# GROWTH, MORTALITY, AND REPRODUCTION OF *EXCIROLANA BRAZILIENSIS* RICHARDSON, 1912 (ISOPODA, CIROLANIDAE) ON THE PRAINHA BEACH, RIO DE JANEIRO, BRAZIL

BY

DUANE B. FONSECA[1,2,4]),VALÉRIA G. VELOSO[3]) and RICARDO S. CARDOSO[3])

[1]) Departamento de Zoologia, Universidade Federal do Rio de Janeiro,
Av. Brigadeiro Trompowsky, s/n, CEP 21941-570 Rio de Janeiro, Brazil
[3]) Laboratório de Dinâmica de Populações Marinhas, Departamento de Ciências Naturais,
Universidade do Rio de Janeiro, Av. Pasteur, n° 296, CEP 22290-240 Rio de Janeiro, Brazil

## ABSTRACT

With the aim of estimating the growth parameters, mortality, and reproduction of a population of *Excirolana braziliensis*, monthly samplings were performed in the period from June 1993 to May 1995 at Prainha Beach, Rio de Janeiro, Brazil. The average size at first sexual maturity was estimated to be 6.9 mm (TL) with an average fecundity of 13 embryos per female. There was a significant linear regression between the clutch size and the length of the female. The growth analyses demonstrated that there is seasonality in growth with smaller rates coincident with lower temperatures. This paper discusses the existence of a size gradient, indicated by an increase in total length with decreasing temperatures.

## RESUMO

Com o objetivo de estimar os parâmetros de crescimento, mortalidade e reprodução de uma população de *Excirolana braziliensis*, amostragens mensais foram feitas no período entre Junho de 1993 e Maio de 1995 na Praia da Prainha (Rio de Janeiro, Brasil). O tamanho médio da primeira maturação sexual foi estimado em 6,9 mm (CT) com fecundidade média de 13 embriões por fêmea. Houve uma significativa regressão linear entre o tamanho da ninhada e o comprimento da fêmea. Foi observada sazonalidade no crescimento, com menores taxas coincidindo com temperaturas mais baixas. Este artigo discute a existência de um gradiente de tamanho, indicado pelo aumento do comprimento total com a diminuição da temperatura.

[2]) Present address: Department of Biology, University of Leicester, Adrian Building, University Road, Leicester LE1 7RH, U.K.
[4]) e-mail: dbf1@le.ac.uk

INTRODUCTION

*Excirolana braziliensis* Richardson, 1912 is a common isopod in the macrofauna of sandy beaches. It has a wide distribution in the Americas and is found along tropical, sub-tropical, and temperate coasts, both in the Pacific and Atlantic Oceans (Glynn et al., 1975; Dexter, 1977; Jaramillo, 1982).

*E. braziliensis* is a scavenger and on the Rio de Janeiro coast; it shares this function with the talitrid *Pseudorchestoidea brasiliensis* (Dana, 1853) (cf. Cardoso & Veloso, 1996; Veloso et al., 1997). Veloso et al. (1997) reported the spatial and temporal variation of the macrofauna of Prainha Beach, where *E. braziliensis* is distributed on the sub-terrestrial fringe and in the midlittoral zone. According to Veloso et al. (1997), no vertical stratification of sizes was observed in the zonation pattern of *E. braziliensis*. Furthermore, a year-round reproduction was observed.

In Panama, Dexter (1977) observed a year-round reproduction, rapid growth, and high adaptability to the physical environment. Zuñiga et al. (1985), studying a population in Chile, also reported rapid growth but unlike Dexter (1977) observed only one annual period of reproductive activity. Zuñiga et al. (1985) compared their results with those of Dexter (1977), and observed differences in some population features (maximum body size of adults, ovigerous females, and juveniles), which were assigned to geographical causes (latitudinal gradient).

This paper compares the results of two previous studies on *Excirolana braziliensis* (cf. Dexter, 1977; Zuñiga et al., 1985) and estimates growth, mortality, and reproductive parameters of a South American Atlantic coast population. Influences of temperature on characteristics of the population are discussed.

MATERIAL AND METHODS

The work was conducted at Prainha Beach, located in the metropolitan area of Rio de Janeiro city, Brazil (23°05′S 43°25′W). This beach was characterized by Cardoso & Veloso (1997) as semi-exposed according to the ranking system of McLachlan (1980), and as an intermediate morphodynamical type in the classification proposed by Short & Wright (1983) and Masselink & Short (1993). The mean sediment grain size is 0.43, i.e., medium sand, according to the classification of Wentworth (Suguio, 1973) and the slope varied from 1/5.29 to 1/17.82 m.

Monthly samples of isopods were taken over a two-year period from June 1993 to May 1995. Sampling was carried out during spring tides. Three transects (200 m spaced) were defined perpendicular to the water line and sampled according to a stratified random design, using zones defined by Dahl (1952): sub-terrestrial fringe zone, 1 stratum; 3 midlittoral strata; 1 stratum in the swash zone. From

each stratum, 4 replicates were taken with a 0.04 m$^2$ metal sampler to a depth of 25 cm. The collected sediment was washed through an 0.71 mm sieve and retained material was taken to the laboratory.

Water and sediment temperatures (20 cm depth) were recorded at the moment of sampling but as the animals were always buried, only the sediment temperature was considered in the statistical analyses. Sediment temperature was taken simultaneously at each stratum in the 3 transects and the overall average was used in statistical analysis. The water temperature was used for comparisons with other studies that did not supply sediment temperature data.

In the laboratory the organisms were preserved (4% formalin), counted, sexed, and measured. Total length (TL), from the anterior tip of the rostrum to the posterior border of the telson (Dexter, 1977), was measured to 0.1 mm.

The two sampling years, June 1993 to May 1994 and June 1994 to May 1995, were studied separately in order to detect any temporal variations in growth and mortality parameters.

The embryos present in the marsupia of ovigerous females were removed and counted. The relationship between clutch size and female TL was obtained by adjusting a linear regression. Significance was estimated by the F-test. The mean length at sexual maturity was defined as the length at which 50% of the females were ovigerous (L50) and it was estimated by the logistic curve

$$P = 1/\{1 + e^{[-r(L-L_m)]}\}$$

where P is the proportion of ovigerous females by length (L), r is the slope of the curve, and $L_m$ is the length that corresponds to a proportion of 50% of ovigerous females (L50) (King, 1995).

To perform the growth analysis, ELEFAN (Electronic Frequency Analysis) routine of the FISAT package (FAO-ICLARM Stock Assessment Tools) was used. This approach assumes that growth is described by the Von Bertalanffy model modified for seasonality (Gayanilo et al., 1994). The original model of Von Bertalanffy (1938) has been applied to a wide variety of species and, according to Garcia & Le Reste (1981), even though there are differences between the physiology of fishes and crustaceans, the model adequately describes the growth of these arthropods as well.

The output of the ELEFAN routine gives estimates of $L_\infty$ (theoretical maximum length attained by the species), k (growth constant), C (amplitude of the seasonal growth oscillation), and WP (winter-point, i.e., the period of growth reduction, expressed as a decimal fraction of the year) associated with an Rn value (goodness of fit index) (Gayanilo et al., 1994). In order to calculate the longevity ($T_{max}$), the maximum observed length and the output of the growth equation were used. To

compare growth parameter estimates, the growth performance index ($\phi'$) (Pauly & Munro, 1984) was calculated. This index is defined as $\phi' = 2\log_{10}(L_\infty) + \log_{10}(k)$.

Total instantaneous mortality (Z) was calculated based on the seasonal length-converted catch curve (FISAT routine) by linear regression $Ln(N_i) = a + bt_i$, where $N_i$ is the number of individuals of length class i, $t_i$ is the age of length class i, a and b are estimated through regression analysis, and b, with sign changed, is an estimate of Z. When seasonal growth is observed, the seasonal length-converted catch curve provides better estimates of Z (Pauly, 1990; Pauly et al., 1995). The annual mortality (A) was obtained from the expression: $A = 1 - e^{-Z}$ (Ricker, 1975).

Statistical comparison of the monthly mean values of sediment temperature was carried out using analysis of variance (ANOVA). Because of logistical problems, the temperature values of May 1994 and May 1995 were not obtained. In all statistical analyses a significance level of 5% was adopted.

### RESULTS

Sediment temperature

During the 24 months of sampling the mean temperature varied with a markedly seasonal pattern. Lowest temperatures occurred in the months of August 1993 and June 1994 (20°C) and the highest in January 1994 (32.25°C) (fig. 1). ANOVA demonstrated significant differences in monthly temperatures during the study period ($P < 0.01$).

Reproduction

During the sampling period, 170 ovigerous females of *Excirolana braziliensis* were collected and 62 of these had only manca embryos. The mean fecundity was 13 embryos per female, varying from 2 to 27. The TL of the ovigerous females varied from 4.6 to 8.9 mm. A statistically significant ($P < 0.01$) linear regression was observed between the TLs of ovigerous females and the numbers of embryos
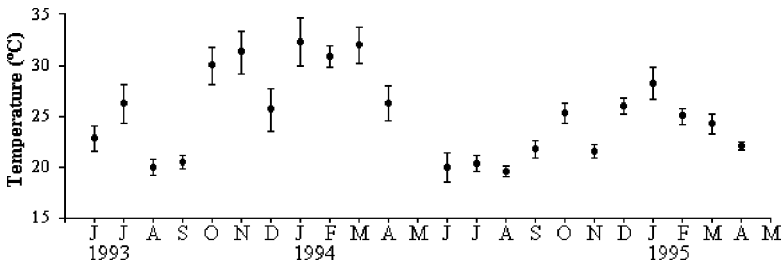


Fig. 1. Sediment temperature (20 cm depth) for the period of study. Means and standard deviations are shown.
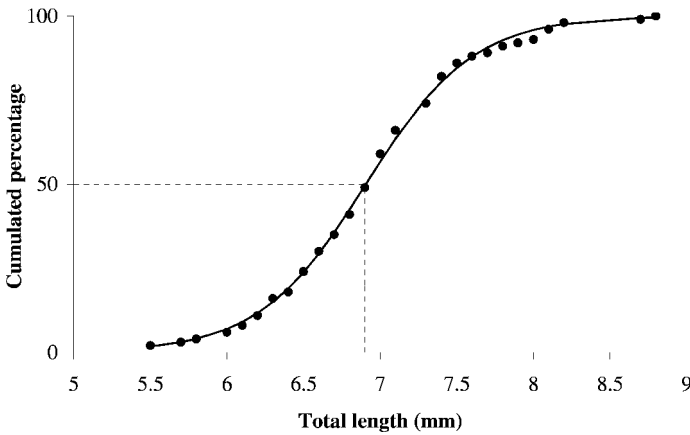
Fig. 2. *Excirolana braziliensis* Richardson, 1912. Mean length at sexual maturity defined as the length at which 50% of females are ovigerous (L50).

TABLE I

*Excirolana braziliensis* Richardson. Growth parameters estimated using the ELEFAN program, and longevity for both years analysed. $L_\infty$ (asymptotic length), k (growth constant), C (amplitude of the seasonal growth oscillation, WP (period of growth oscillation expressed as a decimal fraction of the year) and $T_{max}$ (longevity)

| Period | $L_\infty$ (mm) | k (year$^{-1}$) | C | WP | $T_{max}$ (months) |
|---|---|---|---|---|---|
| June 1993-May 1994 | 9.5 | 1.1 | 0.7 | 0.72 | 26 |
| June 1994-May 1995 | 9.5 | 1.0 | 1.0 | 0.58 | 30 |

carried (Number of embryos = $-17.89 + 4.41$ TL, r = 0.66, $n = 170$). Statistical difference between regressions using only manca stages or all embryo stages was not observed ($P > 0.05$). The mean length at sexual maturity (L50) was estimated to be 6.9 mm (fig. 2).

Growth

A total of 3003 individuals of *Excirolana braziliensis* was sampled, with TL varying between 2.0 and 9.1 mm. The growth parameters, for both years, are shown in table I. The calculated winter-point (WP) in the first year shows a decrease in growth rate in mid-August ($0.72 \times 12 = 8.64$ months), while in the second year it shows a cessation of growth at the end of June ($0.58 \times 12 = 6.96$ months). The estimated parameters for the first year showed an adjustment (Rn) of 0.546, and in the second year of 0.501 (fig. 3).

Mortality

The estimate of total instantaneous mortality (Z) was 2.93 (A $= 0.95 = 1 - e^{-2.93}$) in the first year and 2.74 (A $= 0.93$) in the second year.
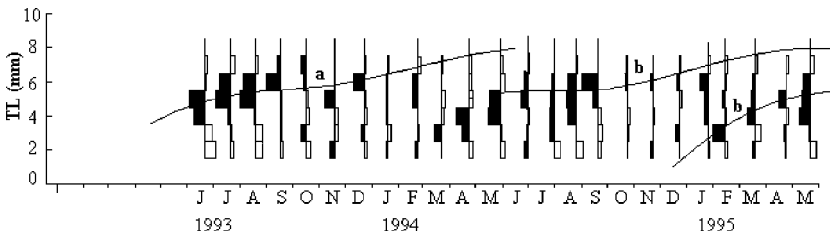
Fig. 3. *Excirolana braziliensis* Richardson, 1912. Growth curves estimated by ELEFAN software. Growth curves were adjusted for two periods: (a) June 1993 to May 1994 ($L_\infty$ = 9.5 mm, k = 1.1/year, C = 0.7 and WP = 0.72) and (b) June 1994 to May 1995 ($L_\infty$ = 9.5 mm, k = 1.0/year, C = 1.0 and WP = 0.58).

## DISCUSSION

### Reproduction

A highly positive correlation between the number of embryos and female length has usually been observed in other species of isopods (e.g., r ≈ 0.90) (Ruyck et al., 1991; Zuñiga et al., 1985). In this work, the correlation coefficient (r) was 0.66. Therefore, 56% of the variation $(1 - r^2)$ (Zar, 1984) in embryo numbers is not explained by regression. Furthermore, regression of number of embryos at manca stage vs. female TL was not significantly different from regression using all embryo stages vs. female TL. Thus, the variance observed cannot be attributed to the presence of different embryo stages (and sizes) in marsupia. Studying the genus *Excirolana*, Klapow (1970) has related the decline of embryo numbers to mortality between embryo stages, and to partial release of juveniles as well. Probably this can explain the variance in our data. However, as we have not quantified mortality and partial release of embryos, we prefer not to draw conclusions about this subject.

### Mortality

*Excirolana braziliensis* and *Pseudorchestoidea brasiliensis* (Dana, 1853), in Prainha Beach, both have similar annual mortality (Cardoso & Veloso, 1996) and field observation has shown that birds prey on the former species. Although we have not seen *E. braziliensis* being preyed, Zuñiga et al. (1985) have reported predation by birds. According to Brusca & Iverson (1985), *E. braziliensis* has an intense swimming activity and Fonseca (pers. obs.) has noticed these isopods swimming in tide pools after a spring tide. Thus, swimming activity could represent a vulnerable condition for *E. braziliensis* to being preyed by fishes. Furthermore, the ghost crab *Ocypode quadrata* (Fabricius, 1787) inhabits the same zone as *E. braziliensis*, which enables this crab to be a possible predator of the isopod. In fact, we believe that predation strongly influences mortality, because cirolanid isopods often have high physiological tolerances and high longevity as well (see below).

Growth

The growth curves obtained exhibit a markedly seasonal pattern. This is often seen in animals with short life cycles (Rosenberg & Beddington, 1988; Dall et al., 1990; Isaac, 1990; Pauly, 1990; Sparre, 1990). In the Von Bertalanffy model, the organism is considered an open system, where growth is the result of the relationship between anabolism and catabolism (Von Bertalanffy, 1938). In this balance, the ingestion of food, the population density, and especially temperature, exert strong influences on growth (Pauly, 1980; Pollock, 1995; Fontoura & Agostino, 1996).

The lowest growth rates in the winter months established in this study have already been reported for other cirolanids (Shafir & Field, 1980; Alava & Defeo, 1991). Lowest temperatures in the period were recorded in August-September 1993 and June-September 1994 ($\approx 20°C$). The estimated values for C (amplitude of the seasonal growth oscillation) equal those observed by Cardoso & Veloso (1996) for the detritivorous talitrid *Pseudorchestoidea brasiliensis*, on the same beach, and for the same period.

With respect to longevity estimates (ca. 30 months) high longevities are observed in other isopods, such as *Excirolana armata* (Dana, 1853), *Cirolana imposita* Barnard, 1955, *Eurydice pulchra* Leach, 1815, *Eurydice affinis* Hansen, 1905, *Tylos capensis* Krauss, 1843, and *Tylos punctatus* Holmes & Gray, 1909 (cf. Fish, 1970; Jones, 1970; Hayes, 1974; Shafir & Field, 1980; Alava & Defeo, 1991; McLachlan & Sieben, 1991). The long life cycle is possibly related to high physiological tolerances that are dependent on behaviour or physiological mechanisms (Brown & Odendaal, 1994). In the laboratory, Dexter (1977) observed the survival of individuals of *Excirolana braziliensis* to extreme conditions of temperature (45°C) and salinity (40). Although not statistically tested, we have two interesting observations about survival to extreme conditions: (a) one individual kept in a plastic tube, with no food or aeration, survived for three weeks, and (b) when the samples were frozen before sorting we usually found live isopods after a night in the freezer.

When we compare the growth parameters obtained in this study with those calculated by Zuñiga et al. (1985), a difference can be observed. Our initial feeling was that Prainha's *E. braziliensis* would have a higher k and a lower $L_\infty$ than the Chilean one (*E. braziliensis* of Antofagasta Beach) in view of the well established relationship between temperature and growth parameters (Beverton & Holt, 1959). However, the results were surprising, because the Chilean k was higher and longevity was markedly lower than that recorded by us (table II). Pauly & Munro (1984) proposed the growth performance index ($\phi'$) to compare estimates of growth parameters. For a given species there is a near constancy of the parameter $\phi'$ (Longhurst & Pauly, 1987). Our calculated value of $\phi'$ is similar

TABLE II

Comparison of growth parameters, longevity, and growth performance index of *Excirolana braziliensis* Richardson and *Excirolana armata* (Dana); $L_\infty$ (asymptotic length), k (growth constant), $T_{max}$ (longevity) and growth performance index ($\phi' = 2\log_{10}(L_\infty) + \log_{10}(k)$)

| Species | Locality | $L_\infty$ (mm) | k (year$^{-1}$) | $T_{max}$ (months) | $\phi'$ | Author |
|---------|----------|-----------------|-----------------|--------------------|---------|--------|
| *E. armata* | Uruguay | 15.8 | 0.4 | 36 | 1.9994 | Alava & Defeo, 1991 |
| *E. braziliensis* | Chile | 12.8 | 1.23 | 14-16 | 2.3043 | Zuñiga et al., 1985 |
| *E. braziliensis* | Brazil | 9.5 | 1.1 | 26 | 1.9968 | This study, 1993-1994 |
| *E. braziliensis* | Brazil | 9.5 | 1.0 | 30 | 1.9954 | This study, 1994-1995 |

to that calculated for a related species (*E. armata*) (cf. Alava & Defeo, 1991), but diverges from the value obtained for *E. braziliensis* by Zuñiga et al. (1985) (table II).

Considering these results, we believe that Zuñiga et al. (1985) may have overestimated k. Two facts support this idea: (a) the high value of the growth performance index, and (b) the low longevity estimate that does not agree with the cirolanid literature.

Zuñiga et al. (1985) suggested a latitudinal gradient for populations of *E. braziliensis*. According to Bergmann's rule (Mayr, 1942) animals inhabiting colder and higher latitudes have larger maximum sizes than their counterparts of lower latitudes. Increase in size with increasing latitude (or temperature) has been reported for various taxonomic groups (Taylor, 1958; Beverton & Holt, 1959; Ricker, 1979; Hartnoll, 1982; Moreau, 1987; Atkinson, 1994; Atkinson & Sibly, 1997).

The reason for this gradient has been controversial (Atkinson & Sibly, 1997; Pauly, 1997). However, it ought to be related to physiological mechanisms which produce the negative relationship between the Von Bertalanffy growth parameters $L_\infty$ and k (i.e., in populations in which asymptotic length is large, k is low, and vice versa) (Beverton & Holt, 1959; Atkinson & Sibly, 1997). Pauly (1980) has given a physiological interpretation of k in which it increases with factors that increase oxygen demand (or cause "stress"), such as temperature. Therefore, temperature would influence the growth constant (k), and k would affect maximum length.

Our results support the temperature gradient in body size of *Excirolana braziliensis*. Table III shows the lengths of juveniles and adults of 3 distinct populations of this species. It can be observed that the size of adults, as well as of juveniles, increases with falling temperature. Another example of this gradient in sandy beach crustacean macrofauna is the mole crab, *Emerita braziliensis* Schmitt, 1935, that is larger on the southern Brazilian coast ($\approx$ 32°S) (Gianuca, 1985) than on the Rio de Janeiro coast ($\approx$ 23°S) (Veloso & Cardoso, 1999). Finally, the swash zone mollusc *Donax hanleyanus* Philippi, 1847 attains a maximum size of 26 mm on the Rio de

TABLE III

*Excirolana braziliensis* Richardson. Comparison of the lengths of juveniles and adults observed in three different studies

| Locality | Latitude | Water temperature range (°C) | Adult TL range (mm) | Juvenile TL range (mm) | Author |
|----------|----------|------------------------------|---------------------|------------------------|--------|
| Panama | 8°55′N | 22.0-29.0 | 2.0-4.7 | 1.0-2.0 | Dexter, 1977 |
| Brazil | 23°27′S | 16.0-28.0 | 3.0-9.1 | 2.0-3.0 | This study |
| Chile | 23°27′S | 13.8-27.2 | 4.0-12.0 | 2.5-4.0 | Zuñiga et al., 1985 |

Janeiro coast (Cardoso pers. comm.), whereas Gianuca (1985) has reported 36 mm from the southern Brazilian coast.

At Prainha, *Excirolana braziliensis* shares a scavenger activity with *Pseudorchestoidea brasiliensis*. Both species have high density (together comprising about 40% of all individuals) and similar secondary production (Cardoso & Veloso, 1996), which shows the importance of the detritus food web. Therefore, *E. braziliensis* is an important species of sandy beach communities, which denotes the importance of this study on the knowledge of growth, mortality, and reproduction processes.

## ACKNOWLEDGEMENTS

## REFERENCES

ALAVA, A. & O. DEFEO, 1991. Distributional pattern and population dynamics of *Excirolana armata* (Isopoda: Cirolanidae) in a Uruguayan sandy beach. Estuarine, Coastal and Shelf Science, **33**: 433-444.

ATKINSON, D., 1994. Temperature and organism size — a biological law for ectotherms? Advances in Ecological Research, **25**: 1-58.

ATKINSON, D. & R. M. SIBLY, 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends in Ecology and Evolution, **12** (6): 235-239.

BERTALANFFY, L. VON, 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology, **10** (2): 181-213.

BEVERTON, R. J. H. & S. J. HOLT, 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: G. WOLSTENHOLME & M. O'CONNER (eds.), The lifespan of animals. CIBA Foundation Colloquia on Ageing, **5**: 142-180. (Churchill, London).

BROWN, A. C. & F. J. ODENDAAL, 1994. The biology of oniscid Isopoda of the genus *Tylos*. Advances in Marine Biology, **30**: 89-153.

BRUSCA, R. C. & E. W. IVERSON, 1985. A guide to the marine isopod Crustacea of Pacific Costa Rica. Revista de Biologia Tropical, **33** (suppl. 1): 1-77.

CADDY, J., 1987. Size-frequency analysis for Crustacea: moult increment and frequency models for stock assessment. Kuwait Bulletin of Marine Science, **9**: 43-61.

CARDOSO, R. S. & V. G. VELOSO, 1996. Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha beach, Brazil. Marine Ecology Progress Series, **142**: 111-119.

— — & – —, 1997. Estratégia amostral para caracterização da macrofauna da região entre-marés em três praias arenosas expostas do Estado do Rio de Janeiro, Brasil. Oecologia Brasiliensis, **3**: 171-182.

DAHL, E., 1952. Some aspects of the ecology and zonation of the fauna of sandy beaches. Oikos, **4**: 1-27.

DALL, W., B. J. HILL, P. C. ROTHLISBERG & D. J. STAPLES, 1990. Moulting and growth. In: J. H. S. BLAXTER & A. J. SOUTHWARD (eds.), The biology of the Penaeidae. Advances in Marine Biology, **27**: 213-250.

DEXTER, D. M., 1977. Natural history of the Pan-American sand beach isopod *Excirolana braziliensis* (Crustacea: Malacostraca). Journal of Zoology, London, **183**: 103-109.

FISH, S., 1970. The biology of *Eurydice pulchra* (Crustacea: Isopoda). Journal of the Marine Biological Association of the United Kingdom, **50**: 753-768.

FONTOURA, N. F. & A. A. AGOSTINO, 1996. Growth with seasonally varying temperatures: an expansion of the Von Bertalanffy growth model. Journal of Fish Biology, **48**: 569-584.

GARCIA, S. & L. LE RESTE, 1981. Life cycles, dynamics exploitation, and management of coastal penaeid shrimps stocks. FAO Fisheries Technical Paper, **203**: 1-215.

GAYANILO, F. C., JR., P. SPARRE & D. PAULY, 1994. The FAO-ICLARM stock assessment tools (FISAT) user's guide: 1-186. (FAO, Rome).

GIANUCA, N. M., 1985. The ecology of a sandy beach in southern Brazil: 1-330. (Ph.D. Thesis, University of Southampton, Southampton, U.K.).

GLYNN, P. W., D. M. DEXTER & T. E. BOWMAN, 1975. *Excirolana braziliensis*, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. Journal of Zoology, London, **175**: 509-522.

HARTNOLL, R. G., 1982. Growth. In: L. G. ABELE (ed.), Embryology, morphology and genetics. The biology of Crustacea, **2**: 111-196. (Academic Press, London).

HAYES, W. B., 1974. Sand-beach energetics: importance of the isopod *Tylos punctatus*. Ecology, **55**: 838-847.

ISAAC, V. J., 1990. The accuracy of some length-based methods for fish population studies. ICLARM Technical Report, **27**: 1-81.

JARAMILLO, E., 1982. Taxonomy, natural history and zoogeography of sand beach isopods from the coast of southern Chile. Studies on Neotropical Fauna and Environment, **17**: 175-194.

JONES, D. A., 1970. Population densities and breeding in *Eurydice pulchra* and *Eurydice affinis* in Britain. Journal of the Marine Biological Association of the United Kingdom, **50**: 635-655.

KING, M., 1995. Fisheries biology, assessment and management: 1-341. (Fishing News Books, Oxford).

KLAPOW, L. A., 1970. Ovoviviparity in the genus *Excirolana* (Crustacea: Isopoda). Journal of Zoology, London, **162**: 359-369.

LONGHURST, A. L. & D. PAULY, 1987. Ecology of tropical oceans: 1-407. (Academic Press, London).

MASSELINK, G. & A. D. SHORT, 1993. The effect of tide range on beach morphodynamics and morphology: a conceptual beach model. Journal of Coastal Research, **9**: 785-800.

MAYR, E., 1942. Systematics and the origin of species: 1-334. (University Press, New York).

MCLACHLAN, A., 1980. The definition of sand beaches in relation to exposure: a simple rating system. South African Journal of Zoology, **76**: 137-138.

McLachlan, A. & P. R. Sieben, 1991. Growth and production of *Tylos capensis* Krauss, 1843 (Isopoda). Crustaceana, **61**: 43-48.

Moreau, J., 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. In: R. C. Summerfelt & G. E. Hall (eds.), Age and growth of fish: 81-113. (Iowa State University Press, Ames).

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil Permanent International pour l'Exploration de la Mer, **39** (2): 175-192.

— —, 1990. Length-converted catch curves and the seasonal growth of fishes. Fishbyte, **8** (3): 33-38.

— —, 1997. Geometrical constraints on body size. Trends in Ecology and Evolution, **12** (11): 442.

Pauly, D. & J. L. Munro, 1984. Once more on growth comparison in fish and invertebrates. Fishbyte, **2** (1): 21.

Pauly, D., J. Moreau & N. Abad, 1995. Comparison of age-structured and length-converted catch curves of brown trout *Salmo trutta* in two French rivers. Fisheries Research, **22**: 197-204.

Pollock, D. E., 1995. Changes in maturation ages and sizes in crustacean and fish populations. South African Journal of Marine Science, **15**: 99-103.

Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, **191**: 1-382.

— —, 1979. Growth rates and models. In: W. S. Hoar, D. J. Randall & J. R. Brett (eds.), Bioenergetics and growth. Fish Physiology, **8**: 677-743. (Academic Press, London).

Rosenberg, A. A. & J. R. Beddington, 1988. Length-based methods of fish stock assessment. In: J. A. Gulland (ed.), Fish population dynamics: the implications for management (ed. 2): 83-104. (John Wiley & Sons Ltd., New York).

Ruyck, A. M. C. de, T. E. Doon, Jr. & A. McLachlan, 1991. Life histories and breeding patterns of three intertidal sand beach isopods. Marine Ecology, **12** (2): 105-121.

Shafir, A. & J. G. Field, 1980. Population dynamics of the isopod *Cirolana imposita* Barnard in a kelp-bed. Crustaceana, **39**: 185-196.

Short, A. D. & L. D. Wright, 1983. Physical variability of sandy beaches. In: A. McLachlan & T. Erasmus (eds.), Sandy beaches as ecosystems: 133-144. (W. Junk, The Hague).

Sparre, P., 1990. Can we use traditional length-based fish stock assessment when growth is seasonal? Fishbyte, **8** (3): 29-32.

Suguio, K., 1973. Introdução à sedimentologia: 1-312. (Blucher/Edusp, São Paulo).

Taylor, C. C., 1958. Cod growth and temperature. Journal du Conseil Permanent International pour l'Exploration de la Mer, **23** (3): 366-370.

Veloso, V. G. & R. S. Cardoso, 1999. Population biology of the mole crab *Emerita brasiliensis* (Decapoda: Hippidae) at Fora beach, Brazil. Journal of Crustacean Biology, **19** (1): 147-153.

Veloso, V. G., R. S. Cardoso & D. B. Fonseca, 1997. Spatio-temporal characterization of the intertidal macrofauna community of Prainha beach (Recreio dos Bandeirantes), State of Rio de Janeiro. Oecologia Brasiliensis, **3**: 213-225.

Zar, J. H., 1984. Biostatistical analysis (ed. 2): 1-718. (Prentice Hall, New Jersey).

Zuñiga, O. R., R. M. Peña & M. G. Clarke, 1985. *Excirolana braziliensis* Richardson, 1912 (Isopoda: Cirolanidae) life history and production. Estudios Oceanológicos, **4**: 9-19.