Latitudinal comparisons of reproductive traits in five Brachyuran species along the Chilean coast

Comparaciones latitudinales de aspectos reproductivos en cinco especies de braquiuros a lo largo de la costa de Chile

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ABSTRACT

Understanding large-scale patterns in reproductive investment and fecundity of marine invertebrates is important for determining the critical environmental variables affecting reproduction and thus, the spatial patterns of population dynamics. However, information on patterns of reproduction of marine invertebrates at large spatial scales are either scarce, or have been conducted by mixing species with contrasting modes of development. Brachyuran crabs are an ideal group to analyze large-scale patterns of reproduction not only because many species are commercially exploited, but also because they show a single mode of larval development and wide distributional ranges. Here, we report latitudinal patterns of reproductive variables in five Brachyuran crab species along the coast of Chile (18-54° S): *Cancer setosus, Paraxanthus barbiger, Homalaspis plana, Ovalipes trimaculatus*, and *Taliepus marginatus*. Five variables were analyzed: brood weight, fecundity, embryo dry weight, embryo volume, and embryo loss. Comparisons between northern (20° S), central (29-33° S) and southern Chile (35-41° S) were conducted for *C. setosus* and between central and southern Chile for the other four species. A total of 378 brooding females were collected and analyzed. Although we did not find a clear and consistent pattern in all reproductive variables in the five crab species analyzed along the coast of Chile, generalizations can be drawn from this study. First, brood weight did not vary between central and southern Chile in most of the species (except *P. barbiger*). Second, embryo loss did not vary between central and southern Chile in four of the species studied. Third, embryo dry weight tended to increase toward high latitudes in four of the five species. We suggest that the costs associated to oxygen provision to broods may explain some of the patterns found, but other factors need also be considered.

Key words: reproductive investment, fecundity, brooding, crabs, embryo loss.

RESUMEN

El estudio de los patrones de inversión reproductiva y fecundidad en invertebrados marinos a escalas espaciales grandes es de vital importancia para determinar las variables ambientales críticas que afectan la reproducción, y así poder entender los patrones espaciales de las dinámicas poblacionales. Sin embargo, la información sobre patrones de reproducción en invertebrados marinos a gran escala es escasa, y en algunos casos ha sido generada tomando en cuenta especies con diferentes modos de desarrollo. Los crustáceos braquiuros son un grupo de gran interés para analizar patrones de reproducción a gran escala no solo por la importancia comercial de muchas especies sino también por presentar un único modo de desarrollo larval y un amplio rango de distribución geográfica. En este trabajo reportamos los patrones reproductivos de cinco especies de braquiuros: *Cancer setosus, Paraxanthus barbiger, Homalaspis plana, Ovalipes trimaculatus* y *Taliepus marginatus*, a lo largo de la costa de Chile (18-54° S). Cinco variables fueron analizadas: peso de la masa de embriones, fecundidad, peso seco del embrión, volumen del embrión y pérdida de embriones. Se realizaron comparaciones entre el norte (20° S), centro (29-33° S) y sur de Chile (35-41° S) para *C. setosus*, y entre el centro y sur de Chile para las otras cuatro especies. Se recolectaron y analizaron un total de 378 hembras ovígeras. Aunque no detectamos un patrón bien definido para todas las variables reproductivas en las especies analizadas a lo largo de la costa de Chile, emergieron al menos tres generalidades. Primero, en la mayoría de las especies el peso de la masa de embriones no varió entre el centro y sur de Chile (exceptuando *P. barbiger*). Segundo, la pérdida de embriones no varió entre el centro y sur de Chile en cuatro de las especies estudiadas. Tercero, el peso seco del embrión tendió a aumentar en poblaciones de latitudes altas en cuatro de las especies analizadas. Proponemos que el costo asociado a la provisión de oxígeno a los embriones puede explicar alguno de los patrones encontrados, aunque otros factores necesitan ser considerados.

Palabras clave: inversión reproductiva, fecundidad, incubación, jaibas, pérdida de embriones.

INTRODUCTION

The understanding of large-scale patterns of reproductive investment and fecundity of marine invertebrates is of importance for several reasons. First, analysis over large spatial scales could help in the identification of potential links between egg production and environmental variables. Second, spatial patterns of reproduction could also help to improve our understanding of spatial patterns of population dynamics, information that could be critical for management of open populations under exploitation. Finally, large-scale analyses of investment in reproduction could also shed lights on our understanding of key aspects shaping life history patterns of marine invertebrates, including large-scale patterns of distribution of modes of development (latitude and depth; Thorson 1950 but see also Spight 1977, Gallardo & Penchaszadeh 2001), and help explain the distribution of species in the oceans. At present, information on patterns of reproduction of marine invertebrates at large-scales are either scarce, or have been conducted by mixing species with contrasting modes of development (e.g., Clarke 1987, Brey 1995).

Studies of reproductive patterns along the coast of Chile offer the opportunity to analyze an extended latitudinal range, with mean temperatures ranging from 6 to 20 °C, contrasting upwelling regimes that affect the oxygen minimum zone (Strub et al. 1998), and dramatic differences in circulation patterns (from northern Chile to the fjords area, Strub et al. 1998). It is unclear if the patterns of investment in reproduction of marine invertebrates respond to the monotic changes of critical environmental variables, such as temperature (Clarke 1987, Brey 1995), or show rather abrupt changes in areas where other environmental variables vary (e.g., oxygen availability for brooding species: Cohen & Strathmann 1996; circulation patterns: Giraldo et al. 2002). Brachyuran crabs are an ideal group of organisms to analyze large-scale patterns of reproduction not only because many species are commercially exploited, but also because they show a single mode of larval development and wide distributional ranges (Boschi 2000). Sea surface temperature shows a clear gradient along the coast of Chile and has been shown to affect several interdependent reproductive variables of Brachyuran crabs (Brante et al. 2003). Temperature affects embryo oxygen consumption, producing changes in patterns of embryo ventilation by females (Fernández et al. 2002), which affects investment in brood care,

reproductive output, and embryo loss (Brante et al. 2003). Thus, embryo loss during incubation along a latitudinal gradient could be an important variable to be included in the evaluation of the cost of reproduction in Brachyuran crabs (Kuris 1991, Fariña et al. 1999, Lardies & Castilla 2001). Latitudinal trends in oxygen concentration in the water column may also be critical in explaining large-scale patterns of reproduction in the ocean given the link between brooding and oxygen provision to the brood (Fernández et al. 2000, Baeza & Fernández 2002). Large-scale patterns of reproductive variables of interest, such as brood weight, fecundity, embryo loss, and egg size are yet unclear (see Jones & Simons 1983, Carvacho et al. 1995, Lardies & Castilla 2001, Brante et al. 2003), as are the relationships between these patterns and environmental variables.

Herein we report latitudinal patterns of reproductive variables in five Brachyuran crab species along the coast of Chile: *Cancer setosus, Paraxanthus barbiger, Homalaspis plana, Ovalipes trimaculatus* and *Taliepus marginatus*. Five variables were analyzed: brood weight, fecundity, embryo dry weight, embryo volume, and embryo loss. Comparisons between northern (20° S), central (29-33° S) and southern Chile (35-41° S) were conducted for *C. setosus* and between central and southern Chile for the other four species. Morphometric and reproductive relationships were established for each species in each region. The presence of a single mode of larval development among Brachyuran crabs is a characteristic of major importance considering that investment in brood care can be substantial and may affect the comparisons of other reproductive variables.

MATERIAL AND METHODS

In order to explore latitudinal trends in some reproductive variables of Brachyuran crabs along the Chilean coast, ovigerous females of the following five species were collected: *Cancer setosus, Paraxanthus barbiger, Homalaspis plana, Ovalipes trimaculatus* and *Taliepus marginatus*. Three regions of Chile were compared (named here north, center and south) and between two and three sites were sampled within each region. The sites sampled in the north were located near Iquique (20°14' S, 70°10' W). The sites sampled in the center were located between Coquimbo (29°58' S, 71°22' W) and San Antonio (33°36' S, 71°38' W) and those in the south between Curanipe (35°50' S, 72°38' W) and Puerto Montt (41°32'

S, 72°59' W; Fig. 1). Females of *C. setosus* were collected in shallow waters in the three regions (latitudinal range: 21 degrees). Mean annual sea-surface temperature was 18 ºC in north, 14 ºC in center, and 10 ºC in south Chile. These temperatures were calculated using information from the last 10 years (Servicio Hidrográfico y Oceanográfico de la Armada de Chile 1996). Unfortunately, we could not find ovigerous females of *P. barbiger, H. plana, O. trimaculatus* and *T. marginatus* in northern Chile, despite that several trips to the north were conducted (and only one or two to the other sites). Thus, data for these species are available only for the central and southern Chile (12 degrees). The collection sites of south Chile were located in the southern limit of the distribution of *P. barbiger* and *T. marginatus* (Fig. 1). Between 11 and 35 crabs incubating early stage embryo masses and between five

and 47 females carrying late stage embryo masses of each species were analyzed for each region (Table 1). Samples were collected by local fishermen between February 1999 and December 2000 (several visits to each sampling site), frozen immediately, and shipped to the Estación Costera de Investigaciones Marinas at Las Cruces where the samples were processed. Each brooding female was categorized according to the developmental stage of the embryos. The following developmental stage categories were used: (1) early (from embryos exhibiting uniformly distributed yolk, absence of cleavage and eyes, to embryos with cleavage and yolk reduced to not less than 75 % of embryo volume; see Fernández et al. 2002), and (2) late (from embryos displaying pigments and visible but undeveloped eyes, to embryos with well developed eyes, heart, and appendages). In order to exclude erroneous
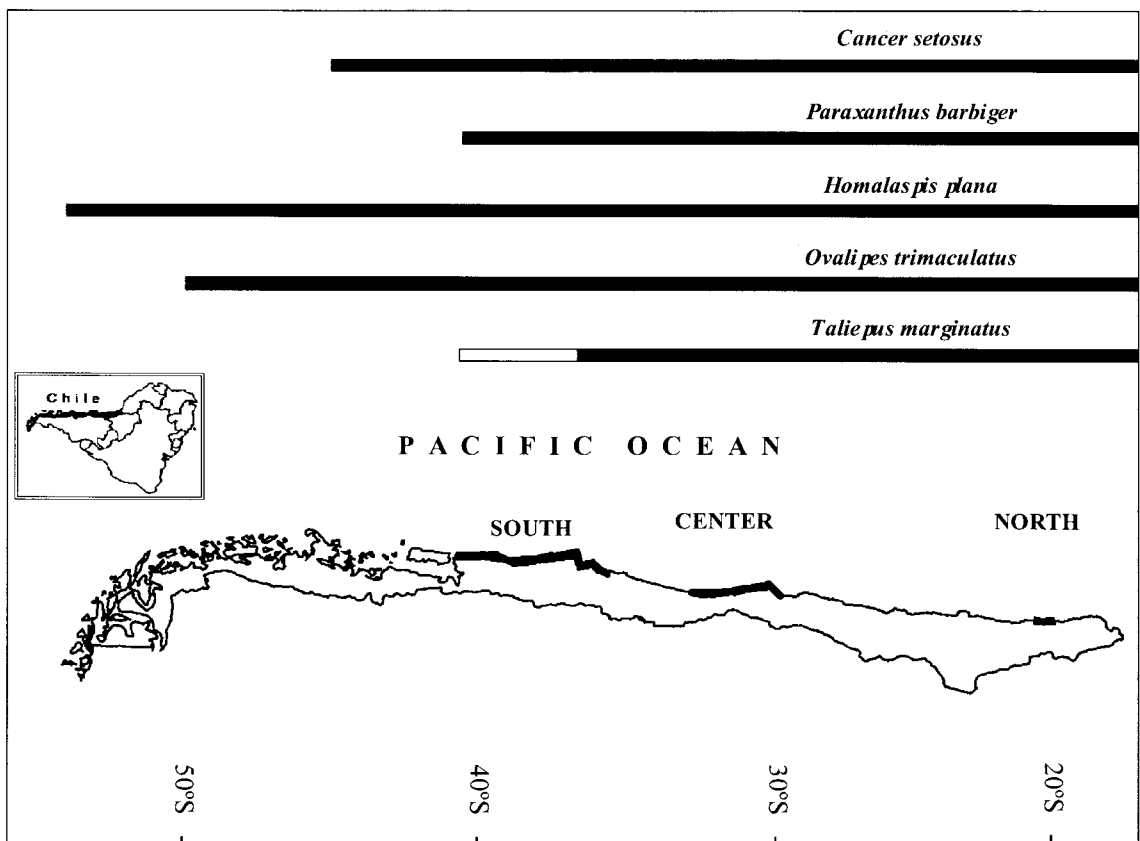

Fig. 1: Map of Chile showing the sampling regions (north, center and south). Horizontal, solid bars show the distributional ranges reported in the literature for each species. Extensions in reported ranges of distribution based on this study are shown with open bars.

Mapa de Chile que muestra las regiones analizadas (norte, centro y sur). Las barras horizontales obscuras muestran el rango de distribución reportado en la literatura para cada especie. Las barras verticales blancas muestran extensiones en el rango de distribución basadas en este estudio.

TABLE 1

Number (n) of females sampled at each region for the five species analyzed.
Mean carapace wide (CW), female dry weight (FDW) and dry weight of embryo
mass (BDW) are also reported. Standard errors are shown in parentheses

Número (N) de hembras analizadas en cada región para las cinco especies estudiadas.
Se muestra el ancho medio de caparazón (CW), peso seco de la hembra (FDW) y peso seco
de la masa de embriones (BDW). Entre paréntesis se muestran los errores estándar

Species	Region	n		CW (cm)		FDW (g)		BDW (g)	
		Early	Late						
Cancer setosus	North	35	40	100.3	(2.1)	74.7	(4.8)	9.7	(0.4)
	Center	25	47	93.3	(2.0)	53.1	(3.3)	10.4	(0.8)
	South	34	18	101.1	(2.9)	85.7	(7.9)	15.5	(1.4)
Paraxanthus barbiger	Center	14	7	44.1	(2.5)	8.9	(1.3)	0.7	(0.1)
	South	30	8	52.9	(1.3)	15.4	(1.0)	1.6	(0.1)
Homalaspis plana	Center	24	28	99.6	(2.7)	97.1	(8.8)	10	(0.8)
	South	23	10	102.3	(3.6)	127.5	(13.0)	13.2	(1.3)
Ovalipes trimaculatus	Center	16	28	79.4	(2.5)	34.2	(3.3)	5.1	(0.4)
	South	19	17	78.7	(1.3)	32.8	(1.4)	4.9	(0.2)
Taliepus marginatus	Center	29	5	42.2	(1.4)	14	(1.5)	1.1	(0.1)
	South	11	7	64.1	(1.0)	50	(3.2)	4.2	(0.2)

estimation in any of the five reproductive variables owing to embryo loss (Kuris 1991) or embryo growth, only females carrying early stage embryos were used to calculate brood weight (g, measured as dry weight of embryo mass), fecundity, embryo dry weight (g), and embryo volume (mm^3). The morphometric relationships between log-carapace wide (cm, CW) and log-female dry weight (g, FDW) was established for each species from each region using linear regressions.

Brood weight

Brood dry weight (g, BDW) and of the brooding females (after removing the embryos) were recorded for each female in the studied regions. All samples were oven-dried for 24 h at 100 °C. We performed ANCOVAs separately for each species to compare mean BDW between regions, using FDW as covariate. Log transformation was used for both variables. Parallelism test was run before ANCOVA. When this assumption was not met, a separate slope model was run. Homogeneity of variance was assessed using the Cochran test.

Fecundity

In order to estimate fecundity, three subsamples (up to 0.005 g), randomly taken

from the border of each embryo mass, were weighed and the number of embryos in those samples were counted under a stereomicroscope. Fecundity of each female was estimated by extrapolating the ratio between number of embryos and dry weight of the sample of the embryos to the total embryo mass. Separate ANCOVAs were performed for each species to compare mean fecundity between regions, using FDW as covariate. Log transformation was used for both variables. Parallelism test was run before ANCOVA. When this assumption was not met, a separate slope model was run. Cochran test was used to assess homogeneity of variance.

Dry weight and volume of embryos

Volume (mm^3) and dry weight (mg) of early stage embryos were calculated from the subsamples of embryos used to estimate fecundity (see above). The longest and shortest diameter of 10 embryos were measured. Embryo volume was calculated for each embryo as the volume of a sphere and the mean of each subsample was estimated. All subsamples were oven-dried for 24 h at 100 °C. Finally, mean embryo dry weight was calculated from the relationship between total weight and the number of embryos in the subsample. For *C. setosus*, embryo dry weight

and embryo volume were compared among regions using a 1 way-ANOVA. A SNK test was conducted for a posteriori comparisons. Student t-tests were used to compare embryo dry weights between central and southern Chile for the other four species. For *H. plana* mean embryo volume was compared using Student *t*-tests (no transformation were needed). Mann-Whitney *U*-tests were performed to compare embryo volume for the other three species (*O. trimaculatus*, *P. barbiger* and *T. marginatus*).

Embryo loss

In order to calculate embryo loss throughout development, fecundity and dry weight of females carrying late stage embryos were calculated (see above). From the relationship between fecundity of females carrying early stage embryos and FDW (see above), the expected fecundity of any given FDW was estimated for all the females carrying late stage embryos. The percentage difference between fecundity of females carrying late stage embryos and expected fecundity of those females when carried early stage embryos (regression) was used to obtain an estimator of embryo loss. Since the relationship between fecundity (at early stage) and female body dry weight of *T. marginatus* from the southern region was not significant, no estimation of embryo loss could be calculated for this species. For *C. setosus*, embryo loss (%) among regions were compared using a one way-ANOVA. A SNK test was conducted for a posteriori comparisons. For the three other species, Student t-tests were used. Data were not transformed.

RESULTS

Mean CW varied considerably among species, from 42.2 cm in *T. marginatus* to 102.3 cm in *H. plana* (Table 1). Similarly, mean FDW showed more than one order of magnitude of difference between the lightest and heaviest species (*P. barbiger* = 8.9 g and *H. plana* = 127.5 g, Table 1). FDW was significantly correlated with CW in all species and regions (Table 2). Females from southern Chile were larger and exhibited a higher FDW than females from the other two regions, with the exception of *O. trimaculatus.*

Brood weight

A wide range of BDW was observed among species when only females carrying early stage embryos are considered (Table 1). *Paraxanthus barbiger* and *C. setosus* showed the lowest and the highest BDW values, respectively. The slope of the allometric relationship between BDW and FDW differed among regions in *C. setosus* (Fig. 2, Parallelism test: $F_{2,88} = 12.36$, P < 0.001), thus a separate slope model was run for this species. Significant differences were detected among regions ($F_{2,88} = 8.76$, P < 0.05). A posteriori tests showed that BDW was lower in the northern region than in the two other localities (P < 0.05). No differences were detected between center and southern regions (P > 0.05). Regarding the other four species, no significant differences in the slopes between regions were found (Parallelism test: *P. barbiger*: $F_{1,40} = 0.27$, P = 0.27; *H. plana*: $F_{1,44} = 0.47$, P = 0.49; *O. trimaculatus*: $F_{1,31} = 0.32$, P=0.57; *T. marginatus*: $F_{1,36} = 1.20$, P =

TABLE 2

Results of regression analysis between log-carapace width (CW) and log-female dry weight (FDW) for the five species analyzed at each region (north, center and south). Females carrying early and late stage embryos were pooled together in the analysis. All regressions were significant (P < 0.001)

Resultados de las regresiones lineales entre log-ancho de caparazón (CW) y log-peso seco de la hembra (FDW) para las cinco especies analizadas en cada región (norte, centro y sur). Hembras con embriones en estado temprano y tardío fueron agrupadas. Todas las regresiones fueron significativas (P < 0,001)

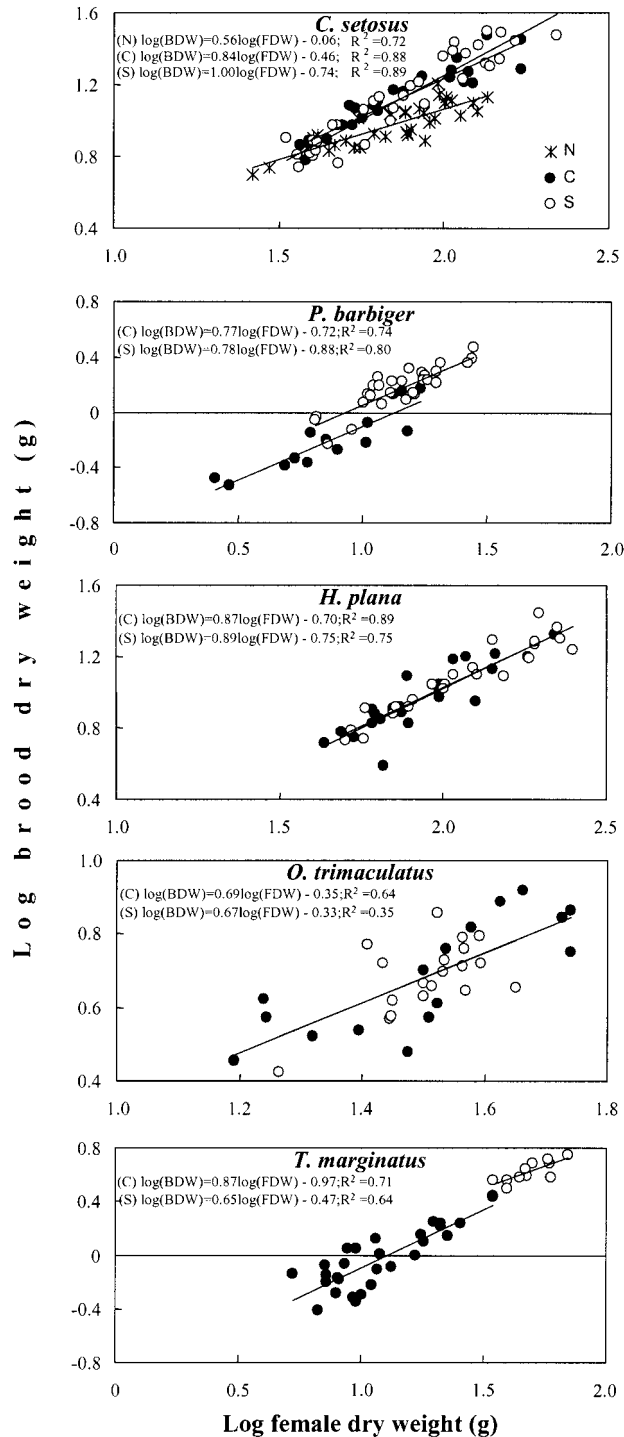| Species	North	Center	South
Cancer setosus	log (FDW) = 3.09(log(CW))-4.35	log (FDW) = 2.77(log(CW))-3.74	log (FDW) = 3.03(log(CW))-4.17
Paraxanthus barbiger		log (FDW) = 2.59(log(CW))-3.34	log (FDW) = 2.77(log(CW))-3.60
Homalaspis plana		log (FDW) = 3.02(log(CW))-4.08	log (FDW) = 2.92(log(CW))-3.80
Ovalipes trimaculatus		log (FDW) = 2.93(log(CW))-4.06	log (FDW) = 1.94(log(CW))-2.17
Taliepus marginatus		log (FDW) = 2.53(log(CW))-3.00	log (FDW) = 3.68(log(CW))-5.00

Fig. 2: Relationship between log-female dry weight (FDW) and log-brood dry weight (BDW) for five Brachyuran species in three regions along the Chilean coast. Data were obtained from female crabs carrying embryos at early stage. The regression equations and the coefficient of determinations (R^2) are also shown for northern (N), central (C) and southern (S) Chile. All regressions were significant ($P < 0.05$).

Relación entre log-peso seco de la hembra (FDW) y log-peso seco de la masa de embriones (BDW) para cinco especies de braquiuros en tres regiones a lo largo de la costa de Chile. Los datos fueron obtenidos de hembras con embriones en estado temprano. Las ecuaciones de regresión y los coeficientes de determinación (R^2) son mostradas para la región norte (N), centro (C) y sur (S). Todas las regresiones fueron significativas ($P < 0,05$).

0.28), and slopes were always below 1 (Fig. 2). BDW did not differ statistically between regions in *H. plana*, *O. trimaculatus*, and *T. marginatus* after removing the influence of female size (Table 3). A significant increase in BDW from the center to the south was detected in *P. barbiger* (Table 3).

Fecundity

The mean number of embryos per brood ranged from 31,407 in *P. barbiger* to 1,381,867 in *C. setosus*. Fecundity was positively correlated with FDW for all species and regions (always P < 0.05; Fig. 3). All slopes from allometric

TABLE 3

Summary of ANOVAs and Student t-tests performed for each species to compare brood dry weight, fecundity, embryo dry weight, embryo volume and embryo losses during incubation among regions (north, center and south). Only female crabs carrying embryos at early stage were used in all cases except for embryo losses. (nd) = no data available for comparisons; (*) the Z-value is reported

Resumen de los ANDEVAs y pruebas t de Student realizados para cada especie para comparar entre regiones (norte, centro y sur): peso seco de la masa de huevos, fecundidad, peso seco del embrión, volumen del embrión y pérdida de embriones durante la incubación. Exceptuando la pérdida de huevos, en todos los casos fueron usadas solamente hembras con embriones tempranos. (nd) = no hay datos disponibles para las comparaciones; (*) se reporta el valor de Z

| Variable and species	Degrees of freedom	F-value (t-value)*	P-value
Brood dry weight			
Paraxanthus barbiger	1, 41	22.0	< 0.001
Homalaspis plana	1, 44	0.15	0.7
Ovalipes trimaculatus	1, 32	0.01	0.91
Taliepus marginatus	1, 37	2.21	0.14
Fecundity			
Paraxanthus barbiger	1, 41	2.11	0.15
Homalaspis plana	1, 44	0.01	0.92
Ovalipes trimaculatus	1, 32	9.08	0.005
Taliepus marginatus	1, 37	2.21	0.14
Embryo dry weight			
Cancer setosus	2, 82	24.36	< 0.001
Paraxanthus barbiger	42	(-2.57)	0.02
Homalaspis plana	46	(0.96)	0.34
Ovalipes trimaculatus	33	(-3.51)	< 0.01
Taliepus marginatus	38	(-11.41)	< 0.001
Embryo volume			
Cancer setosus	2, 82	17.24	<0.01
Homalaspis plana	36	(0.86)	0.40
Paraxanthus barbiger	57	(-3.35)*	<0.001
Ovalipes trimaculatus	28	(-3.9)*	<0.001
Taliepus marginatus	24	(-3.87)*	<0.001
Embryo loss			
Cancer setosus	2, 86	5.55	< 0.005
Paraxanthus barbiger	13	(0.7)	0.5
Homalaspis plana	36	(1.52)	0.14
Ovalipes trimaculatus	41	(3.34)	0.002
Taliepus marginatus	nd		
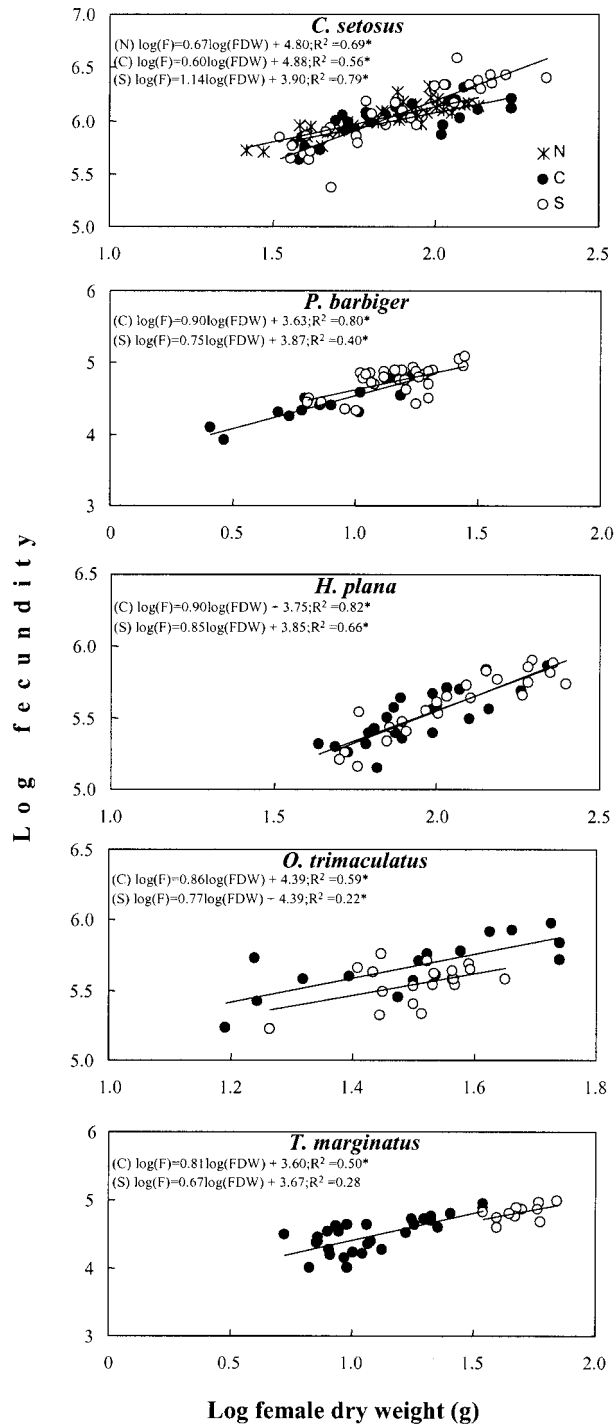
Fig. 3: Relationship between log-female dry weight (FDW) and log-fecundity (F) for five Brachyuran species in three regions along the Chilean coast. Data were obtained from female crabs carrying embryos at early stage. The regression equations and the coefficient of determinations (R^2) are shown for northern (N), central (C) and southern (S) Chile. Asterisks indicate significant relationship between variables ($P < 0.05$).

Relación entre log-peso seco de la hembra (FDW) y log-fecundidad (F) para cinco especies de braquiuros en tres regiones a lo largo de la costa de Chile. Los datos fueron obtenidos de hembras con embriones en estado temprano. Las ecuaciones de regresión y los coeficientes de determinación (R^2) son mostradas para la región norte (N), centro (C) y sur (S). Los asteriscos indican relaciones significativas entre variables ($P < 0,05$).

relationships, except for *C. setosus* from southern Chile, were < 1 (Fig. 3). Regression slopes differed among regions for *C. setosus* (parallelism test: $F_{2,88}$ = 9.91, P < 0.001), therefore a separate slope model was run for this species. Significant differences were detected among regions ($F_{2,88}$ = 9.359, P < 0.05). Although no differences could be detected after using a posteriori tests (P > 0.05), the slope of the relationship FDW and fecundity in the north seemed to be differ from the other two regions. Fecundity of *H. plana*, *P. barbiger* and *T. marginatus* did not show significant differences between regions after female size was controlled for (Table 3).

Fecundity of *O. trimaculatus* was higher in central than in southern Chile (Table 3).

Dry weight and volume of embryos

Mean embryo dry weight ranged between 0.009 to 0.066 mg for *C. setosus* and *T. marginatus,* respectively (Fig. 4A). Mean embryo dry weight was significantly lower in central than in southern Chile for *P. barbiger*, *O. trimaculatus* and *T. marginatus* (Table 3). The other two species did not exhibit significant differences between these two regions (Table 3). However, mean embryo dry weight of *C. setosus* in northern Chile was significantly
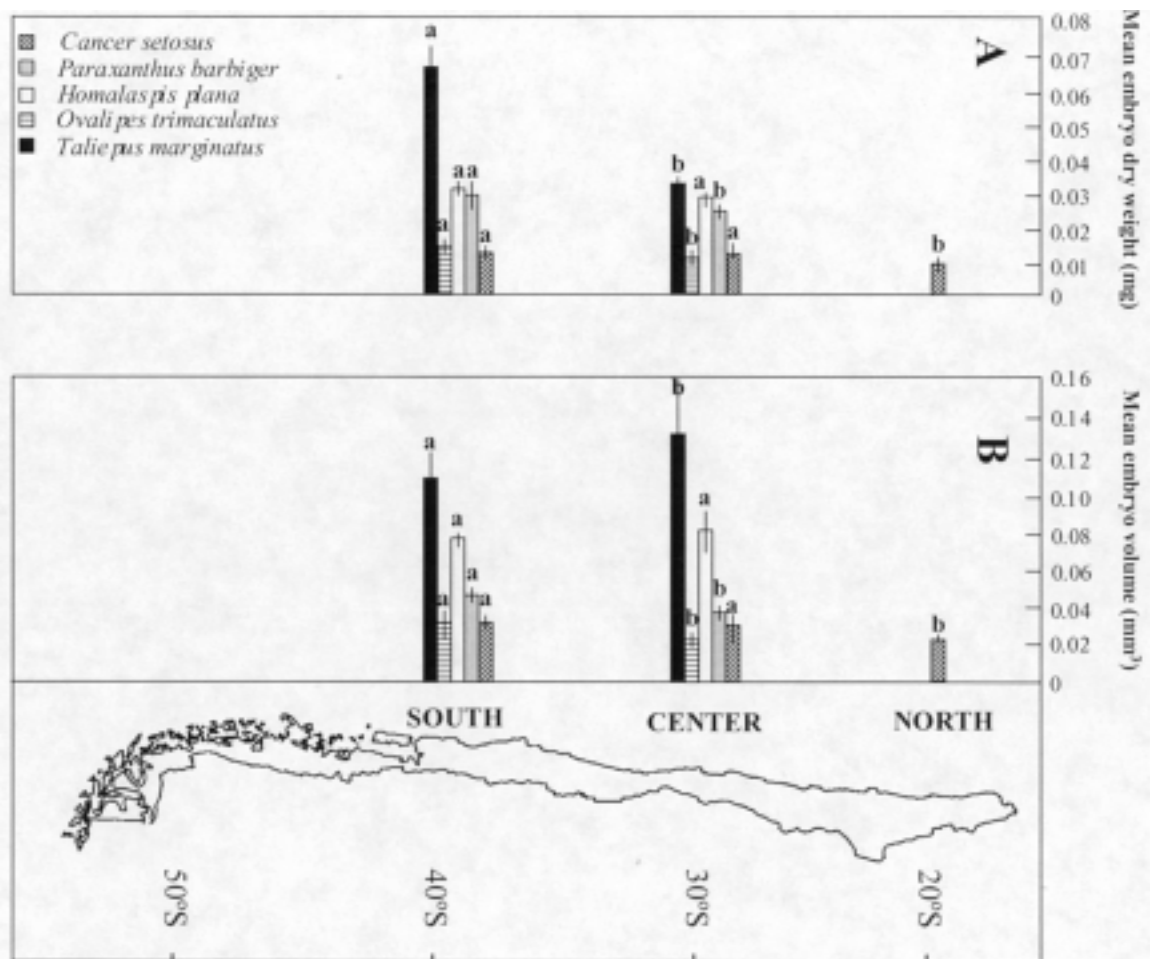

Fig. 4: Latitudinal comparisons of (a) mean embryo dry weight (mg) and (b) mean embryo volume (mm³) of five Brachyuran species in the three study regions along the Chilean coast. Solid lines indicate 1 standard error. Equal symbols above the bars indicate no significant differences among regions within species.

Comparaciones latitudinales de (a) peso seco promedio del embrión (mg) y (b) volumen promedio del embrión (mm³) en cinco especies de braquiuros en las tres regiones estudiadas a lo largo de la costa de Chile. Las líneas continuas indican 1 error estándar. Símbolos iguales sobre las barras indican diferencias intraespecíficas no significativas entre regiones.

lower than in the other two regions (Table 3). Mean embryo volume ranged between 0.021 and 0.126 mm³ in *O. trimaculatus* and *T. marginatus*, respectively (Fig. 4B). In *P. barbiger* and *O. trimaculatus*, embryo volume significantly increased from central to southern Chile (Table 3). In contrast, *T. marginatus* showed the opposite tendency (volume decreased toward the south). No significant differences between central and southern Chile were detected in *H. plana* and *C. setosus* (Tabla 3). However mean volume of embryos was significantly lower in northern Chile for *C. setosus* (Table 3).

Embryo loss

The percentage of embryo loss throughout development varied between 3.6 % for *C. setosus* and 56.7 % for *O. trimaculatus,* respectively (Fig. 5). Only *C. setosus* and *O. trimaculatus* showed significance differences in the percentage of embryo losses among regions (Table 3). A higher percentage of embryo loss was found for *C. setosus* in northern Chile than

in the other two regions, but no significant differences were detected between central and southern Chile. Similarly, a significant increase in the mean percentage of embryo loss towards lower latitudes was detected in *O. trimaculatus*.

DISCUSSION

Although we did not find a clear and consistent pattern in all reproductive variables in the five crab species analyzed along the coast of Chile, some generalizations can be drawn from this study. First, brood weight did not vary between central and southern Chile in four of the five species (the only exception being *P. barbiger*). Second, embryo losses did not vary between central and southern Chile in four of the five species studied. Third, embryo dry weight tended to increase toward high latitudes in four species. Some species (*H. plana, C. setosus*) showed a clear and consistent pattern in all reproductive variables among regions, while different patterns between regions were observed in other species (*P. barbiger, O.*
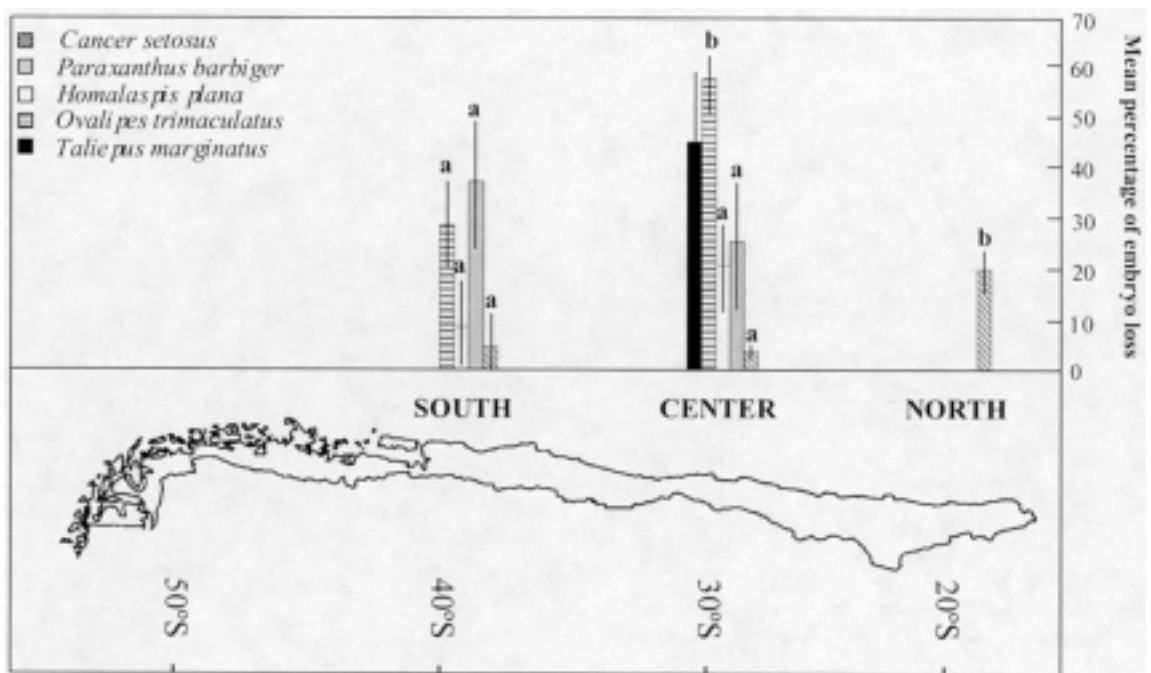

Fig. 5: Latitudinal comparisons of the mean percentage of embryo loss during incubation time of five Brachyuran species in the three study regions along the Chilean coast. Solid lines indicate 1 standard error. Equal symbols above the bars indicate no significant differences among regions within species.

Comparaciones latitudinales de la pérdida de embriones promedio durante el tiempo de incubación en cinco especies de braquiuros en las tres regiones estudiadas a lo largo de la costa de Chile. Las líneas continuas indican 1 error estándar. Símbolos iguales sobre las barras indican diferencias intraespecíficas no significativas entre regiones.

trimaculatus, T. marginatus). Here, we present the first report of *T. marginatus* inhabiting localities south of Talcahuano (36º S).

The most dramatic differences in most reproductive variables occurred between the north and the rest of the areas sampled. Females of *C. setosus* (the only species found brooding in northern Chile) from northern Chile exhibited lower brood weights than females from central and southern Chile. Embryo size, embryo volume, and embryo loss also showed differences between the north, and the rest of the coast. Larger embryos at high latitudes (i.e., where conditions of low temperatures prevail) can be explained by high amounts of yolk, a pattern well known among Brachyuran crabs (Wear 1974). However, smaller and lighter embryos at lower latitudes may also reflect local adaptation to higher mean temperatures (Brante et al. 2003). This interpretation is in line with a general trend observed among marine invertebrates in that relatively cold water temperatures result in large-sized organisms compared with warm water species, because cold waters usually have higher levels of dissolved oxygen (Chapelle & Peck 1999 for amphipods; Pörtner 2002 for cephalopods). This trend may extend to embryo size, which would also benefit from elevated oxygen solubility given the strong oxygen limitation observed in embryo masses during early development (Fernández et al. 2000, Fernández et al. 2002). In fact, the high rate of embryo loss and the low BDW at lower latitudes might be associated to a need for the parents to provide oxygen to the embryos. A higher cost of ventilation at higher temperatures (lower latitudes) seems to affect investment in eggs, decreasing reproductive output (Brante et al. 2003). High embryo loss can also be the result of a high ventilation frequency at high temperatures, which may result from mechanical losses (Kuris et al. 1991, Brante et al. 2003).

Patterns of BDW and fecundity between central and southern Chile were consistent in most of species included in this study. *Cancer setosus*, *H. plana, O. Trimaculatus*, and *T. marginatus* did not show any difference in BDW and fecundity between central and southern Chile. The only species that showed differences in BDW between these two regions was *P. barbiger*, although its fecundity did not change. A similar finding has been reported for *Pinnaxodes chilensis* (Lardies & Castilla 2001). Thus, these two reproductive variables seem to be little affected by variations in temperature or other environmental variables that might have

been expected to affect energy available for reproduction, such as productivity, between 29 and 41º S. An average 18 % decrease in average sea surface temperature and a 28 % increase in chlorophyl-*a* has been reported between central and southern Chile (Thomas 1999). Low temperature conditions, which may lower the cost of brooding (Brante et al. 2003) and higher food availability seemed not to result in higher energy input in eggs. This finding is in line of Hines' (1982) hypothesis, according to which an allometric limitation of available space for yolk accumulation in the body cavity is a major constraint on brood size. The issues of how the brooding cost varies with temperature, how the cost of embryo ventilation affects egg production, and if such trade-off, found in *C. setosus* (see Brante et al. 2003), also occurs in other crab species remains unclear.

Cancer setosus from southern Chile exhibited a different relationship between FDW and BDW, and between FDW and fecundity, than the rest of the species and regions. The slopes of both regressions for all species and regions (except *C. setosus* from southern Chile) were always < 1, indicating that larger crabs have proportionally smaller broods (and lower fecundity) than smaller crabs. Although females of *C. setosus* from central and northern Chile also showed such a relationship, slopes were larger than unity in southern Chile, suggesting that larger females are able to produce more eggs than similarly sized females in lower latitudes (i.e., higher temperatures). The effect of body size on egg production needs further exploration, but a constraint on egg production should be expected for large sized individuals given the cost of oxygen provision to the egg mass (Fernández et al. 2000). The trade-off between egg production and investment in oxygen provision to embryos (Brante et al. 2003) supports this hypothesis. It is important to remark that female size tended to be larger in southern Chile for most of the species. Large brood size, expected in larger females, is more feasible in cold waters (high latitudes) if the costs association to oxygen provision to the brood is an important selective force. Large-sized organisms in cold waters, where dissolved oxygen increases, has also been reported for other groups of marine invertebrates (Chapelle & Peck 1999 for amphipods; Pörtner 2002 for cephalopods).

Embryo loss varied enormously among species and regions, reaching 56.7 % in *O. trimaculatus* in central Chile. This range is similar to those reported for other Brachyuran crabs (Kuris 1991, Fernández et al. 2000,

Lardies & Castilla 2001). Moreover, the higher rate of embryo loss in *O. trimaculatus* coincides well with those reported for other species of the Portunidae family (Kuris 1991), suggesting that losses are substantially higher within this family (above 50 %). Embryo loss has been hypothesized to result from (1) a limitation of space under the cephalotorax to carry the embryos (Corey & Reid 1991, Hines 1982), and (2) from an accidental action during the mechanical process of brood ventilation (Kuris 1991, Fernández et al. 2000). A direct relationship between embryo ventilation and percentage of embryo loss has been reported for *Cancer pagurus, C. setosus,* and *Maja squinado* (Fernández et al. 2000, Brante et al. 2003). We found a higher rate of embryo loss in *C. setosus* at low latitudes, and in *O. trimaculatus* in general, but toward lower latitudes in particular. As shown by Brante et al. (2003), the high rates of embryo losses in *C. setosus* are caused by a higher ventilation frequency at high temperatures (low latitudes). A high ventilation frequency also may be responsible for the relatively high rate of embryo loss found in *O. trimaculatus* between central and southern Chile; this species shows levels of activity that are higher than the other species, which makes it more sensitive to changes in temperature. However, we did not test this hypothesis directly and therefore, alternative explanations can be proposed. For instance, differential rates of parasitism and disease infection, which may also be correlated with ambient temperature, could affect embryo loss through a latitudinal (temperature) gradient. High rates of embryo loss suggest the need to consider this factor in future studies of fecundity or reproductive output, by means of using females carrying early stage embryos to estimate both variables.

Latitudinal patterns observed in brood dry weight can be explained by the combined effects of fecundity and embryo dry weight. With the exception of *T. marginatus*, embryo dry weight showed the same latitudinal pattern as did embryo volume. In general, we found that both embryo dry weight and volume increased with latitude. This is a common trend among marine invertebrates (Barnes & Barnes 1965, Efford 1969, Lardies & Castilla 2001, Brante et al. 2003), but controversial among crustaceans (Diaz 1980, Wooward & White 1981, Jones & Simons 1983). Our data strongly support the trend reported for marine invertebrates, since embryo volume consistently increased toward the south. Although low salinity in the southern region

might explain the increase of embryo volume of *Pinnaxodes chilensis* (Lardies & Castilla 2001), the simultaneous increase of embryo volume and dry weight in most species supports the hypothesis that yolk accumulation rather than environmental variables explain patterns of embryo volume.

It is interesting that *P. barbiger* and *O. trimaculatus* showed differences between central and southern Chile for more variables than any of the other species (brood weight, embryo dry weight, and embryo volume in *P. barbiger* and fecundity, embryo dry weight, embryo volume and embryo losses in *O. trimaculatus*). Both species show their southern end of distribution in our southern study region. This finding suggests that reproductive variables show differences along the distribution of the species, particularly towards the distribution limits, but more studies are needed along this line to explore this hypothesis.

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