Fecundity and embryology of *Pachycheles monilifer* (Dana, 1852) (Anomura, Porcellanidae) at Praia Grande, Ubatuba, SP, Brazil.

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Abstract

A total of 180 ovigerous females of *P. monilifer* were collected at Praia Grande, Ubatuba (SP) as to obtain fecundity estimation for this species. Size of individuals (carapace length, CL) varied from 3.3 to 8.8mm (6.1±1.2mm), and number of extruded eggs (NE) from 2 to 511 (135±126 eggs). The best fitting for the relationship NExCL was provided by the power function $NE=0.0198CL^{4.63}$. The variation of relative average fecundity and percentage of ovigerous females were assessed and tested for correlation with water temperature and photoperiod. No significant associations were detected ($p>0.05$). Eggs were measured throughout embryonic development, which composed nine distinct stages according to morphology, colour and development of main structures. These stages were pooled in three different groups according to their diameter (stages 1-7, 8 and 9), and volume correspondingly. During embryogenesis, the eggs of *P. monilifer* showed a size increase of 38.8 and 78.6% in diameter and volume, respectively.

Key Words: Fecundity, Anomura, Porcellanidae, Reproduction, *Pachycheles*

Introduction

During the recent years, the reproductive biology of decapod crustaceans have been analysed in a rather sectioned fashion, but a combination of complementary studies has promoted a substantial advance towards the preservation of endangered species (Pinheiro and Fransozo, 1995).

Most part of the studies on the fecundity and embryology of crustaceans focus on species of commercial interest, exploited as edible resources for humans worldwide. From those lobsters (Pandian, 1970a,b; Branford, 1978; Attard and Hudon, 1987) and brachyurans (Cheung, 1966; Campbell and Fielder, 1988; Pinheiro and Terceiro, 2000; Paul and Paul, 1997) are particularly targeted. However, smaller decapods forming large populations have been also subject of such studies due to their ecological importance in a variety of biotopes (Jensen, 1986; Pinheiro and Fransozo, 1995).

Porcelain crabs are particularly important in the marine environment, where they are consumed by an array of predators (Ogawa and Rocha, 1976). They also establish symbiotic relationships with hermit crabs (Haig, 1966; Cuadras and Pereira, 1977), shrimps (Jensen, 1986) and sabelariid worms (Gore *et al.*, 1978; Micheletti-Flores, 1997), and may be used as indicators of diversity and structural complexity of coastal biotopes (Werding, 1984).

Fecundity is a parameter frequently measured in crustaceans since it is important for the estimation of reproductive potential and future stock size of a given species (Negreiros-Fransozo *et al.*, 1992). Among a suite of species-specific crustacean features, number of eggs and brooding periodicity indicate the reproductive and ecologic strategy of a species (Sastry, 1983). According to this author, fecundity is not solely determined by the number of eggs extruded in a single batch. Reproductive rhythms and their relation to the life cycle should be also be considered. Yet, most available studies are restricted to the analysis of size-specific fecundity relationships, usually in terms of carapace length (Negreiros-Fransozo, *et al.*, 1992; Pinheiro and Fransozo, 1995) or width (Campbell and Fielder, 1988; Pinheiro and Terceiro, 2000), depending on the taxonomic group considered.

According to some authors (Somerton and Meyers, 1983; Pinheiro and Fransozo, 1995; Mantelatto and Fransozo, 1997), the potential fecundity of pleocyemate decapods may be adequately explained by fitting a power function, but other exponential models (Jensen, 1958; Almaça, 1987) and even straight lines can be used (Jones, 1978; Negreiros-Fransozo *et al.*, 1992).

Average fecundity is usually analysed based on potential fecundity estimates, which can be assessed either monthly or seasonally. Its determination allows the identification of the period of higher breeding intensity, minimizing the effect of size (Pinheiro and Terceiro, 2000).

Embryology is a research topic not frequently addressed in the carcinological literature. Nair (1949) presented a pioneer work on the subject, describing the morphology and organogenesis of the embryos of the shrimp *Caridina laevis*. Boolootian *et al.* (1959) proposed the classification of embryos in ten different development stages, based on observations made on three brachyurans and two anomurans. Other authors, however, used a lower number of divisions for the sake of biological interpretation of analyses or statistical requirements (Valdes *et al.*, 1991; Saint-Marie, 1993; Pinheiro, 1995; Nagao *et al.*, 1999). According to Efford (1969), chromatic change and gradual embryonic growth take place, although being reported in only a few studies (Hartnoll and Paul, 1982; Negreiros-Fransozo *et al.*, 1992). Such information may be useful in the optimization of aquaculture projects and management of wild populations (Anderson, 1982; Nagao *et al.*, 1999).

The purpose of the present study is to analyse the potential and relative average fecundity of the porcelain crab *Pachycheles monilifer* (Dana, 1852). Seasonal variation is assessed and its correlation to water temperature and photoperiod is tested. Embryonic stages are also described, and the biologic coherence of stage groupings is verified. The present results are compared to those already published for other porcelain species.

Material and Methods

Porcelain crabs were collected from August 1996 to May 1997 by sorting them out from samples of sand reefs built by the sabellariid worm *Phragmatopoma cf. (lapidosa) caudata* (Kroÿer) Morch, 1863, at the north-facing rocky shore at Praia Grande, Ubatuba (SP) (23°28'02"S - 45°35'35"W).

Sampled sand blocks were manually processed in plastic trays containing sea water, and porcelain crabs were separated from other organisms and identified according to Melo (1999). Ovigerous *P. monilifer* females were held separately in vials for later analyses.

From each female, a sample of 10 eggs was removed for microscopical analysis. The classification of embryonic development stages followed Boolootian *et al.* (1959). Thirty eggs within each stage were used for morphological description. The larger (LA) and smaller (SA) egg axes, including the corionic membrane, were measured to the nearest 0.1mm under a stereomicroscope provided with a *camera lucida*. Mean egg diameter was calculated for each development stage as the average between egg axes. The LA/SA ratio was also calculated, together with their descriptive statistics and 95% confidence intervals within each development stage, as a means to describe egg shape, *i.e.* whether eggs were spherical (LA/AS = 1) or elliptical (LA/AS ≠ 1). Egg volume was calculated according to its shape. For spherical eggs their volume was calculated following the equation $V=(1/6)\pi d^3$, where *d* stands for the average diameter, and for elliptical ones the equation $V=(1/6)\pi r^2R$ was used, where r = LA/2 and R = SA/2.

A cluster analysis with single linkage was used to verify morphometric similarity regarding diameter and volume and determine eventual groupings (Romesburg, 1984; Krebs, 1989).

The carapace length (CL) of each ovigerous crab was measured from the tip of the rostrum to the postero-median region of the carapace to the nearest 0.1mm using a stereomicroscope supplied with a *camera lucida*. The number of eggs of each female (NE) was determined under a stereomicroscope with the aid of a manual counter. Examined females were fixed in 70% ethanol together with their egg batch.

The size-specific potential fecundity relationship was obtained by relating egg number variation (NE) according to carapace length (CL). The obtained scatter was subjected to regression analyses and the best fitting model was chosen by comparing the obtained determination coefficients (R^2). The same procedure was applied to data obtained in each season, and models were compared to determine the season of highest fecundity.

The relative average fecundity ($\overline{F'}$) was calculated in each season using the potential fecundity data, according Pinheiro and Terceiro (2000).

Temperature data were obtained at the *Base Norte do Instituto Oceanográfico da USP* (IO/USP), and photoperiod data were obtained according to Varejão-Silva and Ceballos (1982), using the latitude of the study region (23°28'02"S).

Egg diameter, egg volume, carapace length, number of eggs, average relative fecundity, water temperature and photoperiod were subjected to one-way ANOVA complemented by Tukey mutliple comparison tests (α=0.05).

The reproductive index (RI) was determined seasonally by multiplying relative average fecundity ($\overline{F'}$) and the percentage of ovigerous females from the total female population, as a means to determine the season of highest reproductive intensity.

Water temperature (T) and photoperiod (P) were tested for significant correlations against average relative fecundity ($\overline{F'}$) and percentage of ovigerous females (OF). The Pearson's linear coefficient (r) was calculated to verify the significance of such correlations (α=0.05).

Results

From August 1996 to May 1997 there were only two porcelain crab species recorded from the sand reefs built by the polychaete species *P. caudata*, both belonging to the genus *Pachycheles: P. laevidactylus* Ortmann, 1892 and *P. monilifer* (Dana, 1852).

For fecundity estimation, a total of 180 ovigerous females were used spanning a size range from 3.3 to 8.8mm CL (6.1±1.2mm), and a potential fecundity from 2 to 511 eggs (135±126 eggs). Average size of sampled breeding females did not vary through seasons ($p>0.01$) (Tab. I), but average NE was higher in autumn compared to the remaining seasons ($p>0.05$). Over the ontogeny of embryos, the eggs of *P. monilifer* showed an increase of 38.8 and 78.6% in diameter and volume, respectively.

In *P. monilifer* the scatterplot obtained for the relationship NExCL showed a curvilinear tendency and rendered a positive correlation between these variables (Fig. 1). The better fit was obtained using the power function, either considering the seasonal groups or the total sample (Tab. II).

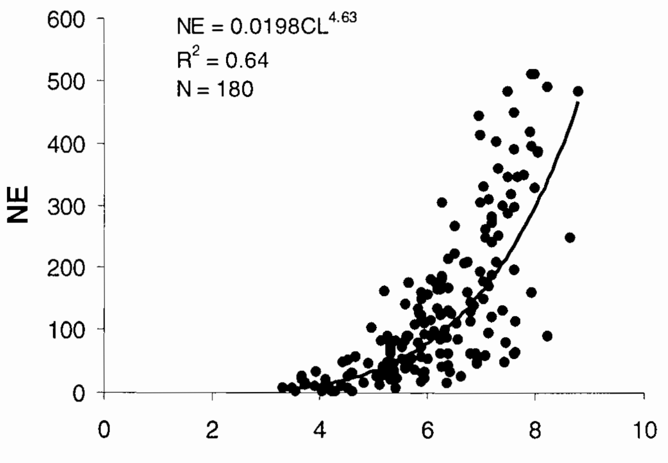

Figure 1: *Pachycheles monilifer* (Dana, 1852). Power function fitted to the relationship between number of eggs (NE) and carapce length (CL) for the specimens collected from August 1996 to May 1997, at Praia Grande, Ubatuba (SP).

Table II: *Pachycheles monilifer* (Dana, 1852). Minimum, maximum, average values and standard deviation of carapace length (CL) and number of eggs (NE) for the ovigerous females collected during the seasons at the north-facing rocky shore of Praia Grande, Ubatuba, SP.

Seasons	N	NE			CL (mm)		
		Min.	Max.	$\bar{x}$ ± s	Min.	Max.	$\bar{x}$ ± s
Summer	51	2	403	142 ± 119 ^{a*}	3.31	8.00	6.24 ± 1.28 ^{a*}
Autumn	55	7	511	167 ± 151 ^{b}	3.54	8.80	6.10 ± 1.39 ^{a}
Winter	36	2	385	75 ± 80 ^{a}	4.11	8.63	6.17 ± 1.07 ^{a}
Spring	38	3	482	136 ± 114 ^{a}	4.29	7.49	5.91 ± 0.78 ^{a}
Total	180	2	511	135 ± 126	3.31	8.80	6.12 ± 1.19

*Average values in a single column followed by the same letter are not statistically different (p>0.05).

Table II: *Pachycheles monilifer* (Dana, 1852). Fitted functions to the relationship between number of eggs (NE) and carapace length (CL), obtained during the seasons at Praia Grande, Ubatuba, SP.

Seasons	N	Equation ($y = ax^b$)	Linearized function ($\ln y = \ln a + b \ln x$)	R^2 (%)
Summer	51	$NE = 0.011CL^{4.94}$	$\ln NE = -4.54 + 4.94 \ln CL$	73.1
Autumn	55	$NE = 0.045CL^{4.32}$	$\ln NE = -3.11 + 4.32 \ln CL$	82.5
Winter	36	$NE = 0.024CL^{4.19}$	$\ln NE = -3.73 + 4.19 \ln CL$	51.5
Spring	38	$NE = 0.001CL^{6.40}$	$\ln NE = -6.91 + 6.40 \ln CL$	60.3
Total	180	$NE = 0.0198CL^{4.63}$	$\ln NE = -3.92 + 4.63 \ln CL$	64.1

hhe highest percentage of ovigerous females was obtained in autumn (91.7), followed by spring (86.4), summer (83.6) and winter (80.0). It may be verified in figure 2A that average relative fecundity ($\overline{F'}$) was higher in spring (0.00295), which did not differ from autumn (0.0028), but contrasted from winter (0.0014). The seasonal reproductive index was highest in autumn, followed by spring, summer and winter (Fig. 2B).

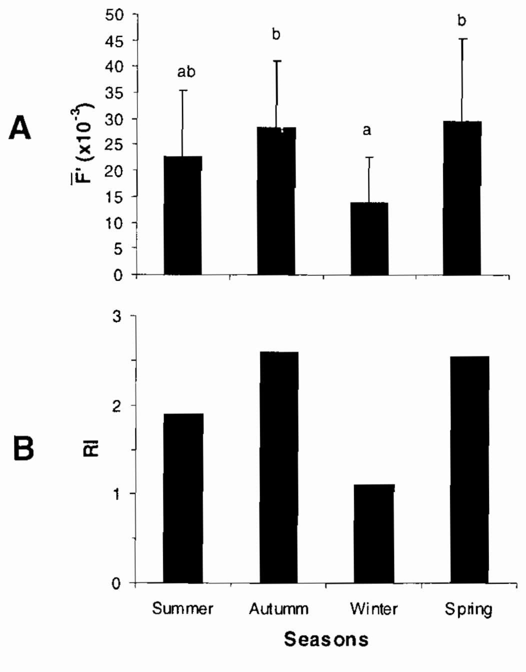

Figure 2: *Pachycheles monilifer* (Dana, 1852). Seasonal variability of average relative fecundity ($\overline{F'}$) (A) and reproductive index (RI) (B), from August 1996 to May 1997.

The highest average water temperature was observed during summer (26.5±1.1°C), contrasting with autumn (23.8±1.8°C) and spring (23.4±1.6°C), which did not differ significantly ($p>0.05$), and winter (21.6±0.9°C) (Fig. 3A). This same figure shows that average values of photoperiod differ among seasons ($p<0.05$), with highest light periods recorded in spring, followed by summer, winter and autumn (Fig. 3B). Neither temperature nor photoperiod presented a significant correlation with average relative fecundity ($\overline{F}'$)or percentage of ovigerous females (OF) ($p>0.05$, Tab. III).

Nine embryonic stages were described for *P. monilifer*. Eggs show a wine colouration during the early development (stages 1 to 4), turning to orange and translucent in later stages (Tab. IV). Over the embryonic development, the proportion LA/AS was significantly different from 1 ($p<0.05$), suggesting that this species' eggs are slightly elliptical. Differences of egg diameter and volume within early stages were not expressive. Egg increase in both diameter and volume was only detected from the fifth stage ($p<0.05$) (Tab. V).

Clustering analysis revealed that embryonic stages can be grouped in three main categories (stages 1-7, 8 and 9) considering both diameter (Fig. 4A) and volume (Fig. 4B).

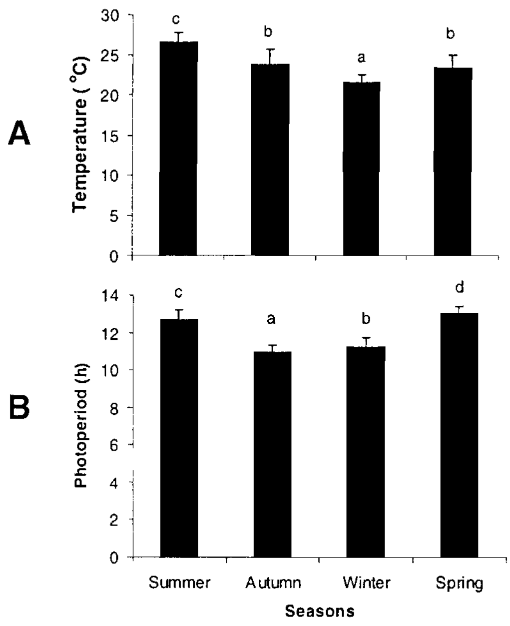

Figure 3: *Pachycheles monilifer* (Dana, 1852). Seasonal variability of water temperature (A) and photoperiod (B) from August 1996 to May 1997. Bars of the same pattern sharing the same letter represent lack of statistical difference ($p>0.05$).

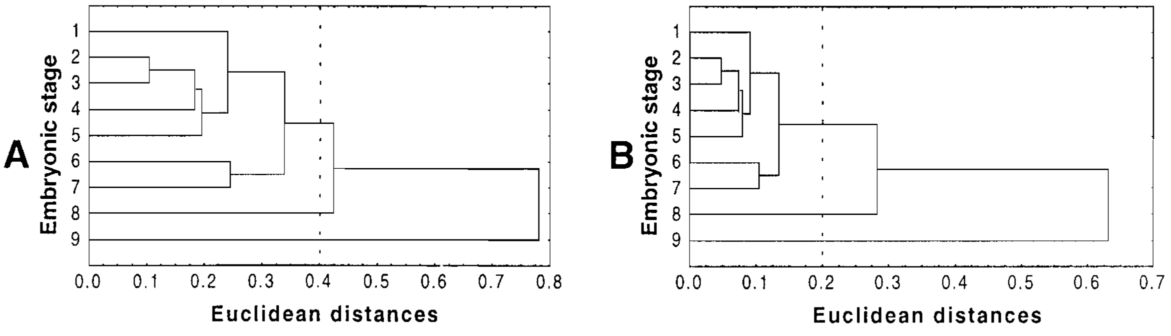

Figura 4: *Pachycheles monilifer* (Dana, 1852). Cluster analysis of embryonic stages based on their diameter (A) and volume (B).

Table III: *Pachycheles monilifer* (Dana, 1852). Regression analyses and respective Pearson's correlation coefficient (r) between abiotic (T = water temperature and P = photoperiod) and reproductive factors (OF = percentage of ovigerous females from the whole sampled population; $\overline{F'}$ = average relative fecundity; N = sample size).

Relation	N	Simple linear equation (y = a + bx)	r
OF vs P	8	OF = 143.42 - 4.59P	- 0.52 ^{ns}
OF vs T	8	OF = 97.52 - 0.3947T	0.33 ^{ns}
$\overline{F'}$ vs P	8	$\overline{F'}$ = - 0.031 + 0.0049P	- 0.12 ^{ns}
$\overline{F'}$ vs T	8	$\overline{F'}$ = 0.003 - 0.0001T	- 0.02 ^{ns}

ns = p>0.05

Table IV: *Pachycheles monilifer* (Dana, 1852). Diagnoses of the embryonic stages according to their morphology, colour pattern and organogenesis.

Stage	Description of embryonic stages
1	Early clivage. Eggs fully filled with yolk, wine. No animal pole visible.
2	Differentiated yolk droplets resulting from clivage are already visible. Eggs dark wine. In a lateral view, the embryo comprised 1/60 (2%) of the egg volume.
3	Eggs wine coloured. Embryo volume comprising 1/25 of the egg volume (4%).
4	Early organization of pigmented cells near the ocular region, yet stil partially covered by yolk. The embryo occupies 1/4 (25%) of the egg volume. Abdomen and maxillipeds more elongated, reaching the ocular region of the embryo. Eggs wine coloured.
5	Onset of pigmentation of the compound eyes, which are oval-shaped in a lateral view and semicircular in a orsal and ventral view. There are two chromatophores in the first and sixth abdominal somites, easily observed in a ventral position. The heart, still small, can be seen beating in a lateral position. Due to the embryonic growth (1/3 of the egg volume), the eggs are now light wine. This stage marks the onset of abdominal pigmentation.
6	The embryo occupies half of the egg volume. Eggs are light wine. The heart is now larger and the pigmentation of the chromatophoric bridge in the cephalotorax begins.
7	Heart beating is more clearly visible and the sixth abdominal somites are now more easily delimited, including the telson furca. The embryo comprises 2/3 of the egg volume. Eggs are light orange. The chromatophoric complex is further developed and the eyes are fully formed, oval-shaped. In a ventral view it is possible to note a chromatophore pair in each abdominal somite linked by a chromatophoric bridge, more developed and double in this stage.
8	The egg is now dark orange. The chromatophoric bridge links the abdominal chromatophores by a thin string. The heart is larger and beating is more evident than in the previous stage. It is now possible to verify the movimentation of maxillipeds.
9	The larva is fully developed and occupies the whole space within the egg. It is possible to observe a few yolk droplets inside the cephalotorax either in a lateral or dorsal position. Eggs are orange. Carapace, maxillipeds and abdominal somites are evident, easily identified through the egg membrane.

Table V: *Pachycheles monilifer* (Dana, 1852). Minimum, maximum, average values and standard deviation of egg diameter and volume in the identified embryonic stages.

Stage	Diameter (mm)			Volume (mm^3)		
	Min.	Max.	$\bar{x} \pm s$	Min.	Max.	$\bar{x} \pm s$
1	0.43	0.54	$0.49 \pm 0.03^{a*}$	0.04	0.08	$0.06 \pm 0.01^{a*}$
2	0.50	0.57	0.54 ± 0.02^{bc}	0.06	0.09	0.08 ± 0.01^{ab}
3	0.48	0.58	0.52 ± 0.02^{b}	0.06	0.10	0.08 ± 0.01^{ab}
4	0.51	0.57	0.54 ± 0.02^{bc}	0.07	0.09	0.08 ± 0.01^{ab}
5	0.48	0.61	0.56 ± 0.02^{c}	0.05	0.11	0.09 ± 0.02^{ab}
6	0.54	0.63	0.59 ± 0.02^{d}	0.08	0.12	0.11 ± 0.01^{bc}
7	0.59	0.68	0.62 ± 0.02^{e}	0.09	0.14	0.13 ± 0.17^{cd}
8	0.64	0.77	0.69 ± 0.03^{f}	0.12	0.22	0.17 ± 0.03^{d}
9	0.69	0.94	0.80 ± 0.08^{g}	0.15	0.41	0.28 ± 0.08^{e}

*Average values in a single column followed by the same letter are not statistically different ($p>0.05$).

Discussion

Reproduction in crustaceans may be either continuous or restricted to some months when better conditions for offspring survivorship are met (Sastry, 1983). Fecundity is a key parameter which allows measuring the reproductive capacity and the turnover potential of a species population (Fonteles-Filho, 1989).

In great part of the studies reporting results on fecundity, the power function is used for size-specific fecundity relationships due to its plasticity in adjusting both linear ($b=1$) and exponential trends ($b>1$) (Pinheiro and Terceiro, 2000). A curvilinear trend, as observed in the swimming crab *A. cribrarius* (Pinheiro and Terceiro, *op. cit.*), is due to the dimensional nature of the related variables and may be overcome by using the carapace dimension raised to the third power (Jensen, 1958). However, some authors that used the power function ($y=ax^b$) have verified $b>3$, as reported by Pinheiro and Fransozo (1995) in *P. laevidactylus* (=*P. haigae*) in which $b=5.24$, and also in *P. monilifer* as verified in the present study ($b=4.63$). Even in studies using a large sample, the amount of scatter can be quite large due to a marked size-specific biological variability of reproductive output, rendering lower determination coefficients ($R^2<0.70$). Yet, there are still grounds for confident extrapolation between variables and reproductive output estimations for this species. Yet, such variability may contrast even between closely related species, as evidenced by comparing the results obtained for the species focused on this study ($N=180$; $R^2=0.63$), and the congener *P. bevidactylus* ($N=157$; $R^2=0.81$) (Pinheiro and Fransozo, 1995).

In most crustaceans, reproduction is tightly associated with certain exogenous factors, of which water temperature (Lowe, 1961; Giese, 1959; Orton, 1920) and photoperiod (Payen, 1981; Meusy and Payen, 1988) seem to be particularly important. According to Boolootian *et al.* (1959), seasonal temperature variations may affect the reproductive period of crustaceans, which could explain the lower average relative fecundity of *P. monilifer* during winter despite of lacking a significant correlation between this parameter and both the average relative fecundity and percentage of ovigerous females. Following Parsons and Tucker (1986), some crustaceans, as it is the case of the shrimp *Pandalus borealis*, produce a higher number of eggs when exposed to lower temperatures, evidencing the effect of this environmental factor on fecundity. Yet, the inverse pattern is more common. Aquatic animals inhabiting areas of higher water temperature often present a higher reproductive potential (Squires, 1968 *apud* Parsons and Tucker, 1986). Failure in detecting a significant correlation between water temperature and reproductive potential in *P. monilifer* may be due to the high thermic stability within the colonies of *P. caudata.*

Armstrong (1988) evidenced an enhanced gonad development in the portunid *Ovalipes catharus* when subjected to a higher photoperiod. Yet, other species do not respond to such a stimulus, as reported by Justo *et al.* (1991) for the prawn *Macrobrachium rosenbergii*. The absence of a significant correlation between photoperiod and reproductive potential in *P. monilifer* may be related to the ecological niche occupied by this species. The penetration of light inside the sand reef galleries built by *P. caudata* is probably null, for what the influence of this environmental factor on the reproduction of *P. monilifer* should be minimal.

A revision of the published results for the family Porcellanidae (Tab. VI) shows that fecundity is slightly larger for *P. laevidactylus* compared to *P. monilifer* at the same study area. Pinheiro *et al.* (1997) recorded a higher abundance of *P. laevidactylus* at the rocky coast of Praia Grande, Ubatuba (SP), indicating a dominance of this species upon the less abundant congener *P. monilifer*. This observation is supported by the results obtained by Hattori and Pinheiro (1999), who verified a wider niche breadth for *P. laevidactylus* compared to *P. monilifer*. However, the range of the reproductive niche is similar between these species and their overlap almost total (92%), which is not surprising for congeneric species with similar trophic niche, thus competing for the same available resources, either in terms of space and food items. This intraspecific competition seems to be generating a seasonal reproductive partitioning since there is an inverse relationship of both reproductive index and the seasonal percentage of ovigerous females between these species.

Table VI: Literature review of fecundity values for porcellanid species examined so far. Carapace length (CL) or carapace width (CW) is considered as the independent variable and number of eggs (NE) the dependent variable.

Species	Author	Localization	Fecundity equation	CL or CW (mm)		NE (units)	
				Min.	Max.	Min.	Max.
Genus *Megalobrachium*							
M. soriatum	Reid and Corey (1991)	Florida, USA	$NE=-196.55+89.02CL$	2.7	3.7	42	131
Genus *Pachycheles*							
P. ackleianus	Reid and Corey (1991)	Florida, USA	$NE=-94.96+42.38CL$	2.8	4.3	24	143
P. laevidactylus (= *P. haigae*)	Ogawa and Rocha (1976)	Fortaleza, CE, Brazil	$NE=-61+22CL$	3.0	8.5	14	147
	Pinheiro and Fransozo (1995)	Ubatuba, SP, Brazil	$NE=0.00494CL^{5.24}$	3.3	9.6	2	775
P. monilifer	Reid and Corey (1991)	Florida, USA	$NE=-347.32+76.59CL$	4.2	8.2	8	286
	Present study	Ubatuba, SP, Brazil	$NE=0.0198CL^{4.63}$	3.31	8.80	2	511
P. natalensis	Ahmed and Mustaquim (1974)	Karachi, Pakistan	$NE=-109.93+35.4CL$	3.0	-	-	-
P. rudis	Van Wik (1982)	California, USA	$NE=0.056CL^{5.12}$	4.1	14.2	2	2400
P. rugimanus	Reid and Corey (1991)	Florida, USA	$NE=-257.42+83.93CL$	3.2	5.9	10	235
P. tomentosus	Ahmed and Mustaquim (1974)	Karachi, Pakistan	$NE=0.363\ CL^{3.19}$	3.0	-	-	-
Genus *Petrolisthes*							
P. armatus	Ogawa and Rocha (1976)	Fortaleza, CE, Brazil	$NE=-97+29CL$	5.0	11.0	36	260
	Reid and Corey (1991)	Florida, USA and Panama	$NE=-686.52+170.58CL$	3.8	9.2	20	1056

Table VI cont.

Species	Author	Localization	Fecundity equation	CL or CW (mm)		NE (units)	
				Min.	Max.	Min.	Max.
P. elongatus	Jones (1977)	Kaikoura, New Zealand	$NE=0.5CL^{2.87}$	5.4	14.3	80	950
P. haigae	Reid and Corey (1991)	Panama	$NE=-757.16+204.7CL$	3.4	6.8	23	711
P. politus	Scelzo (1985)	Cubagua Island, Venezuela	$NE=0.0131\ CL^{4.53}$	4.5	12.5	2	999
P. rufences	Ahmed and Mustaquim (1974)	Karachi, Pakistan	$NE=2.19CL^{2.29}$	4.0	-	-	-
P. zacae	Reid and Corey (1991)	Florida, USA	$NE=-764.63+175.89CL$	4.8	7.0	81	455
Genus *Polyonyx*							
P. gibbesi	Reid and Corey (1991)	Florida, USA	$NE=-3308.76+693.44CL$	5.0	9.6	235	3369
Genus *Porcellana*							
P. platycheles	Smaldon (1972)	Gower Peninsula, UK	$\log NE=1.61+0.12CW$	4.8	13.1	75	2754
	Almaça (1987)	Ericeira, Portugal	$NE=31.3+0.98CL^{3}$	4.0	7.05	54	420
P. sayana	Reid and Corey (1991)	Florida, USA	$NE=-194.72+64.63CL$	5.7	11.8	229	659

Although using a different mathematical model, the trend found for a population of *P. monilifer* in Florida (Reid and Corey, 1991) is similar to what was found in the present study. Probably this similarity is due to the fact that both populations were sampled at similar subtropical regions, where seasonal temperature changes are relatively small. Because of the use of a linear function and the reduced number of specimens used in their study, there are no grounds for discussing latitudinal trends regarding the reproduction of this species. Fecundity variability as a function of latitude were already recorded in other anomuran species (Fusaro, 1980; Bové, 1999).

Early egg stages have wine colouration due to large amount of yolk. As the embryo develops and the yolk is consumed, the colour of eggs turns to orange and becomes translucent in later stages. Colour alterations through embryogenesis is a natural process common in decapod crustaceans (Ghidalia, 1985). According to this author, the colouration of early eggs match the colour of ripe ovaries, which in turn depends on the presence of composed carotenoids (chiefly carotene-lipoproteins), known as lipovitellins. Following Green (1957), the yolk pigment may protect the embryo against UV radiation. Yet, this protective function may be regarded as irrelevant in gallery-dweller species such as *P. monilifer.*

In *P. monilifer* size variation of eggs through development is higher than what was observed for the hermit crab *Paguristes tortugae* by Negreiros-Fransozo *et al.* (1992), in which egg diameter and volume increases 21.6 and 51.2%, respectively.

Environmental conditions do also influence the duration of embryonic development (Furota, 1988; Fukui, 1988), while physiological factors are particularly involved in variations of egg biometry (Efford, 1969; Nishino, 1980). In the other hand, Bas and Spivak (2000) revealed that crustacean embryos may tolerate different osmotic concentrations which may lead to interspecific morphologic variations related to the formation of the corionic membrane of the egg. According to these authors, an incomplete development of the outer egg membrane during the early embryonic stages (1 to 3) prevents an efficient osmotic control, which is only achieved from the fourth stage. Egg increase is a result of both the embryonic growth and water intake due to osmosis during latter stages. The latter is also involved in the corionic breakage at hatching. In most cases, the timing of larval release in crustaceans coincides with the periods of highest temperature and food availability (Nagao *et al.*, 1999).

The crustaceans that produce larger eggs allocate a higher energetic budget for the embryos, implying in a reduction of number of larval stages and thus the shortening of the planktonic phase (Lindley, 1990; Pinheiro *et al.*, 1994). Those authors verified that water temperature markedly influence the duration of larval development, being these variables inversely correlated. The same is true in the case of the incubation period, that is, the development of embryos (Heasman and Fielder, 1983; Nagao *et al.*, 1999).

Morphometric characteristics of the eggs are not sufficient to identify the early embryonic stages of *P. monilifer*. In this species, the relative proportion of the egg volume occupied by the yolk and the embryo, together with the distribution pattern of chromatophores, are also needed as verified by Boolootian *et al.* (1959) for other decapods. The ten embryonic stages proposed by those authors are well suited to examine organogenesis, while further grouping in three stages (initial, intermediate and final) seems particularly useful in studies emphasizing the adult reproductive biology (Mantelatto and Fransozo, 1997; Santos and Negreiros-Fransozo, 1998; Pinheiro and Terceiro, 2000).

The present results show that the main feature allowing the identification of embryonic stages is the relative proportion of the egg volume occupied by the yolk and animal poles. This feature may be used together with information on the internal morphology, morphometry and coloration for a more reliable identification.

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