

Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha Beach, Brazil

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ABSTRACT: The population biology of *Pseudorchestoidea brasiliensis* (Dana, 1853) (Amphipoda: Talitridae) was studied by monthly sampling from June 1993 through May 1995 at Prainha Beach, Brazil. Three transects were established, each with 5 levels parallel to the waterline. From each level, 4 replicates were taken with a 0.04 m² sampler. A stratified distribution was observed, with individuals 3 to 8 mm in length concentrated at the lower levels, while 9 to 12 mm individuals were distributed farther from the waterline. Highest population densities were observed in winter (August 1993 and July 1994) and summer (February 1994 and 1995). Oviparous females and juveniles were observed during the entire sampling period, indicating continuous reproduction of the population. The sex ratio was 1.45 for females. Mean brood size was 2.8 eggs and mean egg volume was 0.04 mm³. The production of small eggs might be linked to small size at maturation of the females, which could increase the population growth rate. Growth and mortality rates were greater for males than females. Annual production was about 0.30 g AFDW m⁻² yr⁻¹ and the P/B ratio varied from 2.16 to 2.3, while life span varied between 12 and 21 mo.

KEY WORDS: Population biology · Secondary production · Brazil · Sandy beaches · Talitridae · *Pseudorchestoidea*

INTRODUCTION

Among those organisms which are part of the macrofauna of exposed sandy beaches, the talitrid amphipods have received special attention because they are one of the faunal dominants (MacIntyre 1963, McLachlan et al. 1981), and because they play an important ecological role as decomposers (Griffiths et al. 1983). Like other intertidal invertebrates, the sandhoppers of sandy beaches occupy various intertidal or supralittoral habitats and can differ in behavior and population characteristics, including reproductive patterns (Marsden 1991). The talitrids are herbivorous or detritivorous and are generally associated with kelp

and wrack cast ashore by waves and tides (Behbehani & Croker 1982, Marsden 1991), feeding on this plant material and debris and migrating up and down the shore in search of food.

Most studies on the Talitridae family are concerned with reproductive biology (Morino 1978, Williams 1978, Wildish 1979, 1982). Marsden (1991), studying *Talorchestia quoyana*, observed that the reproductive strategies of producing several broods, increasing parental care and releasing large hatchlings into the optimal habitat are important for survival in the intertidal sand beach habitat, which has been regarded as the most physically harsh of all marine environments. In most cases, juveniles present a faster growth rate than adults (Wildish 1972, Williams 1978). Marsden (1989) associated the high growth rate of juveniles with their continuous feeding. Van Sensus & McLachlan (1986)

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observed a rapid growth rate and a low mortality for *Talorchestia capensis*, while Wildish (1972) suggests that a slow growth rate would have been a step towards the evolution of primitive terrestrial *Orchestia*.

The genus *Orchestoidea* has been studied by only a few authors: Bowers (1964) described the clumped pattern, nocturnal activity period and reproductive cycle of *O. californiana* and *O. corniculata*. Craig (1971, 1973a, b) observed the behavioral activity, spatial distribution along shore and lunar orientation of *O. corniculata*, while Duarte (1974) investigated the feeding behavior of *O. tuberculata* on the Chilean coast.

The present study is the first to examine the distribution pattern, population and reproductive biology, production and turnover of *Pseudorchestoidea brasiliensis* (Dana, 1853), a species which until recently was classified in the genus *Orchestoidea* (E. L. Bousfield 1982 pers. comm.). *P. brasiliensis* is a common and abundant species in the reflective beaches of Rio de Janeiro State.

MATERIALS AND METHODS

Study area and sampling. Monthly samples were taken from June 1993 through May 1995 at Prainha Beach, Recreio dos Bandeirantes, State of Rio de Janeiro, Brazil (23° 05' S, 43° 25' W).

The collections were made during spring tides on 3 transects, each divided into 5 strata parallel to the waterline. Strata locations were as follows: Stratum 1—below the swash line; Strata 2, 3 and 4—in the lower, middle and upper midlittoral, respectively; Stratum 5—above the drift line (supralittoral). The width of the beach at the time of collection varied between 43 and 65 m. From each level, 4 replicates were taken using a 0.04 m² metal sampler up to a depth of 25 cm.

This beach was characterized by Veloso et al. (in press) as semi-exposed using the McLachlan (1980) ranking system, and as a reflective type in the classification proposed by Short & Wright (1983) and Mase-link & Short (1993). The mean grain size is 0.43 mm (medium sand) and the intertidal slope varies from 1/5.29 to 1/17.82.

Laboratory procedures. The material was sorted using a stereomicroscope and preserved in 10% formalin. Each individual was sexed using the stereomicroscope and sorted into: (a) males, with a developed second gnathopod; (b) females, with oostegites and without a developed second gnathopod; (c) juveniles, lacking both oostegites and a developed second gnathopod; and (d) ovigerous females, with both oostegites and eggs. The individuals were then measured from the beginning of the cephalon to the end of the telson and grouped into 1 mm size classes. Eggs of ovigerous females were

counted and measured. Afterwards the individuals were dried at 70°C for 24 h, weighed, ashed in a muffle furnace for 4 h at 600°C and then reweighed.

The 2 sampling years June 1993 to May 1994 and June 1994 to May 1995 were studied separately in order to analyze the temporal variation of population parameters (growth, mortality and secondary production). Growth and mortality were estimated for males and females separately. Juveniles were divided into 50% males and 50% females to analyze growth and mortality rates.

A χ^2 test was used to test the proportion of males to females, as well as to verify the distribution of length classes and sex categories in the sampling strata. Two-way ANOVA and Duncan's multiple range test were performed to analyse the distribution of length classes and sex categories in the sampling strata. Stratum 1 was excluded from this analysis owing to the absence of any specimens in it during the whole sampling period.

Reproduction. The monthly proportion of males to females (sex ratio) were tested by a χ^2 test.

Fecundity was determined by correlating the length of the 597 ovate females collected with the mean number of eggs per brood. The egg volume, estimated from the egg diameter of 450 eggs, was calculated by: $V = 4/3\pi r^3$, where r is the radius of the eggs (Wildish 1982).

Growth. Growth parameters were estimated using the ELEFAN I routine of the computer program Com-pleat ELEFAN (Version 1.10) which adjusts the von Bertalanffy curve, modified for seasonal oscillation in growth (Pauly & Gaschutz 1979), using the equation:

$$L_t = L_\infty \left\{ 1 - e^{-K \left[(t-t_0) + \frac{C}{2\pi} \sin[2\pi(t-t_s)] \right]} \right\}$$

where L_t is length at time t (mm); L_∞ is asymptotic length (mm); K is von Bertalanffy's growth constant; C is a constant for the amplitude of seasonal oscillation of growth; t_0 is age at zero length; and t_s is the initial point of seasonal oscillation in relation to $t = 0$. The graphical representation of this equation produces a curve of which the agreement is represented by R_n , which is analogous to the parameter r^2 in correlation analysis (Gayanilo et al. 1989). The modified Wetherall method (Pauly 1986) was used to obtain preliminary estimates of L_∞ , for the ELEFAN II routine, thus reducing the iterative process of calculating the growth parameters (Rufino 1991, Urban & Campos 1994). Life span was estimated considering T_{max} as the length at which 99% of the population was represented.

Mortality. Total mortality (Z) was calculated based on the length-converted catch curve of the ELEFAN II routine, using the negative exponential model: $N_t/\Delta t_i =$

$N_0 e^{-Zt_i}$, where N_0 is the number of individuals at time zero, N_i is the number of individuals of length class i , Δt_i is the time necessary for growth within length class i and t_i is the age of mean length of length class i . In all calculations of Z , for the length-converted catch curve, only those points located between the maximum and next last value of the curve were used (Sparre et al. 1989). The annual finite mortality rate (A) was obtained from the expression: $A = 1 - e^{-Z}$ according to Ricker (1975).

Secondary production. Production was estimated by 3 methods: (1) Modified Hynes method or 'size-frequency' (Hynes & Coleman 1968, Hamilton 1969, Benke 1979, Menzie 1980), which is based on survival and increase in mean weight per generation, expressed as follows: $P = \sum (N_j - N_{j+1}) \cdot (W_j W_{j+1})^{1/2}$, where N_j is the number of individuals that grow to the mean size of the size class during $1/i$ of the year (Hamilton 1969); and $(W_j W_{j+1})^{1/2}$ is the mean geometric weight between 2 successive length classes. $N_j = i \cdot N \cdot 365/CPI \cdot P_e/P_a$, where i is the number of length classes, N is the mean number of individuals in the size class, CPI is the time from hatching to death of the largest size class, P_e is the estimated proportion of the life cycle spent in a particular length class ($= 1/i$), and P_a is the actual proportion of the life cycle spent in a particular length class.

(2) Method of production for stocks with recruitment, age classes not separable—Crisp's method 3A. In these calculations it is necessary to measure growth or mortality rates as a function of size and season and to carry out a summation throughout the year for each size class (Crisp 1984). The production is given by the equation: $P = \sum \sum f_i \cdot G_i \cdot w_i \cdot \Delta t$, where f_i is the number of individuals of this size class existing in the population during the period Δt , G_i is the weight-specific growth rate of size class i , w_i is the mean weight of the size class and Δt is the interval of time. G_i can be obtained by $G_i = \ln w_{i+1} - \ln w_i / \Delta t_{(i+1-i)}$.

(3) Allen's (1971) method for populations whose mortality is expressed by the exponential model, and growth by Bertalanffy's model. In these cases, the ratio between production and biomass equals the mortality rate: $P/B = Z$ and thus $P = Z \cdot B$. The mortality rate (Z) used by the Allen method was obtained by the mean of the rates (Z) estimated by Wetherall's method and by the length-converted catch curve.

The relationship between length and dry weight was estimated by linear regression analysis, with the data converted to logarithms in the equation: $\log W = \log a + b \log L$, where W is the monthly mean ash-free dry weight per individual (mg), L is the length of the size class (mm) and a and b are constants. The F -test was used to test the significance of the correlation coefficient.

RESULTS

Population structure

The population of *Pseudorchestoidea brasiliensis* showed the highest densities in the winter (August 1993 and July 1994) and late summer (February 1994 and 1995). The lowest densities were recorded in spring 1993 and 1994, and in autumn 1995 (Fig. 1). The densities of males and non-ovigerous females were similar during both years sampled (Fig. 2). Juvenile individuals (3 and 4 mm) showed 3 density peaks: at the beginning of spring (September 1993), beginning of winter (June 1994) and summer (February 1995). Low densities were observed in spring (October 1993

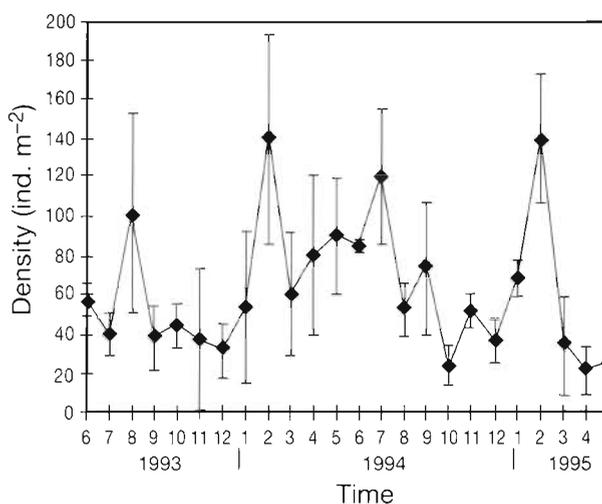


Fig. 1. *Pseudorchestoidea brasiliensis*. Population density for the period June 1993 to May 1995. Vertical bars represent standard deviation

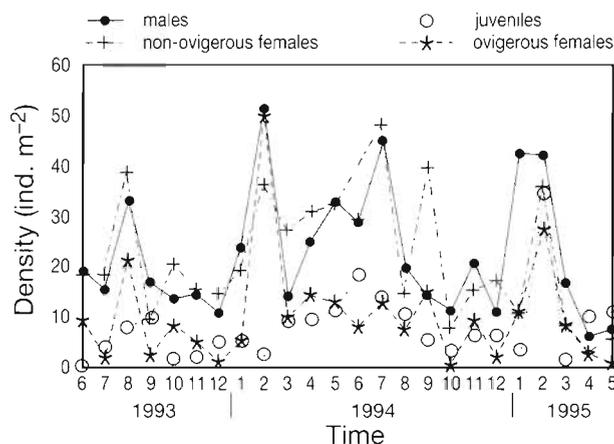


Fig. 2. *Pseudorchestoidea brasiliensis*. Population density of males, non-ovigerous females, ovigerous females and juveniles for the period June 1993 to May 1995

and 1994, November 1993), summer (February 1994) and autumn (March 1995) (Fig. 2). Ovigerous females were captured during all collections, the highest densities being observed during winter (August 1993 and September 1994) and late summer (February 1994 and 1995), while low densities were recorded in spring (September 1993 and October 1994), early summer (December 1993 and 1994) and late autumn (April and May 1995) (Fig. 2). The sex ratio between males and non-ovigerous females was 1:1 ($p > 0.05$), while the sex ratio between males and (ovigerous and non-ovigerous) females was 1:1.5 ($p < 0.05$). The greatest deviations in the sex ratio occurred in October 1993 and March and September 1994 (Fig. 3).

The high standard deviations in Fig. 1 suggest a clumped distribution of individuals mainly on Stratum 2, located in the lower midlittoral (Table 1b).

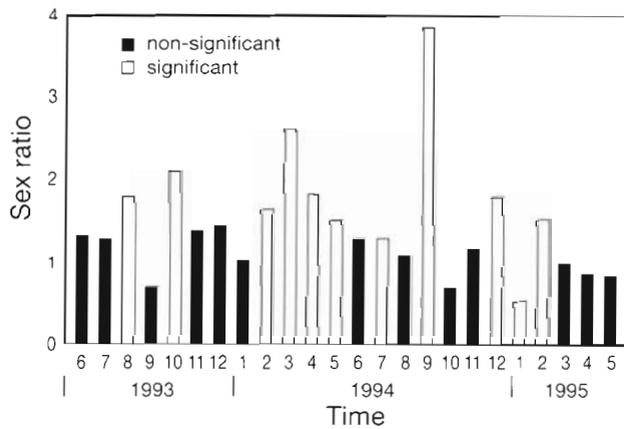


Fig. 3. *Pseudorchestoidea brasiliensis*. Sex ratio during the period June 1993 to May 1995

Table 1 (a) Analysis of variance: 2-way ANOVA. Relation between sampling strata and sex categories of *Pseudorchestoidea brasiliensis*. df = degrees of freedom. p = probability level. (b) Results of Duncan's multiple range test analysis undertaken as a *posteriori* test of multiple comparisons to indicate statistical significance

(a)	df	Sum of squares	Mean squares	F	p
Sampling strata	3	10080.79	3360.26	26.91	0.00
Sex categories	3	4421.97	1473.99	61.34	0.00
Interaction	9	856.83	95.20	1.74	0.08
Residual	368	20157.79	54.77		
Total	383	35517.38			

(b)	Sampling stratum			
	2	3	4	5
Mean abundance	15.97	11.70	7.18	2.28
Non-significance	-	-	-	-

There was no stratification by sex, but all sex categories preferred Stratum 2 (lower part of the midlittoral) (Fig. 4). This was confirmed in a 2-way ANOVA and by Duncan's multiple range test (Table 1a, b). Significant interaction effects were observed between sampling strata and length classes. There is a significant dependence between length classes and spatial location of the individuals on the beach (Table 2). The 3 to 7 mm length classes were preferentially distributed at Stratum 2; 8 mm individuals were found at Stratum 2 as much as at Stratum 3, while 9 mm individuals were distributed over the whole midlittoral (Strata 2, 3 and 4), and 10 to 12 mm individuals occurred in all strata (Fig. 5).

Reproduction

A linear relationship between the mean number of eggs per brood (Y) and the body length of ovigerous females (X) was found (Fig. 6). The highest frequencies of ovigerous females were found at lengths 8 and 9 mm, with a mean length of 8.5 mm. The mean number of eggs per clutch was 2.8, while the mean egg diameter was 0.42 mm, corresponding to a volume of 0.04 mm³ per egg.

Growth

The L_{∞} values determined by the Wetherall method were used as preliminary values for adjusting the growth curves by the ELEFAN I routine (Table 3). The males had higher growth rates as compared to females in both years (Table 3). The values of parameter C (degree of seasonal variation) showed no apparent

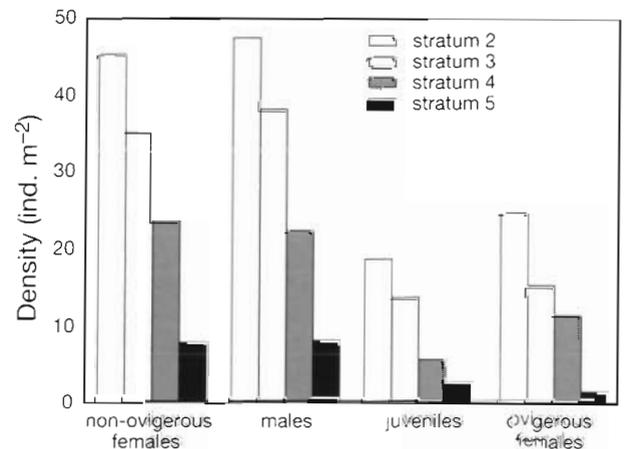


Fig. 4. *Pseudorchestoidea brasiliensis*. Spatial variability of population density of males, non-ovigerous females, ovigerous females and juveniles along the sampling strata

Table 2. Analysis of variance: 2-way ANOVA. Relation between sampling strata and length classes of *Pseudorchestoidea brasiliensis*. df = degrees of freedom. p = probability level

	df	Sum of squares	Mean squares	F	p
Sampling strata	3	2363.14	787.71	59.53	0.00
Length classes	9	6699.80	744.42	56.25	0.00
Interaction	27	1793.76	66.44	5.02	0.00
Residual	920	12174.04	13.23		
Total	959	23030.75			

variation between both sexes and years and were always between 0.9 and 1.0, indicating a strong variation in growth. Values of *WP* (point of lowest growth rate during the year) differed between years and between sexes; however, males and females of the second sampling year showed close *WP* values (September) (Fig 7a, b). Life span of females was greater than that of males during the first year, being a function of the lower growth rates of the females. This did not occur during the second sampling year, because of the smaller difference between growth rates of males and females and the lower T_{max} determined for the females.

Mortality

Mortality rates of males showed no differences when both sampling years were compared; also, no differences were demonstrated between mortality rates of males and females in the second year. However, the males showed higher mortality than females in the first sampling year. Note also that the female mortality rate was significantly higher in the second year, based on both estimation methods used (Table 4). The annual finite mortality rate (*A*) of the males was 0.93 and 0.95 yr⁻¹, respectively, for the first and second years, while that of the females was 0.78 and 0.93 yr⁻¹, respectively.

Table 3. *Pseudorchestoidea brasiliensis*. Von Bertalanffy growth function (VBGF) parameters: $L_{\infty}^{Wetherall}$ and $L_{\infty}^{ELEFAN1}$ = asymptotic length (mm) determined by the modified Wetherall method and ELEFAN 1 routine, respectively; *K* = von Bertalanffy's growth constant; *C* = constant for the amplitude of seasonal oscillation of growth; *WP* = point of lowest growth rate in the year; *Rn* = agreement of the estimated observed growth rates. T_{max} : length (mm) at which 99% of the population was represented and life span estimated for sex categories during the periods

Sex-period	$L_{\infty}^{Wetherall}$	$L_{\infty}^{ELEFAN1}$	<i>K</i>	<i>C</i>	<i>WP</i>	<i>Rn</i>	T_{max}	Life span (mo)
Females-93/94	12.50	12.50	0.90	0.9	0.5 May	0.466	9.95	21.3
Males-93/94	13.39	13.40	1.36	0.9	0.2 Mar	0.501	10.75	14.4
Females-94/95	12.37	13.41	1.41	1.0	0.8 Sep	0.500	9.95	11.5
Males-94/95	13.38	13.38	1.54	1.0	0.75 Sep	0.445	10.60	12

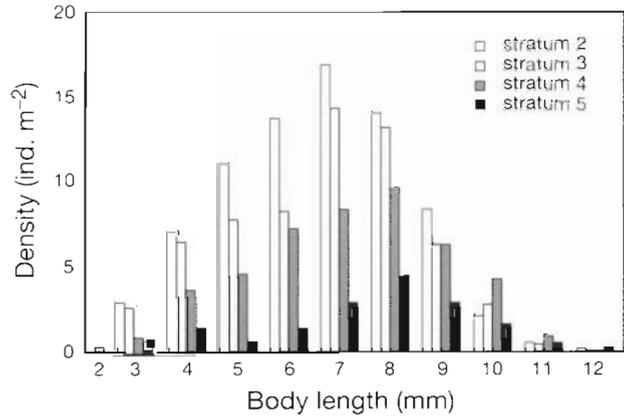


Fig. 5. *Pseudorchestoidea brasiliensis*. Spatial variability of population density in function of body length along the sampling strata

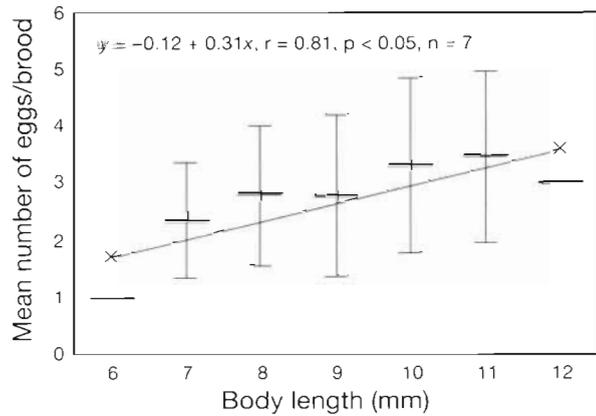


Fig. 6. *Pseudorchestoidea brasiliensis*. Relation between the mean number of eggs per brood and female body length in each size class. Vertical bars represent standard deviation. First and last size classes have only 1 specimen

Secondary productivity

The regression equation between mean weight and length classes for the total population of *Pseudorchestoidea brasiliensis* is expressed as: $\log AFDW = -2.129 + 2.727 \log (\text{length})$; *n* = 214 and *r* = 0.97 (*p* < 0.05).

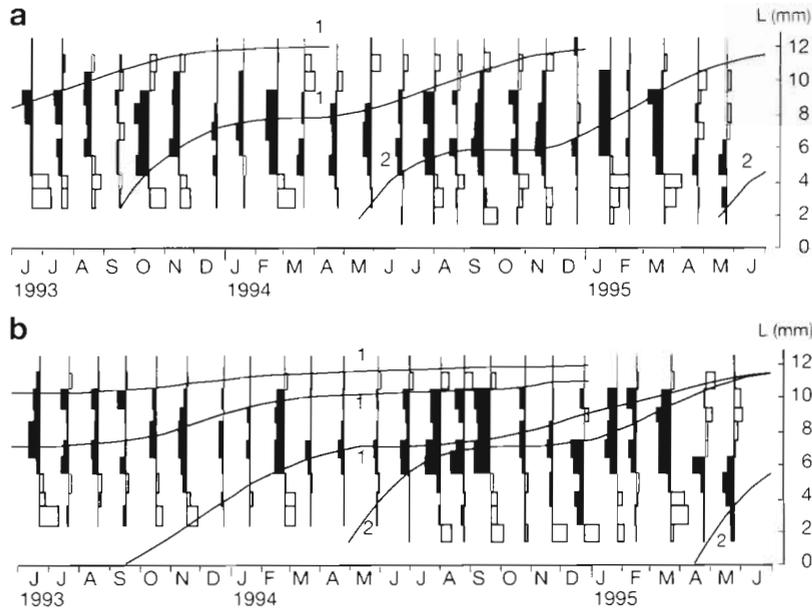


Fig. 7. *Pseudorchestoidea brasiliensis*. Growth curve of (a) males and (b) females estimated by ELEFAN program from 'restructured' length-frequency data set for the period June 1993 to May 1995. 1: June 1993 to May 1994; 2: June 1994 to May 1995

Mean biomass was 0.13 g AFDW m⁻² for the first and second year. Similar production values were found using the different methods in both years (Table 5). The ratios between production and biomass (P/B) using Crisp's and Hynes' methods, respectively, were 2.30 and 2.16 for the first year and 2.21 and 2.26 for the second year.

Table 4. *Pseudorchestoidea brasiliensis*. Z values (mortality) estimated with the length-converted catch curve method and modified Wetherall method, for sex categories during the periods. CI: confidence interval of Z

Sex-period	Z _{Wetherall}	Z _{length-converted catch curve (CI)}
Males-93/94	3.661	2.664 (1.738)
Males-94/95	4.039	2.920 (1.874)
Females-93/94	1.729	1.501 (1.033)
Females-94/95	2.795	2.666 (0.961)

Table 5. *Pseudorchestoidea brasiliensis*. Secondary production in g AFDW m⁻² yr⁻¹ determined by 3 methods: modified Hynes method, Crisp's method 3A and the Allen method

Methods	June 1993 to May 1994	June 1994 to May 1995
Modified Hynes	0.28	0.29
Crisp (3A)	0.30	0.28
Allen	0.33	0.36

DISCUSSION

Fluctuations in population density, indicating periods of intense reproduction, are frequent in talitrids. Marsden (1991) observed higher densities of *Talorchestia quoyana* in summer (February) and late winter (September), a pattern similar to that observed for *Pseudorchestoidea brasiliensis*.

Continuous reproduction was observed in *Talorchestia capensis* by Van Senus (1988) and in the gammarid *Echinogammarus marinus* (Marques & Nogueira 1991), while seasonal reproduction was demonstrated by Marsden (1991) for *Talorchestia quoyana* and by Williams (1978) for *Talitrus saltator*. In Rio de Janeiro State, the continuous reproduction of *Pseudorchestoidea brasiliensis* was characterized by the presence of juveniles and ovigerous females during the entire year, in spite of periods of greater reproductive ac-

tivity. The peaks of ovigerous females and juveniles were not coincident because of the time interval needed for the embryonic development of the eggs. The high densities of ovigerous females in February (late summer) and August (early winter) observed for *P. brasiliensis* were similar to those obtained for *T. capensis* (Van Senus 1988).

Pseudorchestoidea brasiliensis presents greater abundance in the lower midlittoral. Aggregation at Stratum 2 could be related to sediment moisture (Williams 1983), although this was not experimentally tested. Bowers (1964) and Behbehani & Croker (1982) related clumped distribution of *Orchestoidea corniculata* and *Orchestia platensis* to algae location on the debris line.

Pseudorchestoidea brasiliensis showed the same stratified distribution pattern observed for *Orchestoidea corniculata* by Bowers (1964) and Craig (1973b). The location of the small individuals on the lower part of the midlittoral and the larger individuals preferentially on the upper part is probably related to their capacity to resist desiccation. There was no stratification of individuals in relation to sex.

The sex ratio of 1:1 was observed for *Orchestia mediterranea* (Wildish 1970); however, Williams (1978), working with *Talitrus saltator*, and Van Senus (1988), with *Talorchestia capensis*, both verified that the populations of females were greater than those of males, 1:1.45 and 1:1.33, respectively. In *Pseudorchestoidea brasiliensis*, females were 1.54 times more abundant

than males. In the genus *Ampelisca* the deviation of the sex ratio toward females has usually been explained by the drastic decline in numbers of males which undergo ecdysis, copulate and then die (Klein et al. 1975, Hastings 1981, Carrasco & Arcos 1984). In *P. brasiliensis* this has not yet been verified. Another proposal to explain the higher number of females in the population is that their life span is greater than that of the males and they remain longer in the population.

Van Senus (1988) observed a higher proportion of males after the peaks of ovigerous females independent of the season of the year. This would be due to a higher growth rate of juvenile males which may enter the population before the juvenile females, causing an increase in the proportion of males. In *Pseudorchestoidea brasiliensis* the periods in which higher proportions of males were present occurred only 1 or 2 mo after the peaks of ovigerous females in the winter.

The low fecundity observed for *Pseudorchestoidea brasiliensis* corroborates the statement of Marsden (1991) that the fecundity of sand-dwelling animals is lower compared to the supralittoral *Orchestia* species (Wildish 1979) and to gammarids of temperate waters (Steele & Steele 1975). Gammarids show a direct relationship between body length and number of eggs per brood; however, this is less evident in beach sandhoppers. Brood size is strongly dependent on female length in *Talitrus saltator* (Williams 1978) and *Talorchestia capensis* (Van Senus 1988). However, in *Talorchestia quoyana* (Marsden 1991) and *Platorchestia platensis* (Morino 1978) this relationship is more variable, being similar to that found for *P. brasiliensis* (Fig. 6).

Factors such as temperature, humidity, season of the year, photo-period, nutritional level and geographical location can affect the production and mortality of broods, as well as the number and volume of eggs of talitrids (Morino 1978, Steele 1981, Williams 1985, Van Senus 1988). Marsden (1991) suggested that the low fecundity of *Talorchestia quoyana* may be compensated for by the production of larger eggs and by a low

brood mortality, but the mean egg volume observed for *Pseudorchestoidea brasiliensis* does not support this. The mean diameter of the eggs of *P. brasiliensis* is small (0.42 mm) compared to those of other talitrids [*T. quoyana*: 1.39 mm (Marsden 1991); *Talitrus saltator*: ~0.88 mm (Williams 1978); *Platorchestia platensis*: 0.65 mm (Morino 1978); *Orchestia mediterranea* and *O. mediterranea aestuarensis*: 0.72 mm, *Orchestia cavimana*: 0.69 mm and *Orchestia remyi roffensis*: 0.62 mm (Wildish 1979)]. Another hypothesis to explain the low fecundity of intertidal amphipods is their higher survival rate compared to species with a high fecundity (Marsden 1991); this is contradicted by the high mortality rates recorded for *P. brasiliensis* in comparison to other amphipods. The reproductive strategy of *P. brasiliensis* appears to fit other species for which the production of small eggs is related to decrease in the maturation size of females, which in turn allows the production of more than 1 brood, therefore increasing the number of generations and consequently increasing the intrinsic growth rate of the population (Steele & Steele 1975). Such a hypothesis is likely to be correct for *P. brasiliensis*, as the smallest ovigerous female had a length of only 5 mm.

The lower growth rates of females in relation to males must be related to a greater investment of energy in reproduction (production and maintenance of eggs and embryos), since the females do not undergo ecdysis during the period of incubation, making it difficult for them to continue to grow at the same rate as males. The lower life span determined for females of *Pseudorchestoidea brasiliensis* for the second in comparison to the first year can be explained by the combination of higher growth rate with a low T_{max} recorded for them in the second period. Life span differs within and among species of talitrids (Table 6); these differences can be related to different cohorts growing during different seasons of the year, to differences in growth rates among sex categories and to different geographical regions and environmental conditions, or even to different methods of estimation.

Table 6. Comparison of life span of several talitrids from different localities

Species	Life span (mo)	Zonation	Geographical location	Source
<i>Pseudorchestoidea brasiliensis</i>	21 (female) and 14 (male) – 93/94 11.5 (female) and 12 (male) – 94/95	Midlittoral	23° 05' S, 43° 25' W	This study
<i>Talorchestia capensis</i>	18 (cohort 1) and 24 (cohort 2)	Supralittoral	33° 43' S, 25° 50' E	Van Senus & McLachlan (1986)
<i>Talorchestia quoyana</i>	13	Supralittoral	45° S, 172° E	Marsden (1991)
<i>Talitrus saltator</i>	18 (female) and 21 (male)	Supralittoral	54° N, 4° W	Williams (1978)
<i>Talorchestia margaritae</i>	3	Supralittoral	10° N, 64° W	Venables (1981)
<i>Orchestia remyi roffensis</i>	12 to 18	Supralittoral	57° N, 2° W	Wildish (1972)
<i>Orchestia platensis</i>	4–5 (cohort 1) and 8–12 (cohort 2)	Supralittoral	43° 08' N, 70° 37' W	Behbehani & Croker (1982)

Annual mortality rates observed for males and females of *Pseudorchestoidea brasiliensis* are higher when compared to the mortalities of 0.22 and 0.16 yr⁻¹ for the sandhopper *Talorchestia capensis* (Van Senus & McLachlan 1986) and of 0.20 and 0.05 yr⁻¹ for the freshwater hyalid *Parhyale basrensis* (Ali & Salman 1987). These differences may be caused by: (1) latitude [tropical regions show higher mortality rates compared to temperate regions (Ansell et al. 1978)]; (2) the ecosystems [the low mortality recorded for *T. capensis* may have been related to low predation on the beach of Sundays Rivers, South Africa (Van Senus & McLachlan (1986)); or (3) the methods to estimate mortality [Ali & Salman (1987) demonstrated an underestimation of the mortality rate of *Parhyale basrensis*].

Knowing that these parameters influence the catch curve pattern, we may conclude that the lower mortality of females recorded for the first sampling year may be related to the lower growth rate and to the low L_{∞} recorded at that time.

The high production of *Pseudorchestoidea brasiliensis* that was estimated accounts for a large percentage of the overall production of the local macrofaunal community. The great abundance of *P. brasiliensis*, together with *Excirrolana braziliensis* (detritivorous isopod), shows the importance of the detritus food web, as *P. brasiliensis* and *E. braziliensis* comprise about 40% of all individuals from the macrofaunal community (Veloso et al. in press).

The various methods used to estimate the secondary production of *Pseudorchestoidea brasiliensis* gave similar results, varying from 0.28 to 0.36 g AFDW m⁻² yr⁻¹. These values are higher than those observed for the *Ampelisca tenuicornis*, 0.103 g AFDW m⁻² yr⁻¹ (Sheader 1977). The calculation of the ratio between annual production and mean biomass (P/B) is a good method to compare productivities of different species, populations and communities (Ansell et al. 1978). The P/B ratio calculated for *P. brasiliensis* is close to those recorded for *Talorchestia capensis* (2.25 yr⁻¹; Van Senus & McLachlan 1986) and *Parhyale basrensis* (3.06 yr⁻¹; Ali & Salman 1987). The values found for the P/B ratio together with a life span of between 1 and 1.75 yr recorded for *P. brasiliensis* corroborate the observations of Zaika (1973) and Robertson (1979) on the inverse relationship between these parameters. Zaika (1973) suggested that species with a P/B ratio close to 3.0 yr⁻¹ tend to have life expectancies between 1 and 2 yr.

The high mortality rate, rapid growth rate and high P/B ratio value found for *Pseudorchestoidea brasiliensis* as compared to published data may indicate a relationship of these parameters with geographical regions, confirming the conclusions of Ansell et al. (1978). Those authors demonstrated that tropical species exhibit high mortality rates, rapid growth rates and a higher production per unit biomass compared to temperate species.

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