Revista Chilena de Historia Natural
73:705-715, 2000

Natural history of *Emerita analoga* (Stimpson) (Anomura, Hippidae) in a sandy beach of northern Chile

Historia natural de *Emerita analoga* (Stimpson) (Anomura, Hippidae) en una playa arenosa del norte de Chile

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ABSTRACT

Sediment samplings were carried across the intertidal of the beach at Hornitos, northern Chile (22°26´S) during August and November 1996 and March, July and November 1997 for a study of the reproductive and population biology of *Emerita analoga* (Stimpson) (Decapoda, Anomura) in a region of the Chilean coast characterized by persistent upwelling. The highest abundances of *E. analoga* occurred during March and December 1997. During November 1996, March and December 1997, the highest abundances occurred below the effluent line, while in July 1996 and August 1997, most of the stages of *E. analoga* occurred in higher abundances above the effluent line. Ovigerous females were recorded over the entire study period. Juveniles were also present during all sampling months, peaking during March 1997. Body size of ovigerous females varied between 12.6 and 26.4 mm. Fecundity increased significantly with body size of females in all samples analyzed. The analyses of recruitment pattern for males and females suggest the existence of two pulses in the recruitment of *E. analoga* at Hornitos: one between October and December, and another one between February and March. Growth analyses show that females have growth rates a maximum body sizes higher than males. Comparisons with similar studies carried out at the coast of south central Chile (ca. 39° S), a region where upwelling occurs occasionally, show that *E. analoga* from this region have similar growth rates but attain a greater maximum body size than in Hornitos. It is concluded that proximity to areas of persistent upwelling seems not to affect life history of *E. analoga* in northern Chile.

Key words: *Emerita analoga*, sandy beach, northern Chile.

RESUMEN

Se realizaron muestreos de sedimentos en la playa de Hornitos, norte de Chile (ca. 22°26´S) durante Agosto y Noviembre de 1996 y Marzo, Julio y Noviembre de 1997, con el objetivo de estudiar la biología reproductiva y poblacional de *Emerita analoga* (Stimpson) (Decapoda, Anomura) en una región de la costa Chilena, caracterizada por la presencia de surgencias persistentes. Las mayores abundancias de *E. analoga* ocurrieron durante Marzo y Diciembre de 1997. Durante Noviembre de 1996, Marzo y Diciembre de 1997, las abundancias más altas ocurrieron bajo la línea de efluente, mientras que durante Julio de 1996 y Agosto de 1997, la mayoría de las estadios *E. analoga* ocurrieron con mayor abundancia sobre esa línea. Se recolectaron hembras ovigeras durante todo el período de estudio. Los juveniles también estuvieron presentes durante todo el muestreo, registrándose las mayores abundancias durante Marzo de 1997. La talla de las hembras ovigeras varío entre 12,6 y 26,4 mm. La fecundidad aumentó significativamente con la talla de las hembras en cada período estacional analizado. El análisis del patrón de reclutamiento de machos y hembras sugiere la existencia de dos pulsos en el reclutamiento de *E. analoga* en Hornitos: uno entre Octubre y Diciembre, y otro entre Febrero y Marzo. Los análisis del crecimiento muestran que las hembras tienen tasas de crecimiento y tamaños corporales máximos mayores que los machos. Comparaciones con estudios similares realizados en la costa del centro sur de Chile (ca. 39° S), muestran similares tasas de crecimiento y tallas corporales máximas de *E. analoga* mayores en el sur que en la población de Hornitos. Por lo tanto, se concluye que la cercanía a áreas de surgencias persistentes parece no afectar la historia de vida de *E. analoga* en el norte de Chile.

Palabras clave: *Emerita analoga*, playas arenosas, norte de Chile.

INTRODUCTION

Exposed sandy beaches are the most common coastal habitats along the coast of Chile, north of Isla de Chiloé (ca. 42° S). In terms of species richness, the intertidal macroinfauna living in those habitats is characterized by dominance of crustaceans, mainly peracarids (Jaramillo 1987, 1994). In terms of abundance, the anomuran crab *Emerita analoga* (Stimpson) is one of the dominant species along all this coast and contributes more biomass by far than any other species (Jaramillo et al. 1993, 1998), a similar situation to its northern hemisphere counterpart inhabiting sandy beaches of California (Dugan & Hubbard 1996).

In Chile, the reproductive and population biology of *Emerita analoga* has been studied in sandy beaches of central (Osorio et al. 1967, Conan et al. 1975) and south central Chile (Contreras et al. 1999). So far, no studies have been carried out on sandy beaches of northern Chile, a coastal area characterized by persistent upwelling events (Fonseca & Farías 1987, Marín et al. 1993). In contrast, upwelling only occasionally influences coastal areas located further south. It has been argued that primary productivity is enhanced by upwelling waters, which in turn increase secondary production of benthic invertebrates (Tarazona et al. 1988, Arntz et al. 1987, Bosman et al. 1987). Bearing in mind that upwelling waters result in higher primary productivity at the coast of northern Chile (Marín et al. 1993, Rodriguez 1998[1]) and that temperature affects biology of invertebrates (Brusca & Wallerstein 1979), it is reasonable to expect that northern populations of *Emerita analoga* will differ in their reproductive and life history characteristics from populations located further south on the Chilean coast. To evaluate this, we carried out seasonal samplings at a sandy beach located close to the upwelling center of Mejillones (ca. 22° S) and compared the results with that already published for the coast of south central Chile (Contreras et al. 1999).

MATERIAL AND METHODS

Study area and physical measurements

The study beach was located at Hornitos (22° 26' S, 70° 13' W), on the coast of Antofagasta, northern Chile. The length of the beach is approximately 4000 m and is backed by a cliff rising to about 50 m above sea level.

The morphology of the sampling site (i.e., beach face slope at the site of the transects) was determined by Emery´s profiling technique (Emery 1961). Sediment samples for grain size analysis were collected from the uppermost layer (40 mm) of sediment at each macroinfaunal sampling station (see below) with a 35 mm diameter plastic cylinder. The analyses were carried out using a settling tube (Emery 1938). Mean grain size was calculated according to the moments computational method (Seward - Thompson & Hails 1973) and used to estimate sand fall velocity according to the method described by Gibbs et al. (1971). Temporal variability of grain sizes was analyzed with ANOVA (Sokal & Rohlf 1995).

Wave height was estimated by measuring the height of breaking waves (n = 10) with graduated poles against the horizon, and adding the result to the height difference between the location of the observer and the lowest point where the backwash met the next incoming swash bore. The wave period (measured with a stop watch) was the time interval between breaking waves. Temporal variability of that wave characteristics was analyzed with ANOVA (Sokal & Rohlf 1995). From estimated mean wave height, wave period and sand fall velocity, Dean´s parameter (Ω) (Short & Wright 1983) was calculated. Surf water temperature was measured at each sampling period with a mercury thermometer (0.1° C of precision). Water samples collected from the surf zone were used for salinity determinations in the laboratory.

Sampling of Emerita analoga and data analyses

Seasonal samples were collected during spring low tides of July and November 1996 and March, August and December 1997. The specimens of *Emerita analoga* used for this study came from a general intertidal macroinfauna survey. In that survey, sediments were collected with plastic cylinders (250 mm in diameter) at ten equally spaced levels (stations) along four replicated transects (separated by 1 m) extending from above the drift line to the swash zone. The uppermost station of each transect was located above the drift line, the second on the drift line and the last one at the seaward limit of the swash zone (indicated by bore collapse). The sediment was sieved through 1 mm mesh and the specimens were stored in 5 % formalin until sorting. Abundances per m^2 were used to draw kite diagrams to analyze zonation of the different population stages.

Individuals were measured using the length of the cephalothorax (thus, Lc = body size) i.e., from the tip of the rostrum to the distal scoop of the cephalothorax. The smallest individuals (i.e., Lc < 5 mm) were measured using a dissection glass

[1] RODRIGUEZ (1988) Estudios oceanográficos y biológicos en Bahía Mejillones del Sur, Antofagasta, Chile. estados actual. Resúmenes XVIII Congreso de Ciencias del Mar, mayo 1998 Iquique, Chile: 119.

equipped with a graticule, whilst the largest individuals were measured with 0.01 mm precision calipers. Animals were classified as males, females without eggs (hereafter females), ovigerous females and juveniles (i.e. individuals smaller than 4 mm). Sexes were distinguished on the basis of anatomical studies on species of the genus *Emerita* carried out by Knox & Boolotian (1963), Osorio et al. (1967) and Penchaszadeh (1971). Temporal variability of the abundances of the total population and that of each life stage was analyzed with ANOVA on log (n+1) transformed data and the a posteriori LSD (least significant difference) test (Sokal & Rohlf 1995).

Fecundity analyses were carried out for each sampling period, except July 1996 when no ovigerous females were collected. The egg mass was carefully extracted from each female, and the diameters of 10 eggs were measured to estimate mean volume (using the formula for the volume of a sphere). The total number of eggs in each mass was determined by displacement of distilled water in a graduated test tube (0.1 ml accuracy) (Díaz et al. 1983). Fecundity values were log transformed to calculate regressions between number of eggs carried by ovigerous females against body size. Differences of slopes and adjusted averages among regression lines estimated for each season were analyzed with ANCOVA (Sokal & Rohlf 1995).

For the determination of growth parameters, the ELEFAN (Electronic Length Frequency Analyses; see Gayanilo et al. 1989) routine of the FISAT Program (Gayanilo et al. 1996) was applied to the seasonal composition of the population by sizes, discriminated by sex. The method assumes that body growth follows the von Bertalanffy Growth Equation (seasonally oscillating version) (von Bertalanffy 1938), (Hoenig and Hanumara, 1982; Sommers, 1988). For this analysis, class intervals of 2 mm for males and females were chosen following the criteria of Wolff (1989) and Sparre (1989). Longevity was estimated on the basis of the maximum observed length and the growth parameters derived from length - frequency distribution analyses.

The ELEFAN program does not assume normality in the length frequency distributions, but uses the information on the height and shape of the age distributions identified in the length frequency data. It identifies peaks and troughs in the samples and then fits the growth curve which passes trough a maximum number of peaks (Pauly et al. 1984). An index of goodnes of fit, called Rn, is determined by the exponential form of the ESP / ASP ratio (Gayanilo et al. 1989).

To compare different growth rate estimates, the standard growth index ϕ' (phi prime: Pauly & Munro 1984, Vakily 1990) was employed as a measure of overall growth performance (Sparre et al. 1989). This rationale provides a unified parameter of growth performance which does not show variations as large as K and L_∞ values (Sparre et al. 1989).

The recruitment pattern was analyzed through the estimated growth parameters (discriminated by sex) by projecting the length - frequency data backward onto the time axis (Pauly et al. 1984, Gayanilo et al. 1989). Normal distribution patterns in recruitment were distinguished using the maximum likelihood approach «NORMSEP - Hasselblad» contained in the FISAT Program (see Gayanilo et al., 1996 for further details).

RESULTS

Surf and beach characteristics

Water temperature in the surf zone of the beach at Hornitos showed a seasonal trend, with the highest values during March and December 1997 (22 and 24° C, respectively) and the lowest during August 1997 (15 ° C). Water salinity showed little variation, with a range of; 32.2 - 33.6 ‰.

During the the sampling period the wave heights varied between 1188 and 1562 mm, while wave period varied between 12.6 and 16.6 seconds (Table 1). Results of ANOVA and LSD test show that waves were significantly higher during November 1996 and August 1997. No significant differences were found when seasonal wave periods were compared. Mean grain sizes generally corresponded to fine sands (Folk 1980), with a significant increase in grain size during August and December 1997 (means close to 250 microns) (Table 1). The following values of Dean´s parameter (Ω) were estimated: July 1996 = 2.8, November 1996 = 2.3, March 1997 = 3.6, August 1997 = 3.8 and December 1997 = 2.2. According to these values, the beach at Hornitos can be classified as low intermediate (values of Ω between 1 and 6, sensu Short & Wright 1983). The largest change in beach face slope occurred between the first three samplings. The beach was steepest during July 1996 (1/19); between this date and November 1996, the beach slope flattened to 1/29. By March 1997 the slope had steepened once again to 1/24, followed by 1/23 and 1/25 during August and December 1997, respectively.

Abundance and intertidal distribution of Emerita analoga

The total abundance of *E. analoga* peaked significantly during March and December 1997 (65682 and 159354 ind m^{-1}, respectively) (Table 2). Juveniles, males and females peaked significantly at the same months, while ovigerous females had their maximum abundances during March and August 1997 (Table 2). During November 1996, March and December 1997, the highest abundances occurred below the effluent line (water table outcrop), while during July 1996 and August 1997, most of the stages of *E. analoga* occurred in higher abundances above the effluent line (Fig. 1). In general, all stages occupied the same beach levels. However ovigerous females tended to occur lower down in the swash zone than other stages in July 1996 and December 1997 (Fig. 1).

Reproductive biology and fecundity

Ovigerous females were recorded over the entire study period. However, the greatest abundances were registered during the winter sampling of 1997 (August) (Table 2). Juveniles were also present during all sampling months, peaking during March 1997.

Body size of ovigerous females varied between 12.6 and 26.4 mm Lc. Fecundity varied between 1386 and 11937 eggs per ovigerous female (Table 3). Fecundity increased significantly with size of females at each seasonal period analyzed (Table 3, Fig. 2). The estimated fecundity of females with a body size of 20 mm Lc showed its highest value during spring (November) and the lowest at the end of summer (March) (Table 3). The results of ANCOVA analyses showed significant differences between slopes and adjusted means of the seasonal regression lines (Table 4) indicating that the relationship between number of eggs and body size of ovigerous females varied between sampling periods.

Recruitment and growth

As mentioned above, juveniles were collected throughout the study period; they peaked during March 1997 (about 59% of the whole population). The highest frequencies of small males and females occurred during March and December

TABLE 1

Results of the ANOVA and the a posteriori test LSD on the mean of wave heigth, wave period and grain size during the study period. Means linked by lines do not differ significantly

Resultados de los ANDEVA y del test a posteriori LSD de los promedios de la altura de las olas, período y tamaño medio del grano, durante el período de estudio. Los promedios unidos por líneas no difieren significativamente

Source of variation	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
wave height					
Between groups	7581	4	1895	7,38	0,000
Within groups	10786	42	257		
Total	18367	46			
Grouping of means	Nov 96	Aug 97	Jul 96	Mar 97	Dec 97
according LSD test	156 (cm)	147 (cm)	138 (cm)	128 (cm)	118 (cm)
wave period					
Between groups	34	4	9	0,78	0,542
Within groups	493	45	11		
Total	527	49			
Grouping of means	Nov 96	Aug 97	Jul 96	Mar 97	Dec 97
according LSD test	15.7 (s)	12.6 (s)	16.1 (s)	14.9 (s)	16.6 (s)
wave period					
Between groups	16909	4	4227	8,70	0,000
Within groups	21855	45	486		
Total	38764	49			
Grouping of means	Jul 96	Nov 96	Mar 97	Aug 97	Dec 97
according LSD test	227 (mm)	217 (mm)	206 (mm)	250 (mm)	253 (mm)

1997, when they represented a percentage close to 70% (Fig. 3). The analyses of recruitment patterns for males and females (based on FISAT program) suggest the existence of two pulses in the recruitment of *E. analoga* at Hornitos. Thus, the bimodal shape of recruitment (Fig. 4) could be attributed to the presence of a recruitment peak between October and December, and another one around March (cf. Fig. 3).

Growth parameters of *E. analoga* at Hornitos show that females have higher growth rates and greater maximum body sizes than males (see values of $L\infty$ and growth index ϕ' at Table 5). Values of C and Wp (Winter point) suggest seasonal growth oscillations and slowdown of growth during the winter (cf. Table 5 and Fig. 3). The maximum longevity for individuals both sexes was estimated as 3.5 years.

DISCUSSION

The results of this study showed both similarities and differences with previous studies carried out along the distributional range of *E. analoga* on the Pacific coast between Chile and California. As in the present study, it has been reported that *E. analoga* reproduces all year round in sandy

TABLE 2

Results of the ANOVA and the a posteriori test LSD on the mean abundance (ind m -1) of the total population, juveniles, males, females and ovigerous females of *E. analoga*. Mean abundances linked by a lines do not differ significantly

Resultados de los ANDEVA y del test a posteriori LSD de los datos de abundancia promedio del total de la población, juveniles, machos, hembras y hembras ovigeras *de E. analoga*. Las abundancias promedio unidas por líneas no difieren significativamente

Source of variation	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
total					
Between groups	12,6	4	3,2	22,2	0,000
Within groups	2,3	16	0,1		
Total	14,9	20			
Grouping of means	Jul 96	Nov 96	Aug 97	Mar 97	Dec 97
according LSD test	5883	5874	1908	65682	159363
juveniles					
Between groups	29,5	4	7,4	5,3	0,007
Within groups	22,3	16	1,4		
Total	51,9	20			
Grouping of means	Jul 96	Nov 96	Aug 97	Mar 97	Dec 97
according LSD test	1373	158	201	57136	13166
males					
Between groups	10,7	4,0	2,7	30,9	0,000
Within groups	1,4	16,0	0,1		
Total	12,1	20,0			
Grouping of means	Jul 96	Nov 96	Mar 97	Dec 97	Aug 97
according LSD test	2749	4246	14989	79275	174
females					
Between groups	131131,0	4	32782,7	32,8	0,000
Within groups	16008,4	16	1000,5		
Total	147139,0	20			
Grouping of means	Jul 96	Nov 96	Aug 97	Mar 97	Dec 97
according LSD test	1682	1260	634	11430	53126
ovigerous females					
Between groups	1906,0	4	476,5	8,6	0,001
Within groups	892,2	16	55,8		
Total	2798,2	20			
Grouping of means	Jul 96	Nov 96	Dec 97	Mar 97	Aug 97
according LSD test	80	210	90	521	900

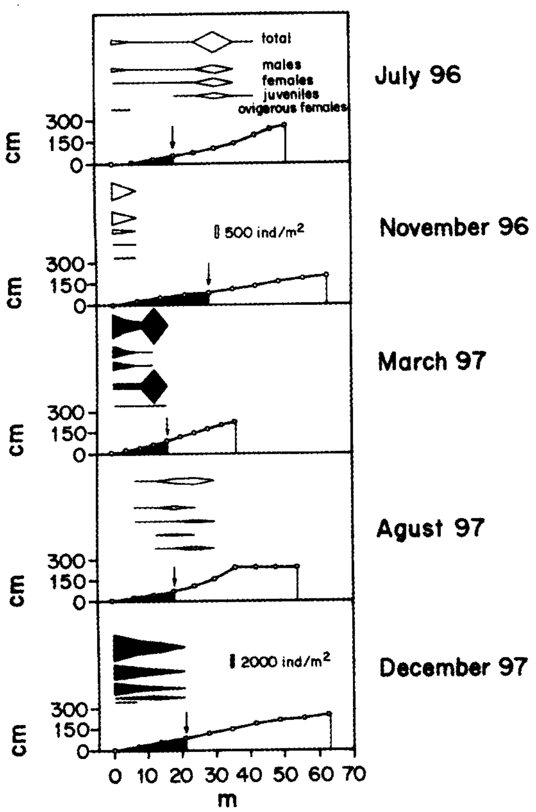

Fig. 1. Intertidal zonation of the different life stages of *E. analoga* at the beach of Hornitos. Beach face slopes are presented for each sampling date. The black areas correspond to the swash and resurgence zones; the arrows indicate the position of the effluent line.

Zonación intermareal de los diferentes estadios de vida de *E. analoga* en la playa de Hornitos. Se presentan los perfiles de playa para cada fecha de muestreo. La áreas negras corresponden a las zonas de resaca y resurgencia; las flechas indican la posición de la línea de efluente.

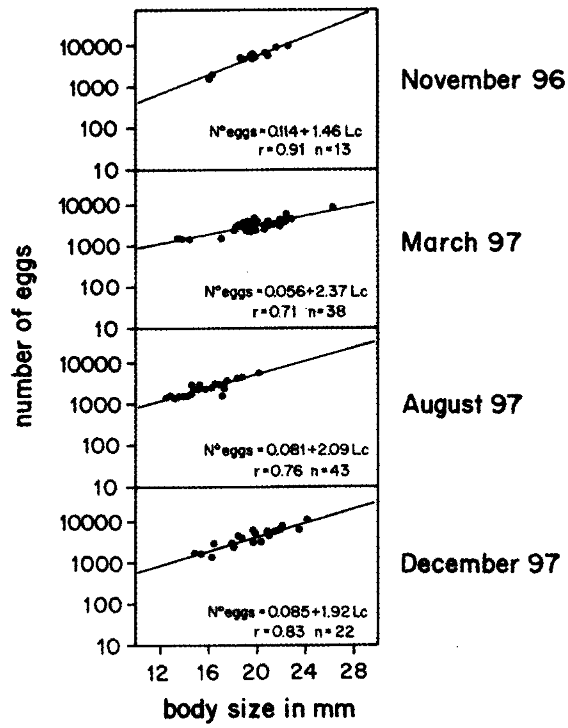

Fig. 2. Comparisons between the number of eggs and body size of ovigerous females of *E. analoga* for each seasonal period.

Comparaciones entre el número de huevos y el tamaño corporal de hembras ovígeras de *E. analoga* en cada período estacional.

beaches of central Chile (Osorio et al. 1967), south central Chile (Contreras et al. 1999) and California (Cox & Dudley 1968). With respect to recruitment, however, Osorio et al. (1967) and Efford (1965), found just one recruitment period occurring during spring in a sandy beach of central Chile (El Tabo, ca. 33°S) and California (ca. 33°N). However, Conan et al. (1975) found two

TABLE 3

Ranges in body size and eggs number carried by ovigerous females of *Emerita analoga*, results of regression analyses between body size and number of eggs, number of data (n) and estimated fecundity for an ovigerous female with Lc = 20.0 mm

Rangos del tamaño corporal y número de huevos portados por las hembras de *Emerita analoga*, resultados de los análisis de regresión entre tamaño corporal y número de huevos, número de datos y fecundidad estimada para una hembra de Lc = 20.0 mm

	body size (range in mm)	eggs number (range)	slope	intercept	r	n	estimated fecundity (Lc = 20.0 mm)
November 96	16.1 - 22.7	1622 - 9417	0,114	1,46	0,91	13	5495
March 97	13.6 - 26.4	1386 - 8625	0,056	2,37	0,71	38	3090
August 97	12.6 - 20.3	1386 - 5968	0,081	2,09	0,76	43	5129
December 97	15.0 - 24.2	1386 - 11937	0,085	1,92	0,83	22	4169

TABLE 4

Results of ANCOVA analyses carried out to compare seasonal regression lines describing the relationships between body size and number of eggs in ovigerous females of *Emerita analoga*. Seasonal sampling (months) linked by a line do not differ significantly

Resultados de los ANCOVA realizados para comparar las líneas estacionales de regresión que describen las relaciones entre tamaño corporal y número de huevos en hembras ovígeras de *Emerita analoga*. Los muestreos estacionales (meses) unidos por líneas no difieren significativamente

Source of variation	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Homogeneity of slopes					
due to regressions	3,11	1,0	3,11	379,34	0,000
among slopes	0,18	3,0	0,06	7,23	0,000
estimated residuals	0,89	108,0	0,01		
total	4,18	112,0			
	Nov 96	Dec 97	Aug 97	Mar 97	
Homogeneity of adjusted means					
among means	0,31	3,0	0,10	12,51	0,000
error	0,89	108,0	0,01		
total	1,19	111,0			
	Nov 96	Aug 97	Mar 97	Dec 97	

recruitment periods (during autumn and spring-summer) at another site in central Chile (Valparaíso, ca. 32°S), a situation similar to that found by Contreras et al. (1999) further south (ca. 39°S). These differences may well be related to recruitment failures reported for coastal benthic invertebrates with planktonic larval stages during sporadic oceanographic events such as ENSO (cf. Moreno et al. 1998). Due to the fact that the larvae of *E. analoga* remain in the plankton for a relatively long time (3-4 months, Johnson 1939), it can be argued that changes in water conditions will affect them, and consequently benthic populations will also be affected. It is also possible that differences in analytical methods could result in the observed differences since both the present study and that of Contreras et al. (1999) used sofisticated statistical packages (i.e., FISAT, Gayanilo et al 1996) for analysis of recruitment patterns, which were not available at the time Osorio et al. (1967) and Efford (1965) carried out their studies.

During the winter samplings of July 1996 and August 1997, most of the population of *E. analoga* was found above the effluent line. That situation did not show any relationship with the seasonal variability of the beach characteristics studied; i.e. wave characteristics and mean grain size did not

TABLE 5

Growth parameters of *Emerita analoga* at the beaches of Hornitos and Mehuín (data from Contreras et al. 1999) estimated by FISAT Program

Parámetros de crecimiento de en las playas de Hornitos y Mehuín (datos tomados de Contreras et al. 1999) estimados usando el Programa FISAT

parameters	♀ from Hornitos	♀ from Mehuín	♂ from Hornitos	♂ from Mehuín
L_∞	28,00	33.00 - 34.00	19,00	23.00 - 26.00
K (1 / year)	0,90	0.60 - 0.80	0,70	0.48 - 0.31
C	1,00	1,00	1,00	1,00
WP	0,60	0.52 - 0.60	0,55	0.50 - 0.81
ϕ'	2,85	2.84 - 2.94	2,40	2.32 - 2.50
Rn[1]	0,25	0.21 - 0.39	0,20	0.21 - 0.52

[1] = goodness of fit index (explained sum of peaks / available sum of peaks) / 10 (see Gayanilo et al. 1989)

differ significantly during that two winter samplings (see Table 1). Since this species is tidal migrant (MacGinitie 1938, Fusaro 1980), it may be argued that the higher shore distribution of *E. analoga* during July 1996 and August 1997, as compared to the other months, is the result of tidal variability. Thus, even when this species moves up and down the beach following the upper limit of the swash, there are some times (e.g. different tidal ranges) when the migrant population may be left behind by the outgoing tide forming patches of stranded animals. Intermediate sandy beaches (such as Hornitos) are the most variable along a gradient of morphodynamic beach types (Short & Wright 1983). Since physical variability in wave energy, grain size, beach face slope and topographic features result in different swash climates (McArdle & McLachlan 1994), it may be hypothesized that intermediate beaches will have more variable swashes which will affect the migration of *E. analoga* and thus its intertidal zonation.

It has been predicted that marine invertebrates living in colder waters or higher latitudes present larger body sizes and lower growth rates than invertebrates living in warmer waters or lower latitudes (Templeman 1936, Abele 1982). Thus, studies carried out on *E. analoga* and other decapods in the northern hemisphere report inverse relationships between size at first maturity and water temperature (Dugan et al 1991, Templeman , 1936). Even though the studies of reproductive biology of *E. analoga* are scarce along the Chilean coast and carried during different seasons, it is possible to make some comparisons. For example, we estimated a body size of 12-13 mm as the minimum size at sexual maturity for crabs collected at Hornitos, whilst Osorio et al. (1967) reported a minimum of 15-16 mm for specimens collected at El Tabo (about 800 km south of Hornitos). Furthermore, Contreras et al. (1999) found that that minimum size at maturity increased to about 16-18 mm at a beach located in south central Chile (Mehuín, about 2000 km south of Hornitos). Previous studies showed that maximum sizes (represented by the parameter L_∞) are higher

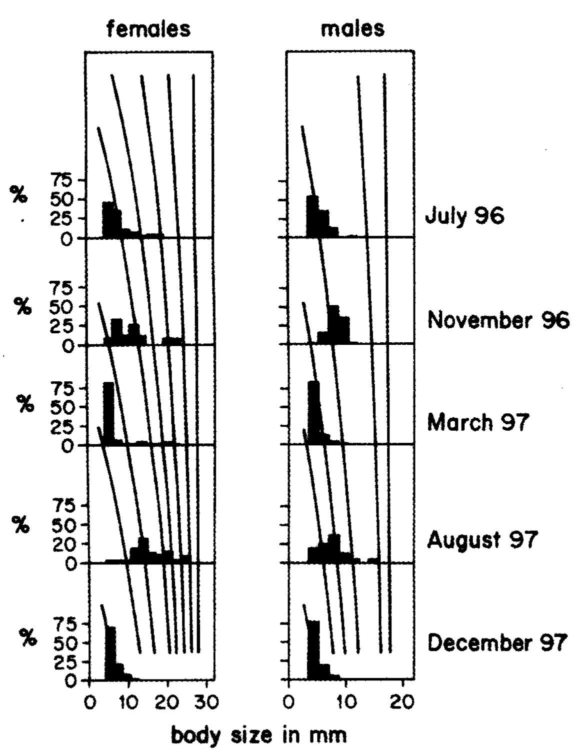

Fig. 3. Size frequency distribution and growth curves of females and males of *E. analoga* estimated by FISAT Program.

Distribución de frecuencias de tallas y curvas de crecimiento de hembras y machos de *E. analoga* estimados a partir del Programa FISAT.

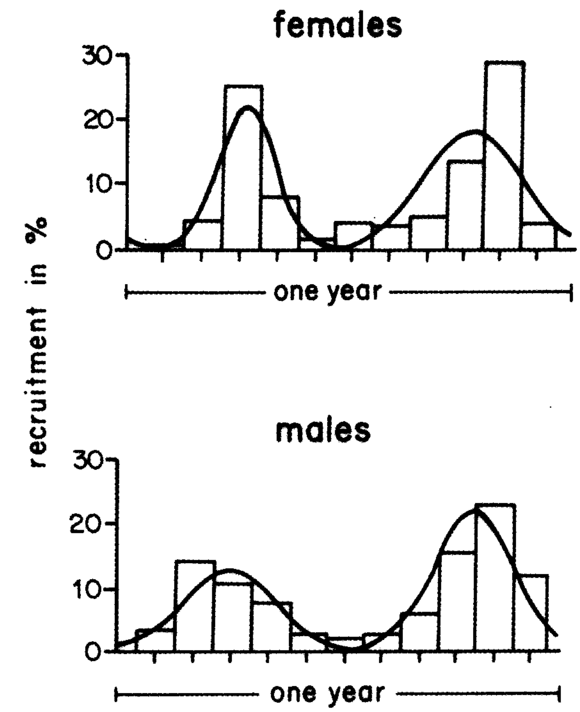

Fig. 4. Recruitment pattern of females and males of *E. analoga* estimated by FISAT Program. The bell shaped curves indicate the number of recruitment pulses throughout the study period.

Patrón de reclutamiento de hembras y machos de *E. analoga* estimado por el Programa FISAT. Las curvas en forma de campana indican los pulsos de reclutamiento a lo largo del período de estudio.

in higher latitudes (Templeman 1936, Abele 1982). Thus, while in this study we estimated a maximum body size of 18 mm and 28 for males and females collected at Hornitos, Contreras et al (1999) registered values between 23-26 mm for males and 33-34 mm for females (Table 5). Although Osorio et al. (1967) and Conan et al. (1975) do not give values of $L\infty$, the maximum length of males was close to 19 mm and that of females about 29 mm. These latitudinal gradients in body sizes of *E. analoga* are similars to those found by Dugan et al. (1991) for Californian populations. On the other hand, growth rates (as shown by the values of parameter ϕ') of males and females at Hornitos were similar to those of southern populations (see Table 5), although the ranges in that parameter were higher at the northern population.

The growth curves reported for *E. analoga* in the present study as well as thus reported by Contreras et al (1999), show a seasonal pattern of growth. Although Osorio et al. (1967) and Conan et al. (1975) do not report growth parameters, both agree that during winter time a slowdown of growth occurs. Seasonality is an important characteristic in growth of short lived animals (Pauly 1990, Sparre, 1990) and is usually the result of environmental variability, primarily oscillations of water temperature between winter and summer (Pauly, 1985). Similarly, Fusaro (1978) reported differences in growth rates of two populations occurring in Californian beaches with differing temperatures.

As mentioned earlier, the beach at Hornitos is close to the upwelling center of Mejillones, a situation which could result in faster growth rates fuelled by enhancement of primary productivity at these northern area of the Chilean coast (cf. Marin et al. 1993). However, no such situation was found in this study, again demonstrating that proximity to a persistent upwelling area does not necessarily result in higher growth rates or larger body sizes of sandy beach invertebrates (cf. Jaramillo et al. 1998). The latitudinal differences observed in reproductive and population biology of *E. analoga* along the Chilean coast show that studies on basic biology of benthic invertebrate species showing an ample distribution along this coast should include latitudinal comparisons (cf. Avellanal et al. 2000). This factor may play a significant role in conservation of benthic communities and the formulation management plans. If, for example, latitudinal comparisons identify differing patterns in biological parameters, differing conservation or management strategies may be required.

ACKNOWLEDGMENTS

To Marcelo Oliva and Rubén Escribano (Universidad de Antofagasta) for logistic support in Antofagasta. To the following students for their help during field samplings: Manuel Rojo, Mauricio Bringas, Héctor Castro, Luis Ossandón, Alvaro Quintana, Luis Vergara and Monique Sánchez (Universidad de Antofagasta). To Marcia González (Universidad Austral de Chile) for laboratory analyses. This study was financed by CONICYT (Proyecto FONDECYT 950001) and the final data analyses and manuscript writing benefitted from the financial support given to EJ and PQ by Proyecto FONDAP O & BM (Programa Mayor nº 3).

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Associated Editor: J. Cancino
Received August 10, 1999; accepted June 27, 2000