

Egg production of *Austropandalus grayi* (Decapoda, Caridea, Pandalidae) from the Magellan region, South America*

INGO S. WEHRTMANN^{1,2} and MARCO A. LARDIES³

¹Universidad Austral de Chile, Instituto de Zoología "Ernst F. Kilian" Casilla 567, Valdivia, Chile.

²present address: Alfred-Wegener-Institut für Polar- und Meeresforschung, Am Handelshafen 12, D-27570 Bremerhaven, Germany.

³Pontificia Universidad Católica de Chile, Facultad de Ciencias Biológicas, Casilla 114-A, Santiago, Chile.

SUMMARY: *Austropandalus grayi* is one of three pandalid shrimp species reported from Chilean waters. Here we describe fecundity, reproductive output, and chemical composition of the incubated embryos of *A. grayi*, providing the first account of such information for a pandalid species inhabiting the southern hemisphere. Ovigerous females (n = 96) were collected during October - November 1994 with an Agassiz trawl in waters off Patagonia and Tierra del Fuego, South America. Both egg production (between 50 and 1858 embryos) and early egg volume ($\bar{x} = 0.069 \text{ mm}^3$) of *A. grayi* were low when compared to values reported from other pandalids. Clutch size increased with maternal size, however, the size of recently-spawned eggs was not linked to female size. Although the egg mass volume remained almost stable during the incubation period, females lost on average 51.1% of their initially-laid embryos; however, this loss was more than compensated by an 88.4% increase of the egg volume during embryogenesis. Mean reproductive output was relatively low (0.133) and not related to maternal size. The RO-data of *A. grayi* and other pandalids seem to indicate an increasing energy allocation for reproduction towards higher latitudes, a trend which would be contrary to the results of studies with other crustaceans. Water was the predominant constituent of the chemical composition of developing embryos and increased from 62.2% to 70.2% during the incubation period. At the same time, organic matter declined and mineral content augmented. Generally, our results are in agreement with previous findings with regard to the chemical composition of developing decapod embryos.

Key words: Pandalidae, reproductive biology, latitudinal cline, southern hemisphere, Chile.

RESUMEN: PRODUCCIÓN DE HUEVOS EN *AUSTROPANDALUS GRAYI* (DECAPODA, CARIDEA, PANDALIDAE) PROVENIENTE DE LA REGIÓN MAGALLÁNICA, AMÉRICA DEL SUR. – *Austropandalus grayi* es una de las tres especies de camarones pandálidos citadas en aguas chilenas. Se describen fecundidad, rendimiento reproductivo y composición química de los embriones de *A. grayi* incubados, representando ésta la primera descripción sobre la biología reproductiva de un pandálido del hemisferio sur. Se recolectaron hembras ovígeras (n = 96) durante octubre-noviembre de 1994 mediante una red de Agassiz en aguas adyacentes a la Patagonia y Tierra del Fuego, América del Sur. La producción de huevos (entre 50 y 1858 embriones) y el volumen de huevos recién puestos ($\bar{x} = 0,069 \text{ mm}^3$) de *A. grayi* fueron bajos comparados con los valores de otros pandálidos. El número de huevos aumentó con el tamaño de la hembra, sin embargo, el tamaño de los huevos recién puestos no mostró relación con el tamaño de la hembra. Aunque el volumen de la masa de huevos permaneció casi estable durante el período de incubación, las hembras perdieron en promedio un 51,1% de los huevos inicialmente producidos. Sin embargo, esta pérdida fue más que compensada por un incremento de un 88,4% del volumen del huevo durante la embriogénesis. El rendimiento reproductivo ("reproductive output"; RO) promedio fue relativamente bajo (0,133) y no relacionado con el tamaño de la hembra. El valor de RO de *A. grayi* y los de otros pandálidos parece que indican un incremento de la asignación energética para la reproducción hacia altas latitudes, tendencia que sería contraria a los resultados en otros decápodos. El contenido de agua en la composición química de los embriones aumentó desde el 62,2% hasta el 70,2% durante el período de incubación. Al mismo tiempo disminuyó la materia orgánica y aumentó el contenido mineral. En general, nuestros datos corroboran resultados anteriores con respecto a la composición química de embriones de decápodos en vías de desarrollo.

Palabras clave: Pandalidae, biología reproductiva, clina latitudinal, hemisferio sur, Chile.

This is AWI contr. no. 1756

*Accepted February 26, 1999.

INTRODUCTION

Members of the family Pandalidae have a worldwide distribution and occur typically in colder waters of both the northern and southern hemisphere (Holthuis, 1980; Hendrickx and Wicksten, 1989). Representatives of several genera of Pandalidae are currently commercially exploited, and species of *Pandalus* and *Heterocarpus* play an important role in the world's shrimp fisheries (Holthuis, 1980; Parsons and Fréchet, 1989). Three species of pandalid shrimps, *Heterocarpus reedi* Bahamonde, 1955, *Plesionika santaecatalinae* Wicksten, 1983, and *Austropandalus grayi* (Cunningham, 1871) inhabit Chilean waters (see Holthuis, 1952; Retamal, 1995). The first species supports the main Chilean crustacean fishery, and several aspects of the fishery biology of *H. reedi* have been investigated (e.g., Hancock and Henríquez, 1968; Bahamonde and Henríquez, 1970; Roa and Ernst, 1996; Wehrtmann and Andrade, 1998). The second species, *P. santaecatalinae*, has been found recently in northern Chile (Retamal, 1995), and its life history in Chilean waters remains to be investigated. Referring to *A. grayi*, virtually nothing is known about the biology and ecology of this shrimp, a shallow water species inhabiting typically the antiboreal region of South America (Holthuis, 1952; Wehrtmann and Carvacho, 1997). A recent study of the decapod fauna of the Magellan zone revealed that *A. grayi* was the most common caridean shrimp in the study area, occurring generally at considerably less than 100 m water depth (Arntz *et al.*, 1999).

The purpose of this paper is to describe and discuss fecundity, reproductive output, and chemical composition of the incubated embryos of *A. grayi*. Furthermore, we compare our data with those published for other pandalids from the northern hemisphere, as such a comparison may contribute to our understanding of life history strategies in caridean shrimps.

MATERIAL AND METHODS

Egg-bearing females ($n = 96$) were obtained from Agassiz trawl catches carried out during October–November 1994 in the frame of the Joint Chilean–German–Italian Magellan “Victor Hensen” Campaign. The cruise covered the Straits of Magellan, the channel system between the Straits of Magellan and the Beagle Channel, and the Beagle Chan-

nel. A detailed description of the study area, location of the stations, and sampling gears employed has been published by Arntz and Gorny (1996). The material used for the present study was obtained in the area between 53°42'8" S, 70°57'4" W and 55°09'2" S, 67°01'6" W; Arntz *et al.* (1999) provide information regarding the exact geographical locations where *Austropandalus grayi* were collected. Ovigerous females of *A. grayi* were stored immediately in a 10%-buffered formaldehyde solution. In the laboratory, we measured total length (TL; distance between the mid-dorsal anterior margin of the carapace and the distal margin of the telson, excluding setae) and carapace length (CL; distance between the distal part of the eye socket to the distal margin of the carapace) of ovigerous females. The entire egg mass was removed from the females, and the total number of embryos was assessed. Thirty eggs were separated from each batch, and length and width were measured to calculate the egg volume (V) using the formula for oblate spheroids $V = 1/6 (\pi d_1^2 \times d_2)$ (see Turner and Lawrence, 1979). The average volume per egg was multiplied with the total number of eggs to estimate the egg mass volume (EMV) of the female. The developmental stage of the embryos per female was determined and divided into three stages according to the following criteria (see Wehrtmann, 1990): Stage I: eggs recently produced; uniform yolk; no eye pigments visible; Stage II: eye pigments barely visible; Stage III: eyes clearly visible and fully developed; abdomen free. To document possible brood mortality during the incubation period, all females were grouped in 2 mm size classes, and their fecundity was estimated according to the regression equations for Stage I - III (see Table 1). Subsequently, estimated egg numbers per size class and developmental stage were compared to obtain estimated values for egg loss.

The removed egg mass per female was divided into three subsamples, and the interstitial water was extracted with filter paper. Aliquots were dried at 60°C

TABLE 1. – *Austropandalus grayi*: regression statistics for log fecundity - log size relation for the three egg stages; abbreviations: n (number of observations), CL (carapace length), and r (correlation coefficient).

Egg stage	n	Slope \pm 95% CL	Intercept \pm 95% CL	r
Stage I	46	1.2378 \pm 0.4089	1.3271 \pm 0.5246	0.42
Stage II	25	2.7549 \pm 0.7657	-0.7323 \pm 0.9099	0.64
Stage III	24	1.5195 \pm 0.5994	0.6806 \pm 0.7215	0.44

TABLE 2. – *Austropandalus grayi*: size (CL) of ovigerous females, and clutch size, egg volume and brood mass during the incubation period; S.D. = standard deviation; n = number of observations.

	Average	± S.D.	Min.	Max.	n
Stage I					
CL (mm)	19.67	2.46	14.44	23.2	46
Egg number	901	421	106	1858	46
Egg volume (mm ³)	0.069	0.087	0.042	0.079	42
Egg mass volume (mm ³)	61.92	28.68	17.28	139.22	42
Stage II					
CL (mm)	15.62	3.09	10.7	20.67	21
Egg number	382	265.92	64	929	21
Egg volume (mm ³)	0.095	0.001	0.072	0.109	21
Egg mass volume (mm ³)	43.17	27.02	6.78	148.18	21
Stage III					
CL (mm)	17.11	3.84	10.94	24.62	29
Egg number	478	313.42	50	1243	29
Egg volume (mm ³)	0.130	0.027	0.103	0.195	29
Egg mass volume (mm ³)	60.58	41.57	7.75	157.81	29

for approximately 48 hours to obtain dry mass; afterwards, eggs were combusted for 3-5 hours at 500°C to obtain ash mass. The mass of the organic material was estimated by subtracting ash mass from dry mass. The same methods were applied for the females, except that dry mass was obtained after 72 hours. Based upon the dry mass of both eggs and female, we calculated the stage-independent reproductive output according to the formula provided by Clarke *et al.* (1991): RO = (wet mass of total egg batch of the female / wet mass of the female without embryos).

RESULTS

Fecundity, egg volume, brood mortality, and reproductive output

The mean size (CL) of ovigerous females analyzed was 17.6 mm (± 3.49 mm standard deviation), ranging from 10.7 mm to 24.6 mm CL. All developmental egg stages were encountered; females with recently spawned embryos were most abundant (Table 2). Females carried a minimum of 50 eggs and a maximum of 1858 eggs, independent of the developmental stage of the embryos (Table 2). The number of recently spawned eggs (Stage I) increased with maternal size (Fig. 1); slopes of the allometric regressions for all three egg stages and maternal size were significantly different ($p < 0.05$) from zero, however, ANCOVA (Sokal and Rohlf,

TABLE 3. – Percent brood mortality in *A. grayi* per maternal size group based upon pairwise comparisons of egg numbers in embryonic stages I and III. Regression equations for Stage I and III were used to estimate average egg numbers per size group; TL = total length of ovigerous females.

Size group (CL, mm)	Number of females	Average egg number (Stage I)	Average egg number (Stage III)	Brood mortality (%)
11	5	413.18	183.23	44.4
13	16	508.09	236.18	46.5
15	13	606.55	293.18	48.4
17	10	708.19	355.03	50.1
19	26	812.72	420.40	51.7
21	17	919.91	489.45	53.2
23	7	1029.55	562.01	54.6
25	2	1141.48	637.93	55.9
Mean mortality for all size groups				51.1

1981) did not detect significant differences ($p > 0.05$) among these regressions. During the incubation period females lost an average of 51.1% of the initially spawned embryos, and brood mortality increased with female size (Table 3). The egg mass volume (EMV) remained almost stable (Stage I: 61.92 ± 28.68 mm³; Stage III: 60.58 ± 41.57 mm³) during embryogenesis while the egg volume augmented steadily from 0.069 mm³ (Stage I) to 0.130 mm³ (Stage III) which represented an 88.4 % egg volume increase (Table 2). Both the volume of recently spawned embryos and RO for Stage-I eggs were variable (Fig. 2), however, no statistically significant relationships were detected between maternal size and initial egg volume ($r = 0.177$; $p = 0.263$; $n = 46$) and RO ($r = -0.203$; $p = 0.197$; $n = 46$). The mean RO was 0.133 (S.D. ± 0.041), and values ranged from 0.070 to 0.243.

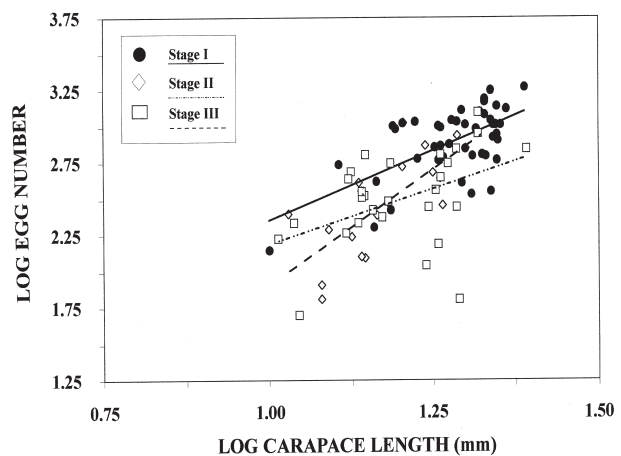


FIG. 1. – *Austropandalus grayi*: relationship between maternal size (CL) and clutch size for three embryonic stages.

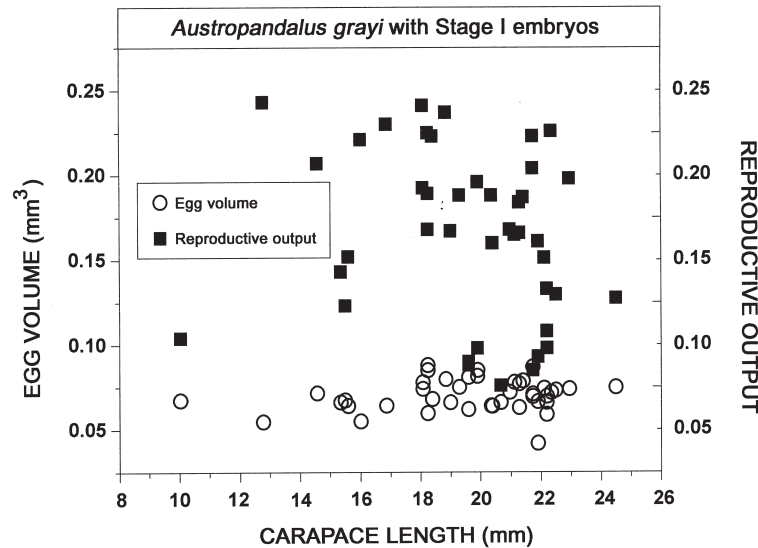


FIG. 2. – *Austropandalus grayi*: relationship of egg volume and reproductive output versus maternal length, considering exclusively females carrying newly-spawned embryos (n = 46).

Chemical composition of developing embryos

Wet and dry mass of recently-laid eggs were 61.15 μg and 21.90 μg , respectively, but while the former increased slightly during embryogenesis, the latter decreased considerably (Table 4). Not surprisingly, water was the predominant component of the developing embryos and increased gradually from 62.2 % to 70.2 %. The organic matter declined and ash content augmented during the incubation period (Table 4).

DISCUSSION

Egg production

Maternal body size is considered to be the principal determinant of egg production in decapod crustaceans (e.g., Hines, 1982, 1991; Corey and

Reid, 1991; Lardies and Wehrtmann, 1997), and our results clearly corroborate this tendency. A comparison with other similar-sized pandalid species reveals that the maximum clutch size of *A. grayi* is the lowest for the species listed in Table 5. It would be interesting to compare also egg volume, egg mass volume, and RO among species, however, such data are unavailable for these similar-sized pandalids. Therefore, it remains to be clarified whether *A. grayi* allocates less energy (in terms of eggs) for reproduction than other species of the same family with ovigerous females covering a comparable size range.

Young embryos of *A. grayi* comprise only half the volume of newly-spawned eggs from the Chilean deep-water pandalid *Heterocarpus reedi* (mean volume: 0.138 mm^3 ; Wehrtmann and Andrade, 1998). Interestingly, freshly-laid eggs of *A. grayi* are approximately 10 times smaller than those of *Pandalus borealis* (see Clarke *et al.*, 1991)

TABLE 4. – Average chemical composition of the three embryonic stages of *Austropandalus grayi*; S.D. = standard deviation; n = number of observations.

	Stage I				Stage II				Stage III			
	μg	$\pm\text{S.D.}$	%	n	μg	$\pm\text{S.D.}$	%	n	μg	$\pm\text{S.D.}$	%	n
Wet mass	61.15	4.38	—	35	61.61	5.57	—	21	62.78	5.41	—	23
Dry mass	21.90	3.32	—	35	20.15	2.56	—	21	17.26	3.06	—	23
Water content	39.25	8.52	62.2	35	41.46	5.03	65.7	21	45.52	4.28	70.2	23
Organic matter	20.39	2.36	35.3	35	18.57	2.18	31.1	21	15.12	2.23	25.5	23
Ash content	1.55	0.63	2.6	35	2.03	0.57	3.2	21	2.48	0.20	4.4	23

TABLE 5. – Comparison of clutch size and maternal size among four pandalid shrimps covering a similar size range; CL = carapace length.

Species	Number of embryos	CL range of ovigerous females	Reference
<i>Austropandalus grayi</i>	50 - 1858	10.7 - 24.6 mm	present study
<i>Dichelopandalus bonnieri</i>	162 - 2639	11 - 21.8 mm	Al-Adhub and Bowers (1977)
<i>Pandalus montagui</i>	200 - 3000	9.5 - 19.0 mm	Allen (1966)
<i>Parapandalus narval</i>	200 - 7500	7.9 - 18.7 mm	Thessalou-Legaki (1992)

and constitute only a minor fraction of the early egg volume reported for two Antarctic shrimps, *Chorismus antarcticus* and *Notocrangon antarcticus* (see Clarke, 1993a). The comparison with these polar species corroborates the tendency of producing larger eggs at higher latitudes (Thorson, 1950; Clarke, 1992).

The volume of Stage I embryos does not increase with maternal size (Fig. 2 and Table 2). This probably implies that there are no maternal size-related differences with regard to energy allocation per embryo in *A. grayi*, which is in contrast to the results obtained from polar caridean shrimps (Clarke, 1993b). In the four species investigated by Clarke (1993b), female size had a positive influence on egg size. This discrepancy between shrimps from polar and temperate zone may be related to environmental conditions (e.g., temperature, food availability, competition). However, the larger size of recently-spawned *A. grayi* eggs from a population inhabiting central-southern Chile (Wehrtmann, unpubl. data) demonstrates intraspecific plasticity in egg size and supports the hypothesis that much of the variability in egg volume among populations may be related to local factors (see Clarke, 1993b).

Intraspecific differences in egg size along a latitudinal gradient have been observed in various decapod species (for caridean shrimps see: Clarke *et al.*, 1991; Gorny *et al.*, 1992; Clarke, 1993b; Lardies, 1995), and *A. grayi* seems to be another example of such a latitudinal cline in the reproductive biology: a limited data set (Wehrtmann, unpubl.) concerning *A. grayi* from Putemún, central-southern Chile, suggests that recently-spawned eggs are substantially larger in the Magellan region compared to those produced in central-southern Chile (mean egg volume: $0.037 \text{ mm}^3 \pm 0.0020 \text{ mm}^3$ S.D.; $n = 7$). Since egg volume is significantly correlated with nutrient content in caridean shrimps (Clarke, 1993a), the above-mentioned difference in early egg volume reflects a real difference in energy investment per embryo.

Austropandalus grayi loses approximately 51.1% of the initially extruded embryos. Some of the egg loss may be attributed to the trawling process (see also Gorny *et al.*, 1992), however, since *A. grayi* was sampled generally from well above 100 m depth, it seems unlikely that the sampling procedure is responsible for an important portion of the calculated brood mortality. The obtained value of 51.1% is not unusual and lies within the range reported from other caridean shrimps (Corey and Reid, 1991; Kuris, 1991; Pandian, 1994). However, the egg loss observed in *A. grayi* is more than compensated by a concomitant increase of egg volume by 88.4%. We assume that the early egg mass almost completely fills the available brood space in *A. grayi*; during the course of the incubation period, the increasing egg mass temporarily outgrows the attachment area which facilitates the mechanical abrasion of the outer embryos (see Kuris, 1991). Our results regarding the EMV (Table 2) suggest that the egg mortality during embryogenesis does not result in an important decrease of the initially-spawned clutch volume of *A. grayi*. However, brood mortality in this pandalid shrimp seems to increase with maternal size (Table 3). Kuris (1991) reviewed the size-specific variability of egg loss among crustaceans and found that only half of the data sets analyzed exhibited a constant proportional loss of embryos over the size range of ovigerous females. Thus, our finding concerning the size-specific brood mortality in *A. grayi* is in accordance with the statement by Kuris (1991) that the relationship between egg mortality and maternal size is highly variable among decapods.

Chemical composition of developing embryos

Water is the major constituent of the developing egg of *A. grayi*, and the water content increases during embryogenesis from 62 to 70%. These values are similar to those reported for a variety of other decapod crustaceans which release planktonic larvae (e.g., Pandian, 1970; Valdés *et al.*, 1991;

Lardies and Wehrtmann, 1997). The overall percent increase of water during the incubation period (16%) is surprisingly low when compared to other decapods such as *Macrobrachium rosenbergii* (74%: Clarke, 1990), *Betaeus emarginatus* (106%: Lardies and Wehrtmann, 1997), *Homarus gammarus* (202%: Pandian, 1970), and *Necora puber* (148%: Valdés *et al.*, 1991), and is relatively close to the water uptake reported for *Crangon crangon* (17%: Pandian, 1967), *Nauticaris magellanica* (27 - 30%: Wehrtmann and Kattner, 1998), *Betaeus truncatus* (12 - 19%: Lardies, 1995), and *Callinectes sapidus* (20%: Amsler and George, 1984). Pandian (1970, 1994) discussed the eco-physiological consequences of water imbibition and demonstrated that marine crustaceans depend heavily on the surrounding environment for water and salt. However, it is still unclear why the egg water content of certain marine decapod species increases substantially during embryonic development whereas other species with a similar initial percent water content show only a slight increase of this component.

Mineral ashes constitute 2.6 % of the dry mass of newly-spawned *A. grayi* eggs (Table 4) which is similar to the ash values reported for early eggs of *Crangon crangon* (1.4%: Pandian, 1967) and *Homarus gammarus* (2.7%: Pandian, 1970). However, most decapods seem to extrude embryos with a considerably higher portion of mineral ashes (e.g., Pandian, 1967; Clarke, 1993a; Amsler and George, 1984; Lardies and Wehrtmann, 1996, 1997). It is speculated that the differences in ash contents in recently produced embryos of different decapods is related to the degree of calcification of the embryonic and larval exoskeleton (see also Clarke, 1990).

The steadily increasing ash content in *A. grayi* is associated with an active absorption of water and reflects the uptake of inorganic salts across the embryonic membranes. Thus, a parallel increase of both water and ash content should be expected and has been reported for many decapods (e.g., *Macrobrachium rosenbergii*: Clarke, 1990; *Crangon crangon*: Pandian, 1967; *Homarus gammarus*: Pandian, 1970; *Callinectes sapidus*: Amsler and George, 1984). In other species, however, ash content remained almost stable or decreased during embryogenesis (*Betaeus emarginatus*: Lardies and Wehrtmann, 1997; *Betaeus truncatus*: Lardies, 1995; *Nauticaris magellanica*: Wehrtmann and Kattner, 1998; *Necora puber*: Valdés *et al.*, 1991).

Reproductive output

Compared to other pandalid species, the RO of *A. grayi* is lower than in *Pandalus borealis* and *P. montagui*, but higher when compared to the Chilean deep-water shrimp *Heterocarpus reedi* (Fig. 3). Although a single low-latitude data point for *H. reedi* strongly influences the relationship presented in Fig. 3, the results seem to indicate an increasing RO toward higher latitudes among pandalid shrimps which is contrary to the results of studies with other caridean shrimps (Clarke, 1987 and references cited therein): polar species of Pandalidae, Hippolytidae and Crangonidae showed a significantly lower RO than temperate species. Referring to intraspecific variability, the fact that *A. grayi* from central-southern Chile produces considerably smaller but approximately the same amount of eggs (Wehrtmann, unpubl. data) than similar-sized females inhabiting the southern tip of America may also suggest that the RO is lower at lower latitude. This would further corroborate the trend among pandalids of an enhanced energy allocation for reproduction at higher latitudes (Fig. 3). However, due to the lack of RO data from other pandalids, such a trend is only suggestive but not conclusive. More data from pandalid species inhabiting different climate zones are indispensable to elucidate the possible relation between reproductive investment and latitude.

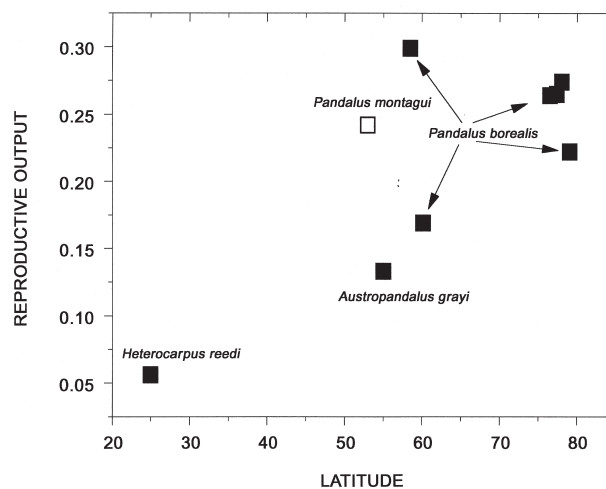


FIG. 3. – Comparison of reproductive output among different pandalid species in relation to latitude (independent of their location in the northern or southern hemisphere). Indicated values are based upon dry mass with the exception of *P. montagui* (wet mass data according to Clarke (1987)). Data regarding *P. borealis* refer to different populations (Clarke *et al.*, 1991). RO-value for *H. reedi* refers to a population from northern Chile (Wehrtmann and Andrade, 1998).

ACKNOWLEDGEMENTS

This study was financially supported by the “Deutscher Akademischer Austauschdienst” (DAAD), “Deutsche Gesellschaft für Technische Zusammenarbeit” (GTZ) and the Universidad Austral de Chile (Dirección de Investigación y Desarrollo, Project N° E-91-1 and S-94-53). We would like to thank the Alfred-Wegener-Institut and especially Prof. Dr. W. Arntz for providing the possibility to carry out this study. Thanks go also to the crew of the RS “Victor Hensen” and to Dr. M. Gorny for their support during the cruise. We are thankful to the Universidad de Magallanes (UMAG), Punta Arenas, Chile, for their logistic support, and to Profs. C. Ríos and E. Mutschke (UMAG) for their kind collaboration. We gratefully acknowledge the assistance of Dr. T. Brey (AWI) and Mr. Roberto Arias (Universidad Austral de Chile) who helped us with the statistical analyses and with the revision of the samples, respectively. M.A. Lardies was supported by a CONICYT doctoral scholarship.

REFERENCES

- Al-Adhub, A.H.Y. and A.B. Bowers. – 1977. Growth and breeding of *Dichelopandalus bonnieri* in Isle of Man waters. *J. mar. biol. Ass. U.K.*, 57: 229-238.
- Allen, J.A. – 1966. Observations on the biology of *Pandalus montagui* [Crustacea: Decapoda]. *J. mar. biol. Ass. U.K.*, 43: 665-682.
- Amsler, M.O. and R.Y. George. – 1984. Seasonal variation in the biochemical composition of the embryos of *Callinectes sapidus* Rathbun. - *J. Crust. Biol.*, 4: 546-553.
- Arntz, W. and M. Gorny. – 1996. Cruise report of the joint Chilean-German-Italian Magellan “Victor Hensen” Campaign in 1994. *Ber. Polarforsch.*, 190: 1-113.
- Arntz, W.E., M. Gorny, R. Soto, M.A. Lardies, M.A. Retamal, and I.S. Wehrtmann. – 1999. Species composition and distribution of benthic decapod crustaceans in the waters off Patagonia and Tierra del Fuego, South America. *Sci. Mar.*, 63(Supl. 1):303-314.
- Bahamonde, N. and G. Henríquez. – 1970. Sinopsis de datos biológicos sobre el camarón nailon *Heterocarpus reedi* Bahamonde, 1955. *FAO Fish. Rep.*, 57: 1607-1627.
- Clarke, A. – 1987. Temperature, latitude and reproductive output. *Mar. Biol. Prog. Ser.*, 38: 89-99.
- Clarke, A. – 1990. The biochemical composition of eggs from *Macrobrachium rosenbergii* in relation to embryonic development. *Comp. Biochem. Physiol.*, 96B: 505-511.
- Clarke, A. – 1992. Reproduction in the cold: Thorson revisited. *Invertebr. Reprod. Develop.*, 22: 175-184.
- Clarke, A. – 1993 a. Egg size and egg composition in polar shrimps (Caridea; Decapoda). *J. Exp. Mar. Biol. Ecol.*, 168: 189-203.
- Clarke, A. – 1993b. Reproductive trade-offs in caridean shrimps. *Funct. Ecol.*, 7: 411-419.
- Clarke, A., C. Hopkins and M. Nilssen. – 1991. Egg size and reproductive output in the deepwater prawn *Pandalus borealis* Krøyer, 1838. *Funct. Ecol.*, 5: 724 - 730.
- Corey, S., and D.M. Reid. – 1991. Comparative fecundity of decapod crustaceans. I. The fecundity of thirty-three species of nine families of caridean shrimp. *Crustaceana*, 60: 270-294.
- Gorny, M., W.E. Arntz, A. Clarke and D.J. Gore. – 1992. Reproductive biology of caridean decapods from the Weddell Sea. *Polar Biol.*, 12: 111-120.
- Hancock, D.A. and G. Henríquez. – 1968. Stock assessment in the shrimp (*Heterocarpus reedi*) fishery of Chile. *FAO Fish. Rep.*, 57: 443-465.
- Hendrickx, M.E. and M.K. Wicksten. – 1989. Los Pandalidae (Crustacea: Caridea) del Pacífico Mexicano, con una clave para su identificación. *Caldasia*, 16: 71-86.
- Hines, A.H. – 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.*, 69: 309-320.
- Hines, A.H. – 1991. Fecundity and reproductive output in nine species of *Cancer* crabs (Crustacea, Brachyura, Cancridae). *Can. J. Fish. Aquat. Sci.*, 48: 267-275.
- Holthuis, L.B. – 1952. Reports of the Lund University Chile Expedition 1948 -49. 5. The Crustacea Decapoda Macrura of Chile. *Lunds Univ. Årsskr. N.F. Avd.2, Bi.*, 47, 10: 1-109.
- Holthuis, L.B. – 1980. FAO Species Catalogue. Vol 1. Shrimps and prawns of the World. *FAO Fish. Synop.*, 125:1-275.
- Kuris, A.M. – 1991. A review of patterns and causes of crustacean brood mortality. In: F.R. Schram (ed.), *Crustacean Egg Production*. Crustacean Issues 7, pp. 117-141. A. A. Balkema, Rotterdam.
- Lardies, M.A. – 1995. *Variación latitudinal en la biología reproductiva de Betaeus truncatus (Decapoda: Alpheidae)*. Lic. thesis, Univ. Austral de Chile.
- Lardies, M.A. and I.S. Wehrtmann. – 1996. Aspects of the reproductive biology of *Petrolisthes laevigatus* (Guérin, 1835) (Decapoda: Anomura: Porcellanidae). I. Reproductive output and chemical composition of eggs during embryonic development. *Arch. Fish. Mar. Res.*, 43(2): 121-135.
- Lardies, M.A. and I.S. Wehrtmann. – 1997. Egg production in *Betaeus emarginatus* (H. Milne Edwards, 1837) (Decapoda: Alpheidae): fecundity, reproductive output and chemical composition of eggs. *Ophelia*, 46: 165-174.
- Pandian, T.J. – 1967. Changes in chemical composition and caloric content of developing eggs of the shrimp *Crangon crangon*. *Helgoländer Meeresunters.*, 16: 216-224.
- Pandian, T.J. – 1970. Ecophysiological studies on the developing eggs and embryos of the European lobster *Homarus gammarus*. *Mar. Biol.*, 5: 154-167.
- Pandian, T.J. – 1994. 3. Arthropoda - Crustacea. In: K.G. Adiyodi and R.G. Adiyodi (eds), *Reproductive Biology of Invertebrates*, Vol. VI, Part B, pp. 39-166. Oxford & IBH Publ. Co. Pvt. Ltd., New Delhi.
- Parson, D.G. and J. Fréchette. – 1989. Fisheries for northern shrimp (*Pandalus borealis*) in the northwest Atlantic from Greenland to the Gulf of Maine. In: J.F. Caddy (ed.), *Marine Invertebrate Fisheries - Their Assessment & Management*, pp. 63-85. J. Wiley & Sons, New York.
- Retamal, M.A. – 1995. *Plesionika santaecatalinae* Wicksten, 1983 en agua chilena. *Gayana Oceanol.*, 3(1): 1-2.
- Roa, R. and B. Ernst. – 1996. Age structure, annual growth, and variance of size-at-age of the shrimp *Heterocarpus reedi*. *Mar. Ecol. Prog. Ser.*, 137: 59-70.
- Sokal, R.R. and F.J. Rohlf. – 1981. *Biometry - The Principles and Practise of Statistics in Biological Research*. W. H. Freeman and Company, New York.
- Thessalou-Legaki, M. – 1992. Reproductive variability of *Parapandalus narval* (Crustacea: Decapoda) along a depth gradient. *Estuar. Coast. Shelf Sci.*, 35: 593-603.
- Thorson, G. – 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25: 1-45.
- Turner, R.L. and J.M. Lawrence, 1979. Volume and composition of echinoderm eggs: implications for the use of egg size in life-history models. In: S.E. Stancyk (ed.), *Reproductive Ecology of Marine Invertebrates*, The Belle W. Baruch Library Mar. Sci. 9, pp. 25-40. Univ. South Carolina Press, Columbia.
- Valdés, L., M.T. Alvarez-Ossorio and E. González-Gurriarán. – 1991. Incubation of eggs of *Necora puber* (L., 1767) (Decapoda, Brachyura, Portunidae). Volume and biomass changes in embryonic development. *Crustaceana*, 60: 163-177.
- Wehrtmann, I.S. – 1990. Distribution and reproduction of *Ambidexter panamense* and *Palaemonetes schmitti* in Pacific Costa Rica (Crustacea, Decapoda). *Rev. Biol. Trop.*, 38(2A): 327-329.
- Wehrtmann, I.S. and G. Andrade. – 1998. Egg production in *Heterocarpus reedi* from northern Chile, with a comparison between iced and living females (Decapoda: Caridea: Pandalidae). *Ophelia*, 49(1): 71-82.
- Wehrtmann, I.S. and A. Carvacho. – 1997. New records and distribution ranges of shrimps (Crustacea: Decapoda: Penaeoidea and Caridea) in Chilean waters. *Proc. Biol. Soc. Wash.*, 110: 49-57.
- Wehrtmann, I.S. and G. Kattner. – 1998. Changes in volume, biomass and fatty acids of developing eggs in *Nauticaris magellanica* (Decapoda: Caridea): a latitudinal comparison. *J. Crust. Biol.*, 18 (3): 413-422.