



Geographical variation in natural history of the sandy beach isopod *Excirolana hirsuticauda* Menzies (Cirolanidae) on the Chilean coast

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Received 23 October 2001; accepted 31 July 2002

Abstract

Monthly samplings were carried out during 1999–2000 at two sandy beaches of the Chilean coast (El Apolillado 29°S and La Misión 39°S), to test the hypothesis that population abundances, reproductive biology and life history characteristics of the cirolanid isopod *Excirolana hirsuticauda* Menzies are affected by latitude. Sediment samples were collected at 2 m spaced levels along two transects separated 2 m apart and extending from the uppermost beach levels down to those levels where no more isopods were found. The isopods were sexed and measured for growth studies through the analysis of month length frequency distribution. The fecundity of ovigerous females was analysed and the relationship between this and the size of the females was estimated with analyses of linear regression and compared with ANCOVA. The population abundances of *E. hirsuticauda* were higher at the northern beach of El Apolillado (up to 48 000–50 000 ind. m⁻¹) as compared to the southern beach of La Misión (up to 13 000 ind. m⁻¹). The reproductive period occurred during early summer (December–January) at both beaches. The fecundity of females increased significantly with body size at both beaches. Results of covariance showed that for a similar body size, fecundity was significantly higher at El Apolillado. Body size of the largest male, smallest and largest ovigerous females and body size at maturity of ovigerous females were larger at La Misión. The intramarsupial stages of the ovigerous females of this beach were significantly larger than that of the ovigerous females from the northern site. The growth and mortality rates were higher at the southern site. It is concluded that population abundances, reproductive biology and growth of *E. hirsuticauda* change along the Chilean coast.

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Keywords: cirolanid isopod; growth; reproduction; Chilean sandy beaches

1. Introduction

The long Chilean coast extends between 18 and 56°S crossing different environmental conditions strongly associated with latitude (Fig. 1). One of the main oceanographic features of northern and central Chile is the persistent upwelling which sustains one of the richest pelagic fisheries of the world. Sea surface temperatures (SSTs) decrease gradually from about 16–18 °C in the north, to nearly 12 °C at 40°S and even lower further south. The Andes Mountains run close and parallel all

along the coast, creating special climatic conditions, including an arid coast (from about 18 to 27°S), a semiarid coast between 27 and 32°S, a central coast between approximately 32 and 42°S and a fjord coast further south. Sandy beaches are one of the most common coastal habitats north of 42°S; in south central Chile (36–40°S), exposed sandy beaches alternate with estuarine outlets.

Cirolanid isopods are typical macroinfaunal organisms of the upper and middle shore intertidal levels of temperate and tropical sandy beaches around the world (e.g. McLachlan & Jaramillo, 1995). Three cirolanid isopods are currently known from sandy beaches of Chile: *Excirolana braziliensis* Richardson, *Excirolana hirsuticauda* Menzies and *Excirolana monodi* Carvacho

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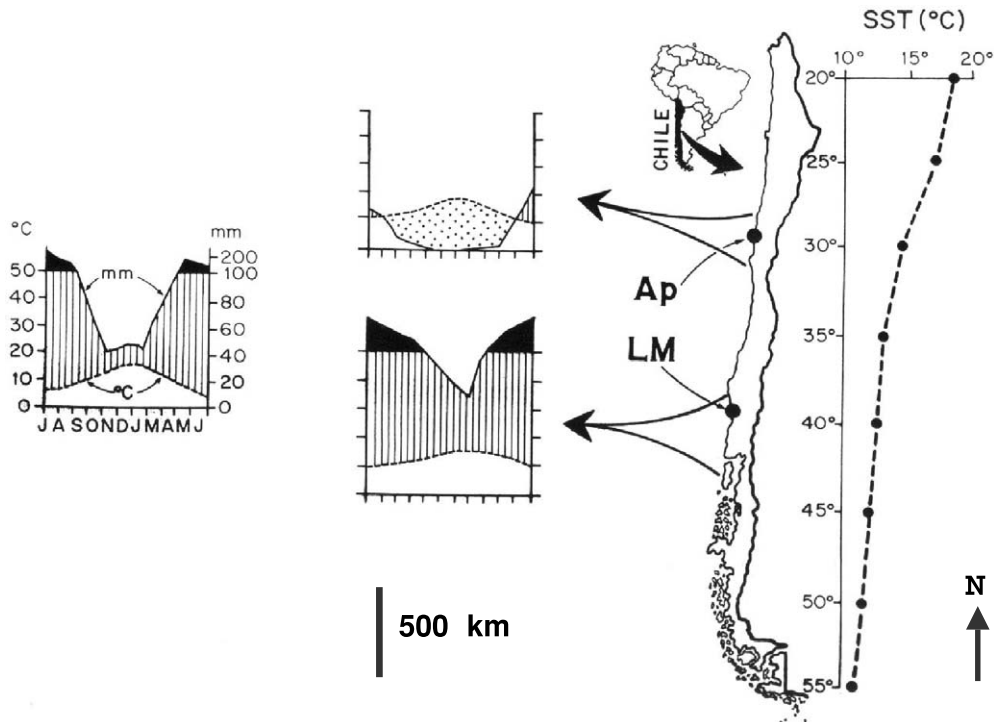


Fig. 1. Location of the beaches of El Apollado (Ap) and La Misión (LM) on the Chilean coast. Walter's climatic diagrams (temperature and rainfall) of two selected localities from the coastal areas where these beaches are located are also presented (figures taken from di Castri & Hajek, 1976). The scales of this representation are shown in the diagram of the left side. Map of the Chilean coast and latitudinal distribution of SST adapted from Fernández et al. (2000).

(Jaramillo, 1982, 1987, 1994, 2001). While *E. braziliensis* has a widespread distribution along the Pacific and Atlantic coast of the Americas from Mexico south to Chile (Dexter, 1977; Glynn, Dexter, & Bowman, 1975; Jaramillo, 1994), *E. hirsuticauda* and *E. monodi* are endemic species of the Chilean coast from about 26 to 42°S (Jaramillo, 1994; Jaramillo, Carrasco, Quijón, Pino, & Contreras, 1998). These isopods are ovoviviparous; i.e. eggs are retained in a brood chamber or marsupium until the manca stage is reached; after an incubation period which may vary 1–4 months, young isopods are released to the environment (Dexter, 1977; Klapow, 1970; de Ruyck, Donn, & McLachlan, 1992). While buried during low tides, cirrolanid isopods are active swimmers during high tides (Brusca, 1980; Jaramillo & Fuentealba, 1993).

It has been shown worldwide that community and population parameters of the sand beach macroinfauna are related to beach morphodynamics (McLachlan, Fisher, Al-Habsi, Al-Shukairi, & Al-Habsi, 1998; McLachlan & Jaramillo, 1995; McLachlan, Jaramillo, Donn, & Wessels, 1993; McLachlan, de Ruyck, & Hacking, 1996). But there are also other factors that vary geographically such as water temperature and food which seem to be important in the regulation of life history traits (Dugan, Hubbard, & Wenner, 1994; Dugan, Wenner, & Hubbard, 1991). Bergmann (1847)

argued that vertebrates of colder waters are usually larger than those of warmer areas; thus, body size would increase with latitude. A similar relationship has been reported for invertebrates (e.g. Frank, 1975; Volker, Bundgaard, & Barker, 2000). In marine organisms the relationship between body size and latitudinal gradient has been reported for fishes (Boehlert & Kappenman, 1980), molluscs (Frank, 1975) and crustaceans (Steele, 1983). Similar trends of higher body sizes versus higher latitudes have been also found for sandy beach crustaceans. For example, Contreras, Jaramillo, and Quijón (2000) reported larger body sizes for the anomuran crab *Emerita analoga* (Stimpson) at a sandy beach of southern Chile (ca. 39°S) as compared with another one from northern Chile (ca. 22°S). Dugan et al. (1994) found a gradient of increasing body sizes of *E. analoga* along a decrease in water temperatures in sandy beaches of the coast of California, USA. Other traits of the life history (e.g. fecundity, size of eggs and reproductive strategies) also vary between populations from different geographical areas. For example, Thorson (1950) showed that invertebrates inhabiting polar regions tend to produce larger eggs than those of lower latitudes.

Bearing in mind the oceanographic and climatic gradients mentioned above for the Chilean coast, and that sea water temperature affects life history of coastal

invertebrates (e.g. Abele, 1982; Dugan et al., 1994, 1991; Fusaro, 1980) it is reasonable to expect that populations of sandy beach crustaceans located at different areas of this littoral should show differences in their life history characteristics and reproductive biology. The wide geographic distribution and presence of *Excirrolana hirsuticauda* along the Chilean coast, make this species a suitable organism to test the hypothesis regarding variability in life history characteristics and reproductive biology with relation to geographic ranges and environmental variability. This study analysed these characteristics at two beaches of the Chilean coast, to test the hypothesis that these characteristics are different.

2. Materials and methods

2.1. Study area

Fig. 1 shows the location of the two sandy beaches studied: El Apolillado (29°10'S, 71°29'W) and La Misión (39°14'S, 73°29'W). El Apolillado is about 1200 km north of La Misión. The sampling area is included in the Peruvian or Transition Zoogeographic Zone whose southern limit is located at about 42°S (Isla de Chiloé) (Dell, 1971; Knox, 1960; Marincovich, 1973). El Apolillado and La Misión closely represent the northern and southern borders of the Martin's (1923) warm zone where the mean temperature for the warmest month varies from about 15 to 20 °C, and for the coldest month from 10 to 13 °C. Brattström and Johanssen (1983) state that the annual rainfall increases from about 110 mm at 30°S to 760 mm at 37°S and still higher further south. According to Brattström and Johanssen (1983), La Misión (ca. 39°S) lies within the rainy zone (38–56°S) of Martin (1923). The mean annual temperatures at a latitude close to La Misión is about 14.5 and 7.2 °C, during the warmest and coldest months, respectively. These climatic characteristics are graphically displayed by Walter's climatic diagrams (Fig. 1). In this representation, the abscissa represent the months of the year, while the two ordinate axes represent temperature (°C) and rainfall (mm) (graph to the left in Fig. 1). Aridity (dotted area) is indicated when the curve of rainfall is located below the curve of temperature. With the exception of periods exceeding 100 mm rainfall which are black, humid periods are conventionally represented by vertical lines (di Castri & Hajek, 1976). While El Apolillado is typical of the warm zone delimited by Brattström and Johanssen (1983) where the arid period occurs during most of the year, La Misión is typical of the rainy zone where there is an excess of rainfall during the year (Fig. 1). Minimum and maximum mean surf water temperatures during this study were 12–17 and 10–13 °C for El Apolillado and La Misión, respectively (unpublished data). The approxi-

mate lengths of these beaches are 1500 and 400 m, respectively. Both are intermediate beaches (sensu Short & Wright, 1983), with maximum intertidal widths close to 80 m. Mean sizes of sand grains are close to 350 and 290 µm for El Apolillado and La Misión, respectively (unpublished data).

2.2. Sampling

Sediment samples were collected monthly from December 1998 to December 1999. The samples were collected with plastic cylinders (20 cm in diameter) at 2 m spaced levels (stations) along two replicated transects (2 m apart) extending from the uppermost beach levels down to those beach levels where no more isopods were found (usually at the uppermost levels of the swash zone). The sediment was sieved through 1 mm mesh and the specimens were stored in a seawater–formalin solution (10%).

2.3. Data analysis

Values of population abundances m^{-2} were transformed to abundances per linear meter of beach ($ind. m^{-1}$) to account for between-site variability in the width of the intertidal. The intramarsupial stages of ovigerous females were counted to compare fecundity among populations. These stages were categorized as eggs, embryos and intramarsupial juveniles (i.e. juveniles in the brood chamber). The relationship between fecundity and size of ovigerous females (see below) was estimated with analyses of linear regression, preceded by log transformation of data. Differences of slopes and adjusted means between regression lines estimated for each population were analysed with ANCOVA (Sokal & Rohlf, 1995).

After collection, isopods were sexed and measured. Sexes were distinguished on the basis of the study of Jaramillo (personal communication). Body sizes of *Excirrolana hirsuticauda* were defined as the distance from rostrum tip to telson tip. The number of ovigerous females and juveniles was counted. Analyses of life history characteristics included: body size of the largest male, body size of the smallest and largest ovigerous females and body size at maturity of females. The smallest size of ovigerous females corresponded to the fifth percentile size determined from the cumulative number of isopods, while the largest size of ovigerous females and male isopods corresponded to the 99th percentile size. The mean body size at sexual maturity was estimated according to Restrepo and Watson (1991).

For growth analyses, class intervals of 1 mm were chosen following the criteria of Sparre (1989) and Wolff (1989). Individual growths were determined by analysing the month length frequency distribution. The

normal component of each sample was separated with the routine NORMSEP included in the software FISAT (Gayanilo, Sparre, & Pauly, 1996). This analysis allows identification of means and standard deviations of each cohort. An age–body size key for each population was obtained following the methodology of Gomez and Defeo (1999). Each cohort was followed along time; a value of absolute age was assigned to each of these cohorts (from time zero or birth). Time zero (t_0) was defined as minimum size of recruits into the beach. Since significant differences were found between sizes of intramarsupial juveniles and juveniles in the beach between populations, the following values of t_0 were used: 2.5 and 3.3 mm for El Apollillado and La Misión, respectively. The results of this were fitted to the von Bertalanffy growth function (VBGF) with seasonal oscillation (Hoenig & Hanumara, 1982; Sommers, 1988):

$$L_t = L_\infty [1 - \exp[-K(t - t_0) + (KC/2\pi) \sin 2\pi(t - WP) - (KC/2\pi) \sin 2\pi(t_0 - WP)]]$$

where L_t is the length at age t , L_∞ the asymptotic length, K the curvature parameter, t_0 the computed age at length zero, C the parameter reflecting the intensity of seasonal growth oscillation and winter point (WP) was defined as the time (expressed as a decimal fraction of the year) when growth is slowest (Pauly & Gaschütz, 1979). The parameters of VBGF were estimated with a non-linear method of optimization by using the Marquardt–Levenberg algorithm included in the software Sigmaplot (Marquardt, 1963; Ress, Flannery, Teukolsky, & Vetterling, 1986; Shrager, 1972). An analysis of the residual sum of squares (ARSS) was employed to compare the VBGF between populations. The F -statistics was calculated as Chen, Jackson, and Harvey (1992), Defeo, Gomez, and Lercari (2001), and Gomez and Defeo (1999):

$$F = \frac{(RSSp - RSSs)/(3(K - 1))}{RSSs/(N - 3K)}$$

where $RSSp$ is the residual sums of square (RSS) of the VBGF fitted by pooled data (samples from both population pooled), $RSSs$ the sum of the RSS of each VBGF fitted to each populations, K is the number of samples in the comparison and N is the total sample size. The calculated F value was then compared with the critical F , with $3(K - 1)$ and $N - 3K$, degree of freedom for the numerator and denominator, respectively.

To compare different growth rate estimates, the standard growth index ϕ' (phi prime: Pauly & Munro, 1984; Vakily, personal communication) was employed as a measure of overall growth performance (Sparre, Ursin, & Venema, 1989). This index was calculated as follows:

$$\phi' = 2 \log_{10}(L_\infty) + \log_{10} K$$

This rationale provides a unified parameter of growth performance which does not show large variations as do K and L_∞ values and it has been used frequently in similar studies (Contreras et al., 2000; Defeo et al., 2001; Gomez & Defeo, 1999).

The instantaneous rate of natural mortality (M) of each population was estimated by length-converted catch curves and growth parameters estimated with the equation given by Pauly, Moreau, and Abad (1995), for species which have growth with seasonal oscillation (i.e. when $C > 0$, Gayanilo et al., 1996):

$$\ln(N) = a - b \times t'$$

where N is the number of individuals in a pseudo-cohort “sliced” by means of successive growth curves, t' the relative age of individuals in the pseudo-cohort, a the regression intercept and b (with sign changed) provides an estimate of M (cf. Defeo et al., 2001; Gayanilo et al., 1996; Gomez & Defeo, 1999; Pauly et al., 1995). This equation gives an estimate of total mortality; and since the species studied does not have fishing mortality (F), then $Z = M$. An ANCOVA was used to compare M between the populations of El Apollillado and La Misión, using age as the covariate.

3. Results

3.1. Population abundances

The population abundances of *Exciorolana hirsuticauda* were higher at the northern beach of El Apollillado as compared to the southern beach of La Misión (Fig. 2). Mean population abundances as high as 48 000–50 000 ind. m^{-1} (March–April 1999) and 61 000 ind. m^{-1} (July 1999) were estimated for El Apollillado, as compared with 13 000 ind. m^{-1} (August 1999) as the highest value estimated for La Misión.

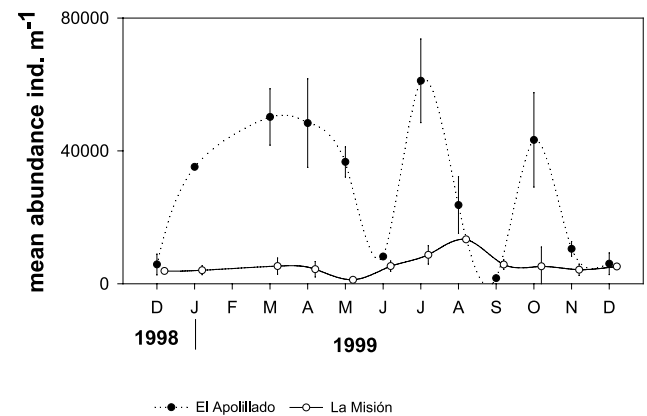


Fig. 2. Mean population abundances (± 1 standard deviation) of *Exciorolana hirsuticauda* at the beaches of El Apollillado and La Misión.

3.2. Reproductive biology

The maximum reproductive period of *Excirolana hirsuticauda* (deduced from the abundances of ovigerous females) occurred during early summer (December–January) at both beaches (Fig. 3a). However, in the northern site the ovigerous females were collected only between December and March, while in the southern beach, ovigerous females were collected during most of the study period. During the reproductive period in early summer, the number of ovigerous females represented up to 73% (El Apolillado) and 75% (La Misión) of the total number of females included in the size ranges of ovigerous females. (Fig. 3b). During the spring, the ovigerous females represented around 50% at La Misión. Juveniles had a higher representation at the beach of El Apolillado (Fig. 3c); at both beaches they

had their highest abundances 2–3 months after the peaks of ovigerous females.

The fecundity of females increased significantly with body size at both beaches (Fig. 4a). The results of covariance analyses (Table 1) showed no significant differences in the slopes of the regression lines for each population; however, intercepts were significantly different. Thus, for a similar body size, fecundity was significantly higher at El Apolillado (cf. Fig. 4a and Table 1). Size of intramarsupial stages varied between a mean of 1.08 and 1.32 mm (eggs) to 1.91 and 2.26 mm (intramarsupial juveniles) at El Apolillado and La Misión, respectively. Fig. 4b shows that the size of eggs, embryos and manca was significantly larger at the southern beach of La Misión. No significant relationships ($P > 0.05$) were found between sizes of the different brood stages with fecundity or body size of ovigerous females.

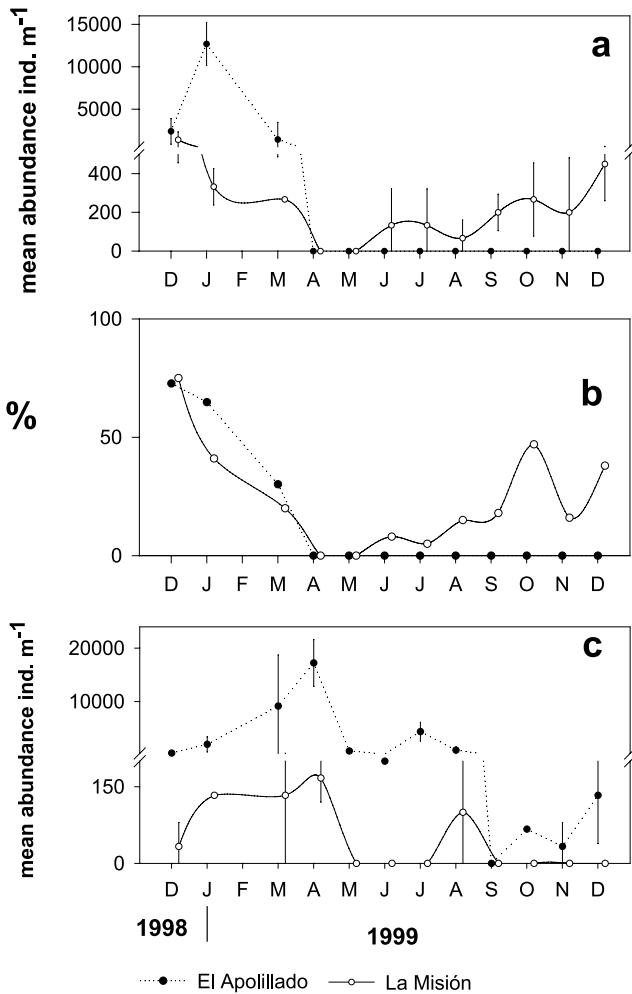


Fig. 3. (a) Mean population abundances of ovigerous females of *Excirolana hirsuticauda* at the beaches of El Apolillado and La Misión. (b) Percentual representation of these ovigerous females in relation to the total number of females. (c) Mean population abundances of juveniles at each beach. The values of abundances are means \pm 1 standard deviation.

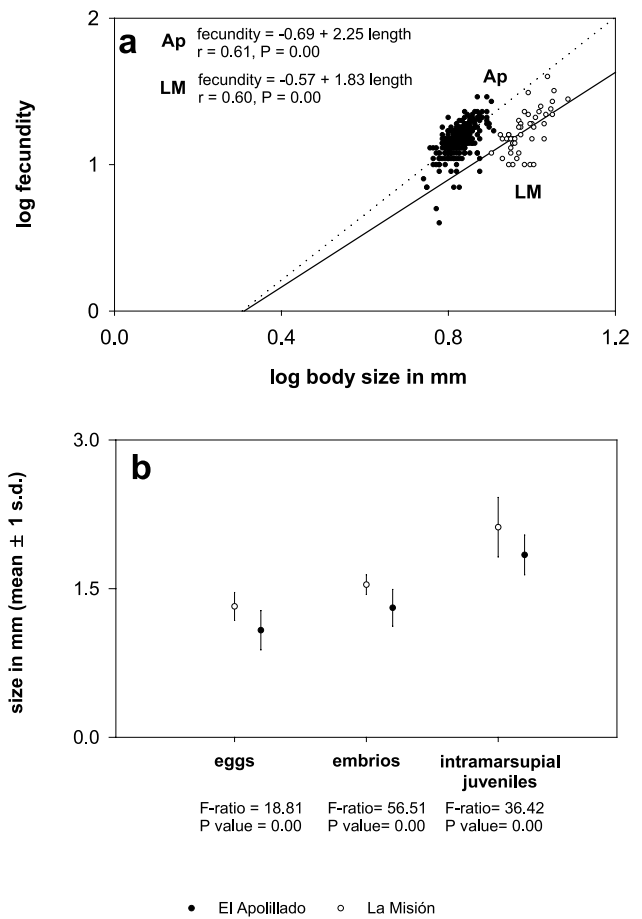


Fig. 4. (a) Fecundity versus body size of ovigerous females of *Excirolana hirsuticauda* from El Apolillado and La Misión; eggs, embryos and intramarsupial juveniles are included in the fecundity figures. (b) Mean sizes of eggs, embryos and intramarsupial juveniles. ANOVA was used to compare inter-site variability in sizes of these stages; thus, values of F and P are given for each comparison.

Table 1

Results of ANCOVA carried out to compare regression lines describing the relationship between body size and fecundity of ovigerous females of *Excirolana hirsuticauda* from El Apolillado and La Misión

Source of variation	Sum of squares	DF	Mean square	F-ratio	P-value
Homogeneity of slopes					
Due to regressions	1.50	1	1.49	164.95	0.000
Among slopes	0.01	1	0.013	1.44	0.232
Estimated residuals	2.64	292	0.009		
Total	4.15	294			
Homogeneity of adjusted means					
Among means	0.72	1	0.72	79.54	0.000
Error	2.66	293	0.01		
Total	3.38	294			

3.3. Growth and body size

The growth curves generated for *Excirolana hirsuticauda* by VBGF were different for both populations; the curve for the southern beach of La Misión was over that of El Apolillado. This was corroborated by the ARSS analyses ($P = 0.05$, Fig. 5). The values of L_{∞} and maximum body size were higher at La Misión, while the value of K was lower (Table 2). The seasonality in growth was similar at both populations (values of C around 0.50), with values of WP indicating a minimum growth around June in El Apolillado and August in La Misión (Table 2). The values of ϕ' were higher for the population of La Misión indicating a higher growth rate as compared with the population sampled at El Apolillado (Table 2).

The largest isopods at both beaches were ovigerous females (Table 3). Body sizes of the largest and smallest ovigerous females (99th and fifth percentiles, respec-

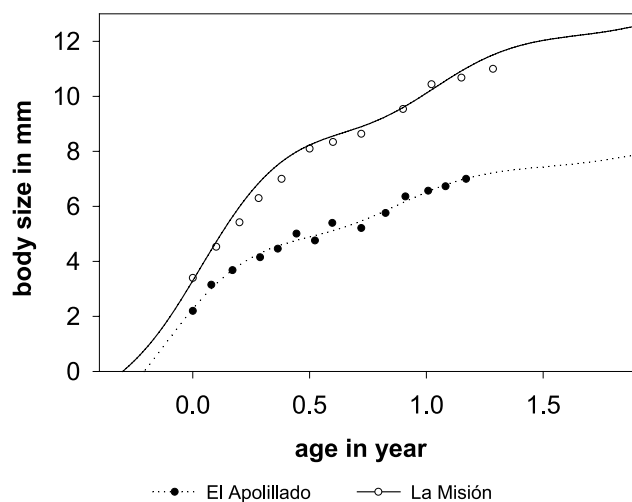


Fig. 5. Growth curves generated by VBGF for the studied populations of *Excirolana hirsuticauda*.

Table 2

Growth parameters, maximum body size observed and natural mortality (M) of *Excirolana hirsuticauda* from El Apolillado and La Misión

Growth parameters	El Apolillado		La Misión	
	Coefficient	P	Coefficient	P
L (mm)	9.30	0.00	14.45	0.00
K (1/year)	1.05	0.02	0.94	0.03
t_0	-0.21	0.04	-0.30	0.04
C	0.48	0.01	0.50	0.07
WP	0.49	0.00	0.62	0.00
ϕ'		1.96		2.30
Adj R^2		0.98		0.96
Maximum body size observed (mm)		8.90		13.50
Natural mortality (M)		2.27		3.13

tively), as well as the size of the largest male were larger at the southern beach of La Misión. Thus, the body sizes of largest ovigerous female, smallest ovigerous female and largest male were 1.6, 1.4 and 1.3 times greater in La Misión than in the northern population. Also, body size at maturity of females was larger at La Misión ($L_{50} = 8.86$ mm) as compared with El Apolillado ($L_{50} = 6.22$) (Table 4).

3.4. Mortality

The natural mortality rate (M) of *Excirolana hirsuticauda* was higher at La Misión (3.13) as compared with El Apolillado (2.27) (Table 2). Results of ANCOVA showed significant differences of natural mortality rates between both populations ($P = 0.021$).

4. Discussion

The results of this study show marked differences in population abundances, reproductive biology and growth of *Excirolana hirsuticauda* at two sandy beaches of the Chilean coast separated by about 1200 km. While population abundances and fecundity of ovigerous females were higher at the northern site of El Apolillado, growth and body sizes reached higher values at the southern site of La Misión affected by colder waters. Similar trends of higher body sizes with relation to lower

Table 3

Smallest (fifth percentile) and largest (99th percentile) body size (mm) of *Excirolana hirsuticauda* from El Apolillado and La Misión

	El Apolillado	La Misión
Male 99th percentile	7.5	9.5
Ovigerous females		
Fifth percentile	5.8	8.2
95th percentile	7.8	12.2

Table 4

Parameters of the maturity function (see Section 2) and average size at sexual maturity ($L_{50\%}$) of *Exciorolana hirsuticauda* from El Apolillado and La Misión

	El Apolillado		La Misión	
	Coefficient	<i>P</i>	Coefficient	<i>P</i>
<i>C</i>	0.96	0.002	0.87	0.003
<i>a</i>	1.51	0.049	1.41	0.051
<i>b</i>	9.39	0.044	12.49	0.055
R^2	0.96		0.91	
$L_{50\%}$ (mm)	6.22		8.86	

water temperatures have been also found in many marine invertebrates, especially crustaceans (Abele, 1982; Barnard, 1962; Contreras et al., 2000; Dugan et al., 1994; Frank, 1975; Garth, 1957; Poulsen, 1965).

Differences in seawater temperature have been commonly reported as the key factor behind these patterns of geographic variability in life history characteristics of marine invertebrates (Abele, 1982; Donn & Croker, 1986; Dugan et al., 1994; Ray, 1960). On an average, the maximum surf water temperature at El Apolillado was about 4°C higher than that measured at La Misión, implying that this difference is large enough to produce the observed differences in growth parameters of *Exciorolana hirsuticauda*. Usually, higher temperatures result in an increase in the values of parameter *K* but a decrease in L_{∞} (Beverton & Holt, 1959). Other factors which may affect growth or body size of the sandy beach crustaceans are: food availability and beach characteristics related to morphodynamics (Defeo et al., 2001; Dugan et al. 1994, 1991; Gomez & Defeo, 1999). Dugan et al. (1994) found positive correlations between life history characteristics of *Emerita analoga* and chlorophyll *a* in surf waters along sandy beaches of California concluding that as food supply increases, sizes of the smallest and largest body sizes of ovigerous females and female size at maturity, increase. Dugan et al. also found that quality of sediments related to beach types were also important to explain the geographic variability in these characteristics. Specifically, they found that body size of the largest male, and body size of the smallest and largest ovigerous females, increase at those beaches with finer and better sorted sands and gentler slopes. Gomez and Defeo (1999) and Defeo et al. (2001) found differences in growth parameters of the talitrid amphipod *Pseudorchestoidea brasiliensis* (Dana) and the anomuran decapod *Emerita brasiliensis* Schmitt inhabiting different types of beaches on the coast of Uruguay. Since the sites of El Apolillado and La Misión are morphodynamically similar, beach morphodynamics cannot explain the observed variability in reproductive biology or life history characteristics observed in this study. This similarity was the key factor that only El Apolillado and La Misión were chosen as

study sites; since both are modally intermediates, it was intended to avoid the confounding effect of beach morphodynamics on the reproductive biology and life history characteristics of *E. hirsuticauda*. Life history regulation related to population has been less documented in sandy beach organisms. Among the few studies is that by Dugan et al. (1991) which found that body size of *Emerita analoga* is inversely related to population density.

Genetic differences and reproductive isolation have been invoked to explain the variability in some aspects of the natural history of marine organisms (Boehlert & Kappenman, 1980; Janson, 1982). For example, Lessios and Weinberg (1994), showed important genetic variability among populations of the isopod *Exciorolana braziliensis* along 500 km of the coast of Panamá. They showed higher similarity among closer populations as compared with that located further away. In general, a lower genetic flux and lower genetic similarity have been reported for invertebrates without planctonic stages; in other words, with lower capability of dispersion (Grant & Da Silva-Tatley, 1997; Palumbi, 1994). Also, Janson (1982) found an important genetic component in the observed differences of growth rates of the gastropod *Littorina saxatilis*. Thus, even though no studies have aimed to evaluate genetic differentiation in *Exciorolana hirsuticauda* along the Chilean coast, the possibility that such sort of differentiation results in the observed differences in growth and body size of this species cannot be excluded.

While the population abundances of *Exciorolana hirsuticauda* from the southern beach of La Misión, showed a well defined pattern of seasonal variability in population abundances, that from El Apolillado showed non-seasonal temporal variability. Production of multiple broods has been invoked to explain non-seasonal temporal variability in population abundances of sand beach isopods (de Ruyck, Donn, & McLachlan, 1991). Since the data suggest just one brood per year in El Apolillado and two in La Misión, variability in population abundances of *hirsuticauda* must have another cause. This cause may well be related to the alongshore patchiness which characterize sand beach species and introduces variability in population abundances (e.g. Brazeiro, Rozbaczylo, & Fariña, 1998; Shepherd, Knott, & Eliot, 1988). For example, Brazeiro et al. (1998) found that in an intermediate sand beach of central Chile (ca. 33°S), population abundances of cirrolanid isopods tended to be larger in bays than in cusps. Since bays and cusps are typical features of intermediate beaches (Short, 1996; Short & Wright, 1983), it can then be implied that in a long term, the along shore variability in beach topography of El Apolillado is larger than in La Misión, a situation which could be related to the longer extent of the first beach which allows for a full development of cusps and bays. Moreover, Jaramillo

(personal communication) has shown that sediment loss related to winter storms significantly affects population abundances of cirrolanid isopods in a sandy beach of southern Chile close to La Misión. Thus, the higher probability of beach erosion in the rainy coast of southern Chile might well result in higher variability of abundances and mortality rates in the southern populations of *E. hirsuticauda*.

While fecundity of ovigerous females of *Excirrolana hirsuticauda* was higher at the northern population, the southern population exhibited larger sizes of intramarsupial stages. The increase in size of brooding stages towards higher latitudes has been interpreted as an adaptation to protect them against lower temperatures, via an increase in the amount of energy stored in larger eggs (Efford, 1969; Lardies & Castilla, 2001; Thorson, 1950). The limiting factor in the production of eggs in crustaceans is the body size of ovigerous females (Corey & Reid, 1991; Hines, 1982, 1991). However, environmental variables such as water temperature and salinity have been also mentioned as factors affecting fecundity (Lardies & Wehrtmann, 2001; Vernberg, 1962), especially the second one for subtidal organisms (Lardies & Wehrtmann, 2001; Pandian, 1970). Thus, in coastal areas with higher temperatures, a higher fecundity and lower size of eggs are usually observed (Kerfoot, 1977; Lardies & Wehrtmann, 2001; Steele & Steele, 1975; Vernberg, 1962). Consequently, a crustacean female can produce smaller but more eggs or larger but fewer eggs (Christiansen & Fenchel, 1979; Lardies & Wehrtmann, 2001). Finally, the higher fecundity of *E. hirsuticauda* at El Apollillado may explain the higher recruitment at this northern site.

In conclusion, this study has shown that reproductive biology and life history traits of a cirrolanid isopod commonly distributed along sandy beaches of the Chilean coast, differ according to latitude. It is not known if these changes are gradual or uneven along this long coast. However, this study provides a first insight into this variability, and may help to understand large-scale patterns in the natural history of other intertidal marine invertebrates. In turn, these results may well help ecologists trying to preserve coastal diversity, and also, resource managers involved in the planning of conservation strategies.

Acknowledgements

We thank Andrés Sepúlveda, Marcia González and Sandra Silva for field and laboratory work. We also thank Omar Defeo for his continuous help in growth analyses of crustaceans and two anonymous reviewers who improved an earlier manuscript. Financial support for this study was provided by CONICYT-CHILE (Proyecto FONDAP Oceanografía and Biología Marina, Pro-

grama Mayor no. 3). H.C. and E.J. appreciate the financial support of CONICYT and Universidad Austral de Chile (Dirección de Investigación y Desarrollo), respectively, which provided the funds to attend the workshop “Beaches—What Future? An Integrated Approach to the Ecology and Evolution of Beaches and Sand Dunes” held in Florence, Italy, during October 2001.

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