid declined particularly strongly (by 79% in Antofagasta; 58 and 84% in Puerto Montt at 19 and 12°) (Figure 2), as also reported for *Nauticaris magellanica* (Wehrtmann and Kattner, 1998). SAT and MUFA are usually major fatty acids of triacylglycerols which are storage lipids in most organisms. Their decrease during egg development shows clearly the utilization for energetic requirements. In contrast, PUFA are necessary for cell differentiation and thus for the membrane formation during embryogenesis. This is in agreement with the observed quantitative retaining of the n-3 PUFA, eicosapentaenoic acid (EPA, 20:5(n-3)) and docosahexaenoic acid (DHA, 22:6(n-3)). In addition, the importance of these fatty acids has been attributed to maintaining membrane flexibility (Chapelle, 1986; Morais et al., 2002; Figueiredo et al., 2008a). For copepods a seasonal increase in body DHA content was interpreted as mechanism to maintain membrane fluidity at lower temperatures (Farkas, 1979). In the present study, eggs sampled in the field had higher proportions of EPA than DHA. Eggs produced in Puerto Montt (~11°C) showed a slightly higher percentage of DHA (10%) than eggs produced under warmer conditions in Antofagasta (~19°C; 8% DHA). The elevated proportions of EPA and moreover of 16:1(n-7) reflect a dietary input based primarily on a diatom source (Dalsgaard et al., 2003). However, eggs produced in captivity at 19°C had the highest proportion of DHA (15%) and thus do not fit into this latitudinal pattern (Table 5). The eggs produced in captivity originated from females, that prior to egg laying, were fed exclusively on *Perumytilus purpuratus*, which may be the source of DHA. These PUFA are essential in Crustacea since they can not be synthesised *de novo* (Anger, 2001), and thus are a reflection of the female food intake. They are considered an important part of crustacean and finfish-broodstock diet, leading to enhanced egg-quality (Harrison, 1990; Wiegand, 1996; Brooks et al., 1997).

4.3 Adaptive importance of latitudinal variation in egg traits

Although eggs at all three temperatures in Puerto Montt showed a similar decrease of 1.4 µg carbon from blastula to pre-hatching (Table 4; Fig. 1), almost twice as much fatty acids were utilized at 12°C (-1.15 µg/egg) compared to 19°C (-0.62 µg/egg) (Table 6). Since lipids composed of fatty acids make up about 80% of the total lipid fraction, the remaining decrease in carbon content must largely be based on utilization of proteins. On a mass basis protein contains about 40% less energy than lipids. The utilization of protein may lead to a saving of the energetically richer lipids.

The most pronounced utilization of fatty acids took place at 12°C in Puerto Montt (-60%), which is a typical temperature of egg incubation for this location close to the species southern distributional range (Fischer and Thatje, 2008). Blastula eggs at Puerto Montt at 12°C were provided by 30% more fatty acids as blastula eggs produced in Antofagasta at 19°C. This advantage is largely compensated by the prolonged larval development at the lower temperature. However, when exposed to the higher Antofagasta temperatures (19°C), eggs from Puerto Montt maintain their higher initial investment in fatty acids throughout development.

This clearly indicates an increased conversion efficiency of embryos incubated at higher temperatures in *C. setosus*, as reported also for the American lobster *Homarus americanus* (Sasaki et al., 1986). In this respect, at least for *C. setosus* the production of larger, energy richer eggs at the colder location, is not solely an adaptation to the prolonged development faced by the hatching larvae (Weiss et al., under revision), but also a necessity to meet the energetic demands of the prolonged egg development.

5 Conclusions

Cancer setosus produces larger, energy richer eggs at lower temperatures. This higher investment in the single offspring appears to be an energetic necessity due to the reduced metabolic efficiency of egg development at low temperatures and thus is only partly carried over to later larval stages.

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Tables

Table 1. *Cancer setosus*. Overview of ovigerous females sampled throughout egg development (stages: I blastula, II gastrula, III eye-placode and IV pre-hatching) until hatching of the zoea 1 at different temperatures of incubation and number of replicates used for the ANOVAs.

T (°C)	Egg stages I, III, IV DM, C, N, V	Egg stages I, IV fatty acids	Zoea 1 larvae DM, C, N
Antofagasta			
16 ± 0.5	3 (+II)		3
19 ± 0.8	3 (+II)	3	3
19 ± 0.8 "captivity"	3 (+II)	3 (+II, III)	3
Puerto Montt			
12 ± 0.3	6	6	3
16 ± 0.5	2		2
19 ± 0.3	3	3	1

Table 2. *Cancer setosus.* Sampling days after oviposition, elemental composition DM, C, N (µg/ind^{-1}), C:N ratio and volume of eggs (V, mm^3 x10^{-4}) from blastula stage (I) to pre-hatching stage (IV) until zoea 1 larvae hatching (Z1) in Antofagasta and Puerto Montt (arithmetic mean values ± SD); for number of replicates see table 1.

Stage	Days	DM	C	N	C:N	V
Antofagasta 16°C						
I	~2.0	9.6 ± 0.2	5.1 ± 0.1	0.99 ± 0.02	5.2	176 ± 6
II	15.0 ± 1.7	9.6 ± 0.3	5.0 ± 0.2	1.02 ± 0.04	4.9	194 ± 9
III	22.3 ± 1.2	9.6 ± 0.4	4.9 ± 0.1	0.98 ± 0.03	5.0	226 ± 32
IV	37.0 ± 1.0	8.7 ± 0.2	4.0 ± 0.1	1.02 ± 0.02	4.0	330 ± 8
Z1	38.7 ± 1.5	10.0 ± 0.7	3.1 ± 0.1	0.80 ± 0.03	3.8	
Antofagasta 19°C						
I	~2.0	10.2 ± 1.5	5.4 ± 0.7	1.13 ± 0.13	4.8	181 ± 18
II	13.0 ± 1.0	10.3 ± 1.2	5.3 ± 0.6	1.04 ± 0.12	5.1	206 ± 23
III	20.3 ± 0.6	10.2 ± 1.4	5.0 ± 0.7	1.07 ± 0.12	4.7	289 ± 3
IV	28.0 ± 1.0	9.9 ± 1.5	4.4 ± 0.7	1.09 ± 0.17	4.0	357 ± 52
Z1	30.0 ± 1.0	9.4 ± 0.4	3.2 ± 0.3	0.77 ± 0.07	4.1	
Antofagasta 19°C “captivity”						
I	2.0	10.0 ± 0.4	5.3 ± 0.2	1.06 ± 0.06	5.0	174 ± 8
II	14.0 ± 0.0	10.1 ± 0.5	5.2 ± 0.2	1.10 ± 0.07	4.7	214 ± 21
III	20.0 ± 0.0	7.5 ± 0.7	3.8 ± 0.3	0.83 ± 0.09	3.4	197 ± 9
IV	28.0 ± 0.6	7.2 ± 0.7	3.3 ± 0.3	0.79 ± 0.06	3.1	276 ± 12
Z1	30.7 ± 0.6	8.6 ± 0.1	3.0 ± 0.3	0.75 ± 0.03	4.1	
Puerto Montt 12°C						
I	~2.0	12.0 ± 0.1	6.4 ± 0.4	1.21 ± 0.06	5.3	219 ± 16
III	36.0 ± 5.1	11.6 ± 0.7	6.0 ± 0.4	1.22 ± 0.10	4.9	296 ± 46
IV	59.7 ± 4.3	10.9 ± 0.8	5.0 ± 0.3	1.19 ± 0.08	4.2	437 ± 30
Z1	66.0 ± 0.6	12.4 ± 1.4	4.0 ± 0.4	0.95 ± 0.08	4.2	
Puerto Montt 16°C						
I	~2.0	13.1 ± 1.1	7.2 ± 0.6	1.37 ± 0.10	5.2	263 ± 16
III	15.0 ± 0.0	13.3 ± 1.1	7.1 ± 0.6	1.41 ± 0.09	5.0	295 ± 57
IV	29.0 ± 1.4	12.1 ± 0.9	5.8 ± 0.6	1.26 ± 0.09	4.6	418 ± 35
Z1	31.5 ± 3.5	11.5 ± 0.2	4.5 ± 0.4	0.95 ± 0.07	4.7	
Puerto Montt 19°C						
I	~2.0	13.1 ± 1.4	7.1 ± 0.7	1.37 ± 0.13	5.2	251 ± 29
III	15.7 ± 2.5	13.0 ± 1.4	6.9 ± 0.9	1.38 ± 0.16	5.0	291 ± 19
IV	30.3 ± 5.5	12.3 ± 1.3	5.7 ± 0.7	1.28 ± 0.14	4.5	457 ± 90
Z1	26.0	10.4	4.4	1.04	4.2	

Table 3. *Cancer setosus.* Percentage changes in elemental composition (DM, C, N), and volume (V) during egg development from stage I (blastula) to stage IV (pre-hatching) and from stage I to freshly hatched zoea 1 larvae (Z1)(calculated solely for females with zoea 1 sampled). The results of ANOVA, testing for the differences (μg/ind^{-1}) between stage I and IV eggs as shown by raised letters. Different letters indicate significant differences (Tukey HSD at $\alpha = 0.05$). For number of replicates see table 1.

T	stage IV as % of stage I				Z1 as % of stage I		
°C	DM	C	N	V	DM	C	N
Antofagasta							
16	90^{A}	78^{ABC}	103^{C}	187	104	60	81
19	96^{BC}	81^{BC}	96^{ABC}	197	92	59	69
19 “captivity”	72^{C}	62^{C}	75^{BC}	158	87	57	70
Puerto Montt							
12	91^{A}	78^{A}	98^{BC}	200	101	61	77
16	92^{A}	82^{AB}	92^{A}	159	87	62	69
19	94^{AB}	81^{AB}	94^{AB}	182	75	58	72

Table 4. *Cancer setosus.* Absolute fatty acid composition (µg/200 eggs) in egg stages I-IV in Antofagasta captivity (19°C) and in stages I and IV for field produced eggs in Antofagasta (19°C) and Puerto Montt (12 & 19°C) ± SD. SFA: saturated fatty acids, MUFA: monounsaturated fatty acids, PUFA: polyunsaturated fatty acids.

Fatty acid	A (capt.) ~ 19°C (n=3)				A (field) ~ 19°C (n=3)		PM 19°C (n=3)		PM 12°C (n=6)	
	I	**II**	**III**	**IV**	**I**	**IV**	**I**	**IV**	**I**	**IV**
14:0	3.9 ± 1.0	3.4 ± 0.8	2.5 ± 1.0	1.0 ± 0.1	6.5 ± 1.7	1.0 ± 0.6	6.1 ± 0.9	2.6 ± 0.2	6.4 ± 1.0	0.9 ± 0.3
15:0	3.3 ± 0.7	3.0 ± 0.4	2.3 ± 0.5	1.1 ± 0.1	1.8 ± 0.3	0.5 ± 0.3	3.0 ± 0.9	1.5 ± 0.5	1.8 ± 0.5	0.4 ± 0.1
16:0	48.4 ± 6.0	45.6 ±2.5	37.3 ± 3.9	21.9 ± 1.1	49.1 ± 11.3	19.0 ± 10.2	59.0 ± 4.4	36.1 ± 5.8	62.3 ± 7.8	21.2 ± 2.7
17:0	3.0 ± 0.5	2.9± 0.3	2.6 ± 0.3	1.8 ± 0.2	1.5 ± 0.1	0.5 ± 0.5	2.4 ± 0.4	2.0 ± 0.7	1.7 ± 0.5	1.0 ± 0.2
18:0	13.8 ± 1.7	14.0 ± 1.1	12.9 ± 1.3	11.6 ± 0.9	15.1 ± 2.2	9.0 ± 1.3	17.4 ± 0.3	15.3 ± 2.8	19.6 ± 6.2	9.3 ± 0.9
20:0	0.5 ± 0.0	0.7 ± 0.0	0.8 ± 0.0	0.9 ± 0.0	1.1 ± 0.2	1.0 ± 0.2	1.6 ± 0.7	1.6 ± 0.4	1.7 ± 0.6	1.1 ± 0.2
∑ SFA	**73.0**	**69.7**	**58.5**	**38.2**	**75.0**	**31.0**	**89.5**	**59.1**	**93.5**	**33.9**
16:1(*n*-7)	26.3 ± 6.3	20.6 ± 3.8	14.8 ± 3.2	5.4 ± 1.1	36.7 ± 12.7	7.6 ± 7.0	42.9 ± 10.2	18.2 ± 5.3	35.4 ± 8.9	5.5 ± 1.4
18:1(*n*-9)	30.0 ± 1.1	28.7 ± 0.9	23.4 ± 1.3	13.6 ± 0.7	38.5 ± 11.7	14.7 ± 8.7	51.7 ± 9.5	30.0 ± 6.7	56.3 ± 10.9	17.2 ± 4.6
18:1(*n*-7)	14.4 ± 0.7	14.0 ± 1.0	11.9 ± 1.1	7.7 ± 0.2	17.6 ± 2.1	8.3 ± 3.1	24.1 ± 6.1	16.9 ± 5.3	29.0 ± 2.9	12.1 ± 1.5
20:1(*n*-7)	4.1 ± 0.2	4.0 ± 0.2	3.3 ± 0.2	1.8 ± 0.1	3.5 ± 0.6	1.2 ± 0.7	5.2 ± 1.8	2.3 ± 0.7	6.1 ± 1.5	1.6 ± 0.5
20:1(*n*-9)	8.5 ± 0.3	8.3 ± 0.5	7.2 ± 0.5	3.9 ± 0.3	2.8 ± 0.3	1.2 ± 0.4	3.7 ± 1.4	3.5 ± 0.9	5.0 ± 0.9	1.8 ± 0.8
20:1(*n*-11)	2.7 ± 0.4	2.6 ± 0.2	2.1 ± 0.1	0.9 ± 0.1	3.2 ± 1.7	1.0 ± 1.0	5.5 ± 2.9	1.4 ± 1.2	4.9 ± 2.4	1.0 ± 0.5
22:1(*n*-7)	1.1 ± 0.1	1.1 ± 0.0	0.9 ± 0.2	0.6 ± 0.1	4.0 ± 1.6	2.3 ± 1.6	2.4 ± 0.7	1.7 ± 0.3	4.6 ± 2.6	1.6 ± 1.0
∑ MUFA	**87.0**	**79.3**	**63.6**	**33.9**	**106.3**	**36.2**	**135.6**	**74.0**	**141.4**	**40.8**
16:2(*n*-4)	0.6 ± 0.3	0.5 ± 0.4	0.4 ± 0.3	0.1 ± 0.0	1.7 ± 1.1	0.2 ± 0.1	1.5 ± 0.1	1.2 ± 1.0	1.2 ± 0.5	0.2 ± 0.0
16:3(*n*-4)	10.4 ± 6.4	10.7 ± 6.7	5.3 ± 5.5	4.0 ± 0.8	4.3 ± 2.7	1.5 ± 1.9	2.9 ± 0.3	1.5 ± 0.4	2.4 ± 0.8	0.5 ± 0.2
18:2(*n*-6)	3.9 ± 0.2	3.7 ± 0.2	2.9 ± 0.2	1.5 ± 0.1	3.0 ± 0.5	1.0 ± 0.4	2.3 ± 0.4	1.2 ± 0.4	4.9 ± 3.2	1.0 ± 1.0
18:3(*n*-3)	2.2 ± 0.3	1.9 ± 0.2	1.4 ± 0.2	0.5 ± 0.0	6.1 ± 1.3	4.7 ± 0.9	6.6 ± 1.4	5.4 ± 1.1	5.9 ± 0.5	4.7 ± 0.5
18:4(*n*-3)	1.0 ± 0.1	0.8 ± 0.1	0.6 ± 0.2	0.2 ± 0.0	1.0 ± 0.2	0.2 ± 0.2	1.2 ± 0.3	0.6 ± 0.3	1.6 ± 0.3	0.3 ± 0.1
20:2(*n*-6)	1.3 ± 0.1	1.3 ± 0.3	1.2 ± 0.2	1.0 ± 0.2	2.3 ± 1.0	1.6 ± 0.9	2.5 ± 0.9	2.3 ± 0.8	3.3 ± 0.5	1.9 ± 0.4
20:4(*n*-6)	11.2 ± 0.8	10.9 ± 0.3	9.3 ± 0.2	7.2 ± 0.5	12.4 ± 3.5	7.0 ± 4.4	9.2 ± 4.3	6.8 ± 3.7	7.3 ± 2.3	3.9 ± 0.9
20:4(*n*-3)	0.9 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.3 ± 0.1	1.3 ± 0.1	0.2 ± 0.1	1.8 ± 0.8	0.8 ± 0.3	2.8 ± 1.5	0.4 ± 0.2
20:5(*n*-3)	29.1 ± 3.9	28.6 ± 2.9	25.1 ± 2.5	23.9 ± 2.0	42.5 ± 15.5	23.8 ± 1.9	50.4 ± 14.6	39.4 ± 9.3	54.8 ± 8.8	31.9 ± 4.0
22:5(*n*-3)	5.0 ± 0.8	4.7 ± 0.6	3.9 ± 0.4	2.3 ± 0.4	7.4 ± 4.6	5.5 ± 2.4	16.4 ± 1.8	11.0 ± 3.6	15.0 ± 5.0	7.2 ± 3.2
22:6(*n*-3)	39.5 ± 2.3	37.6 ± 3.0	32.8 ± 1.9	23.4 ± 1.0	21.6 ± 4.2	14.1 ± 2.3	35.7 ± 8.1	29.5 ± 9.9	36.0 ± 7.9	20.0 ± 4.5
∑ PUFA	**105.1**	**101.4**	**83.5**	**64.6**	**103.5**	**59.7**	**130.6**	**99.9**	**135.1**	**71.9**
∑ Total	**265.1**	**250.3**	**205.5**	**136.7**	**284.9**	**127.0**	**355.7**	**232.9**	**370.0**	**146.5**
% of FA left in stage IV				**51.6**		**44.6**		**65.5**		**39.6**

Table 5. *Cancer setosus.* Relative fatty acid compositon (% of total fatty acids) in egg stages I-IV in Antofagasta captivity (19 °C) and in stages I and IV for field produced eggs in Antofagasta (19 °C) and Puerto Montt (12 & 19 °C) ± SD. SFA: saturated fatty acids, MUFA: monounsaturated fatty acids, PUFA: polyunsaturated fatty acids.

Fatty acid	A (capt.) ~ 19 °C (n=3)				A (field) ~ 19 °C (n=3)		PM 19 °C (n=3)		PM 12 °C (n=6)	
	I	**II**	**III**	**IV**	**I**	**IV**	**I**	**IV**	**I**	**IV**
14:0	1.5 ± 0.2	1.3 ± 0.2	1.2 ± 0.3	0.7 ± 0.0	2.3 ± 0.6	0.7 ± 0.1	1.7 ± 0.3	1.1 ± 0.2	1.7 ± 0.1	0.6 ± 0.2
15:0	1.2 ± 0.1	1.2 ± 0.1	1.1 ± 0.1	0.8 ± 0.0	0.6 ± 0.1	0.4 ± 0.1	0.8 ± 0.2	0.6 ± 0.2	0.6 ± 0.4	0.3 ± 0.1
16:0	18.3 ± 0.9	18.2 ± 0.4	18.1± 0.3	16.1 ± 0.1	17.1 ± 1.7	14.5 ± 2.1	16.6 ± 0.2	15.5 ± 0.4	17.2 ± 0.9	14.5 ± 0.7
17:0	1.1 ± 0.1	1.2 ± 0.0	1.2 ± 0.0	1.3 ± 0.1	0.5 ± 0.1	0.5 ± 0.5	0.7 ± 0.1	0.8 ±0.2	0.6 ± 0.3	0.7 ± 0.2
18:0	5.2 ± 0.1	5.6 ± 0.1	6.3 ± 0.1	8.5 ± 0.5	5.4 ± 1.0	7.5 ± 1.5	4.9 ± 0.5	6.5 ± 0.1	5.3 ± 1.0	6.4 ± 0.4
20:0	0.2 ± 0.0	0.3 ± 0.0	0.4 ± 0.1	0.7 ± 0.0	0.4 ± 0.0	0.8 ± 0.1	0.5 ± 0.2	0.7 ± 0.1	0.4 ± 0.2	0.7 ± 0.1
∑ SFA	**27.5**	**27.8**	**28.4**	**28.0**	**26.4**	**24.4**	**25.2**	**25.4**	**25.9**	**23.2**
16:1(*n*-7)	9.9 ± 2.3	8.2 ± 1.2	7.2 ± 1.1	4.0 ± 0.6	12.7 ± 2.8	5.3 ± 2.9	12.0 ± 0.3	7.8 ± 1.7	9.5 ± 1.7	3.7 ± 0.8
18:1(*n*-9)	11.4 ± 0.7	11.5 ± 1.0	11.5 ± 1.1	10.0 ± 0.4	13.4 ± 2.5	11.0 ± 2.3	14.5 ± 2.0	12.9 ± 1.8	14.3 ± 2.1	11.6 ± 2.1
18:1(*n*-7)	5.4 ± 0.5	5.6 ± 0.7	5.6 ± 0.6	5.6 ± 0.4	6.2 ± 0.4	6.5 ± 0.3	6.8 ± 1.4	7.2 ± 1.4	7.4 ± 1.4	8.2 ± 0.4
20:1(*n*-11)	1.0 ± 0.1	0.6 ± 0.1	1.0 ± 0.0	1.0 ± 0.1	1.1 ± 0.4	0.7 ± 0.5	1.6 ± 1.0	0.5 ± 0.5	1.4 ± 0.6	0.7 ± 0.4
20:1(*n*-9)	3.2 ± 0.3	2.9 ± 0.2	3.3 ± 0.4	3.5 ± 0.4	1.0 ± 0.2	0.9 ± 0.1	1.0 ± 0.3	1.6 ± 0.7	1.6 ± 0.6	1.2 ± 0.4
20:1(*n*-7)	1.6 ± 0.1	1.8 ± 0.2	1.6 ± 0.2	1.3 ± 0.0	1.2 ± 0.1	0.9 ± 0.2	1.5 ± 0.6	1.0 ± 0.2	1.6 ± 0.4	1.1 ± 0.4
22:1(*n*-7)	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.0	1.4 ± 0.4	1.7 ± 1.2	0.7 ± 0.2	0.7 ± 0.1	1.1 ± 0.6	1.0 ± 0.6
∑ MUFA	**32.9**	**31.7**	**31.0**	**24.8**	**32.0**	**27.1**	**38.1**	**31.8**	**36.9**	**27.7**
16:2(*n*-4)	0.2 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.0	0.6 ± 0.5	0.2 ± 0.1	0.4 ± 0.1	0.6 ± 0.6	0.3 ± 0.1	0.1 ± 0.0
16:3(*n*-4)	3.9 ± 2.2	4.2 ± 2.5	2.4 ± 2.3	3.0 ± 0.5	1.5 ± 0.7	0.9 ± 0.9	0.8 ± 0.0	0.6 ± 0.1	1.4 ± 1.9	0.3 ± 0.1
18:2(*n*-6)	1.5 ± 0.1	1.5 ± 0.1	1.4 ± 0.0	1.1 ± 0.0	1.1 ± 0.0	0.8 ± 0.0	0.6 ± 0.1	0.5 ± 0.1	1.4 ± 0.6	0.7 ± 0.6
18:3(*n*-3)	0.8 ± 0.0	0.8 ± 0.1	0.7 ± 0.0	0.4 ± 0.0	2.1 ± 0.1	3.9 ± 0.8	1.8 ± 0.2	2.3 ± 0.1	1.5 ± 0.4	3.3 ± 0.7
18:4(*n*-3)	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	0.2 ± 0.1
20:2(*n*-6)	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.7 ± 0.2	0.8 ± 0.3	1.2 ± 0.2	0.7 ± 0.3	1.0 ± 0.3	0.8 ± 0.2	1.3 ± 0.2
20:4(*n*-6)	4.2 ± 0.2	4.4 ± 0.2	4.5 ± 0.3	5.3 ± 0.2	4.3 ± 0.9	5.2 ± 1.4	2.5 ± 1.1	2.9 ± 1.3	2.3 ± 1.0	2.6 ± 0.4
20:4(*n*-3)	0.4 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.5 ± 0.0	0.2 ± 0.1	0.5 ± 0.3	0.4 ± 0.2	0.7 ± 0.5	0.3 ± 0.1
20:5(*n*-3)	10.9 ± 0.4	11.4 ± 0.7	12.2 ± 0.1	17.5 ± 0.7	15.2 ± 5.6	20.1 ± 5.7	14.3 ± 4.2	17.1 ± 4.0	14.0 ± 2.1	21.8 ± 1.4
22:5(*n*-3)	1.9 ± 0.2	1.9± 0.1	1.0 ± 0.1	1.7 ± 0.2	2.5 ± 1.4	4.2 ± 0.7	4.6 ± 0.6	4.8 ± 1.2	3.9 ± 2.1	4.9 ± 2.2
22:6(*n*-3)	14.9 ± 0.9	15.0 ± 1.2	16.0 ± 1.4	17.1 ± 0.6	7.7 ± 2.0	11.7 ± 2.3	10.0 ± 1.6	12.4 ± 2.3	10.4 ± 2.2	13.6 ± 2.4
∑ PUFA	**39.6**	**40.5**	**40.6**	**47.2**	**36.6**	**48.5**	**36.7**	**42.9**	**37.2**	**49.1**

Table 6. *Cancer setosus.* Fatty acid content (FA µg/egg) and as percentage of DM and C in egg stages I and IV.

T (°C)	FA µg/egg		FA as % of DM		FA as % of C	
	I	IV	I	IV	I	IV
Antofagasta						
19 “captivity”	1.33	0.68	13.3	7.1	25.2	15.7
19	1.42	0.63	13.9	6.4	26.5	14.6
Puerto Montt						
19	1.78	1.16	13.6	9.5	25.0	20.3
12	1.85	0.73	15.5	6.7	28.9	14.6

Figures

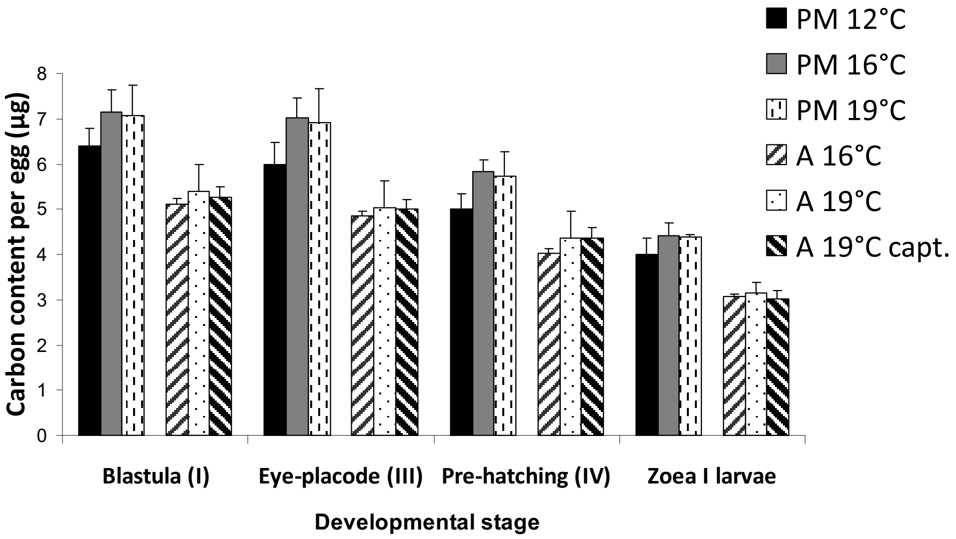

Figure 1. *Cancer setosus.* Carbon content throughout egg development and in freshly hatched zoea 1 larvae in Puerto Montt (PM) and Antofagasta (A) at different incubation temperatures. With the exception of “A 19°C capt.” all eggs were produced in the field.

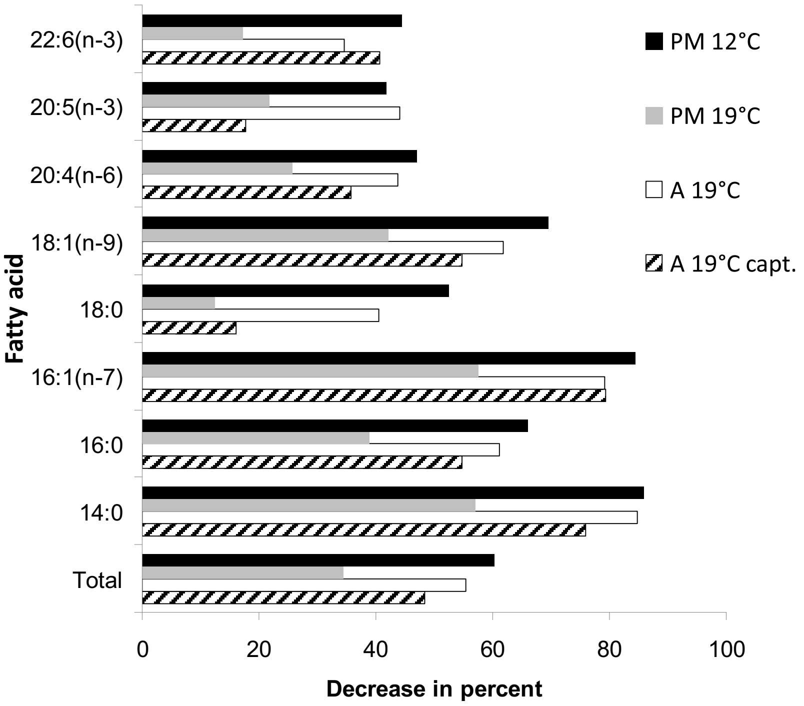

Figure 2. *Cancer setosus.* Percentage change in the total of fatty acids and in the most abundant fatty acids from the start (stage I) to the end of the incubation period (stage IV) at 12 and 19°C in Puerto Montt (PM) and at 19°C in Antofagasta (A; field and captivity produced eggs). Decrease in percent refers to changes in the absolute mass (µg) per fatty acid.

Brachyuran crabs in the Humboldt Current System: temperature effects on life-history traits cause challenges to fisheries management

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Abstract

Owing to the influence of the Humboldt Current many cold-water adapted brachyuran crabs of commercial interest have vast (>40°latitude) distributional ranges along the Pacific Coast of Peru and Chile. Development of artisanal diving and trapping fisheries on these crabs (mainly Cancridae and Xanthidae) is either uncontrolled (Peru) or existing management measures, like the minimum landing size of 12 cm and the prohibition to catch ovigerous females, are poorly enforced (Chile). Under El Niño conditions, occurring on average every 4 years, the upper temperature limit of these temperate species can be exceeded in Peru leading to mass mortalities of adult crabs and a breakdown of the artisanal crab fishery. Temperature changes (latitudinal or in the course of El Niño Southern Oscillation) may have pervasive effects on reproduction and early life history stages as represented for *Cancer setosus,* which ultimately determine the recruitment of crabs to the fishery. The recent development of the fishery, namely the decline of the landings of *C. setosu*s and *Homalaspis plana* in Central- to Northern Chile, compensated by the rapidly developing fishery on *C. edwardsii* in Southern Chile is presented and discussed in the light of temperature effects on the crabs (reproductive-) biology.

1 Introduction

Artisanal “shellfish-fisheries” in the near coastal zone of Chile and Peru are inferior in landings compared to the large-scale industrial fisheries operating in the pelagic upwelling waters of the Humboldt Current (e.g. anchovies, jumbo squid and squat lobster). Nevertheless, among the more than 60 species of benthic invertebrates caught (e.g. bivalves, gastropods, sea urchins, tunicates, giant barnacles and crabs) many are of high economic value on the domestic- and export markets (Bustamente and Castilla, 1987). Shellfish are gathered by hand at low tide or caught from small boats with traps and by “hooka-diving”, which is the most widely employed artisanal fishing technique in Chile and Peru. These fisheries are quite selective and do relatively little direct harm to the ecosystem. However, the sheer number of artisanal fishermen, ~70 000 in Chile (SERNAPESCA 2008) and ~38 000 in Peru (IMARPE 2005) combined with the *de facto* open access to the fishery have caused some of the most valuable resources, like the muricid gastropod *Concholepas concholepas* to collapse (e.g. resulting in a closure of the Chilean fishery from 1989 to 1992) (Castilla and Fernández, 1998). Learning from the collapse of *C. concholepas,* a law for the design of “management and exploitation areas for benthic resources” (MEABR) has been fully enacted in Chile in 1995 (Castilla, 1996; Bernal et al., 1999). “Territorial user rights in fisheries” (TURFs) are granted to local fisheries cooperations, who are then responsible for the monitoring and co-management of benthic invertebrates in MEABR (Castilla, 1996), but with very limited ability to prevent poaching (Castilla and Gelcich, 2006). The number of fishermen and the size of MEABRs vary, but in few cases can reach up to 150 individuals in larger syndicates and 150 ha in area (Thatje et al., 2008). MEABRs (506 in 2007) were primarily created in the areas of the highest productivity of *C. concholepas*, but nowadays also key-hole limpets (*Fissurella sp.*) and sea urchins (*Loxechinus albus*) are managed on the basis of annual stock assessments (Stotz, 2007). While this approach seems promising for these semi-sedentary invertebrates, the benefits for brachyuran crab resources in smaller MEABRs is hampered by their mobility (Fernández and Castilla, 1997, 2000; Castilla and Fernández, 1998). Therefore, the crabs *Cancer setosus* and *Homalaspis plana,* considered valuable “secondary resources”, are presently only caught outside the MEABR due to the lack of management plans for these species (Stotz, 2007).

Brachyuran crab landings have greatly increased in the last two decades in Chile and Peru. The Chilean landings of 6500 t in 2008 were mainly based on *Cancer edwardsii, C. setosus* (Cancridae) and *Homalaspis plana* (Xanthidae) (SERNAPESCA, 2008), while in Peru landings of ~1600 t in 2007 were based on *C. setosus, C. porteri* and *Platyxanthus orbignyi* (Xanthidae) (IMARPE, 2008). Despite the long fishing tradition, the scientific knowledge as a basis for management guidelines, has not kept pace with their rates of exploitation (Fernández and Castilla, 2005). In Peru, there are no management guidelines of brachyuran fisheries at all, while in Chile a uniform minimum carapace width of 120 mm and the prohibition to land ovigerous females represent the only legal management measures. So far, basic life-history parameters for the majority of exploited brachyuran crabs in the HC are poorly known (e.g. reproductive periods and size of maturity).

This paper aims to give an overview of brachyuran crab ecology, highlighting the challenges for fisheries management in Chile and Peru. Based on the results, we advocate that the adaptive management of shellfish species with wide latitudinal distribution needs to consider the local responses of stocks to macroecological driving factors in order to be effective.

2 Distribution of cold water adapted crabs in the Humboldt Current

Cancer crabs and many other species of evolutionary cold-faunal origin owe their wide distributional ranges along Pacific South America to the influence of the cold Humboldt Current (MacKay, 1943; Nations, 1975; Nations, 1979). The reported northern distributional limits of *C. setosus*, *C. edwardsii*, *H. plana,* and *P. orbignyi* (~ 2°S) coincide with the limit of the Humboldt Current (Figure 1) (Rathbun, 1930; Garth, 1957; Retamal, 1981) and support MacKay (1943) stating that *Cancer* crabs are principally restricted to surface waters colder than 24°C. What may seem like an exception is the more tropical distribution of *C. porteri*, which appeared to avoid the higher temperatures through a deeper distribution below the thermocline (Garth, 1957). More recently, it was revealed that the morphological differences of the deep-water form of Central America actually represent a distinct species, *C. johngarthi* (Carvacho, 1989; Carvacho and Bonfil, 1989).

Under El Niño conditions, occurring on average every 4 years, temperatures may surpass the limits of the cold-temperate adapted fauna and flora. In the 1982/83, El Niño sea surfaces temperatures rose above 30°C (+ 10°C compared to the long-term mean) in Northern Peru, causing mass-mortalities of the commercially important crabs *C. setosus* and *P. orbignyi* and a migration to deeper waters of *C. porteri* (Arntz et al., 1988). These effects of El Niño were reflected by collapsing brachyuran catches in Peru (Figure 2). The “tropicalization” of the Humboldt Current under the 1982/83 El Niño allowed for a southward range extension by 13° latitude of penaeid shrimps (e.g. *Xiphopenaeus riveti*; *Penaeus stylirostris*) and swimming crabs from Ecuador (e.g. *Euphylax robustus*, *E. dovii*, *Callinectes arcuatus*) and Peruvian fishermen adjusted their fishing methods to catch great quantities of shrimps (Barber and Chavez, 1983, 1986; Arntz et al., 1988). However, by-catches of swimming crabs that occurred were rather considered a nuisance (despite their marketable size and their consumption throughout Central America) (Fischer and Wolff, 2006) to the recently established shrimp fishery through net entanglment and their attacking of the targeted shrimp (Arntz et al., 1988). Distributional ranges of commercial benthic invertebrates may thus show pronounced shifts of several latitudinal degrees in the HC associated to the warm and cold phases of the El Niño Southern Oscillation (ENSO) (for the bay scallop *Argopecten purpuratus* Wolff, 1987, 1988; Wolff and Mendo 2000; for the surf clam *Mesodesma donacium* Arntz et al., 1987; Riascos, 2008).

The actual northern distribution limit of C*. edwardsii* and *H. plana*, reported by early taxonomists to range into Southern Ecuador, remains obscure (Figure 1). These brachyurans are of high commercial importance in Central-Southern Chile, but their presence has not been confirmed for Peru in the last decades (Haig, 1968; Méndez, 1982)(Mendo pers. observation). On the contrary, based on occasional captures in king crab traps, the reported range of *C. edwardsii* has been extended southward from the Magellan Strait to the Beagle Channel (56°S) (Vinuesa et al., 1999).

3 Latitudinal variation in life history traits: *Cancer setosus* as a model organism

Throughout *C. setosus’* wide range of more >40° latitude, mean annual SST ranges from roughly 10 to 20°C, which has implications for this crabs reproductive biology and early life history traits. In Ancud (43°S) oviposition occurs annually in late winter, and thus follows the typical seasonal reproductive pattern of *Cancer* crabs (Shields, 1991), while slightly warmer winter temperatures in Concepción (12°C vs. 10°C in Ancud) allow for continuous reproduction leading to the output of more than 3 annual clutches (Fischer and Thatje, 2008). At increasingly higher temperatures ovigerous females are observed year-round, but their annual clutch number decreases towards Northern Peru (~2 in Coquimbo 29°S, and ~1 in Casma 9°S), which was attributed to the higher metabolic costs of life at warmer temperatures (Fischer and Thatje, 2008). In Coquimbo, the growth efficiency of mature female *C. setosus* was lowered by ~50% compared to males due to the energetic investment in two annual ovipositions (Wolff and Cerda, 1992). However, it remains speculative as to how temperature dependent differences in annual clutch-number affect female growth rate. The size of first massive maturity (CW_{mass}) and apparently also the maximum size in both sexes (CW_{max}) increase by roughly 25% from Casma (9°S) to Chiloé (42°S) (Table 2). Larger *C. setosus* females were found to produce significantly larger eggs and thus possibly make a higher contribution to the recruitment as explained by their size specific higher fecundity alone (Fischer et al., 2009).

Changes in the temperature regime appear to not only affect the number of annual clutches produced, but also the energetic investment per egg. Eggs produced in Puerto Montt (43°S) at ~11°C were 32% higher in size, dry mass, carbon, nitrogen and fatty acids compared to eggs produced under conditions representative for the species upper thermal range (~19°C) in Antofagasta (23°S). This trend appears to be a result of *C. setosus*' physiological plasticity in response to environmental settings, as females from Puerto Montt (43°S) were observed to produce smaller eggs when reared in aquaria under higher pre-oviposition temperatures (Fischer et al., 2009). Increased energetic investment per egg under lower temperatures is discussed as an adaptive maternal response, providing the hatching larvae with more energy needed for its prolonged development under cold conditions. However, a significant proportion of the "surplus" energy invested per egg at lower temperatures is already consumed during egg development. Eggs incubated at 12°C required almost twice as much fatty-acid based energy until larvae hatching as compared to eggs incubated at 19°C (-1.1 and -0.6 µg fatty acids per eggs, respectively). Along this line, the higher energetic investment under lower temperatures might also represent an energetic requirement for the reduced metabolic efficiency of low-temperature egg development (Fischer et al., in press). The duration of egg development decreased from 65 days at 12°C to 23 days at 22°C. Above temperatures of 22°C, which may be reached in Peru under moderate El Niño conditions, eggs failed to attach to the female abdomen at oviposition or they died few days thereafter (Fischer and Thatje, 2008). *C. setosus* larvae hatching in Antofagasta (21°S) successfully developed within the temperature range of 16 to 20°C (Weiss et al., under revision), while larvae in Concepción (36°S) finished their development at lower temperatures of ~14°C (Quintana, 1981). Both the initial energetic investment per egg, and the conditions experienced throughout egg development may have pervasive effects on later life history stages (Giménez, 2006). Changes in temperature conditions, throughout the crabs latitudinal range and as influenced by ENSO variability, show effects on life-history traits, which may translate into recruitment and later life history stages. The high degree of plasticity of *C. setosus* in life history traits is seen as the key to the species wide range under conditions of high, and unpredictable environmental stochasticity.

4 Chile – fisheries shifting South

Brachyuran crab catches in Chile (composed of 8 species), steeply increased from ~ 1 000 t annually in the early 1980s to 5 000 – 6 000 t in recent years, which was partly driven by changes in market structure from domestic consume to international export of processed crab meat. However, not all species increased in catches. Decreasing landings of *C. setosus* and *H. plana* occurring at least since 1991 throughout the country (regions I to VIII) were masked and overcompensated by the rapidly developing *C. edwardsii* fishery in Chiles southernmost regions (X to XII) nowadays contributing ~85% of the countries brachyuran crab landings (Figure 2). Prior to 1991, landings were not reported to the species level, but it was estimated that for the period from 1970 to 1983 *C. edwardsii* contributed to no more than 1/3 of Chiles brachyuran landings (CORFO, 1984). Therefore, it seems reasonable to conclude that formerly higher crab landings in Central- to Northern Chile, were mainly composed of *C. setosus*, *H. plana* and *C. porteri* (Table 1; Figure 3). The higher historical importance of *C. setosus* and *H. plana* over that of *C. edwardsii* is reflected in the number of published scientific works. The population dynamics, reproductive parameters, feeding ecology, and the trophic role in the ecosystem of *C. setosus* (syn. *C. polyodon*) have been studied primarily in the II, IV and VIII regions (Gutiérrez and Zúñiga, 1976; Veaz, 1981; Wolff and Cerda, 1992; Wolff and Soto, 1992; Cerda and Wolff, 1993; Jesse, 2001; Ortiz and Wolff, 2002b; Jesse and Stotz, 2003; León and Stotz, 2004). For *H. plana,* feeding ecology, recruitment pattern and catch per unit effort (CPUE) trends were studied in Central Chile (V region) (Morales and Antezana, 1983; Fernández and Castilla, 1997, 2000) and clutch-size, sex-ratio and the reproductive period in the X region (Steffen, 1975; Retamal and Quintana, 1980; Carvacho et al., 1995).

The size of first massive maturity of *C. edwardsii* in the X region was recently estimated to be 103 mm CW for females (confidence intervals 88 – 129 mm CW) based on the presence of egg masses, and 118 mm CW for males based on allometry in chelae-growth (Pardo et al., 2009). These findings well support the minimum landing size of 120 mm CW, which if properly enforced, would allow most specimens of both sexes to reproduce at least once before exposure to the fishery in the X region. Given the presently uncontrolled fishery development, roughly 80% of *C. edwardsii* caught are below 120 mm CW in the X region, threatening the reproductive potential of the stock (Figure 4) (Pool et al., 1998; Olguín et al., 2006). Throughout most of Chile, hooka-diving represents the main crab capture technique, while the fishery on *C. edwardsii* in the sparsely populated Chilean South (regions X-XII) to 90% is based on trapping (Olguín et al., 2006). In the remote XI region fishermen construct temporal living sites in the regions of crab-trapping and the crabs are transported by larger vessels to the landing sites further north for processing of crab meat (Olguín et al., 2006). In the XI region most of the *C. edwardsii* caught are still larger 120 mm CW and the size composition has not changed in the past years, which is explained by the processor demanding crabs of preferably larger 130 mm CW or with large chelae (Olguín et al., 2006) (Figure 4). However, ongoing exploitation in the X region is likely to lead to an increase in fishing pressure in the more southerly regions. Growth and population dynamics have not been studied in *C. edwardsii*, but *C. magister*, *C. pagurus* and *C. setosus* (see Table 2) all show a considerable reduction in growth rate and higher size of first maturity with lower temperature (Methot, 1989; Shields, 1991). A pronounced break to lower temperatures and thus an important biogeographic boundary occurs in the HC south of ~42°S (Brattström and Johanssen, 1983) (mean winter SST of 10.3 and 5.3°C for Ancud and Puerto Chacabuco in the X and XI region, respectivly; Figure 1) and, therefore, it seems likely that *C. edwardsii* may be particulary sensitive to the ever-increasing fishing pressure in the XI region.

5 Current knowledge into management

The development of guidelines for brachyuran fisheries management in Peru is seriously hampered by strong El Niño events leading to mass mortalities of the main target species (Figure 2). However, the year-round spawning activity of *C. setosus* should counteract environmental stochasticity as long as sufficient competent larvae are transported in the HC from more southerly populations less affected by El Niño.

Based on the current knowledge, a stricter enforcement of the minimum landing size of 120 mm CW should enable for a rebuilding of the stocks of *C. setosus* and *H. plana* in Central to Northern Chile and should maintain catches at a high level for *C. edwardsii* in the X region. Given the current level of exploitation, targeting mainly sublegal sized *C. edwardsii* in the X region is likely to cause recruitment overfishing and is also economically detrimental considering that larger specimen are demanded for processing of crab meat. Escape vents, which are mandatory in the *Cancer magister* and *Callinectes sapidus* fishery in the US (Methot, 1989; Guillory and Hein, 1998), should be introduced to permit the free passage of sublegal (<120 mm CW) crabs from traps in the X region. From a precautionary point of view, a larger minimum size may be required in the XI region (130 mm CW is proposed); Research on the reproduction and the size of first maturity is urgently needed to evaluate the likely possibility of slower growth and higher size of maturity of *C. edwardsii* under the colder conditions prevailing in the XI region. Marine protected areas should be implemented throughout the species range (see Castilla, 1996) to mitigate effects of size selective fishing pressure on large specimen, selecting against fast growing genotypes (Taggart et al., 2004) (Kuparinen and Merilä, 2007), and as reference sites to study the population dynamics and ecological role of these benthic predators in the absence of fisheries mortality.

6 Future research direction

The largest uncertainty in the management of brachyuran crab fisheries arises from their high individual variability in growth and the absence of calcified hard structures for aging purpose (like otoliths) (Hartnoll, 1978; Botsford, 1985; Hartnoll, 2001; Miller and Smith, 2003; Smith and Addison, 2003; Wahle, 2003). This situation has been partly overcome by the development of the lipofuscin analysis technique. Lipofuscin, also referred to as age pigment, accumulates with time in post mitotic tissue (e.g. the brain and eyestalks) and has been successfully used to assess the age structure of several slow growing commercial Crustacea including *Cancer pagurus* (Sheehy et al., 1998; 1999; Sheehy and Bannister, 2002; Sheehy and Prior, 2008). However, this technique seems too demanding in terms of infrastructure and costs to be realized soon for the commercial Brachyura in the HC. As a more feasible approach, a regular monitoring of size and sex-composition of landed crabs, their sizes of maturity and the reproductive periods is encouraged to be implemented throughout the crabs distributional range. Reference data of brachyuran and other invertebrate distributional patterns in relation to El Niño Southern Oscillation (ENSO), would be also of high interest given a predicted increase in El Niño frequency with ongoing greenhouse warming (Timmermann et al., 1999). Experiments under controlled conditions, so far conducted for *C. setosus*, are needed to determine the critical upper and lower temperature limits of early life-history stages (egg, larvae, juvenile), which represent bottlenecks in species distribution.

7 Conclusions

Whilst it is always desirable to conduct further research into unknowns in order to optimise fisheries management, the present study provides clear evidence that very often the already available information is not sufficiently implemented in management approaches. Here, we summarize the ongoing decline of *C. setosus* and *H. plana* in Central to Northern Chile, which is attributed to the lack of enforcement of the legal minimum size. The fishery of *C. edwardsii* in the X region, and particularly in the XI region is postulated to follow the same way unless enforcement of fisheries legislation steps up to the rapid fisheries development.

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Tables

Table 1. Brachyuran landings (t) in the 12 administrative regions of Chile, (I-XII; from north to south; see Fig. 1) in 5-year intervals (1971-2008) (SERNAPESCA, 2008).

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1971-75	7	23	4	70	66		40	676		27	3	
1976-80	17	9	4	121	103	62	100	485	9	244	3	
1981-85	31	44	55	422	216	91	54	381		769	292	1
1986-90	22	73	188	280	131	34	92	448	1	2735	166	5
1991-95	26	82	34	146	101	24	253	677		2604	557	0
1996-00	29	70	43	170	127	19	126	314		2984	1227	11
2001-05	23	18	16	96	68	9	14	113		4409	1169	145
2006-08	21	26	14	110	195	7	24	304		3757	1280	89

Table 2. *Cancer setosus*. Carapace widths of first massive maturity (CW_{mass}), defined as size were 50% of the females (F) are ovigerous at peak-spawning and as inflection point of allometric chela growth for males (M), and maximum observed carapace widths (CW_{max}). The size of the smallest observed ovigerous female is given in brackets.

Location	Lat.		CW_{mass}	CW_{max}	
Casma	9°S	F	75 (54)	119	Moya (1995)
		M	99	134	
Independencia Bay	13°S	M	100	151	Lang (2000)
Mejillones	23°S	F	(79)	158	Gutiérrez and Zúñiga (1976)
		M		163	
La Herradura Bay	30°S	F	98 (67)	150	Soto (1990)
		M	124	197	
Concepción Bay	36°S	F	104 (84)	136	Veaz (1981)
		M		151	
Chiloé	42°S	F	100 (70)	164	Pool et al. (1998)
		M	123	194	
		M		199	Olguín et al. (2006)

Figures

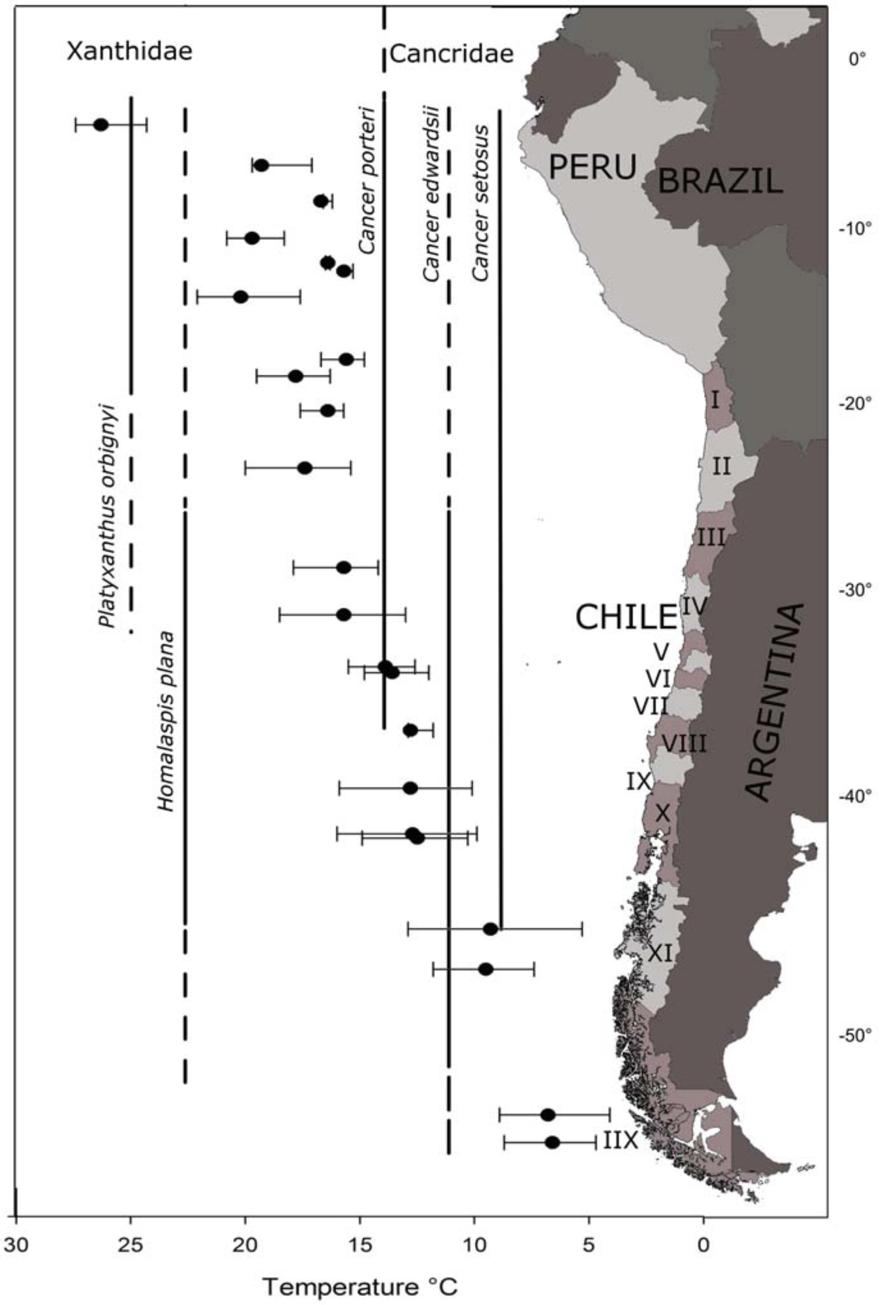

Figure 1. Distributional ranges of *Cancer edwardsii*, *C. setosus, C. porteri* (Cancridae) and of *Homalaspis plana*, and *Platyxanthus orbignyi* (Xanthidae) along the coast of Peru and Chile (continuous lines: range of regular fisheries captures; hatched lines: reported maxium range) (Rathbun, 1930). The long-term mean SST (1996 to 2006) is shown for various coastal locations. The seasonal temperature oscillation is indicated by the “error bars”: the left hand side being the mean SST in January (austral-summer) and the right hand side the mean SST in July (austral-winter) (IMARPE 2008, CENDHOC, 2008). The administrative regions of Chile are indicated (I-XII) as in 2007.

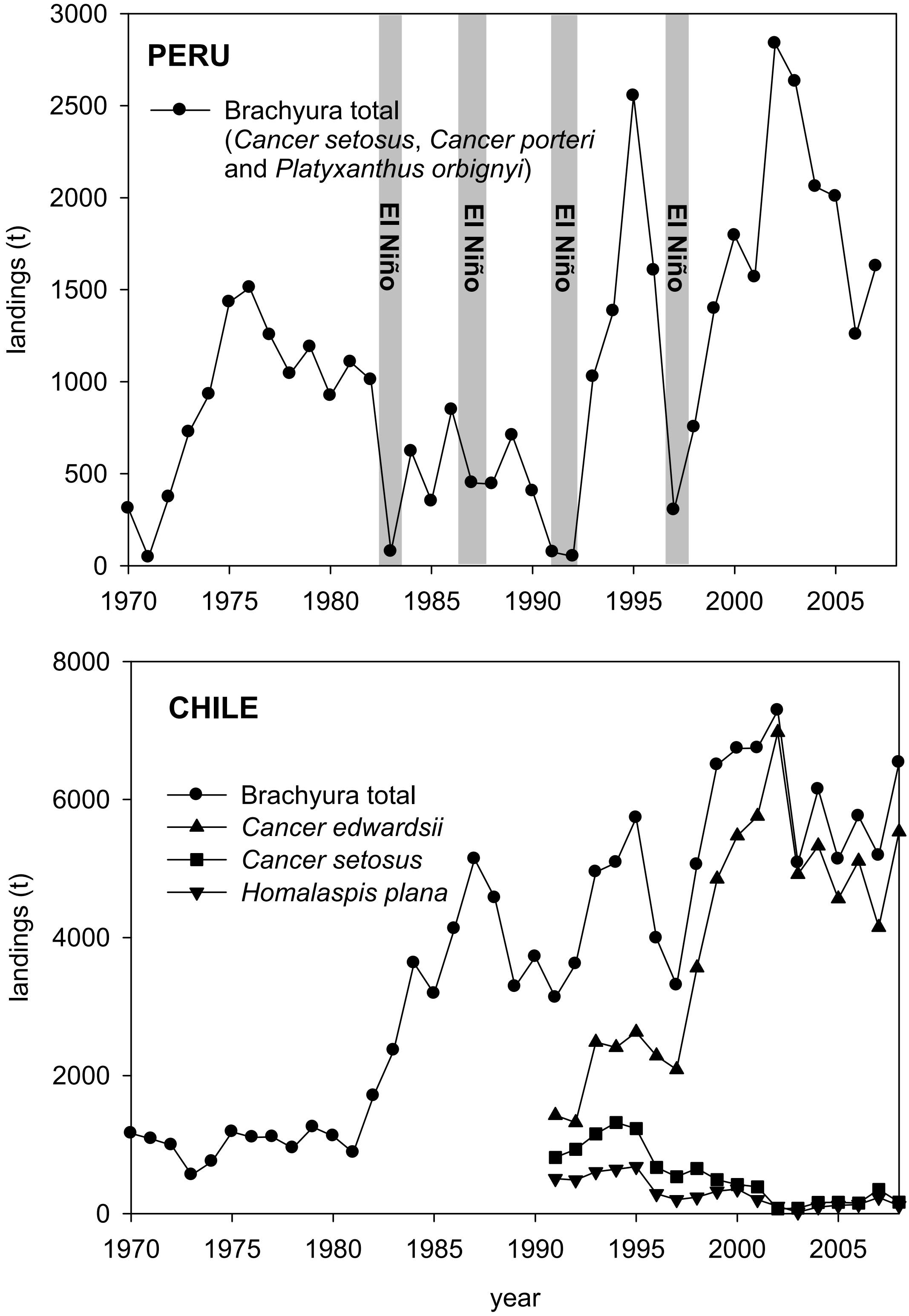

Figure 2. Temporal development of brachyuran crab landings in Peru and Chile (1970-2008) (IMARPE, 2008; SERNAPESCA, 2008). In Peru landings of *Cancer setosus*, *Cancer porteri*, and *Platyxanthus orbygnii* are reported together. In Chile landings of 8 brachyuran crab species are reported to the species level since 1991 (*C. edwardsii*, *C. setosus*, and *H. plana* contribute to 95% of the landings). The major El Niño periods are indicated (ENSO Index >2) (Trenberth, 1997).

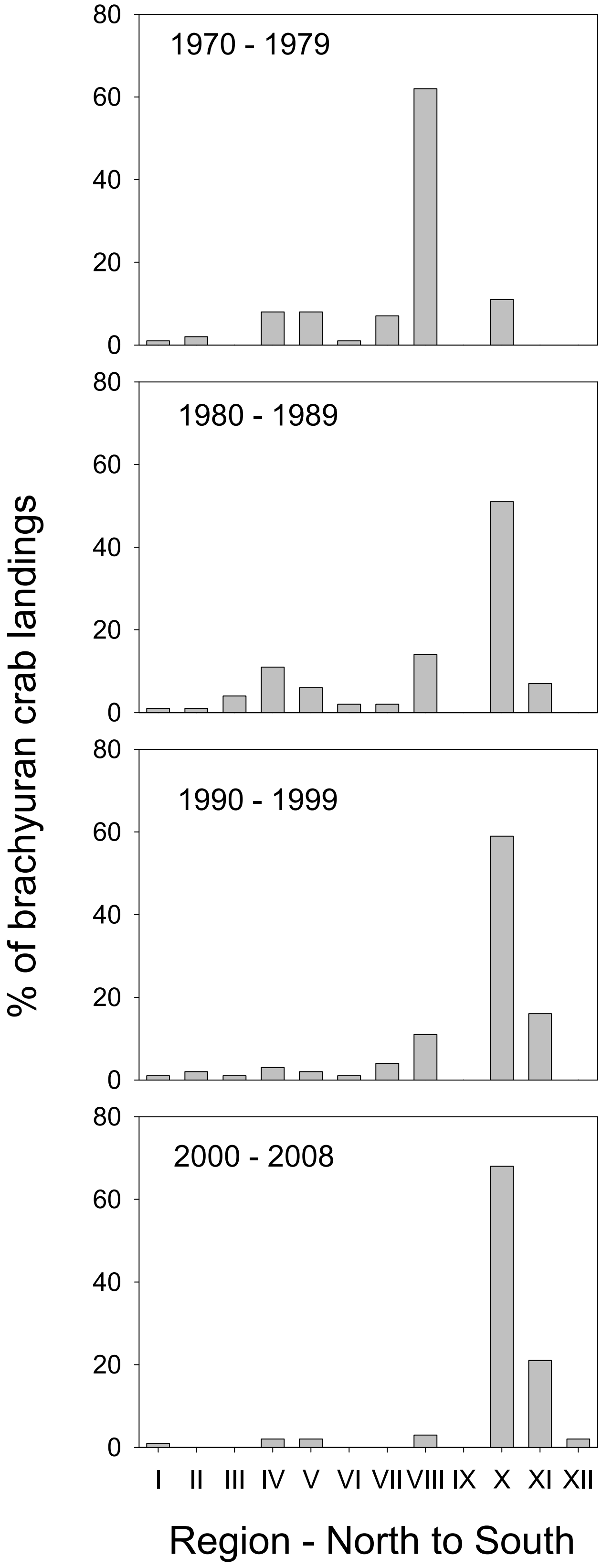

Figure 3. Brachyuran crab landings of Chile in 10-year intervals. Percentage contribution of the different administrative regions; from north to south **I-XII** (SERNAPESCA, 2008).

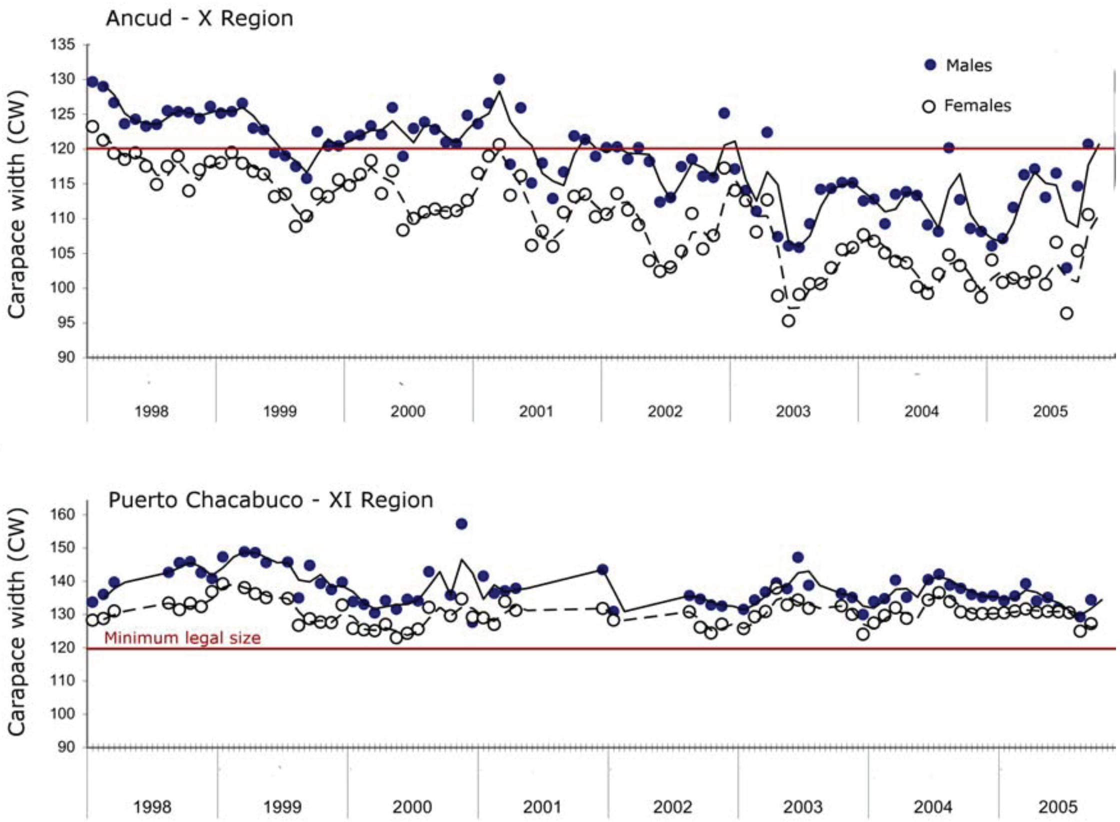

Figure 4. *Cancer edwardsii***.** Mean carapace width for males and females in landings in the X region (Ancud) and the XI region (Puerto Chacabuco) for the period 1998 – 2005. The minimum legal size of 120 mm CW is indicated; modified after Olguín et al. (2006).

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