

Population dynamics of *Hyale nigra* (Haswell, 1879) (Amphipoda, Hyalidae) associated to *Bryocladia thyrsgera* (J. Agardh) at Peruipe beach, Itanhaém (SP), southeastern Brazil

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Abstract

The size-class structure, abundance trends, sex-ratio, net reproductive rate, generation time and per capita rate of population growth were established for a population of *Hyale nigra* from the intertidal region at the *Bryocladia thyrsgera* belt. Marine algae often forms habitat patches occupied by an associated fauna composed mainly, by crustacean such as amphipods and isopods. Collections were taken once a month from March/1997 to February/1998. A total of 26909 individuals were sampled. There were two reproductive peaks one smaller in May and another one throughout the warmer months from November to February imposing, with the continual reproduction, the overlapping of generations. A sex ratio biased in favor of females was recorded in all sampling dates, a common pattern in epifaunal species. *H. nigra* appears to be r_1 strategist, with iteroparous females and multivoltine cycle. The net reproductive rate estimated was 3.1190 ± 3.2615 , the generation time 4.6889 ± 0.6549 and the per capita rate of population growth, 0.1388 ± 0.1884 . The reproductive strategy is related to the high-risk littoral habitat of the species which is exposed to variations in tide, osmotic pressure and thermal shock.

Key words: *Hyale nigra*, population dynamics, coastal area, marine environment.

Introduction

Hyalidae species occur in dense populations in a wide range of intertidal habitats (Barnard 1979). The genus dominates the phytal communities of the rocky intertidal shores in abundance and number of species (Lancelloti and Trucco 1993). Leite *et al.* (2000) registered a temporal increase of abundance of *Hyale* species, from 1972 to 1997 at sheltered sites of the southeastern Brazilian coast indicating the replacement of species less tolerant to antropic pollution by more tolerant and generalist ones as *Hyale nigra*. Species of these groups present as a rule continuous reproduction, with females carrying their embryos in a ventral pouch and adjusting their reproduction cycles in order to be able to quickly explore favorable environmental conditions.

Hyale nigra appears to be a monotonic colonizer (*in* Martin-Smith 1994 sense), *i.e.*, a species

that presents a rapid increase of abundance when the environment conditions are favorable, with iteroparous female, a multivoltine cycle, low number of eggs per brood, sex ratio biased towards females and recruitment throughout the year. It has been shown that low number and volume in amphipods associated to continuous reproduction is part of a reproductive strategy related to high-risk littoral habitat (Valerio-Berardo and Flynn 2002).

Life history traits of aquatic amphipods seem to follow patterns that respond to geographical and ecological aspects of the habitat. Trends related to the latitude, productivity and predictability have been recorded. These trends can be summarized in the r-K-A selection hypothesis and are related to the species longevity, maturity and fecundity (Saint-Marie 1991).

The aim of this paper was to describe the population structure of *Hyale nigra* from a shel-

tered coastal site, by constructing monthly life tables and presenting information on reproductive period, net reproductive rate, extinction risk and per capita rate of population growth.

Material and Methods

Collections were made at the low mark of spring tides once a month from March/1997 to February/1998, from the *Bryocladia trysigera* belt at Poço de Anchieta, Peruipe Beach, Itanhaém, State of São Paulo, Brazil (Fig. 1). As the amphipods are quite strongly attached to the substrata (Muskó 1990), an amount of approximately 200 ml of algae was scrapped randomly from the algae belt in order to cover a possible spatial variability and carefully placed on plastic bags with sea water. Then, the algae and associated fauna were preserved in alcohol 70% and taken to the laboratory where the material was sorted using a stereomicroscope and the specimens of *Hyale nigra* separated for further analysis. Details of other amphipod species captured in these samples are given in (Valério-Berardo and Flynn 2002). The algae were dried for 2 days at 60°C in a stove and weighted. The population abundances are expressed as number of individuals per 50 g of the algae dried weight.

Each *Hyale nigra* individual was sexed and sorted into four categories (Serejo 1999): first, males, presenting a developed second gnathopod; second, females, with oostegites and without a developed second gnathopod; third, ovigerous fe-

males, with both oostegites and eggs; and fourth, juveniles, lacking both oostegites and a developed second gnathopod. The individuals were measured from the beginning of the cephalon to the end of the telson and grouped in 1 mm size class.

The proportion of males to total females, as well as females to ovigerous females were calculated for each month. The monthly adult sex ratio was used to estimate the number of female juveniles, since it was as used as the parameter to estimate inside the category juvenile the proportion of males and females. Fecundity was already determined by correlating the length of ovigerous females with the mean number of eggs per brood (Valério-Berardo and Flynn 2004). The monthly proportion of females to ovigerous females was used to correct the age-specific fecundity each month. Females were grouped in 1 mm size classes for the construction of a monthly static life table. The individual density N_x at each class was recorded and ratio of survivors (l_x) calculated dividing the number of individuals of each size class by the number of individuals that initiate the generation (N_0),

$$l_x = N_x / N_0 \quad (1)$$

Age fecundity was considered from the linear regression that related average number of eggs per hatch (x) and the female body size in mm (y) taking in account the abundance of ovigerous females,

$$y = 0.1811x + 3.0855 \quad (2)$$

The net reproductive rate (R_0) was calculated by the total sum of the product $l_x m_x$ of each size class express by,

$$R_0 = \sum l_x m_x \quad (3)$$

The generation time (T) was esteemed by the total sum of the product $l_x m_x x$ divided by the net reproductive rate,

$$T = \sum l_x m_x x / \sum l_x m_x \quad (4)$$

The per capita rate of population growth (r) was calculated directly from the relation,

$$r \approx \ln(R_0) / T \quad (5)$$

The logistic equation was used to represent the population dynamics of the species.

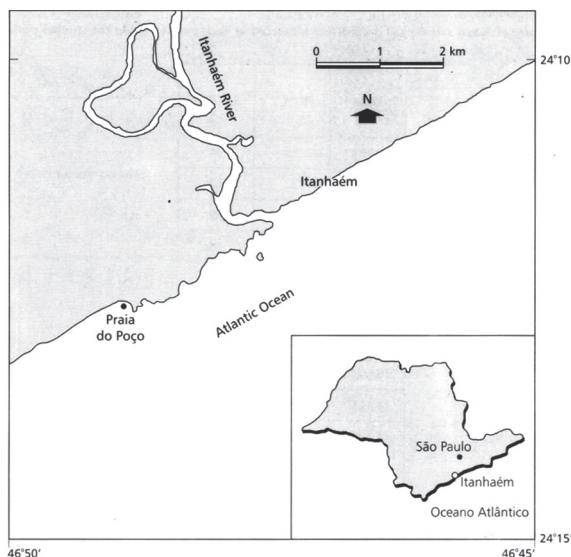


Figure 1. Study area Poço Beach (Itanhaém, SP, Brazil).

$$N(t) = K/1 + [(K-N_0)/N_0] e^{-rt} \quad (6)$$

The average logistic curve was obtained considering an average life table.

The initial population was defined for each month as $N_0 = 1000$ e the environmental carrying capacity (K) was considered as the maximum number of individuals in 50 g of seaweed.

Results

A total of 26909 individuals were sampled. Of this total, 6110 were females, 1068 were ovigerous females, 2021 were males and 17710 were juveniles. The population of *Hyale nigra* showed the highest abundance in late autumn (May, 1997) and in summer (December, 1997 and January-March, 1998). The lowest abundance was recorded in spring (October, 1997). The same pattern was observed for females, ovigerous females, males and juvenile. Juveniles dominated throughout the year with the exception of May and August when total females were more abundant. The total population abundance increased from early summer to late autumn and attained a maximum of 5281 individuals per 50 g of algae in March. The population then decreased and reached a minimum of 125 individuals per 50 g of algae in October 1997 (Fig. 2).

Small juveniles constituted the bulk of the population throughout the year with the exception of May when females dominated. Males and females presented length ranged between 2 to 10 mm, with higher values in May and June. Sex ratio fluctuated throughout the study period. A sex ratio favorable to females was recorded in all sam-

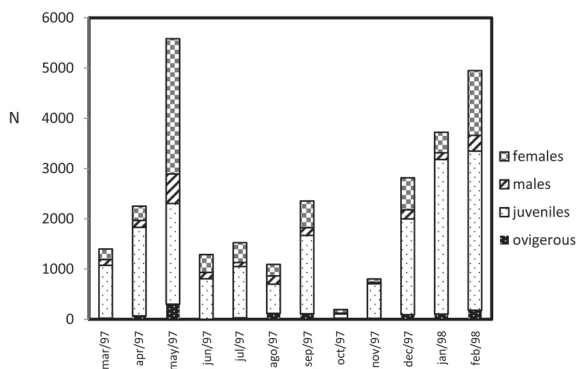


Figure 2. Temporal variation of females, ovigerous females, males and juveniles abundances.

pling dates, with a marked increase on the proportion of females in May and July.

Monthly static life table were constructed (Tab. I), considering only females (adult females and juveniles females) adjusted to 1000 individuals. Fecundity was estimated by female length and values of mx adjusted by the proportion of ovigerous females at each month.

The values of the net reproductive rate (Ro), generation time (T) and the per capita rate of population growth (r) varied throughout the year (Tab. II). For r, the equation (5) supplies a better approach when $Ro \approx 1$, that is, when the size of the population remains relatively constant (Begon et al. 2006).

The net reproductive rate has increased in March and April projecting the peak that occurred in May, followed by a decrease in June. In August, September and October, the net reproductive rate was high signaling the next reproductive period beginning in early spring (Fig. 3). The correlation between the per capita rate of population growth (r) and population abundances (N) was -0.020 (Fig. 4).

The logistic curves representing hypothetically the population growth for each monthly sampled population are graphically represented, with $N_0 = 1000$, $K = 5281$ and the variable r (Fig. 5). Each curve presented a peculiar behavior.

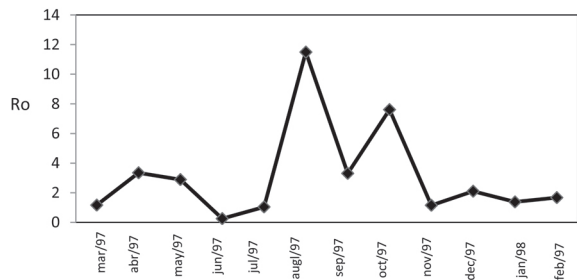


Figure 3. Temporal variation of the net reproductive rate (Ro).

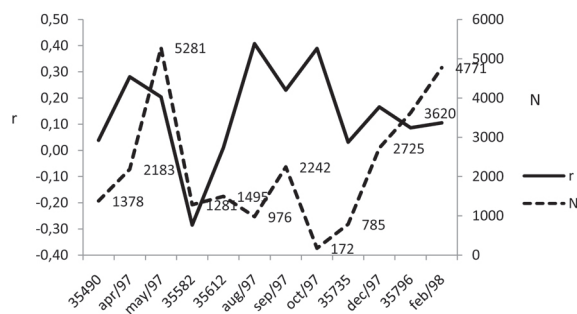


Figure 4. Temporal variation of the per capita rate of population growth (r) and abundance (N) with correlation value.

Table I. Monthly static life table: size-class in mm, N_x adjusted female abundance, l_x ratio of survivors and m_x age specific fertility adjusted for the ratio of ovigerous females.

	Size class	Total females in size class	N_x	l_x	Fertility	m_x
March/97	2-3	102,56	1.000,00	1,00		
	3-4	205,13	885,24	0,89		
	4-5	362,88	655,73	0,66	7,81	0,78
	5-6	128,69	249,72	0,25	13,33	1,33
	6-7	63,00	105,73	0,11	18,85	1,89
	7-8	21,00	35,24	0,04	24,38	2,44
	8-9	10,50	11,75	0,01	29,90	2,99
	9-10					
April/97	2-3	416,69	1.000,00	1,00		
	3-4	430,89	717,41	0,72	2,29	0,55
	4-5	311,84	425,19	0,43	7,81	1,87
	5-6	87,93	213,71	0,21	13,33	3,19
	6-7	71,00	154,08	0,15	18,85	4,51
	7-8	127,80	105,93	0,11	24,38	5,84
	8-9	0,00	19,26	0,02		
	9-10	28,40	19,26	0,02	35,42	8,48
May/97	2-3		1.000,00	1,00		
	3-4	496,12	1.000,00	1,00		
	4-5	1074,92	885,81	0,89		
	5-6	755,44	638,40	0,64	13,33	1,50
	6-7	1210,95	464,53	0,46	18,85	2,12
	7-8	403,65	185,81	0,19	24,38	2,74
	8-9	269,10	92,91	0,09	29,90	3,36
	9-10	134,55	30,97	0,03	35,42	3,98
June/97	2-3	29,56	1.000,00	1,00		
	3-4	177,33	968,79	0,97		
	4-5	354,67	781,56	0,78		
	5-6	171,96	407,09	0,41	13,33	0,26
	6-7	89,00	225,53	0,23	18,85	0,37
	7-8	124,60	131,56	0,13	24,38	0,48
	8-9					
	9-10					
July/97	2-3	42,58	1.000,00	1,00		
	3-4	255,50	965,76	0,97		
	4-5	569,80	760,32	0,76	7,81	0,58
	5-6	179,78	302,16	0,30	13,33	0,99
	6-7	137,20	157,60	0,16	18,85	1,39
	7-8	58,80	47,28	0,05	24,38	1,80
	8-9					
	9-10					
August/97	2-3	17,28	1.000,00	1,00		
	3-4	120,95	970,03	0,97		
	4-5	120,95	760,26	0,76		
	5-6	34,56	550,49	0,55		
	6-7	121,13	490,55	0,49	18,85	9,43
	7-8	69,30	280,46	0,28	24,38	12,19
	8-9	57,75	160,26	0,16	29,90	14,95
	9-10	34,65	60,10	0,06	35,42	17,71
September/97	2-3	182,81	1.000,00	1,00		
	3-4	487,50	895,52	0,90		
	4-5	487,50	616,91	0,62		
	5-6	114,04	338,30	0,34	13,33	2,79
	6-7	132,75	273,12	0,27	18,85	3,94
	7-8	265,50	197,26	0,20	24,38	5,09
	8-9	79,65	45,52	0,05	29,90	6,25
	9-10					

Table I (Cont.). Monthly static life table: size-class in mm, N_x adjusted female abundance, l_x ratio of survivors and m_x age specific fertility adjusted for the ratio of ovigerous females.

	Size class	Total females in size class	N_x	l_x	Fertility	m_x
October/97	2-3	11,12	1.000,00	1,00		
	3-4	29,66	924,93	0,92		
	4-5	29,66	724,74	0,72		
	5-6	11,11	524,56	0,52	13,33	3,96
	6-7	18,50	449,58	0,45	18,85	5,60
	7-8	37,00	324,70	0,32	24,38	7,24
	8-9	11,10	74,93	0,07	29,90	8,89
	9-10					
November/97	2-3	251,46	1.000,00	1,00		
	3-4	251,46	561,09	0,56		
	4-5	15,56	122,18	0,12	7,81	1,90
	5-6	7,78	95,03	0,10	13,33	3,24
	6-7	23,33	81,45	0,08	18,85	4,58
	7-8	23,33	40,73	0,04	24,38	5,92
	8-9					
	9-10					
December/97	2-3	148,98	1.000,00	1,00		
	3-4	670,43	929,98	0,93		
	4-5	723,54	614,91	0,61	7,81	1,10
	5-6	265,89	274,88	0,27	13,33	1,88
	6-7	127,60	149,92	0,15	18,85	2,66
	7-8	127,60	89,95	0,09	24,38	3,44
	8-9	31,90	29,98	0,03	29,90	4,22
	9-10	31,90	14,99	0,01	35,42	4,99
January/98	2-3	699,55	1.000,00	1,00		
	3-4	1049,32	744,86	0,74		
	4-5	685,45	362,15	0,36	7,81	1,96
	5-6	164,00	112,15	0,11	13,33	3,35
	6-7	123,00	52,34	0,05	18,85	4,74
	7-8	20,50	7,48	0,01	24,38	6,12
	8-9					
	9-10					
February/98	2-3	255,65	1.000,00	1,00		
	3-4	1533,87	933,55	0,93		
	4-5	639,11	534,88	0,53		
	5-6	579,67	368,77	0,37	13,33	1,86
	6-7	451,85	218,11	0,22	18,85	2,63
	7-8	322,75	100,66	0,10	24,38	3,40
	8-9	64,55	16,78	0,02	29,90	4,17
	9-10					

In April, May, August, September and October the population presented high growth rates, reaching the carrying capacity after approximately 30 generations. Sampled populations with intermediate growth rates had occurred in December, January and February, when carrying capacity were reached in 70 generations approximately. Lower rates were obtained in March, July and November. A local extinction was predicted in June, when population was extinguished in less than 15 generations. The average logistic curve for the monthly sampled populations shows a great uncertainty in the attempt to foresee the population behavior in future generations (Fig. 6).

Table II. Monthly values for R_0 (net reproductive rate); T (generation time) and r (the per capita rate of population growth).

	R_0	T	r
mar/97	11.655	39.694	0.0386
apr/97	33.472	42.999	0.2810
may/97	28.883	51.895	0.2044
jun/97	0.2526	48.277	-0.2850
jul/97	10.413	39.530	0.0102
aug/97	115.027	59.913	0.4077
sep/97	33.083	51.908	0.2305
oct/97	76.158	52.108	0.3896
nov/97	11.533	45.404	0.0314
dec/97	21.029	44.843	0.1658
jan/98	13.798	37.310	0.0863
feb/98	16.706	48.782	0.1052

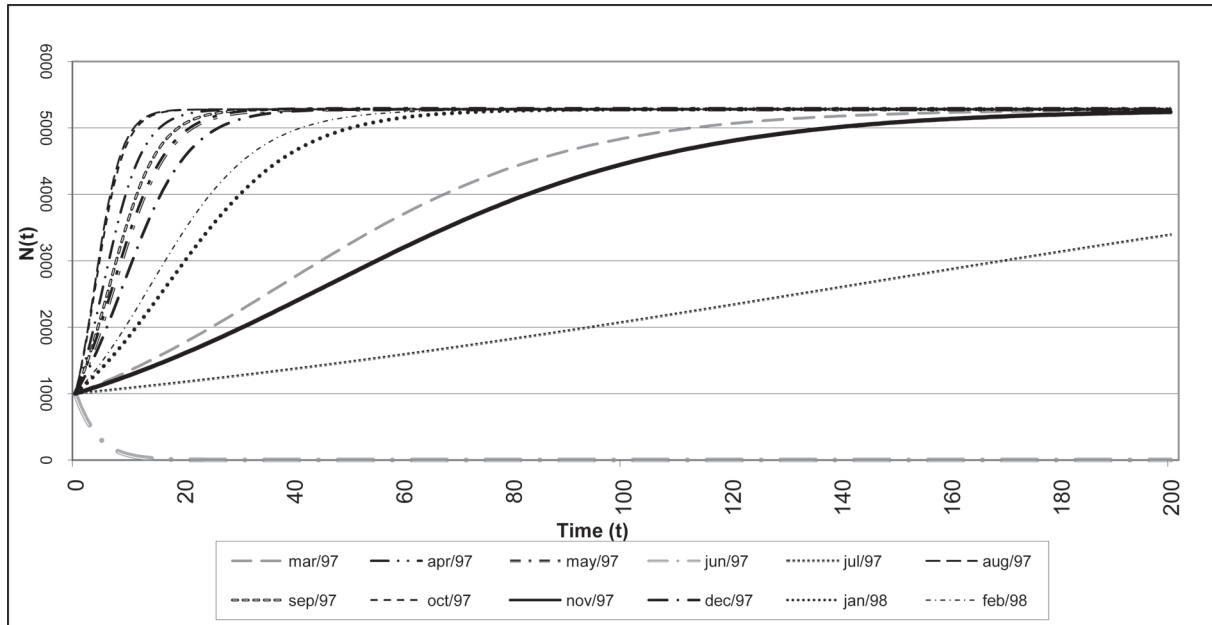


Figure 5. Logistic curves for each of the monthly sampled population.

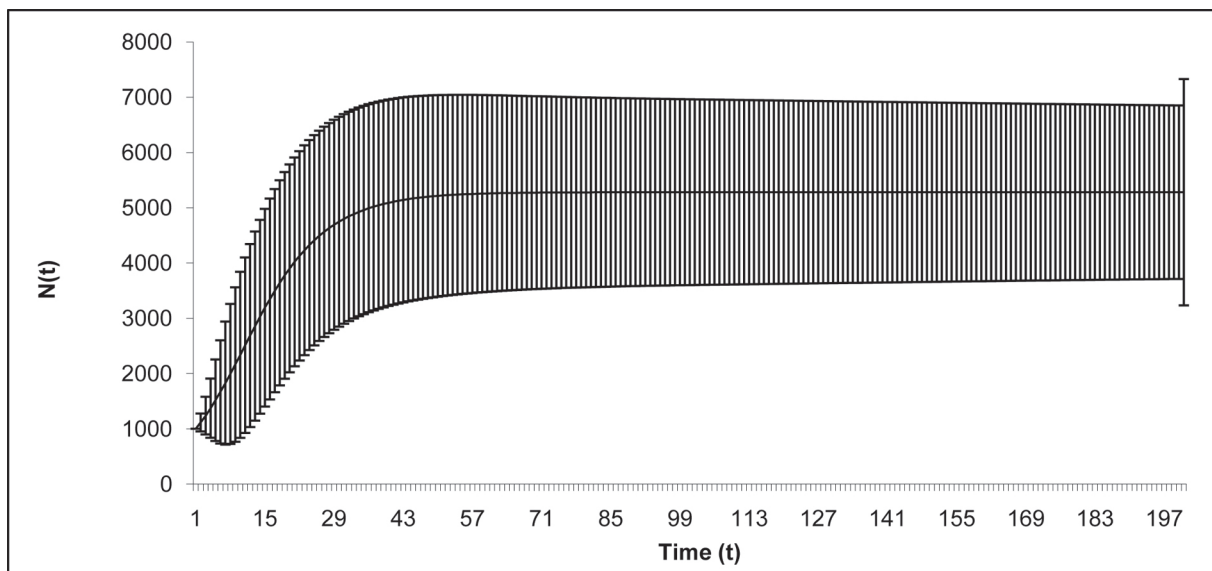


Figure 6. Average logistic curve and standard deviation.

Discussion

The population dynamics pattern displayed by *Hyale nigra*, iteroparous semiannual and multivoltine, is consistent with the opportunistic behaviour of coastal species in physically controlled and frequently disturbed habitats. Unpredictable habitats such as the littoral area exposed to variations in tide, osmotic pressure and thermal shock is considered as an environmentally stressed system thus occupied by r -selected organisms with short

longevity and high fecundity (van Dolah and Bird 1980; Martin-Smith 1994), where the evolution of opportunistic strategies such as a continuous sexual activity throughout the year should be expected (van Dolah and Bird 1980; Martin-Smith 1994).

Although incubating females were present all year round, *Hyale nigra* has two main breeding periods during the year, in autumn and late spring/summer (Valério-Berardo and Flynn 2004). Juveniles constituted the major proportion of the total

population throughout the year, a consequence of the year-round breeding activity of females and an important strategy to enhance the net reproductive rate (Wildish 1988; Saint-Marie 1991; Jeong *et al.* 2007). The year-long presence of juvenile and reproductive females (ovigerous) in the population of other peracaridans is strong evidence of continuous reproduction as an advantageous strategy for small animals that, as *Hyale* spp., carry few eggs (Lewis 1998). Fluctuations in population density indicate periods of intense reproduction with high densities of females in May, December and January, representing peaks of reproduction. Reproduction seems to be deterred from June to October. The reproduction of amphipods is constrained mainly by low winter temperatures (Cunha *et al.* 2000) but the latitudinal variation in temperature enables the extended breeding period from October to February allowing the production of two or more generations per year at low latitudes. In *Hyale nigra* a sex ratio of 1:3.38 has been documented by Valério-Berardo and Flynn (2002). The sex bias toward females is a common feature in amphipods populations and explained by different mortality between males and females over the year (Hasting 1981; Carrasco and Arcos 1984; Dauvin 1988; Marques and Nogueira 1991; Valério-Berardo and Flynn 2004).

Parameters such as type (semelparous or iteroparous) of reproduction, fecundity and generation time indicate the life strategy used by a particular species (Winemiller and Taphorn 1989). Iteroparity is typical for most gammaridean amphipods including the coastal shallow-water *Hyale* spp. The high variation of the net reproductive rate (R_0) with the consequent variation of the per capita growth rate (r) points to it. It may be advantageous to spread reproduction over different periods of time if there is a risk of losing all offspring if they are born at an unfavorable condition (Gotelli 2001). The occurrence of multiple overlapping generations is usual in shallow coastal areas, consistent with an opportunistic behavior of epifaunal species from physically controlled communities according to the stability-time theory (Sanders 1969). Generation time is an elusive concept for populations with continuous growth since it is the average age of the parents of all the offspring produced by a single cohort (Caughley 1977). Thus, the rate of population increase is higher for organisms with short generation times. The reproductive strategy of the *H. nigra* compensates the small number of

eggs per brood by a decrease in the maturation size of females, which in turn allows the production of more than one brood, decreasing the generation time and consequently increasing the per capita growth rate. This assumption is corroborated by the evidence of low post-marsupial mortality in *Hyale media* associated to the small number of eggs per female (Leite, 1996 a and b)

These traits associated with the population structure yield a trichotomous continuum with three distinct tactics. The first tactic, K-strategy, associated to high juvenile and adult survivorship, low fecundity, long generation time, iteroparity and relatively stable population density. The second tactic, r_1 -strategy, is associated with low juvenile and adult survivorship, high fecundity, short generation time, iteroparity, and variable population densities. The third tactic, r_2 strategy, is characterized by low juvenile but high adult survivorship, high fecundity, long generation time and large fluctuation in population density. *Hyale nigra* is considered as r_1 strategist (Valério-Berardo and Flynn 2004), they minimize the generation time duration while increasing the reproductive potential. In this way, r is maximized (May 1976). The strategy seems to work well because just one possibility of extinction is predicted for the population.

When a population is inserted in a physically stressed environment, the intrinsic growth rate can be density-independent which means that the population growth is not correlated directly with the mortality and natality rates, but with the changing environmental, *i.e.* the environmental stochasticity (Lewontin and Cohen 1969). Therefore, the growth tax r varies in accordance to some external law, unrelated to the population abundances (N), as supported here by the low correlation between r and N . The attempt to foresee the behavior of the population analyzed here lead us to conclude that this population size should be predicted considering the environmental stochasticity, which seems more appropriated in view of the monthly changes of r unrelated to the monthly fluctuations in the abundance of the *Hyale nigra* population here registered. The mean logistic curve representing the population growth shows that the variance in population size increases with time typical of a population growing with environmental stochasticity. The further in the future the prediction, the more uncertain is the estimation of the population size. This uncertainty stabilizes when the carrying capacity is attained.

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