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Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast

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Abstract The pinnotherid crab *Pinnaxodes chilensis* is a common commensal of the edible sea urchin *Loxechinus albus* along the Chilean coast. Several aspects of the reproductive biology of *P. chilensis* were examined between April and June 1999, along temperature and salinity gradients, at three sampling sites along the Chilean coast (23°45'S–39°24'S). Results demonstrated significant differences in egg number, egg volume, dry egg weight, and reproductive output of ovigerous females, between the studied populations of northern and central-southern Chile. Egg volume, egg dry weight, and reproductive output of females decreased from high to low latitudes, while egg number increased from high to low latitudes, exhibiting a clear trade-off with egg volume. It has been shown that changes in environmental conditions (e.g. temperature, salinity) along a latitudinal gradient, can generate clines in reproductive characteristics in both free-living and parasitic species.

Introduction

A major point of dispute in life-history theory is whether or not the traits that compose an organism's life history are coadapted and the result of natural selection (Stearns 1976). When environments within the biogeographical range of a species differ, it is unlikely that any single phenotype will confer higher fitness in all situations (Via et al. 1995). Hence, variation in reproductive features would be the result of local genetic variation

due to natural selection (Endler 1986), and/or it may reflect phenotypic plasticity that is largely environmentally determined (Via and Lande 1985). Our current understanding of variation in life-history biology is based mainly on studies done on free-living organisms (Roff 1992; Stearns 1992). However, it is unknown what occurs with organisms living in highly specific microenvironments, such as many parasites and commensals, where the main factor of influence on the parasite is the biotic environment of the host (Rohde 1984). In these cases, commensals tend to adjust their morphology, physiology, reproduction and behavior to the physics, physiological features and even movements of their hosts (Bell and Stancyk 1983). On the other hand, commensals are benefited by their hosts by receiving a constant habitat, along with enough food to increase their survival rate considerably. Moreover, when comparing species of marine parasites with related free-living species, the former usually show higher reproductive potentials (Rohde 1982).

The majority of decapod species belonging to the family Pinnotheridae are commensals during their adult life, and live in a facultative and/or obligate association with their hosts (Stevens 1990). The pinnotherid *Pinnaxodes chilensis* (H. Milne Edwards, 1837) is a commensal species, with a range of distribution over 50° of latitude, from the Galapagos Islands and the coast of Ecuador, to the west canal of the Magellan Strait (Fenucci 1967). This crab lives at the end of the intestine of the edible sea urchin *Loxechinus albus* (Molina, 1782), which provides great environmental homogeneity for the crab (Báez and Martínez 1976). Similarly, from the Chilean central zone it has been reported that *P. chilensis* has continual spawning throughout the year (Báez and Martínez 1976), probably because of the unlimited or very high food availability (Gutiérrez-Martínez 1971). Therefore, we hypothesized that the latitudinal effects for different reproductive attributes described for free-living organisms would be diminished among parasitic and commensal organisms. Using *P. chilensis* as a model, we tested this prediction. We compared various

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parameters of the reproductive biology of *P. chilensis*, such as: egg number and size, egg losses and the reproductive output of females at three sites along the Chilean coast, spanning approximately 16° of latitude.

Materials and methods

Study sites

Specimens were collected from the following localities on the coast of Chile: Caleta Coloso (23°45'S; 70°27'W), near Antofagasta in northern Chile; El Quisco (33°23'S; 72°41'W), in central Chile; and Mehuín (39°24'S; 73°13'W) in southern Chile (Fig. 1). Ovigerous females of *Pinnaxodes chilensis* were extracted by means of dissection from the intestines of *Loxechinus albus*, which were collected from the subtidal zone (3–7 m of depth) by autonomous divers during April–June of 1999, and comprised all the sea urchin size ranges in each population. The number of sea urchins sampled were 131 (Caleta Coloso), 128 (El Quisco) and 126 (Mehuín), with

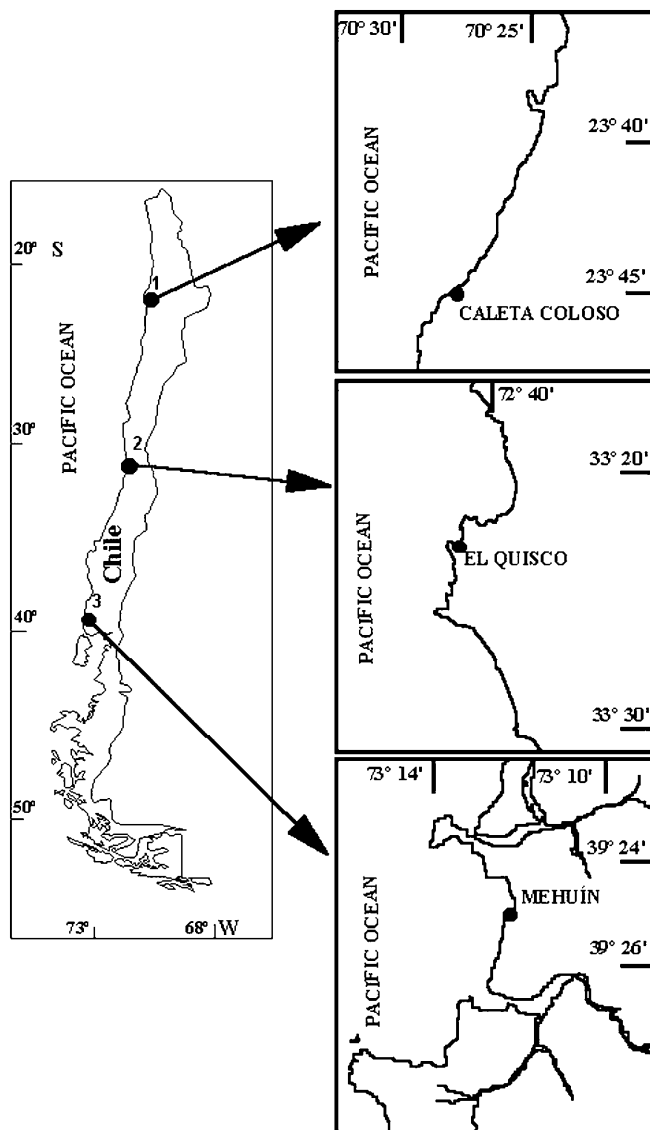


Fig. 1 Location of the three study sites along the Chilean coast

41, 45 and 35 ovigerous females of *P. chilensis*, respectively. Crabs were placed in individually labeled bottles and fixed in seawater-diluted formaldehyde (10%) for analysis in the laboratory.

Latitudinal gradient information

The sea surface temperature (SST) decreases gradually from northern towards southern Chile. The mean annual SST at Antofagasta is 17.6°C (1946–1995), ranging between 20.9°C and 15.0°C. Off Valparaíso (33°01'S; 71°38'W), the mean annual SST (1945–1995) is 13.9°C, ranging between 16.7°C and 12.1°C. Off Valdivia (39°48'S; 73°14'W), near Mehuín, the mean annual SST is 12.2°C (1982–1995), ranging between 15.3°C and 9.8°C (Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996). Off Antofagasta, throughout the year, the seawater surface salinity remains very stable, showing a mean of 34.9 ppt (1985–1995), ranging from 34.7 to 35.0 ppt in June and February, respectively. However, salinity varies seasonally in southern Chile (i.e. Valdivia), with lowest salinity values in the austral winter (32.1 ppt in July) and maximum values in the austral summer (33.6 ppt in February), showing a mean (1985–1995) of 32.8 ppt. Near Valparaíso, surface salinity values do not show the marked changes evident off Valdivia, and values range between 34.0 ppt (July) and 34.7 ppt (November), with an annual mean of 34.3 ppt (1985–1995) (Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996).

Analysis of *P. chilensis* females and eggs

For each female, we measured carapace length (CL), using a vernier caliper with a precision of ± 0.1 mm. The eggs were removed from each female, and the embryonic stage was determined. Then, three subsamples containing between 150 and 300 eggs were taken from the egg mass. Each subsample was washed four times with distilled water, and the interstitial water was extracted with filter paper. Each subsample, and the rest of the egg mass, was dried for 48 h at 60°C and then weighed with an analytical balance with a precision of ± 0.01 mg. We computed the average dry weight of each egg, and with this information we estimated the total number of eggs carried by a female. Females were dried for 72 h following the above methodology. To avoid errors in estimating species egg number, the measurement was made only on females with eggs in stage I (recently produced), assuming that crustaceans frequently lose eggs during their embryonic development (see Kuris 1991). The stage of embryonic egg development was determined using a microscope equipped with a calibrated ocular micrometer. Eggs were divided into three stages according to the criteria proposed by Wehrmann (1990): (1) stage I, eggs recently produced, uniform yolk, no eye pigments visible; (2) stage II, eye pigments barely visible; and (3) stage III, eyes clearly visible and fully developed, abdomen free. Thirty eggs were separated from each female; length (L) and width (W) were measured to calculate the egg volume (EV) using the formula for the volume (V) of an ellipsoid ($V = \pi L W^2 / 6$). A mean EV value was calculated per female. The average volume per egg was multiplied by the total number of eggs to estimate the clutch volume.

Increase in EV during embryonic development was computed for each analyzed population, based on the mean percent volume increase for the three stages of embryonic development. To estimate probable egg loss we used loss-profit percentages between three stages (I–II, II–III and I–III). In this paper, we assume that females in stage I did not suffer any egg loss. With egg number versus CL regression values (stage I) from each site, we calculated individually the number of eggs that females with eggs in stages II and III would have had in stage I. Then, using the difference between the estimated number of eggs in stage I and the real number, at stages II and III, we obtained the female loss-profit percent. To detect possible differences in biomass (per clutch invested per female) among the three populations studied, we calculated the reproductive output (RO) based on the dry mass of ovigerous females, following the formula presented by Clarke et al. (1991).

Statistical analysis

All data were tested for normality and homoscedasticity. Percent values were not normally distributed ($P < 0.05$) and were arcsine transformed (Sokal and Rohlf 1981). To test for differences between egg volumes, both at the intra-population (different developmental stages) and at the inter-population level (comparison among similar stages), we used a one-way ANOVA. The same analysis was used to estimate differences in female egg number, egg loss, CL, clutch volume, RO, and dry egg weight between the three sites along the coast of Chile. When differences in the means were significant at the $P < 0.05$ level, they were also tested with a posteriori Tukey (HSD) (Sokal and Rohlf 1981).

Results

Size of ovigerous females

The average size of ovigerous females of *Pinnaxodes chilensis* (Table 1) was found to be significantly different among the three studied sites ($F = 100.0$, $df = 2, 117$, $P < 0.001$). A posteriori Tukey (HSD) test showed that mean female size was significantly smaller in Caleta Coloso (average of 12.22 mm CL) than at the other two sites ($P < 0.001$). The largest ovigerous females were found in Mehuín, showing an average of 18.59 mm CL, and the maximum size was 20.30 mm CL; females from El Quisco showed an intermediate value of 16.39 mm CL (range: 10.75–20.00 mm CL) (Table 1).

Egg production

The average number of eggs varied from 4,553 in Caleta Coloso (range: 2,134–9,456) to 8,358 in El Quisco (range: 2,376–15,898) (Fig. 2), and 8,082 in Mehuín (range: 5,045–15,432). We found an exponential relationship between CL and the number of eggs in the populations studied (Fig. 2). As there was little or no overlap of ovigerous female size among the three populations analyzed, we used a correction to compare them and estimate the number of eggs produced per unit of female body weight (Fig. 3). The statistical analysis indicated significant differences in egg production between the populations of Caleta Coloso–El Quisco and Caleta Coloso–Mehuín ($F = 114.3$, $df = 2, 117$, $P < 0.001$; a posteriori Tukey test, $P < 0.001$).

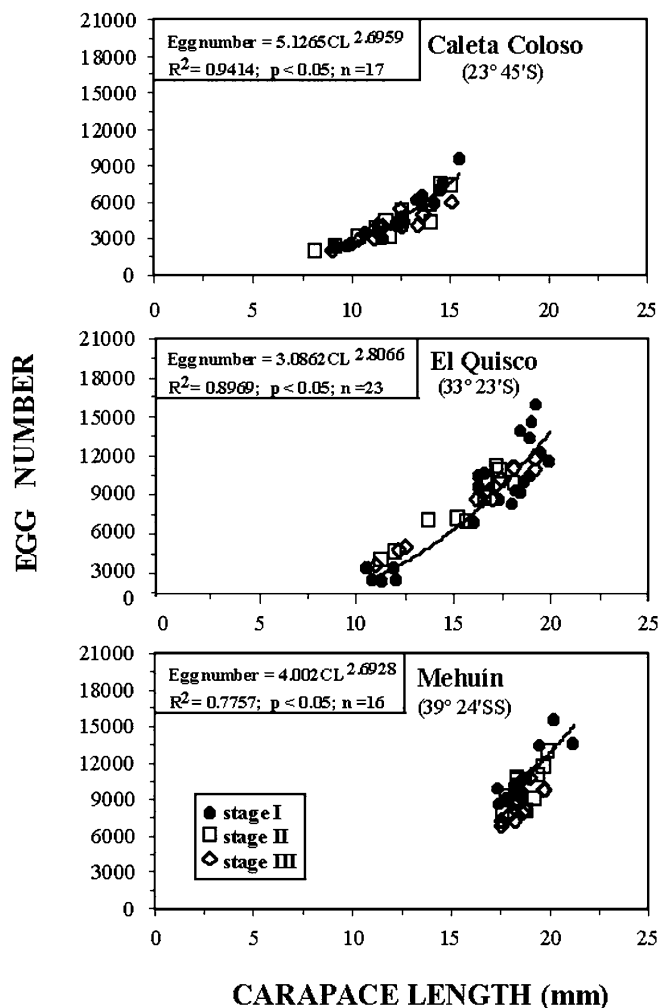


Fig. 2 *Pinnaxodes chilensis*. Fecundity at the three study sites along the Chilean coast. The regressions are based on data obtained from females carrying freshly extruded eggs (stage I) (CL carapace length; n number of observations)

The smallest eggs were found in northern Chile, at Caleta Coloso, where the average EV increased from 0.048 mm³ (stage I) to 0.076 mm³ (stage III) (Figs. 3, 4), showing a 58.4% volume increase during embryonic development (Table 2). Females in the El Quisco and Mehuín populations produced considerably larger eggs (stage I: El Quisco: 0.070 mm³; Mehuín: 0.072 mm³)

Table 1 *Pinnaxodes chilensis*. Carapace length (CL), clutch volume (in mm³), and clutch volume per unit weight (g) of female of ovigerous females, collected in Caleta Coloso, El Quisco and Mehuín (SD standard deviation; n number of females)

	Caleta coloso (23°45'S)			El Quisco (33°23'S)			Mehuín (39°24'S)		
	CL (mm)	Clutch volume (mm ³)	Clutch volume (g ⁻¹ female)	CL (mm)	Clutch volume (mm ³)	Clutch volume (g ⁻¹ female)	CL (mm)	Clutch volume (mm ³)	Clutch volume (g ⁻¹ female)
Average	12.22	270.14	226.38	16.39	724.10	335.59	18.59	864.38	374.41
±SD	1.85	102.92	61.36	2.66	318.35	101.13	0.77	207.03	113.72
Minimum	8.20	110.37	139.24	10.75	166.10	207.63	17.40	463.48	206.75
Maximum	15.50	462.96	370.93	20.00	1,385.60	538.55	20.30	1,365.82	555.48
n	41	41	41	45	45	45	35	35	35

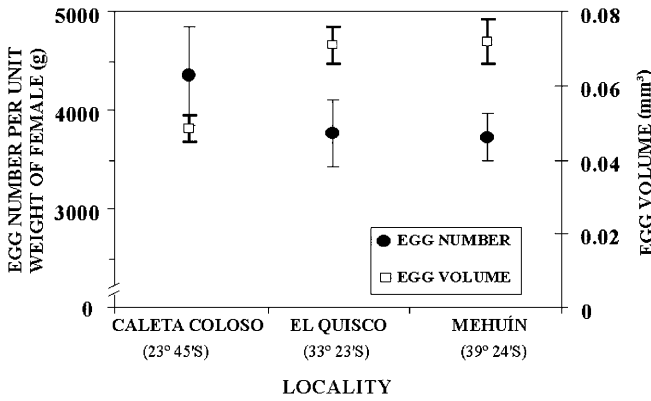


Fig. 3 *Pinnaxodes chilensis*. Mean egg volume of freshly extruded eggs (stage I) and egg number per weight unit of females (mean values \pm standard deviation; based on grams dry weight) from populations collected in Caleta Coloso, El Quisco and Mehuín

than the population in Caleta Coloso (0.048 mm³) (Fig. 4). Similarly, a larger increase in EV was observed in both El Quisco (70.2%) and Mehuín (76.8%) (Table 2), than for eggs from Caleta Coloso. The recently extruded EV was significantly different between Caleta Coloso–El Quisco and Caleta Coloso–Mehuín ($F=7.765$, $df=2$, 49 , $P<0.001$; a posteriori Tukey test, $P<0.001$), but not between the populations El Quisco–Mehuín (a posteriori Tukey test, $P=0.071$) (Fig. 4). The largest increase in EV was observed during later embryogenesis (stages II–III) in Caleta Coloso and El Quisco, while in Mehuín a greater increase was observed during early embryonic development (Table 2). The clutch volume was significantly different for the three studied populations ($F=69.93$, $df=2$, 117 , $P<0.001$). The smallest clutch volume was found in Caleta Coloso, with 270.14 mm³ on average, and the largest in Mehuín, with 864 mm³ on average. In El Quisco, females presented mean clutch volume values of 724.10 mm³ (Table 1). When the values were standardized by body weight, significant clutch volume differences were observed ($F=25.35$, $df=2$, 117 , $P<0.001$; a posteriori Tukey test, $P<0.001$) between populations from Caleta Coloso–El Quisco and Caleta Coloso–Mehuín (Table 1).

Table 2 *Pinnaxodes chilensis*. Egg volume increase and egg loss during incubation period (stages I–III). Comparison of data obtained for three populations along the Chilean coast (see “Materials and methods”)

	Caleta Coloso (23°45'S)	El Quisco (33°23'S)	Mehuín (39°24'S)
Egg volume increase (%)			
Stages I–II	23.90	27.70	37.00
Stages II–III	27.80	33.30	29.00
Stages I–III	58.40	70.20	76.80
Number eggs lost (%)			
Stages I–II	–	–	9.40
Stages II–III	5.00	5.10	8.80
Stages I–III	2.80	0.80	19.10

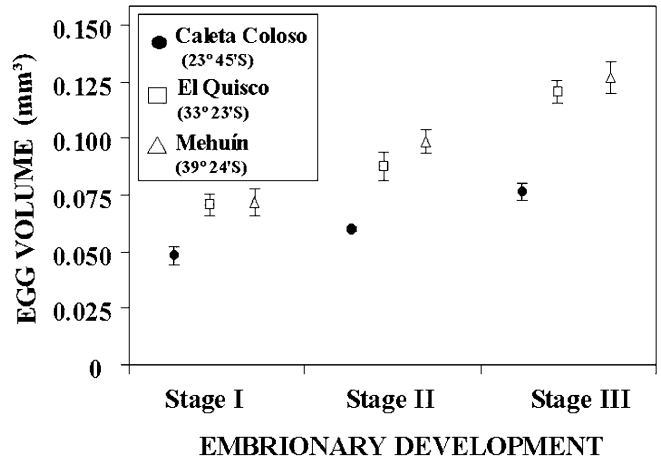


Fig. 4 *Pinnaxodes chilensis*. Egg volume during embryogenesis (stages I–III), comparison of mean values \pm standard deviation of the three populations

Dry weight of eggs and females

The dry weight of eggs decreased gradually throughout embryonic development in the three studied populations (Table 3). The dry weight of recently extruded eggs (stage I) was significantly smaller ($F=12.35$, $df=2$, 47 , $P<0.001$; a posteriori Tukey test, $P<0.001$) in Caleta Coloso (20.2 μ g) than in the populations from El Quisco and Mehuín, between which there were no significant differences. The same trend was observed for eggs of embryonic stages II and III.

Egg losses

Egg loss was detected in the three studied populations throughout embryonic development (Table 2), with very little loss in the populations from Caleta Coloso and El Quisco (2.8% and 0.8%, respectively), and with a significantly higher percentage of eggs lost in Mehuín (19.1%) ($F=9.85$, $df=2$, 47 , $P<0.001$; a posteriori Tukey test, $P<0.001$) (Table 2). For all populations, egg loss occurred principally at the end of embryonic

Table 3 *Pinnaxodes chilensis*. Dry weight of eggs and ovigerous females of the three populations analyzed. Means (\pm standard deviation) of all embryonic stages of eggs (μ g) and females (g) (n number of samples)

	Caleta Coloso (23°45'S)	El Quisco (33°23'S)	Mehuín (39°24'S)
Embryonic development (μg)			
Stage I	2.02 \pm 0.19 ($n=17$)	2.24 \pm 0.21 ($n=23$)	2.29 \pm 0.26 ($n=12$)
Stage II	1.84 \pm 0.27 ($n=12$)	2.09 \pm 0.37 ($n=11$)	2.15 \pm 0.46 ($n=10$)
Stage III	1.71 \pm 0.24 ($n=12$)	2.00 \pm 0.36 ($n=11$)	2.08 \pm 0.35 ($n=12$)
Ovigerous female (g)	1.20 \pm 0.40 ($n=41$)	2.21 \pm 0.92 ($n=45$)	2.49 \pm 0.72 ($n=35$)

development (stages II–III), except in the population at Mehuín, where ovigerous females lost the same amount of eggs throughout embryonic development (Table 2).

Reproductive output

The RO for Caleta Coloso, El Quisco and Mehuín (Fig. 5) was 0.70 (± 0.03), 0.80 (± 0.04) and 0.81 (± 0.02), respectively. There were significant differences in RO between the populations from Caleta Coloso–El Quisco and Caleta Coloso–Mehuín ($F=101.81$, $df=2$, 117, $P<0.001$; a posteriori Tukey test, $P<0.001$). However, there were no significant differences between the *P. chilensis* populations from El Quisco and Mehuín (a posteriori Tukey test, $P=0.062$).

Discussion

Ovigerous females

The size of ovigerous females of *Pinnaxodes chilensis* exhibits a latitudinal pattern, with the smaller crabs inhabiting low latitudes and the larger crabs high latitudes. Several authors have agreed that marine invertebrates, especially decapod crustaceans, show an increase in their size towards higher latitudes (Garth et al. 1967; Boschi et al. 1969; Steele 1983; Arntz and Gorny 1991). These results also coincide with the latitudinal cline found in the size of fish ectoparasites (Rohde 1985; Poulin 1995). Our study shows that females of *P. chilensis* produce smaller eggs at Caleta Coloso compared with females at El Quisco and Mehuín. This latitudinal cline in first-spawning size has also been found in a mud crab, *Helice crassa* (Jones and Simons 1983), and in a caridean shrimp, *Betaeus truncatus* (Lardies 1995). Experimentally

it has been demonstrated that temperature is a key factor stimulating growth and early development of the ovary in crustaceans (Efford 1970; Kinne 1970; Annala et al. 1980; Nelson et al. 1988a,b). Since the surface waters off the Chilean coast have a relatively higher average temperature, with small oscillations in the northern zone (Caleta Coloso), compared to lower average temperatures and larger fluctuations in the central (El Quisco) and southern zones (Mehuín) (Viviani 1979; Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996; Strub et al. 1998), it is possible to suggest that temperature may be one of the important causes of the observed differences in the minimum spawning size of ovigerous females of *P. chilensis*. Another proposed factor that could explain the observed size variation is female nutritional condition, since, in crustaceans, nutrition directly influences maturity (Harrison 1990). Nevertheless, food does not seem to be a limiting factor for *P. chilensis*, as the organism bases its alimentation on the accumulated leftovers inside the sea urchin rectum (Gutiérrez-Martínez 1971). This observation is supported by the idea that parasite organisms would normally have a superabundance of resources (Rohde 1991), where the only limiting factor in the abundance of those species would be the recruiting of larvae and juveniles (Sousa 1994).

Production of eggs

When considering egg production in equally sized ovigerous females of *P. chilensis*, the number of eggs per unit weight of the female increased from high to low latitudes (Fig. 3). Similar observations have been reported in the amphipod *Hyaella azteca* (France 1992), the harpacticoid copepod *Scottolana canadiensis* (Lonsdale and Levinton 1985), the caridean shrimp *Betaeus truncatus* (Lardies 1995) and for the anomuran crab *Petrolisthes laevigatus* (Lardies and Wehrtmann 1996). The differences can be explained by the fact that egg size is negatively correlated with the number of eggs. Assuming that the same amount of energy is invested in egg production, one species can produce a large quantity of small eggs or a lesser quantity of large eggs (Christiansen and Fenchel 1979; Wägele 1987; Giangrande et al. 1994). In the case of *P. chilensis*, EV clearly increases with latitude (Figs. 3, 4). This tendency has been documented in many marine invertebrates (Efford 1969; Lonsdale and Levinton 1985; Wehrtmann and Kattner 1998). Increase of EV toward high latitudes has been interpreted as an adaptation for the protection of the embryo against low temperatures, along with sufficient internal energy provision (yolk) to survive during long periods of incubation (Thorson 1950; Efford 1969). Similar reasons seem to be valid for *P. chilensis*, since surface water temperatures (SST) are lower in El Quisco and Mehuín than in northern Chile (Caleta Coloso) (Viviani 1979; Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996; Strub et al. 1998); therefore, females could

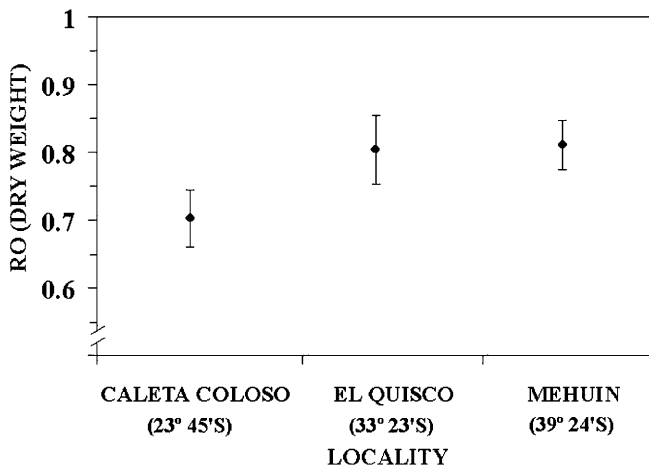


Fig. 5 *Pinnaxodes chilensis*. Reproductive output (mean \pm standard deviation; based on dry weight) of females from Caleta Coloso ($n=41$), El Quisco ($n=45$) and Mehuín ($n=35$) (RO reproductive output)

increase the number of eggs, while diminishing their total volume (see Table 2).

EV in *P. chilensis* increases throughout embryonic development (stages I–III), ranging from 58.4% (Caleta Coloso) to 76.8% (Mehuín). This variation is within the range reported for other Chilean crustaceans (Lardies and Wehrtmann 1996, 1997). The larger EV increase in the southern locality (Mehuín) may be related to greater fluctuations in environmental factors, such as temperature and salinity. Salinity may be a particularly important factor in this zone, which is characterized by high rainfall and river input (Viviani 1979). Throughout the year, salinity is higher and more stable in northern Chile, compared to the central and southern zones (Viviani 1979; Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996; Strub et al. 1998). This is an important factor since the EV is considered to be an adaptive response to different environmental variables in the habitat (Belk et al. 1990). Mashiko (1982, 1983, 1987) and Walsh (1993) demonstrated that shrimps from fresh water extrude eggs with significantly different sizes, compared to populations inhabiting estuarine environments. In habitats subject to high fluctuations, salinity is the most important factor affecting the reproduction and development of crustaceans (Pêqueux 1995). This increase in EV primarily is due to water incorporation during embryonic development (Pandian 1970, 1994; Lardies and Wehrtmann 1996). Pandian (1970) suggests that one of the ecophysiological advantages of water incorporation into eggs is that water acts as a buffer against environmental variations produced outside the embryo. We think that the low variability of factors such as temperature and salinity in the northern zone (Caleta Coloso) may determine the production of small eggs with a low increase in volume throughout the embryonic development of *P. chilensis*, relative to the central and southern populations (El Quisco and Mehuín).

Egg size has been considered a good estimator of the energy content of the egg (Herring 1974; Jaekle 1995). Clarke (1993) observed a significant relationship between EV and nutrient content in eggs (yolk) of decapods. It was concluded that differences in egg size reflect real differences in maternal investment per embryo. Dry egg weight was significantly different between the population from Caleta Coloso and the two other populations studied (El Quisco and Mehuín), and the values increased from north to south. Given the significant differences in dry weight of recently extruded eggs of *P. chilensis*, it seems reasonable to assume that eggs from Caleta Coloso may contain a lower amount of yolk than those produced in the central and southern populations of Chile. The low quantity of yolk could be explained by the presence of more stable habitat conditions in northern Chile (e.g. temperature, salinity and food availability for larvae). Consequently, the size of larvae at release should be smaller in Caleta Coloso than in populations from El Quisco and Mehuín. This assumption is supported by observations done in caridean shrimps (*B. truncatus*: Lardies 1995; *B. emarginatus*:

López 1996), where small larvae hatch from small eggs. This suggests that *P. chilensis* larvae in El Quisco and Mehuín should be larger and contain more internal reserves to withstand continued environmental changes, which are typical in temperate and polar regions (Thorson 1950; Bauer 1992).

Seasonal variation in water temperature, a pattern which is strongly tied to latitude, has always been considered an important proximate factor or environmental stimulus triggering and maintaining gametogenesis and other reproductive characteristics of marine invertebrates. In accordance with several authors (Thorson 1950; Pearse et al. 1991; Bauer 1992), we believe that the important selective pressure acting on reproductive characteristics (i.e. timing of reproduction, egg size, reproductive effort) in marine invertebrates with planktotrophic larvae might be the temporal variation of larval food supply, that is, the seasonal pattern of primary and secondary productivity. Thus, the temporal availability of larval food supply has been reported to be the ultimate factor for the observed variation in aspects of reproductive biology in benthic invertebrates (Bauer 1992; Clarke 1992; Olive 1992). Hence, temperature and salinity (proximate factors) may well be correlated with hydrographic conditions, leading to the variations in larval food supply that account for the clinal variation in the reproductive characteristics of *P. chilensis*. Since, the temporal patterns of plankton productivity are negatively correlated with latitude (Bauer 1992), at high latitudes larger eggs may produce large larvae or may produce larvae that hatch with larger amounts of yolk reserves remaining, which sustain the larvae in the plankton until and/or among pulses of productivity in the same season.

Egg losses

The physical space available to carry eggs under the cephalothorax is a limiting factor of egg production in decapods (Corey and Reid 1991; Hines 1992). Since eggs tend to increase in volume during embryonic development and, generally, the available space is filled, some eggs are lost, reducing the size of the original egg mass. Also, factors like disease and egg predators can be responsible for egg losses (for review see Kuris 1991). *P. chilensis* loses only a small number of eggs on average when compared to other free-living decapods (Kuris 1991; Norman and Jones 1993; Lardies and Wehrtmann 1996), even though the increase in volume is around 70% during embryonic development. Certainly, the internal habitat of the host, which is constant and provides protection for incubation of the eggs by the female diminishes their loss, and, additionally, the immobility of the commensal may diminish egg loss due to mechanical effects. The relatively small amount of eggs lost during the incubation period of *P. chilensis* in Caleta Coloso (2.80%) corroborates the hypothesis that small increases in egg size are probably associated with reduced egg loss

(Reid and Corey 1991). Furthermore, only in the population of Mehuín was a larger egg loss experienced, this was probably related to the large increase of the EV prior to hatching (see Fig. 4).

Reproductive output

Available data in the literature suggest that the RO of polar species is substantially lower when compared with species in temperate zones (Clarke 1987). Observed values in *P. chilensis* do not agree with this pattern, since RO increases towards higher latitudes. However, our results confirm reports for other decapods: a decrease in egg number associated with an increase in latitude (Lonsdale and Levinton 1985; Clarke and Gore 1992; Gorny et al. 1992). *P. chilensis* has a high average RO (0.77) compared with free-living decapods in Chilean waters: *B. emarginatus* (0.09; Lardies and Wehrmann 1997), *P. laevigatus* (0.06; Lardies and Wehrmann 1996), *Heterocarpus reedi* (0.06; Wehrmann and Andrade 1998) and *B. truncatus* (0.14; Lardies 1995). Such high RO values for *P. chilensis* corroborate findings on parasitic and commensal Pinnotheridae species, which show a higher reproductive potential than free-living species (Hines 1992). Our results indicate that females of *P. chilensis* collected from El Quisco and Mehuín invest significantly more biomass (dry weight) in egg production, than females from Caleta Coloso. This suggests that individuals at high temperatures concentrate more energy towards rapid growth and high metabolism, and invest less energy towards reproduction (Díaz 1980). Inversely, the slow growth and low metabolism of species in zones with low temperatures (Brey and Clarke 1993) allow more energy investment in egg production, since the eggs contain larger internal reserves (Woodward and White 1981). Despite the fact that the quantity of eggs produced by equally sized *P. chilensis* females is greater in northern Chile compared to central and southern populations, clutch volume is larger in localities from central and southern Chile (Table 1). Unfortunately, we do not know the number of egg batches produced per year for each population, and therefore, we cannot estimate the annual RO for each population studied, which could change the direction of our results.

Hines (1982, 1988, 1991, 1992) analyzed RO in a number of brachyuran crabs and concluded that the average weight of egg mass in these decapods is generally 10% of the female weight. Based on dry weight, the average egg mass in all populations of *P. chilensis* is 77% of the female's body weight. These values are over the range of 3–22% given for brachyuran crabs (Hines 1992). Similar results were found for two species of pinnotherids: *Pinnotheres ostreum* and *Fabia subquadrata*, in which egg batches represented 66% and 97% of female body weight (Hines 1992). Since available space inside the cephalothorax is limiting for egg batches in brachyurans, it is curious that such species show values

above this range. According to Hines (1992), there are two factors which may explain such high values: (1) ovaries in this species are extended out of the cephalothorax into the abdomen, providing extra space for egg accumulation, which apparently does not exist in species outside of the family Pinnotheridae (ovaries are typically confined to the cephalothorax); and (2) females of this family have a very small quantity of calcium carbonate deposited in their exoskeleton, which diminishes female body weight and, also, makes the exoskeleton more flexible, allowing the body to distend during egg accumulation (Bell and Stancyk 1983; Hines 1992). These observations agree with features presented by ovigerous females of *P. chilensis* (Lardies, personal observation). The large RO of pinnotherids is an adaptation to the parasitic niche of these species (Hines 1992). Its larvae can suffer great mortality during the search for a more specialized place for settlement (sea urchin hosts) than larvae of free-living crabs. As with the other members of the family Pinnotheridae, the large reproductive output of *P. chilensis* could help to offset high larval mortality.

Latitudinal effects on an endocommensal

The trends documented in this work, i.e. increases in individual size, first-spawning size of females, RO of females and egg size of *P. chilensis* with increases in latitude, are in agreement with similar latitudinal influences reported for free-living marine invertebrates (Thorson 1950; Lonsdale and Levinton 1985; Bauer 1992; Clarke 1992). That is, the macroenvironment of *P. chilensis*, defined as the host environment (Rohde 1984), directly affects the biology of the parasitic organism. Poulin (1995) found a positive correlation between latitude and some reproductive parameters, such as size and egg number in copepod ectoparasites of fishes. However, in relation to other parameters, e.g. female size, latitude did not have any effect. The positive relationship between latitude and the variability of the studied parameters in *P. chilensis* is the first such report for a commensal organism, and questions the assertion that, in endoparasitic groups, the nature of the host has a greater influence than the survival of infective larvae (Poulin 1995). In *P. chilensis*, apart from the large female reproductive output which is a typical feature of parasitic species, an equilibrium was observed between the external environmental conditions (e.g. temperature, salinity) in which free-living larvae develop and the reproductive strategy of the species in each locality.

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