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Influence of temperature on the zoeal development and elemental composition of the cancrid crab, *Cancer setosus* Molina, 1782 from Pacific South America

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ABSTRACT

Temperature changes during ENSO cause mass mortalities of adult *Cancer setosus*, but the effects on early life stages are unknown. The influence of temperature on survival, development and biochemical composition was studied in larvae of the hairy crab, *C. setosus*, from a population off the northern Chilean coast. In rearing experiments conducted at four different temperatures (12, 16, 20, 22 °C), zoeal development was only completed at 16 and 20 °C, after 78 and 36 days, respectively. Instar duration was negatively correlated with temperature. A multiple linear model relating larval body mass (in carbon) to temperature and developmental time suggests that successful larval development is possible within a narrow temperature range only. The biochemical composition, measured as carbon, hydrogen, and nitrogen (*C, H, N*) content, show in general the typical oscillating changes during the moult cycle of brachyuran crab larvae. However, at high (22 °C) and low (16 °C) temperatures, CHN values show deviations from the typical pattern, indicating threshold temperatures for larval activity and survival. These findings indicate that the larval development of *C. setosus* is compromised under conditions of El Niño, with temperatures exceeding the upper thermal temperature tolerance threshold of larvae. Effects of El Niño on early life history stages and recruitment rates should be increasingly taken into account in fisheries management strategies.

1. Introduction

Most cancrid crabs are found in cold temperate and boreal waters (MacKay, 1943) and provide a huge proportion of crustacean fisheries in those regions (Bennett, 1995; Johnson and Shanks, 2002). Due to their commercial importance population structure and recruitment of cancrid crabs have been the subject of several studies (e. g. Hankin et al., 1997; Eaton et al., 2003; Taggart et al., 2004; Fischer and Thatje, 2008; Fischer et al., 2009). Successful recruitment is based on larval development. Larval hatching normally occurs during spring when food availability (plankton bloom) (Park et al., 2007) and temperatures are favourable for larval growth. This seasonal dependency is not valid for larvae in the highly productive upwelling region of the Humboldt Current, which provides a huge amount of plankton year-round during upwelling periods. The persistent stable temperate conditions in a broad range of the Humboldt Current allow larvae to develop all year round (for review see Fischer and Thatje, 2008). As one of the world's most productive ecosystems, the Humboldt Current supports one of the world's largest fisheries (Bertrand et al., 2004) which is of high economical importance for the adjacent countries (Ryther, 1969; Urban and Tarazona, 1996; Food and Agricultural Organization, 2006). The availability of resources is highly dependent on the global coupled ocean-atmosphere phenomenon El Niño Southern Oscillation (ENSO) (Lehodey et al., 2006). During El Niño various abiotic and biotic conditions change: i.e., temperature rises, salinity is reduced, sedimentation and turbidity increases in some regions, radiation increases due to clear oceanic water in others, predation and competition increase by invaders and food shortage occurs (Arntz et al., 1988). Those changing conditions during El Niño have some positive effects like immigration of commercially valuable tropical species (e.g. the shrimp *Xiphopenaeus riveti*) and an outbreak of some commercial exploited local species, such as the scallop *Argopecten purpuratus* (Arntz et al., 1988). However, the negative effects and damage caused by collapsing local populations of other important species, like the hairy crab, *Cancer setosus*, likely caused by the sudden and drastic temperature rise prevails by far in local artisanal fisheries (Arntz et al., 1988). Only few artisanal fishermen are able to take advantage of the immigration of tropical species during El Niño since they do not have the right fishing gears (O'Riordan, 1998).

Cancer setosus (Molina 1782; synonymous *C. polyodon* Poeppig 1836) ranges in its distribution from Guayaquil in Ecuador (2°13′ S, 79°53′ W) to the Peninsula of Taitao in Southern Chile (46°00′ S, 75°00′ W) (Garth and Stephenson, 1966; Fischer and Thatje, 2008) and its commercial value for the Chilean and Peruvian artisanal fishery increased during the last decades (Wolff and Soto, 1992; SERNAPESCA, 2006; Thatje et al., 2008). The early ontogeny, which in *C. setosus*

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consists of five planktotrophic zoeal stages (zoea I–V = Z I–V) and one megalopa before reaching the first crab stage (Quintana and Saelzer, 1986), is considered as the most delicate part within the life cycle of brachyuran and in particular cancrid crabs (Anger, 2001; Weiss et al., in press). A unique physiological plasticity to respond to latitudinal and seasonal changes in temperature, has been observed in early egg traits of *C. setosus*. Among the most conspicuous characteristics is a synchronization of a single egg batch release with seasonality at the species southernmost distribution boundary in central southern Chile, contrasted by multiple annual ovipositions in northern Chile (Antofagasta). In addition, a correlation of changes in egg energy contents and temperature was observed along latitude as well as in subsequent ovipositions in the same female (Fischer et al., 2009).

Temperature affects all levels of biological organization ranging from cellular to organismal level (Guderley and St-Pierre, 2002) and cause changes in the metabolic efficiency or fitness of an organism (Pörtner, 2001; Pörtner et al., 2005), which presumably is reflected in its elemental and biochemical composition (Dahlhoff, 2004). In this study we draw a picture of larval destiny during ENSO temperature oscillations to improve our knowledge of mechanisms of temperature adaptations in *C. setosus* larvae. We define the temperature window of *C. setosus* larvae for the Antofagasta region (northern Chile), and reveal the influences of temperature changes throughout ENSO on larval elemental composition and survival.

2. Materials and methods

2.1. Sampling and maintenance of adults

Ovigerous *C. setosus* (carapace width, CW 101 to 120 mm) were caught between February and May 2007 by fishermen of the "Caleta Colosso" (23°45′ S, 70°27′ W) by scuba diving and were immediately transferred to the laboratory of the Instituto de Investigaciones Oceanológicas of the Universidad de Antofagasta, Chile. Animals were maintained individually in flow-through seawater aquaria (12 l) at ambient temperature ~16.0 °C and salinity 34 psu in a 12:12-h light/dark cycle and fed *ad libitum* with living *Perumytilus purpuratus*.

2.2. Experimental set-up

Freshly hatched larvae were collected in filters receiving water from the overflow of the aquaria. Since most larvae hatched at night, samples were taken every morning. Filters were cleaned every evening to ensure daily larval age did not vary by more than 12 h (after Lovrich et al., 2003). Solely actively moving larvae were transferred to bowls with 16 °C filtered seawater and afterwards were allowed to acclimate to the experimental temperature in the corresponding temperature chamber for the experiments.

2.2.1. Influence of temperature on larval survival and development

Randomly selected larvae from one randomly selected female (A) were kept individually in glass bowls containing 100 ml filtered seawater. For each experimental temperature (12, 16, 20, 22 °C) an initial number of 100 larvae was cultured in order to describe larval development and mortality. Water was changed daily; larvae were daily checked for moults or mortality and fed *ad libitum* with freshly hatched *Artemia* spp. nauplii. Survival rates and time of development for each instar was recorded. The mean duration of instars was calculated from all larvae that successfully passed through the moult into the subsequent stage.

2.2.2. Influence of temperature on elemental composition

Larvae from a randomly selected second female (B) were reared at 16, 20 and 22 °C. 12 °C as rearing temperature was excluded in this experiment, as the instar duration experiment showed extremely extended developmental times and exceptionally high mortality. Larvae were kept in 500 ml glass bowls (20 to 30 individuals/bowl) and provided with water and alimentation as described above. At each temperature an initial amount of 1000 larvae were randomly distributed into 35 glass bowls. At 20 °C, due to unforeseen technical problems, all larvae died, and a second set of experiments was conducted at 20 °C with larvae of a third female (C).

For the analyses of dry weight (W) and carbon (C), hydrogen (H) and nitrogen (N) content throughout larval development, it was inevitable to pool specimens from the same hatch and developmental day in order to reach minimum required sample W. Each sample consisted of 30 individuals in the zoea I (Z I) on the day of hatching, but less (see Table 1) in the following days and (larger) instars, in order to obtain minimum sample W necessary for elemental analysis. Samples for elemental analyses were immediately taken after hatching and later every second day at 20° and 22 °C. At 16 °C samples were taken every fourth day due to the extended developmental time at lower temperatures. Three replicates of pooled larvae from the same hatch and developmental day were collected. Number of replicates was reduced, when too few larvae were available.

2.3. Elemental analyses (CHN)

Carbon (C), hydrogen (H), nitrogen (N) contents were determined following Anger and Dawirs (1982). In brief: larvae were gently rinsed in distilled water, blotted on filter paper, placed into pre-weighed tin cartridges and stored at −80 °C. Afterwards samples were vacuum-dried for 48 h in a Virtis Benchtop SLC freeze dryer at −70 ° C and a pressure below 0.01 mbar before being stored in airtight boxes with silica gel. At the home institute samples were dried again, at 50 °C in a dry oven for 24 h and weighed to the nearest 0.1 μg on a Sartorius M2P microbalance. CHN content was measured with a HEKAtech EURO EA 3000 CHNS-Analyzer using Acetanilid as a standard.

2.4. Statistical analyses

All data were tested with the Mahalanobis distances test (Mahalanobis, 1936) to exclude outliers from analysis. The effects of temperature and instar on instar duration and carbon gain per instar were analysed with a full interaction analysis of covariance (ANCOVA). Data were Box-Cox transformed (Sokal and Rohlf, 1981) to reach the best transformation to approach the normal distribution of residuals. An ANOVA was conducted to test for significant differences in the biochemical composition (C, H, N) between freshly hatched larvae of 9 females including female B and C. To test whether slopes and intercepts of C % and C:N with time are significantly different from zero, we conducted a slope analyses. A general additive model (Hastie and Tibshirani, 1990) including an ANOVA was used to describe larval mass (μg C) as a function of time (t, days) and temperature (T, Kelvin):

$$C_{BC} = a + b_1 \times t + b_2 \times f(T) + b_3 \times t \times f(T) \quad [\mu g, d, K]$$

where C_{BC} is the Box-Cox transformed larval mass (Sokal and Rohlf, 1981) and $f(T)$ a function that models the temperature effect according to a skewed normal distribution with mean M_T, standard deviation SD_T and skewing factor SK_T following the method described in Weiss et al. (in press):

$$f(t) = 1 / \left(SD_T \times \sqrt{2\pi}\right) \times e^{-0.5 \times (((T - M_T) + SK_T \times (T - M_T)) / SD_T)^2} \quad \text{for } T >= M_T$$

$$f(t) = 1 / \left(SD_T \times \sqrt{2\pi}\right) \times e^{-0.5 \times (((T - M_T) - SK_T \times (T - M_T)) / SD_T)^2} \quad \text{for } T < M_T$$