ORIGINAL ARTICLE

Production of *Excirolana armata* (Dana, 1853) (Isopoda, Cirolanidae) on an exposed sandy beach in southeastern Brazil

Marcelo Petracco · Ricardo Silva Cardoso ·
Alexander Turra · Thais Navajas Corbisier

Abstract The somatic and gonad productions of the cirolanid isopod *Excirolana armata* were analyzed by taking monthly samples from December 2003 to November 2005 on Una beach, São Paulo state (24°S), southeastern Brazil. Sampling was performed along three fixed transects established from the base of the foredunes to the waterline. Weight-specific growth rate was used to estimate the *E. armata* somatic production for 2004 and 2005, separately. The gonad production was estimated based on the monthly reproductive potential (mean number of eggs/embryos per female × monthly abundance of ovigerous females with near-release broods) for 2004. The annual somatic production of *E. armata* population varied from 15.57 to 17.25 g AFDW m^{-1} $year^{-1}$ and the somatic production/biomass ratio (P_s/B) from 3.55 to 3.14 $year^{-1}$ for 2004 and 2005, respectively. The P_s/B ratios were higher for males (4.02 and 3.19 $year^{-1}$ for 2004 and 2005) than for females (3.10 $year^{-1}$ for both years). The annual gonad production ($P_g = 1.07$ g AFDW m^{-1} $year^{-1}$) contributed about 15 and 6% to the total production ($P_s + P_g$) of females and the population, respectively. The proportion of gonad to somatic production of females (P_g/P_s) increased with individual size (ca 90% in the 7.5 mm size class), and the annual weight-specific gonad production (P_g/B ratio) was estimated to 0.24 $year^{-1}$. The high P_s/B ratios estimated for *E. armata* derive from the fast growth of individuals and show the importance of this population to the energy flow on Una beach ecosystem. However, the low percentage of juveniles verified in this population and in other studies of populations of the genus *Excirolana* is discussed as an important source of underestimation of P_s/B ratio.

Keywords Somatic production · Gonad production ·
P/B ratio · Sandy beaches · *Excirolana armata* · Brazil

M. Petracco (✉) · A. Turra · T. N. Corbisier
Depto. Oceanografia Biológica, Instituto Oceanográfico,
Universidade de São Paulo (USP), Praça do Oceanográfico, 191,
Cidade Universitária, São Paulo, SP CEP 05508-120, Brazil
e-mail: mpetracco@uol.com.br

R. S. Cardoso
Depto. Ecologia e Recursos Marinhos, Instituto de Biociências,
Universidade Federal do Estado do Rio de Janeiro (UNIRIO),
Av. Pasteur, 458, Urca, Rio de Janeiro,
RJ CEP 22290-240, Brazil

Introduction

Somatic production of macrozoobenthos is an important parameter for the study of ecosystem dynamics and a quantitative measure of a population's function in the ecosystem (Dolbeth et al. 2005). In natural populations, secondary production is mainly a function of individual growth, recruitment patterns, and mortality observed in nature (Sardá 1997). Therefore, it is directly related to the life-cycle of any given species and a key parameter in population ecology (Sardá et al. 2000). Studies of secondary production have been used to improve the understanding of important ecological issues such as energy transfer within communities, monitoring of benthic communities (Wilber and Clarke 1998), rational management of aquatic resources (Downing 1984), and food web analyses (Benke 1998). Moreover, measures of production are informative because they represent the rate at which organic matter is made available to higher trophic levels and reflect the relative importance of organisms as consumers and nutrient recyclers (Taylor 1998).

Population production is often expressed as the annual production to biomass ratio (*P/B*) in hopes of yielding standardized production values that can be compared among species or populations with differing biomasses (Plante and Downing 1989). The *P/B* ratio, also called turnover rate, is generally correlated with different biotic and environmental variables such as life span, body weight, and temperature (Robertson 1979; Banse and Mosher 1980; Schwinghamer et al. 1986; Sprung 1993; Cusson and Bourget 2005). However, few estimates of productivity of isopods are available, particularly when compared to marine amphipods (sensu Cusson and Bourget 2005). Isopods are among the most abundant species of the sandy beach macrofauna. They are generally scavengers (McLachlan and Brown 2006) and regulate the energy flow in the beach ecosystem (sensu Hayes 1974). Thus, estimates of production of species of this group are important to understand the energy flow on sandy beaches.

Cirolanid isopods are conspicuous members of the supralittoral and intertidal fringes of sandy beaches around the world (McLachlan and Jaramillo 1995) and might be one of the dominant groups in terms of abundance, biomass, and production (Glynn et al. 1975; Dexter 1977; Lercari and Defeo 2003; Veloso et al. 2003; Petracco 2008). The genus *Excirolana* is the most ubiquitous intertidal invertebrate in low-latitude temperate, subtropical, and tropical sandy beaches of the Americas (McLachlan and Brown 2006). *Excilorana armata*, a representative of this genus, occurs along the Atlantic coast of South America, from the state of Rio de Janeiro, Brazil, to Buenos Aires Province, Argentina (Castro and Brum 1969). This highly substratum-specific species shows a clear preference for fine sand (Defeo et al. 1997; Yannicelli et al. 2002; Lozoya et al. 2010) and is abundant on dissipative and intermediate morphodynamic beaches. On the other hand, the other representative of *Excirolana* in Brazil, *E. braziliensis*, occurs on beaches with a wider range of morphodynamic states (Defeo et al. 1992, 1997; Giménez and Yannicelli 1997; Defeo and Martínez 2003; Petracco et al. 2010).

The scavenger *E. armata* is a primary consumer, exposed to high predation pressure (Lercari et al. 2010), and is used as food by fishes of economic importance (Bergamino et al. 2011). On Una beach, *E. armata* is one of the dominant species in terms of abundance and biomass and showed stable isotope signature of nitrogen close to the filter feeders (Petracco 2008; Petracco et al. 2010). Thus, considering the scarcity of information on the contribution of *E. armata* and other cirolanid isopods to the energy flow in beach ecosystems, and that estimates of production of *E. armata* population are essential to determine the amount of food available to subsequent links in the food web, this study aims to estimate the somatic and gonad productions of *E. armata* on this beach.

Materials and methods

Study area

Una beach (24°27′S; 47°06′W) is an exposed beach (sensu McLachlan 1980) located in the Ecological Station Jureia-Itatins, São Paulo state, Brazil. The sampling area is situated in the northern segment of the beach, with a dissipative morphodynamic state (Souza and Souza 2004) and gentle profile (mean slope = 2.46%; SD ± 0.27), with sands ranging from fine to very fine (mean grain size = 0.13 mm; SD ± 0.01). The mean surf zone temperature and salinity were 23.00°C (SD ± 2.15) and 32.77 (SD ± 1.77), respectively. For more details of the study area, see Petracco et al. (2010).

Sampling and laboratory procedures

Sampling was carried out monthly during spring low tides from December 2003 to November 2005. Three fixed transects (placed 8 m apart) were sampled from the base of the foredunes to the waterline. Between December 2003 and April 2004, sampling units were obtained every 8 m along each transect with a metallic cylinder (20 cm in diameter) and to a depth of 20 cm. From May 2004 to the end of the study, the sampling units were obtained every 4 m. The samples were sieved using a 0.5 mm mesh and the isopods retained were fixed in 4% buffered formalin. For logistic reasons, the samples of *E. armata* in February 2004 and January 2005 were not collected. Individuals were measured from the tip of the cephalon to the end of the telson and grouped into 0.5 mm size classes. Each individual was sexed under a stereomicroscope, according to Dexter (1977). Individuals were classified as juveniles (length < 3 mm; Petracco et al. 2010) and adults. Adults were categorized as females, ovigerous females (with presence of eggs/embryos), and males.

Eggs/embryos incubated in the marsupium of females collected in the first year (December 2003 to November 2004) were removed, counted, and categorized into four developmental stages according to Jones (1970) and Martínez and Defeo (2006) (see also Petracco et al. 2010). In order to obtain the ash-free dry weight, the individuals were pooled into 0.25 mm length classes and dried at 70°C for 48 h to measure the dry weight (DW). Ash weight (AW) was obtained after burning the dried individuals in a muffle furnace for 4 h at 500°C. Ash-free dry weight (AFDW) was calculated by subtracting the ash weight from the dry weight.

Length–weight relationship and secondary production

The relationship between length and weight for each sex was calculated by linear regression analysis, with the data

converted into logarithms using the equation: $\log W = \log a + b \cdot \log L$, where W is the ash-free dry weight per individual (g AFDW), L is the length of the size class (mm), and a and b are constants.

Annual somatic production (P_s) was estimated by the weight-specific growth rate method (Crisp 1984; Brey 2001) from the length-frequency distribution obtained from all pooled samples, the length-weight relationship, and the von Bertalanffy growth function parameters. The annual production is given by the equation:

$$P_s = \sum \sum f_i \cdot w_i \cdot G_i,$$

where f_i is the annual mean number of individuals in length class i, w_i is the mean individual weight in the length class i, calculated from the mean length in length class i, and G_i is the weight-specific growth rate in length class i obtained through the equation:

$$G_i = b \cdot K \cdot [(L_\infty/L_i) - 1],$$

where b is the exponent of the length-weight relationship, K and L_∞ are von Bertalanffy growth function parameters estimated for *E. armata* (see Petracco et al. 2010), and L_i is the mean length in length class i. For the estimates of somatic production, the juveniles were divided equally in males and females, since the sex ratio did not differ significantly from 1:1 (Petracco et al. 2010).

Production was expressed in running meter (g and mg m^{-1} year^{-1}) and also in square meter (g m^{-2} year^{-1}) to enable it to be compared with other studies of production. The P_s/B ratio was calculated by the ratio between annual somatic production (P_s) and annual mean biomass (B). The somatic production and the P_s/B ratio were estimated for the two sampling years separately; December 2003 to November 2004 (2004: first year) and December 2004 to November 2005 (2005: second year). Monthly productions of males and females were calculated from the monthly length-frequency distributions (see Petracco et al. 2010) obtained from samples pooled from the three transects. The monthly P_s/B ratio of females was estimated from the production in each month and the respective biomass.

Annual gonad production (P_g) was estimated for the first year of study (December 2003 to November 2004), according to Shafir and Field (1980), as the product of number of eggs/embryos per female and the monthly abundance of ovigerous females with broods in late developmental stages. Since the incubation period estimated for *E. armata* is longer than 1 month (ca 2 months; Petracco et al. 2010), only the ovigerous females bearing embryos in the developmental stages three and four described by Martínez and Defeo (2006) were considered to estimate the abundance of eggs/embryos in each month. Annual gonad production (P_g) is given by the equation:

$$P_g = \sum A_i \cdot Ne_i \cdot We,$$

where A_i is the monthly abundance of ovigerous females (ind. m^{-1}) bearing embryos in the developmental stages three and four in length class i; Ne_i is the number of eggs/embryos female^{-1} in length class i, obtained from the length-fecundity relationship (Petracco et al. 2010), and We is the individual weight of the last marsupial developmental stage (manca stage). The individual weight of the last marsupial developmental stage (We = 0.0445 mg AFDW) was obtained by measuring 50 individuals ($L = 1.39$ mm $\pm$ 0.16 SD) and from the length-weight relationship. The gonad production was estimated for the period between June and November 2004 because the number of ovigerous females sampled between December 2003 and May 2004 was very low (≤ 3 individuals/month) to estimate the percentage of ovigerous females bearing embryos at stages three and four. However, the fact that ovigerous female abundances between June and November totaled 90% of the annual abundance of ovigerous females allowed a reliable estimate of gonad production to be obtained. Moreover, in 2 years of study, *E. armata* showed the same proportion of ovigerous females (ca 25%; Petracco et al. 2010).

Correlation analyses were used to assess the relationship between monthly P_s/B ratio of females and ovigerous female abundance, and between monthly P_s/B ratio of females and monthly mean length of females. Nested one-way ANOVA was used to test the null hypothesis that there was no significant difference in the abundance of ovigerous females between years and among months, with months nested in years. Nested one-way ANOVA was also employed to test the null hypothesis that there was no significant difference in the mean length of females between years and among months.

The annual weight-specific gonad production (GP) was estimated by the ratio between the annual gonad production (P_g) and the population mean annual biomass (GP = P_g/B; Brey 1995). On the population level, this measure of reproductive output is a measure equivalent to the P_s/B ratio, generally used to describe somatic productivity in benthic invertebrate populations (Brey 1995).

Results

The observed relationships between length and weight obtained for females ($\log W_{(g\ AFDW)} = -4.074 + 2.458 \cdot \log L_{(mm)}$, $n = 54$, $r^2 = 0.89$, $P < 0.0001$) and males ($\log W_{(g\ AFDW)} = -4.718 + 2.558 \cdot \log L_{(mm)}$, $n = 56$, $r^2 = 0.94$, $P < 0.0001$) were used for biomass and production estimates. The annual somatic production estimated for males (8.10 and 7.87 g AFDW m^{-1} year^{-1}) and females

(7.47 and 9.38 g AFDW m^{-1} $year^{-1}$) resulted in annual somatic productions of population of 15.57 and 17.25 g AFDW m^{-1} $year^{-1}$ for 2004 and 2005, respectively. These annual somatic values of production of population were similar to those calculated from the sum of monthly productions (16.91 and 17.10 g AFDW m^{-1} $year^{-1}$ for 2004 and 2005, respectively). The mean annual biomass of males (2.01 and 2.47 g AFDW m^{-1}) and females (2.41 and 3.03 g AFDW m^{-1}) totaled mean annual biomasses of 4.42 (2004) and 5.50 g AFDW m^{-1} (2005). The somatic production of males and females was concentrated between August 2004 and March 2005 with a high peak in November 2004 (Fig. 1a).

The P_s/B ratios for males ranged between 4.02 and 3.19 $year^{-1}$ for 2004 and 2005, while, for females, the P/B ratio was 3.10 for both years. The P_s/B ratios of the population ranged between 3.55 $year^{-1}$ (2004) and 3.16 $year^{-1}$ (2005). The monthly P_s/B ratios of females were higher from January to May and lower between June and November in both years of study, i.e., there was an inverse pattern of temporal distribution of mean length of females and of abundance of ovigerous females ($n = 21$, $r = -0.88$, $P < 0.0001$ and $n = 21$, $r = -0.58$, $P < 0.01$, respectively; Fig. 1b). The abundance of ovigerous females and the mean length of females differed among months (nested ANOVA $F_{20,44} = 6.89$, $P < 0.0001$; nested ANOVA $F_{20,44} = 4.87$, $P < 0.0001$, respectively), but not between years.

The distribution of annual production for the length classes of males showed the same pattern in both years. A

high peak of production in 3.5 mm length class and a high production in other intermediary length classes (4.0–4.5 mm) were observed (Fig. 2a, b). For the females, a different distribution pattern of production occurred between the years. However, high productions also occurred in intermediary length classes (3.5 and 4.5 mm) with a decrease in production in the 4.0 mm class (Fig. 2c, d).

The gonad production (P_g: 1.07 g AFDW m^{-1} $year^{-1}$) amounted to 15 and 6% of female production and total population production (somatic + gonad production), respectively. A higher gonad production occurred in 5.5 and 6.0 mm length classes. The proportion P_g/P_s increased with individual size (ca 90% in the 7.5 mm size class; Fig. 3). The annual weight-specific gonad production (P_g/B ratio) was 0.24 $year^{-1}$.

Discussion

High productions of males and females of *E. armata* on Una beach between August 2004 and March 2005 can be explained by the high abundance in this period (Petracco et al. 2010), since these variables were strongly related for both males ($n = 21$, $r = 0.88$, $P < 0.0001$) and females ($n = 21$, $r = 0.87$, $P < 0.0001$). The higher P_s/B ratios estimated for males in relation to females, mainly in 2005, can be attributed to the high abundance of individuals of the 3.5 mm length class. These small individuals grow fast and, consequently, have a high weight-specific growth rate contributing to 30% of the annual production of males which is twice the percentage observed for female individuals of this class.

The somatic production of *E. armata* on Una beach was higher than the value estimated for this species on a dissipative beach situated in southern Brazil (Souza 1998), despite the similarity in annual mean biomass (ca 0.18 g AFDW m^{-2}; Table 1). The higher production of *E. armata* in the Una beach was due to the higher curvature parameter (K) and asymptotic length (L_∞) (see Petracco et al. 2010) and, consequently, to the higher weight-specific growth rate (G).

The P_s/B ratios estimated for *E. armata* on Una beach and for *E. braziliensis* on Chilean (Zuñiga et al. 1985) and Uruguayan beaches (Lercari et al. 2010) are the highest values obtained for the genus *Excirolana*. The considerable P_s/B ratios of *E. armata* on Una beach derived from fast growth (Petracco et al. 2010). Furthermore, the low life span of this population can explain these considerable values as P_s/B ratios of peracarids were significantly correlated with life span ($n = 27$, $r = -0.61$, $P < 0.001$), but not with mean individual weight, seawater temperature, and latitude (Table 1). The lowest P_s/B ratios of *Excirolana* populations (1.6–1.9 $year^{-1}$) are similar to the values
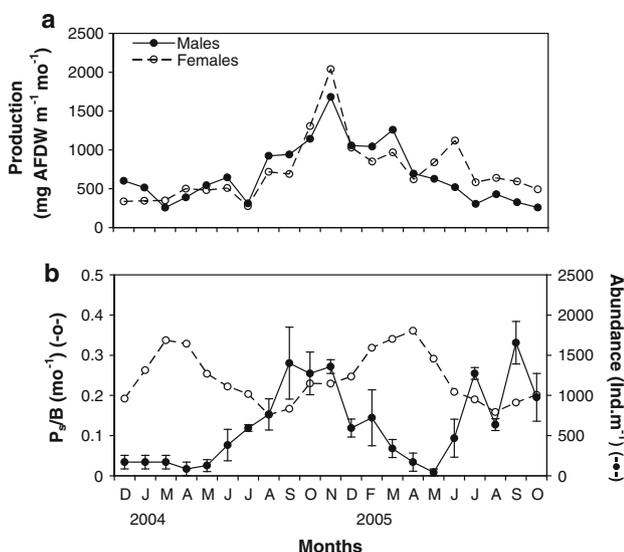
Fig. 1 a Monthly variation in somatic production of males and females; b monthly variation in somatic turnover rate (P_s/B; *open circles*) of females and in abundance (*closed circles*; mean ± SE) of ovigerous females from December 2003 to October 2005 on Una beach
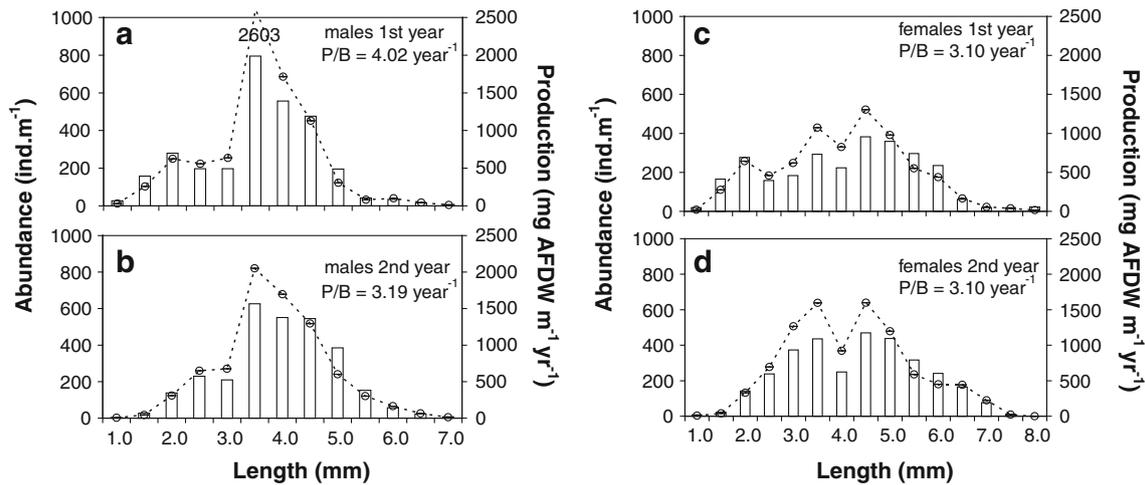
Fig. 2 Annual distribution of production (*open circles*) and abundance (*bars*) of **a**, **b** males and **c**, **d** females for different length classes from December 2003 to November 2004 (first year) and December 2004 to November 2005 (second year) on Una beach
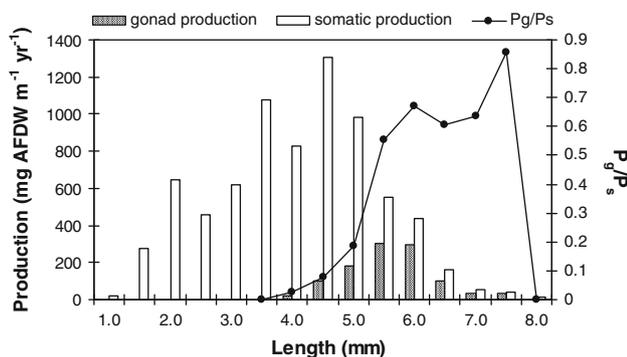
Fig. 3 Annual distribution of somatic production (P_s), gonad production (P_g), and the P_g/P_s ratio for females of different length classes from December 2003 to November 2004

obtained for oniscid isopods (1.5 year^{-1}), which showed very high life spans (4.0 years). On the other hand, the higher P_s/B ratios of *Excirolana* (2.2–3.8 year^{-1}) were similar to most of the estimates of amphipods (Table 1).

Life history traits of *E. armata* show latitudinal variation with a significant decrease in mortality from subtropical to temperate beaches ($n = 11$, $r = -0.86$, $P < 0.001$), while the life span and the mean individual weight follow the inverse pattern ($n = 11$, $r = 0.89$, $P < 0.001$ and $n = 9$, $r = 0.97$, $P < 0.0001$; Table 2). When four estimates of Z of *E. armata* (Lozoya and Defeo 2006:1.50–1.95 year^{-1}) were used as proxies of P_s/B ratios, the latter decreased significantly with the latitude and life span ($n = 11$, $r = -0.67$, $P < 0.05$ and $r = -0.79$, $P < 0.01$), but was not related with mean individual weight. Similarly, considering all *Excirolana* populations (Table 2), significant relations between latitude and the biotic variables, mortality, life span, and mean individual weight were observed. Similarly to *E. armata*, *Excirolana* P_s/B was negatively correlated

with life span ($n = 20$, $r = -0.52$, $P < 0.05$), but not related to the mean individual weight. However, *Excirolana* P_s/B was not related to the latitude either. The relationships between P_s/B ratios and life span verified for the peracarids, *E. armata* and *Excirolana* populations confirm that, for marine macroinvertebrates, life span is the variable which is most related to P_s/B ratios (Cusson and Bourget 2005). As life span is strongly and negatively correlated with mortality and the latter is equal to the P_s/B ratio (Allen 1971), a negative and strong relation between P_s/B and life span is expected.

Besides latitude, some factors acting on a local scale, such as inter and intraspecific interactions as well as the morphodynamic state of the beach, influence the growth and mortality of populations (Defeo and Martínez 2003; Lozoya and Defeo 2006) and, consequently, the P_s/B ratios. For instance, at similar latitudes on Uruguayan beaches, contrasting P_s/B estimates for *E. braziliensis* were obtained (Lercari et al. 2010: $P_s/B = 0.95$ and 3.78 year^{-1}). The low value of P_s/B ratio of *E. braziliensis* can be attributed to the interspecific interaction with *E. armata*, which decreases the growth rate of both species (Defeo et al. 1997; Defeo and Martínez 2003). However, as verified for the other life history traits, P_s/B ratios of *Excirolana* populations were expected to undergo a latitudinal variation, as verified for *Donax* populations (Cardoso and Veloso 2003; Herrmann et al. 2009). However, despite showing lower life span and higher mortality rate in relation to the Uruguayan *Excirolana* populations, unexpected lower and conservative P_s/B estimates were observed for most of the *Excirolana* populations of Brazilian sandy beaches ($P_s/B \leq 2$ year^{-1}) (Tables 1, 2). The productivity of Brazilian *Excirolana* populations were obtained from the weight-specific growth rate method (WSGRM), based on

Table 1 Somatic production (P_s: g AFDW m^{-2} year^{-1}), somatic turnover rate (P_s/B: year^{-1}), and life span (LS: years) of sandy beach peracarid crustaceans (Isopoda: I; Amphipoda: A) of different latitudes

	Species	P_s	P_s/B	LS	Latitude	Source
I	*Excirolana braziliensis*	0.29	1.81	1.66	23°02′S	Petracco (2000), Veloso et al. (2003)
I	*Excirolana braziliensis*	0.26	1.82	1.66	23°02′S	Petracco (2000), Veloso et al. (2003)
I	*Excirolana braziliensis*	0.13	1.62	1.58	23°03′S	Caetano et al. (2006)
I	*Excirolana braziliensis*	0.56	2.24	1.65	23°03′S	Caetano et al. (2006)
I	*Excirolana braziliensis*[a]	3.07[a]	3.62	1.25	23°27′S	Zuñiga et al. (1985)
I	*Excirolana armata*	0.45	3.55	0.89	24°27′S	This study (first year)
I	*Excirolana armata*	0.56	3.16	0.84	24°27′S	This study (second year)
I	*Excirolana armata*	0.35	1.86	1.55	25°20′S	Souza (1998)
I	*Excirolana armata*		2.39	2.15	33°40′S	Lozoya and Defeo (2006), Lercari et al. (2010)
I	*Excirolana braziliensis*		0.95	2.30	33°40′S	Cardoso and Defeo (2004), Lercari et al. (2010)
I	*Excirolana braziliensis*		3.78	2.15	34°36′S	Cardoso and Defeo (2004), Lercari et al. (2010)
I	*Tylos capensis*		1.38	4.50	34°00′S	McLachlan and Sieben (1991)
I	*Cirolana harfordi*		2.10	2.00	36°37′N	Johnson (1976a)
I	*Tylos europaeus*	0.08	1.58	3.50	40°07′N	Gonçalves et al. (2005)
A	*Pseudorchestoidea brasiliensis*	0.29	2.23	1.46	23°02′S	Cardoso and Veloso (1996)
A	*Pseudorchestoidea brasiliensis*	0.29	2.19	0.98	23°02′S	Cardoso and Veloso (1996)
A	*Atlantorchestoidea brasiliensis*		2.32	1.08	33°40′S	Gómez and Defeo (1999), Lercari et al. (2010)
A	*Talorchestia capensis*		2.25	1.75	34°00′S	Van Senus and McLachlan (1986)
A	*Atlantorchestoidea brasiliensis*		2.33	1.17	34°36′S	Gómez and Defeo (1999), Lercari et al. (2010)
A	*Talorchestia brito*	0.22	7.48	0.54	37°00′N	Gonçalves et al. (2003)
A	*Talitrus saltator*	0.61	7.26	0.58	37°00′N	Marques et al. (2003)
A	*Talitrus saltator*	0.74	5.69	0.75	40°07′N	Marques et al. (2003)
A	*Talorchestia brito*	0.19	5.94	0.63	40°12′N	Gonçalves et al. (2003)
A	*Talitrus saltator*	0.12	8.21	0.63	42°37′N	Marques et al. (2003)
A	*Haustorius canadensis*	1.25	1.48	2.00	43°07′N	Donn and Croker (1986)
A	*Ampelisca brevicornis*	1.18	2.82	1.16	54°05′N	Hastings (1981)
A	*Ampelisca brevicornis*	1.29	3.13	1.16	54°05′N	Hastings (1981)

[a] Values converted to AFDW based on Ricciardi and Bourget (1998)

length-frequency distributions (LFDs), as opposed to the estimates for Uruguayan *Excirolana* populations, which were obtained by balanced ecosystem models (Lercari et al. 2010). Thus, it is possible to refer to the LFDs to understand these conservative P_s/B ratios. The LFDs of *E. armata* (Fig. 2a, b, c, d) and *E. braziliensis* (Petracco 2000; Defeo and Martínez 2003) show low proportions of juveniles. This low proportion of juveniles and the consequent decrease in P_s/B ratio can be explained by: (1) fast growth of juveniles, which makes it difficult to accurately represent the abundance of these individuals by monthly sampling, and (2) sampling selectivity against smaller organisms due partly to their possible escape through the mesh (Defeo, pers. com.).

According to Allen (1971), the instantaneous mortality rate (Z) of a population is equal to the P_s/B ratio of such population if the individual growth of population is describable by the von Bertalanffy growth function. However, Z estimates calculated with the length-converted catch curve

(LCCC) (Pauly 1983) are higher than the P_s/B ratios obtained with the WSGRM when the population shows gear selectivity against smaller individuals (Brey, pers. com.). The high values of r^2 (0.88–0.99) of the LCCC fitted for *E. armata* and *E. braziliensis* (Defeo and Martínez 2003; Caetano et al. 2006; Petracco 2008) show that the single negative exponential model is appropriate to estimate the mortality of these species and provides reliable estimates of Z. Specifically for *E. armata* on Una beach, the similarity of the initial number of individuals calculated from the LCCC of males and females (330) and the number of individuals estimated from the annual number of embryos (450) reinforce this idea. The Z estimated for *Excirolana* populations were significantly higher than the P_s/B ratios calculated with the WSGRM (paired t test: $t_{1,14} = 4.12$, $P < 0.001$; Table 2). Moreover, the relationship between these two variables described by a significant linear model shows a significantly lower slope than that of Allen's relation ($Z = P_s/B$, slope = 1; $t_{1,22} = 2.66$,

Table 2 Life span (LS: years), turnover rate (P_s/B ratio: year^{-1}), and instantaneous rate of mortality (Z: year^{-1}) estimated for males (M), females (F) and populations of *Excirolana armata* (Souza 1998; Lozoya and Defeo 2006; Lercari et al. 2010; this study) and *E. braziliensis* (Zuñiga et al. 1985; Fonseca et al. 2000; Veloso et al. 2003; Defeo and Martínez 2003; Caetano et al. 2006; Lercari et al. 2010)

Species	LS		P_s/B		Z		Latitude	Source
	M	F	M	F	M	F		
E. armata[a]	0.78	0.99	4.02	3.10	5.53	4.90	24°27′S	This study (first year)
E. armata[a]	0.79	0.88	3.19	3.10	6.43	7.36	24°27′S	This study (second year)
E. armata[a]	1.20	1.90	1.64	2.13	3.23	3.42	25°20′S	Souza (1998)
E. armata[b]	2.15		2.39		2.23		33°40′S	Lozoya and Defeo (2006), Lercari et al. (2010)
E. armata	2.20	2.40			1.95	1.50	33°50′S	Lozoya and Defeo (2006)
E. armata	2.10	1.90			1.85	1.65	33°50′S	Lozoya and Defeo (2006)
E. braziliensis[a,b]	1.66		1.62		2.95		23°02′S	Fonseca et al. (2000), Veloso et al. (2003)
E. braziliensis[a,b]	1.66		1.78		2.74		23°02′S	Fonseca et al. (2000), Veloso et al. (2003)
E. braziliensis[a]	1.72	1.45	1.50	2.00	2.82	4.06	23°03′S	Caetano et al. (2006)
E. braziliensis[a]	1.91	1.40	2.92	1.62	2.20	3.22	23°03′S	Caetano et al. (2006)
E. braziliensis[a,b]	1.25		3.62		3.00[c]		23°27′S	Zuñiga et al. (1985)
E. braziliensis[b]	2.30		0.95		0.90		33°40′S	Defeo and Martínez (2003), Lercari et al. (2010)
E. braziliensis[b]	2.15		3.78		2.97		34°36′S	Defeo and Martínez (2003), Lercari et al. (2010)

[a] P/B ratios obtained with the weight-specific growth rate method

[b] Value relative to the population

[c] Value of Z according to Cardoso and Defeo (2004)

$P < 0.05$; Fig. 4). The difference between the P_s/B ratio and Z reinforces the hypothesis of underestimation of P_s/B ratios for Brazilian *Excirolana* populations due to a sampling selectivity and/or an inadequate (monthly) sampling regime.

From the negative relationship between the monthly P_s/B ratios of females and ovigerous female abundance, it is possible to characterize two distinct annual periods of P_s/B ratio of females. In the period with lower abundance of ovigerous females, females show lower lengths and, consequently, higher P_s/B ratios than in the period characterized by higher abundance of ovigerous females.

Despite the fact that fecundity increases with the length of females (Petracco et al. 2010), higher gonad production occurred at 5.5 and 6.0 mm length classes, due to the higher abundance of ovigerous females in these classes (mean length of ovigerous females = 5.87 mm). However, the higher proportion of gonad production compared with the somatic production at larger length classes (6.0–7.5 mm) derived from low somatic production in these classes because older individuals invest more energy in reproduction than in growth.

The contribution of gonad production, compared with the total population production (somatic + gonad production) estimated for *E. armata* (6%), was lower than those observed for the cirolanids *Cirolana imposita* (15%; Shafir and Field 1980) and *C. harfordi* (13%; Johnson 1976a). However, when comparing the gonad production of
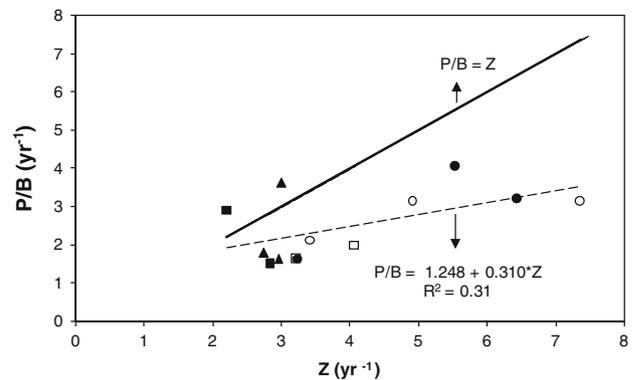
Fig. 4 *P/B* ratios obtained with the weight-specific growth rate method plotted against the instantaneous mortality rate (Z) (*dashed line*) obtained for males (*filled circles*) and females (*open circles*) of *Excirolana armata* (Souza 1998; this study), and for males (*filled square*), females (*open square*) and populations (*triangle*) of *E. braziliensis* (Zuñiga et al. 1985; Fonseca et al. 2000; Veloso et al. 2003; Caetano et al. 2006); Allen's relationship: *P/B* = Z (*full line*)

E. armata to the total production of females calculated from the length reached by females at sexual maturity (length ≥ 4 mm), a considerable contribution of gonad production (ca 20%) was observed. According to Shafir and Field (1980), the high percentage of productive energy channeled into reproduction of *C. imposita* was strongly supported by the fact that ovigerous females were present in samples throughout the year. *C. harfordi* also showed ovigerous females throughout the year and in high

percentage (Johnson 1976b). In *E. armata*, low abundance of ovigerous females was observed over a long period of time (December 2003 to May 2004), although ovigerous females occurred throughout the year and with a considerable mean percentage (25%). This fact contributed to the smaller relative contribution of gonad production of *E. armata* when compared with the other two cirolanids.

The P_g/B ratios of *E. armata* (0.24 year^{-1}) and *C. harfordi* (0.30 year^{-1}; Johnson 1976a) were similar to each other but much lower than that estimated for *C. imposita* (0.86 year^{-1}; Shafir and Field 1980). This similarity between *E. armata* and *C. harfordi* P_g/B ratios is not in accordance with the positive relation between P_g/B ratio and temperature (Clarke 1987; Brey 1995). *C. harfordi* and *C imposita* live at a seawater temperature (15°C), which is lower than the temperatures measured on Una beach (23°C). However, the fact that *E. armata* and *C. harfordi* live in the intertidal zone of sandy beaches, while *C. imposita* occurs in kelp beds in depths between 12 and 16 m, may contribute to the difference in P_g/B ratios. In populations of intertidal invertebrates, energetic costs increase with aerial and wave exposure (Sebens 2002). Moreover, food availability influences positively the P_g/B ratio (Clarke 1987; Brey 1995). A kelp bed is a high productive ecosystem, mainly when compared with the intertidal zone of sandy beaches. A higher P_s/B ratio estimated for *C. imposita* (4.80 year^{-1}), when compared with *E. armata*, despite the higher seawater temperature on Una beach, indicates fast growth, supported by high food availability typical of the environment of kelps.

In summary, the high production and P_s/B ratios of *E. armata* in relation to other *Excirolana* populations suggest that this species is an important component of the energy flow on Una beach. However, like other *Excirolana* populations of lower latitudes, the productivity of *E. armata* on Una beach is probably underestimated due to the low percentage of juveniles in the population. Therefore, fortnightly sampling frequency and mesh with smaller aperture than 0.5 mm must be employed in studies on the production of this genus, mainly on tropical/subtropical beaches where the individuals recruit with smaller length and grow faster than their relatives on temperate beaches (Cardoso and Defeo 2003, 2004; Petracco et al. 2010). The considerable contribution of gonad production (~20%) compared with the total production of females at sexual maturity (length ≥4 mm) shows that gonad production must be included in production studies of species of the genus *Excirolana*.

References

Allen KR (1971) Relation between production and biomass. J Fish Res Board Can 28:1573–1581

Banse K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. Ecol Monogr 50:355–379

Benke AC (1998) Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. Ecology 79:899–910

Bergamino L, Lercari D, Defeo O (2011) Food web structure of sandy beaches: temporal and spatial variation using stable isotope analysis. Estuar Coast Shelf Sci 91:536–543

Brey T (1995) Temperature and reproductive metabolism in macrobenthic populations. Mar Ecol Prog Ser 125:87–93

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 1.2. Alfred Wegener Institute for Polar and Marine Research, Germany. http://www.thomas-brey.de/science/virtualhandbook. Accessed 26 Nov 2010

Caetano CHS, Cardoso RS, Veloso VG, Silva ES (2006) Population biology and secondary production of *Excirolana braziliensis* (Isopoda: Cirolanidae) in two sandy beaches of southeastern Brazil. J Coast Res 22:825–835

Cardoso RS, Defeo O (2003) Geographical patterns in reproductive biology of the Pan-American sandy beach isopod *Excirolana braziliensis*. Mar Biol 143:573–581

Cardoso RS, Defeo O (2004) Biogeographical patterns in life history traits of the Pan-American sandy beach isopod *Excirolana braziliensis*. Estuar Coast Shelf Sci 61:559–568

Cardoso RS, Veloso VG (1996) Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha Beach, Brazil. Mar Ecol Prog Ser 142:111–119

Cardoso RS, Veloso VG (2003) Population dynamics and secondary production of the wedge clam *Donax hanleyanus* on a high energy, subtropical beach of Brazil. Mar Biol 142:153–162

Castro AL, Brum INS (1969) Sobre as espécies de *Excirolana* Richardson do litoral Atlântico das Américas (Isopoda: Cirolanidae). Bolm Mus Nac RJ 271:1–21

Clarke A (1987) Temperature, latitude and reproductive effort. Mar Ecol Prog Ser 38:89–99

Crisp DJ (1984) Energy flow measurements. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. IBP Handbook 16. Blackwell, Oxford, pp 284–372

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297:1–14

Defeo O, Martínez G (2003) The habitat harshness hypothesis revisited: life history of the isopod *Excirolana braziliensis* in sandy beaches with contrasting morphodynamics. J Mar Biol Ass UK 83:331–340

Defeo O, Jaramillo E, Lyonnet A (1992) Community structure and intertidal zonation of the macroinfauna in the Atlantic coast of Uruguay. J Coast Res 8:830–839

Defeo O, Brazeiro A, de Alava A, Riestra G (1997) Is sandy beach macroinfauna only physically controlled? Role of substrate and competition in isopods. Estuar Coast Shelf Sci 45:453–462

Dexter DM (1977) Natural history of the Pan-American sand beach isopod *Excirolana braziliensis* (Crustacea: Malacostraca). J Zool Lond 183:103–109

Dolbeth M, Lillebo AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. J Exp Mar Biol Ecol 326:115–127

Donn TE, Croker RA (1986) Seasonal patterns of production in the sandy-beach Amphipod *Haustorius canadensis*. Estuar Coast Shelf Sci 22:675–687

Downing JA (1984) Assessment of secondary production: the first step. In: Downing JA, Rigler FH (eds) A manual on the assessment of secondary productivity in fresh waters. IBP Handbook 17. Blackwell, Oxford, pp 1–18

Fonseca DB, Veloso VG, Cardoso RS (2000) Growth, mortality, and reproduction of *Excirolana braziliensis* Richardson, 1912 (Isopoda, Cirolanidae) on the Prainha beach, Rio de Janeiro, Brazil. Crustaceana 73:535–545

Giménez L, Yannicelli B (1997) Variability of zonation patterns in temperate microtidal Uruguayan sandy beaches with different morphodynamic types. Mar Ecol Prog Ser 160:197–207

Glynn PW, Dexter DM, Bowman TE (1975) *Excirolana braziliensis*, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. J Zool Lond 175:509–522

Gómez J, Defeo O (1999) Life history of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda) in sandy beaches with contrasting morphodynamics. Mar Ecol Prog Ser 182:209–220

Gonçalves SC, Marques JC, Pardal MA, Bouslama MF, El Gtari M, Charfi-Cheikhrouha F (2003) Comparison of the biology, dynamics, and secondary production of *Talorchestia brito* (Amphipoda, Talitridae) in Atlantic (Portugal) and Mediterranean (Tunisia) populations. Estuar Coast Shelf Sci 58:901–916

Gonçalves SC, Pardal MA, Cardoso PG, Ferreira SM, Marques JC (2005) Biology, population dynamics and secondary production of *Tylos europaeus* (Isopoda, Tylidae) on the western coast of Portugal. Mar Biol 147:631–641

Hastings MH (1981) The life cycle and productivity of an intertidal population of the amphipod *Ampelisca brevicornis*. Estuar Coast Shelf Sci 12:665–667

Hayes WB (1974) Sand-beach energetics: importance of the isopod *Tylos punctatus*. Ecology 55:838–847

Herrmann M, Carstensen D, Fisher S, Laudien J, Penchaszadeh PE, Arntz WE (2009) Population structure, growth, and production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from Northern Argentinean beaches. J Shellfish Res 28:511–526

Johnson WS (1976a) Population energetics of the intertidal isopod *Cirolana harfordi*. Mar Biol 36:351–357

Johnson WS (1976b) Biology and population dynamics of the intertidal isopod *Cirolana harfordi*. Mar Biol 36:343–350

Jones DA (1970) Populations densities and breeding in *Eurydice pulchra* and *Eurydice affinis* in Britain. J Mar Biol Ass UK 50:635–655

Lercari D, Defeo O (2003) Variation of sandy beach macrobenthic community along a human-induced environmental gradient. Estuar Coast Shelf Sci 58S:17–24

Lercari D, Bergamino L, Defeo O (2010) Trophic models in sandy beaches with contrasting morphodynamics: comparing ecosystem structure and biomass flow. Ecol Model 221:2751–2759

Lozoya JP, Defeo O (2006) Effects of a freshwater canal discharge on an ovoviviparous isopod in an exposed sandy beach. Mar Freshw Res 57:421–428

Lozoya JP, Gómez J, Defeo O (2010) Modelling large-scale effects of estuarine and morphodynamic gradients on distribution and abundance of the sandy beach isopod *Excirolana armata*. Estuar Coast Shelf Sci 87:472–478

Marques JC, Gonçalves SC, Pardal MA, Chelazzi L, Colombini I, Fallaci M, Bouslama MF, Gtari ME, Charfi-Cheikhrouha F, Scapini F (2003) Comparison of *Talitrus saltator* (Amphipoda, Talitridae) biology, dynamics, and secondary production in

Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations. Estuar Coast Shelf Sci 58S:127–148

Martínez G, Defeo O (2006) Reproductive biology of the isopod *Excirolana braziliensis* at the southern edge of its geographical range. Helgol Mar Res 60:273–280

McLachlan A (1980) The definition of sand beaches in relation to exposure: a simple rating system. S Afr J Zool 76:137–138

McLachlan A, Brown A (2006) Sandy beaches as ecosystems. Elsevier, Amsterdam

McLachlan A, Jaramillo E (1995) Zonation on sandy beaches. Oceanogr Mar Biol Annu Rev 33:305–335

McLachlan A, Sieben PR (1991) Growth and production of *Tylos capensis* Krauss 1843 (Isopoda). Crustaceana 61:43–48

Pauly D (1983) Length-converted catch curves: a powerful tool for fisheries research in the tropics (part I). Fishbyte 1:9–13

Petracco M (2000) Produção secundária das espécies mais abundantes da macrofauna bentônica da zona entremarés da Prainha, Estado do Rio de Janeiro. Dissertation, Universidade Federal do Rio de Janeiro, Brazil

Petracco M (2008) Produção secundária da macrofauna bentônica da zona entremarés no segmento norte da praia do Una, litoral sul do estado de São Paulo. PhD thesis, Universidade de São Paulo Brazil

Petracco M, Cardoso RS, Corbisier TN (2010) Population biology of *Excirolana armata* (Dana, 1853) (Isopoda, Cirolanidae) on an exposed sandy beach in Southeastern Brazil. Mar Ecol 31:330–340

Plante C, Downing JA (1989) Production of freshwater invertebrate populations in lakes. Can J Fish Aquat Sci 46:1489–1498

Ricciardi A, Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. Mar Ecol Prog Ser 163:245–251

Robertson AI (1979) The relationship between annual production:biomass ratio and lifespan for marine macrobenthos. Oecologia 38:193–202

Sardá R (1997) The use of general relationships to estimate secondary production in coastal habitats: a revision based on a case study. Publ Espec Inst Esp Oceanogr 23:11–22

Sardá R, Pinedo S, Dueso A (2000) Estimating secondary production in natural populations of polychaetes: some general constraints. Bull Mar Sci 67:433–447

Schwinghamer P, Hargrave B, Peer D, Hawkins CM (1986) Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar Ecol Prog Ser 31:131–142

Sebens KP (2002) Energetic constraints, size gradients, and size limits in benthic marine invertebrates. Integr Comp Biol 42:853–861

Shafir A, Field JG (1980) Importance of a small carnivorous isopod in energy transfer. Mar Ecol Prog Ser 3:203–215

Souza JRB (1998) Produção secundária da macrofauna bentônica de praia de Atami—PR. PhD thesis, Universidade Federal do Paraná, Brazil

Sprung M (1993) Estimating macrobenthic secondary production from body weight and biomass: a field test in a non-boreal intertidal habitat. Mar Ecol Prog Ser 100:103–109

Taylor RB (1998) Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. Mar Ecol Prog Ser 172:37–51

Van Senus P, McLachlan A (1986) Growth, production, and a partial energy budget for the amphipod *Talorchestia capensis* (Crustacea, Talitridae) in the Eastern Cape, South Africa. PSZN Mar Ecol 7:165–179

Veloso VG, Cardoso RS, Petracco M (2003) Secondary production of the intertidal macrofauna of Prainha beach, Brazil. J Coast Res 15(SI):385–391

Wilber DH, Clarke DG (1998) Estimating secondary production and benthic consumption in monitoring studies: a case study of the

impacts of dredged material disposal in Galveston Bay, Texas. Estuaries 21:230–245

Yannicelli B, Palacios R, Giménez L (2002) Swimming ability and burrowing time of two cirolanid isopods from different levels of exposed sandy beaches. J Exp Mar Biol Ecol 273:73–88

Zuñiga O, Peña R, Clarke M (1985) Historia de vida y producción de *Excirolana braziliensis* Richardson, 1912 (Isopoda: Cirolanidae). Estud Oceanol 4:9–19