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Comparative reproductive effort and fecundity in the spider crabs, *Leurocyclus tuberculosus* and *Libinia spinosa* (Majoidea, Brachyura).

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Abstract

A comparative analysis of the reproductive effort, fecundity and egg weight was conducted in two species of spider crabs, Leurocyclus tuberculosus and Libinia spinosa during one-year period. Ovigerous females were collected from Patagonia-Argentina $(42^{\circ}56'S, 64^{\circ}21'W)$ and were measured (CW = carapace width). Each egg brood was weighed, dried and the number of eggs (F = fecundity) counted. Scatterplot from relative fecundity (RF = F / CW) was submitted to regression analyses. Mean F and RF was calculated for each season to assess seasonal variation of reproductive intensity. Mean F was 35 000 eggs in L. tuberculosus and 30 000 eggs in L. spinosa being these values intermediate in comparison with other Majoidea. The RF was approximately 18 % higher in L. tuberculosus that presented an average dry weight egg 45 % less than L. spinosa. Although in both species F showed a positive correlation with CW, less than the 20 % of the variation in the number of eggs could be explained by female's size, suggesting there are other factors that influence F. The proportion of body energy devoted to reproduction (reproductive effort), exhibited significant differences between species. In Leurocyclus tuberculosus reproductive activity is significantly different along the 12-month suggesting that the conditions for an "optimal" egg production change throughout the year. In *Libinia spinosa* mean fecundity did not reveal significant differences over seasons. These results are central in studies of life-history theory and in the development of life-history models because it is directly related to energy allocation and partitioning.

Key words: reproductive effort; fecundity; Majoidea; Leurocyclus; Libinia.

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Introduction

Knowledge of egg production in a species is essential for estimating the reproductive potential, future stock size of a resource and provides basic elements for understanding the reproductive strategies, spatiotemporal dynamics and evolution of a given population (Wenner and Kuris, 1991; Ramírez-Llodra, 2002; Cobo and Okamori, 2008).

The female reproductive potential is usually defined as the proportion of body energy devoted to reproduction and it is determined by the number of offspring produced during lifetime, the number of stages of growth, the number of offspring produced by stage of maturity and life expectancy (Ramírez-Llodra, 2002). One of the most studied parameter of the reproductive investment is the reproductive effort (also named " reproductive output") defined as the ratio of the dry weight of the egg mass and total dry weight of the female (Hines, 1982). It is commonly associated with the number of eggs released by a female during a single spawning event or specific period of its life history or fecundity (Hines, 1982; Sastry, 1983; Ramírez-Llodra, 2002; Hartnoll, 2006).

This definition has been adopted by many carcinologists and the estimate of fecundity is always obtained using mathematical models fitted to scatterplots relating number of eggs to size (usually carapace width, CW or carapace length, CL) (Haynes et al., 1976; Somerton and Meyers, 1983; Negreiros-Fransozo et al., 1992; Sainte-Marie, 1993; Bryant and Hartnoll, 1995; Lardies and Wehrtmann, 1997; Comeau et al. 1999; López-Greco et al., 2000; Pinheiro and Terceiro, 2000; Okamori and Cobo, 2003; Bas et al., 2007; Diez and Lovrich, 2009).

Majoidea (Ng et al., 2008) represents a widespread group commonly known as "spider crabs" involving many species relevant for fisheries (as *Maja* and *Chionoecetes*) or ornamental purposes (as *Mithraculus*). Fecundity and reproductive potential estimation have been studied in some species of the genus *Chionoecetes* (Haynes et al.,

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1976; Somerton and Meyer, 1983; Paul, 1984; Sainte Marie, 1993; Comeau et al., 1999; Webb, 2009), *Epialtus* (Cobo and Barros, 2009), *Halicarcinus* (Dunnington, 1999; Van den Brink, 2006; Diez and Lovrich, 2010), *Leucippa* (Varisco and Vinuesa, 2011), *Libidoclaea* (Schejter and Spivak, 2005), *Maja* (Carmona-Suárez, 2003; Verísimo et al., 2011), *Maiopsis* (Villalejo-Fuerte et al., 1998), *Microphrys* (López-Greco et al., 2000), *Mithraculus* (Cobo and Okamori, 2008), *Stenocionops* (Villalejo-Fuerte et al., 1999) and *Stenorhymnchus* (Okamori and Cobo, 2003) (Table 1).

These species generally exhibit a trend of positive correlation between size and fecundity similar to other Eubrachyura (Haynes et al., 1976; Hines, 1992; Sainte-Marie, 1993; López-Greco et al., 2000; Van den Brink, 2006; Diez and Lovrich, 2010; Varisco and Vinuesa, 2011; Verísimo et al., 2011), but, generally, in Majoidea is very low the variation in the number of eggs that could be explained by the size of the female (Table 1). Fecundity is a highly plastic feature and variations in fecundity to seasonality, the number of spawnings, the natural loss of eggs and the condition of primiparous (individuals that produced their first egg clutch following the pubertal molt) or multiparous (females with hard carapace when they extrude their second and subsequent annual egg clutches), pointing differences in the reproductive strategies (Paul, 1984; Sainte Marie, 1993; Dunnington, 1999; Diez and Lovrich, 2010; Verísimo et al., 2011) have been recognised.

Leurocyclus tuberculosus (H. Milne Edwards and Lucas, 1842) and *Libinia spinosa* (H. Milne Edwards, 1834) are endemic American species coexisting in northern patagonian gulfs (41°-43°S 64°-65°W) (González-Pisani, 2011). *Leurocyclus tuberculosus* (Inachoididae, Majoidea) (Ng et al., 2008) occurs in coastal Southern and Southeastern Brazil, from Rio de Janeiro to Rio Grande do Sul State, Uruguay and Argentina (Melo 1996). *Libinia spinosa* (Epialtidae, Majoidea) (Ng et al., 2008) is

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restricted to the southwestern Atlantic, from Espírito Santo (Brazil) south to Uruguay and Argentina (Tavares and Santana 2012).

The aim of this study was to compare in two species of spider crabs, *Libinia spinosa* and *Leurocyclus tuberculosus* the reproductive effort (RE), the fecundity (F) and the mean weight per egg, and their possible variations during the annual cycle of spawning. This information is important to understanding the reproductive strategies and spatio temporal dynamics, and to integrate geographic distribution patterns in phylogenetic related species having about the same distribution pattern and sharing similar habitats. This may also allow the comparison with other Majoidea.

Materials and methods

Ovigerous females of *Leurocyclus tuberculosus* (CW from 40.30 to 68.79) and *Libinia spinosa* (CW from 41.91 to 62.76 mm) were monthly collected by baited traps and diving by SCUBA divers from Cracker Bay, Patagonia-Argentina (42°56'S, 64°21'W) during 12 month period (January 2008 to December 2008) at depths between 5 and 45m. Crabs were kept with seawater and transported to the laboratory. Once in the laboratory the ovigerous mass of each female was examined under the microscope to determine their development stage as described by González-Pisani (2011). Only females with eggs in segmentation period (blastula-gastrula) were used for analyses, thus minimizing underestimates due to egg loss. Those females was measured the maximum carapace width (CW) with a caliper to 0.01 mm precision and each mass of eggs was extracted from the abdomen using a dissecting forceps fine tip.

The number of eggs per brood (fecundity, F) was estimated gravimetrically, and 3 subsamples of 300 eggs were counted under a binocular magnifying glass (40×) (Carmona-Suarez, 2003). After oven-drying at 80 °C to constant weight, the subsamples were weighed. An earlier study using subsamples of varying numbers of eggs (100 200,

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300, 400 and 500) was carried out to determine the optimum sample size that would allow us to obtain a reasonable estimate of fecundity according to Verísimo et al. (2011). The dry weight of the female (DWF), the dry weight of the spawning (DWS) and of each egg subsample were determined with a Mettler H80 analytical microbalance.

The dependent variable (F) was plotted as a function of the independent variable (CW) and the resulting scatterplots submitted to regression analysis. Models were fitted to these scatterplots, and the one with the highest determination coefficient (R^2) was chosen to represent them. The relative fecunditdy (RF) was calculated as the average of F / CW. Resulting equations, fecundity, reproductive effort (RE) as the average of DWS / DWF * 100 (Hines 1982) and the dry weight per egg (DWE) as the average of DWS / F, were compared to equivalent data found in other species of Majoidea. Mean F and RF were calculated in each season.

For the study of optimal egg subsample size Tukey test was used. Differences in F, RF, RE and DWE were compared between species and was tested with Kruskal Wallis non-parametric test. Also, differences in the fecundity between seasons were tested using the same test (Sokal and Rohlf, 1995).

Results

Leurocyclus tuberculosus: Fecundity and size of 85 ovigerous females analyzed varied from 1 175 – 75 922 eggs (35 199 ± 16 735 eggs) and CW from 40.30 to 68.79 mm (52.61 ± 5.32 mm). The RE was 4.96 % and the dry weight per egg (DWE) was $29.36 \pm 1.21 \mu g / egg$ and RF was $661 \pm 300 eggs / mm$ CW (Table 2). Scatterplots revealed a linear association y = a + bx in the relationship F / CW was the mathematical model providing the better fit in all regression analyses. Regression analyses indicated

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that the number of eggs (F) is positively correlated with CW (p < 0.001) and the linear regression between F and CW was significant (p < 0.0001, R² value = 0.19) (Fig. 1). *Libinia spinosa:* Fecundity and size of 95 ovigerous females analyzed varied from 8 613 – 55 342 eggs (29 164 \pm 9 787 eggs) and CW from 41.91 to 62.76 mm (53.04 \pm 4.05 mm). The RE was 6.9 % and the dry weight per egg (DWE) was 54.45 \pm 6.48 µg / egg (Table 2). The average relative fecundity (RF) was 547 \pm 172 eggs / mm CW (Table 2). Scatterplots revealed a linear association *y* = a + bx in the relationship F / CW was the mathematical model providing the better fit in all regression analyses. Regression analyses indicated that the number of eggs (F) is positively correlated with CW (p < 0.001) and the linear regression between F and CW was significant (p < 0.0001, R² value = 0.16) (Fig. 1).

Comparing species, the relative fecundity (RF) was 18 % greater in *Leurocyclus tuberculosus* but the dry weight per egg was significantly lower (< 45 %) than *Libinia spinosa*. However, the reproductive effort (RE) of *Libinia spinosa* was significantly greater than *Leurocyclus tuberculosus* (p < 0.05) (Table 2).

During the studied period from January 2008 to December 2008 and for both species ovigerous females in winter (june to august), spring (september to november) and summer (december to february) were collected. In *Leurocyclus tuberculosus* values of number of eggs (F) and relative fecundity (RF) showed significant differences (p < 0.0001) per season (Fig. 2). Generally, in winter (F = 40 000 eggs) and spring (F = 50 000 eggs), the broods reflected similar mean fecundity, greater than in summer (F = 20 000 eggs) (Fig. 2). In *Libinia spinosa* no statistical differences were found between seasons (p > 0.05) being approximately 30 000 eggs per female along the three periods (Fig. 2). The mean dry weight *per* egg for both species, within the annual breeding cycle, did not present significant differences (p > 0.05).

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Discussion

In Eubrachyuran crabs highlights two indicators of reproductive potential, one is the amount of sperm stored in seminal receptacles and the other is the number of eggs carried by female estimated as fecundity (Sainte-Marie et al., 2002; Bas et al., 2007; Webb, 2009; Diaz and Lovrich, 2010). The reproductive potential, estimated as reproductive effort, measured as the percentage of female body weight represented by a brood is a good indicator of the resources (energy and tissue components) invested by a female in egg production (Lardies and Wehrtmann, 1997). The values of RE in Libinia spinosa and Leurocyclus tuberculosus, 6.9 % and 4.9 % respectivemently, are three quarters and half of the value of 10 % estimated as being the mean investment in egg production of brachyurans in general (Hines, 1982, 1992; Brante et al., 2004). However, Majoidea species usually present important differences (Table 1). In comparation, L. spinosa has a similar RE than Inachus dorsettensis (RE = 8.9), Loxorhynchus crispatus (RE = 8.7), Pugettia producta (RE = 8.1) and Puggettia richii (RE = 8.1). L. tuberculosus has a RE value close to Libinia emarginata (RE = 4.7), Loxorhynchus grandis (RE = 5.2) and Mimulus foliatus (RE = 5.2) (Table 1) (Hartnoll, 2006). This would indicate, that the reproductive effort is not specific to each genus, RE of Libinia spinosa is greater than Libinia emarginata. According to Ramírez-Llodra (2002) egg production requires an optimal allocation of energy into growth and reproduction for the maximization of parental fitness.

Fecundity measurements are also influenced by factors that include the stage of embryonic development of the egg (Gardner, 1997; Tuck et al., 2000) and the method of estimation used (Tuck et al., 2000). Therefore, in the present study for all females the fecundity was determinate in the initial of the cycle brood and the method used was for gravimetric (Verísimo et al., 2011). However, fecundity comparisons within Majoidea

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show high variability ranging from less 149 eggs in *Epialtus bituberculatus* (6.6 ± 0.75 mm of CW) (Cobo and Barros, 2009) to more 400,000 eggs for *Chionoecetes bairdi* (91.0 ± 8.7 mm CW) and *Maja brachydactyla* (132.5 to 191.3 mm CL) (Table 1) (Haynes et al., 1976; Varísco et al., 2011). Such variability has been attributed to biological factors such as body size (Hines, 1982), time elapsed from the previous moult, and subsequent broods (Sainte-Marie, 1993) and to environmental factors as temperature (Ouellet and Plante, 2004; Brillon et al., 2005), food availability, (Ramírez-Llodra, 2002), and geographic area (Tuck et al., 2000). In this study, *Leurocyclus tuberculosus* and *Libinia spinosa* present similar size but significantly differences in fecundity (Table 1). Additionally, when relative fecundity is compared among Majoidea, the average values obtained in this study (661 eggs / mm for *Leurocyclus tuberculosus* and 547 eggs / mm for *Libinia spinosa*) and those reported for *Microphrys bicornutus* (López-Greco et al., 2000) and *Leucippa pentagona* (Varisco and Vinuesa, 2011) (Table 1) shows that these smaller species have more number of eggs than bigger species.

However the variability is not only between species but there are also intraspecific differences. Many studies in Majoidea have recognized factors that would explain intraspecific differences; the great variation in the number of eggs within a same size range could indicate the presence of more than one spawning in the annual period (Mantelatto et al., 2002; Varisco and Vinuesa, 2011). In *Chionoecetes opilio* the different spawnings *per* reproductive period have differences in the fecundity (Comeau et al., 1999). In *Maja brachydactyla* the size of the broods during two breeding cycles and of subsequent broods exhibited significant differences in terms of both fecundity and brood dry weight, the first broods contained fewer, larger eggs (a greater energy investment per egg), whereas subsequent broods contained more, smaller eggs (less

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energy investment per egg) (Verísimo et al., 2011). The variability in the number of eggs for the same female size was also observed in *Paguristes tortugae*, where the authors stated that this difference may be caused by multiple spawning in the same reproductive period and/or low fecundity observed in primiparous females (Mantelatto et al., 2002; Ramírez-Llodra, 2002). This could be an explanation for our studied species, although in this work not discriminated in primiparous and multiparous, because both species have 1 to 3 spawnings in one reproductive cycle (Gonzalez-Pisani, 2011).

A positive relationship between carapace width and fecundity was found in the present study and has been documented in previous studies (Table 1, Fig. 1) (Sainte-Marie, 1993; López-Greco et al., 2000; Van den Brink, 2006; Diez and Lovrich, 2010; Verísimo et al., 2011). However, in the present work only about 15 to about 20 % of the variation in the number of eggs could be explained by female's size. This suggests that besides size other factors influence in the fecundity. This variability has been attributed to environmental factors too such as temperature (Ouellet and Plante, 2004; Brillon et al., 2005) or food availability (Ramirez-Llodra, 2002). This may be reflected in *Leurocyclus tuberculosus* and *Libinia spinosa* because both species have a widespread reproductive period, the annual breeding cycle of female in the northern patagonian gulfs (41°-43°S 64°-65°W) starts in july and continues until march so there is a possible variation in egg production during the breeding cycle. The availability of food is an important determinant of egg production (Hines, 1982; Henmi, 2003; Bas et al., 2007) and it has been demonstrated that the seasonal variability in food resources reduces the fecundity (Hines, 1982, 1992; Bas et al., 2007). During the year, the seasonal data for the entire study period showed that ovigerous females of *Leurocyclus tuberculosus* had higher relative frequency (> 90%) during spring (september to november) and summer

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(december to march) while during winter (june-august) the relative frequency was the lower (<10%). In *Libinia spinosa*, ovigerous females had a relative frequency over 75% during summer and winter and, during the spring (march to may) the relative frequency was below 15% (González-Pisani, 2011). So probably this factor is reflected in the significant differences in fecundity between spring, summer and winter are seen in accordance to the large thermal range (8°C-18°C) in waters of the Nuevo gulf between seasons (Dellatorre, 2010).

Gayoso and Fulco (2006) indicated that the seasonal pattern of phytoplankton bloom in the Nuevo gulf has two peaks: one in autumn and one in spring. Taking into account this pattern it could be estimated that there is a synchronization between periods of maximum fecundity (spring) with periods of high primary productivity contributing to optimal developmental conditions for growth of larvae and juveniles.

These interannual variations in the fecundity of *Leurocyclus tuberculosus* in the Nuevo gulf and other species of Majoidea, such as *Inachus dorsettensis* (Bryant and Hartnoll, 1995), *Chionoecetes bairdi* (Somerton and Meyers, 1983), and *C. opilio* (Sainte-Marie, 1993), may also be attributed to the causes like time elapsed since the terminal moult, and food availability. Therefore, the first spawning of *Maja brachydactyla*, associated with lowest values of fecundity, occurs in winter when environmental conditions are unfavorable and females have not yet built up sufficient reserves in their bodies to invest in reproduction, because they are still recovering from the energy expended in carrying out the terminal moult and reproductive migration (Verísimo et al., 2011). In contrast, subsequent broods, with higher values of fecundity, are produced in spring and summer when environmental conditions (food and temperature) are more favorable (Verísimo et al., 2011). This means that females have more resources to be devoted to reproduction. This could be the cause of differences in

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fecundity in *L. tubeculosus* during the reproductive cycle that in spring the females of the species have higher fecundity and lower during summer. By contrast, in *L. spinosa* the mean number of eggs produced did not change along the year as was observed by Okamori and Cobo (2003) and Cobo and Okamori (2008) for the spider crabs, *Stenorhynchus seticornis* and *Mithraculus forceps* respectively.

Another involved feature is the correlation of sperm content in the seminal receptacles and egg production. *Halicarcinus cookii* spawns regardless of the amount of sperm available (Van den Brink, 2006), unlike *Chionoecetes bairdi* where females do not spawn if there is not enough sperm in the receptacles to fecundate the oocytes (Paul and Adams, 1984). *Leurocyclus tuberculosus* and *Libinia spinosa* are similar in this aspect to *H. cookii* because the females lay eggs regardless of the amount of sperm content in the seminal receptacles (Gonzalez-Pisani, 2011). Therefore, we can infer that this independence between spawning and sperm load could be one of the factors contributing to the wide variation in fecundity for the same female size, since it is possible that not all oocytes produced by the female can be fertilized.

In terms of biometric characteristics of the eggs, by volume and weight, the eggs from two studied species follow the rule for Eubrachyuran crabs, that higher fertility is accompanied with lower egg size/weight. The fecundity being approximately 18 % higher in *Leurocyclus tuberculosus* presented an average egg weight 45 % lesser than *Libinia spinosa* (Hines, 1982; Sainte Marie, 1993; Diez and Lovrich, 2010). The dry weight per egg (DWE) did not differ between seasons which may indicate that the difference in fecundity is not due to differences in egg's size.

The presented results show a significant knowledge of the reproductive potential of these two species of Majoidea with a wide geographic distribution that coexistent in Nuevo gulf, Argentina. It highlights the variations in species showing the tendency for

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crustaceans in general and its possible modulating factors. Both species show significant amplitude in the number of eggs related to body size, suggesting that external factors besides size affect fecundity. On the other hand these species present differences in the interannual cycle, in *Leurocyclus tuberculosus* seasonality plays an important role, suggesting that the conditions for an "optimal" fecundity change throughout the year but *Libinia spinosa* inhabiting the same habitat does not. These variations in these species from the same breeding cycle shed some light on reproductive strategies that differ from each other in the way they use structural and energetic resources to produce a small quantity of large eggs or a large number of small eggs, depending on the environmental conditions.

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Figure legends

Figure 1. Relationship between fecundity (n° of eggs, F) and carapace width (mm, CW) of the all females of *Leurocyclus tuberculosus* (N = 85) and all females of *Libinia spinosa* (N = 95). Regression equations and coefficients of determination are presented for each relationship.

Figure 2. Fecundity (F, mean \pm SD) and relative fecundity (RF, mean \pm SD) in winter (W; N = 34), spring (Sp; N = 20) and summer (S; N = 31) of *Leurocyclus tuberculosus* (N = 85) and in winter (W; N = 50), spring (Sp; N = 30) and summer (S; N = 15) of *Libinia spinosa* (N = 95). Different letters indicate significant differences (p < 0.05) among seasons.

Table

Table 1. Comparative analyses of the relationships between number of eggs (Fecundity) against carapace width (CW) or carapace length (CL), the dry weight per egg (DWE), reproductive effort (RE) and the interannual variations in the fecundity among Majoidea species.

Table 2. Fecundity, relative fecundity, reproductive effort and dry weight per egg for all females of *Leurocyclus tuberculosus* (N = 85) and *Libinia spinosa* (N = 95). Different letters indicates significant differences (p < 0.05) between species.





Relationship between fecundity (n° of eggs, F) and carapace width (mm, CW) of the all females of Leurocyclus tuberculosus (N = 85) and all females of Libinia spinosa (N = 95). Regression equations and coefficients of determination are presented for each relationship.



Fecundity (F, mean \pm SD) and relative fecundity (RF, mean \pm SD) in winter (W; N = 34), spring (Sp; N = 20) and summer (S; N = 31) of Leurocyclus tuberculosus (N = 85) and in winter (W; N = 50), spring (Sp; N = 30) and summer (S; N = 15) of Libinia spinosa (N = 95). Different letters indicate significant differences (p < 0.05) among seasons.



Table 1. Comparative analyses of the relationships between number of eggs (Fecundity) against carapace width (CW) or carapace length (CL), the dry weight per egg (DWE), reproductive effort (RE) and the interannual variations in the fecundity among Majoidea species.

Family	Species	Reference	Locality or Latitude	CW(mm)	Fecundity	Dry weight per egg (DWE)	Relationship F/CW	Reproductive effort	Interannual variations in the fecundity
				or CL (mm)	(mean or range) (eggs)	(μg/egg) or Diameter μm	\mathbf{R}^2	RE	
Epialtidae	Epialtus bituberculatus	Cobo & Barros 2009	Brazilian (23°23′S, 45°03′W)	6.6 ± 0.75 (CW)	_149 ± 122.90	пр	$R^2 = 0.10$	пр	np
	Leucippa pentagona	Varisco & Vinuesa 2011	Bustamante Bay, <u>Argentina</u> (45.11°S, 66.56°W)	18 to 24 (CL)	645 to 7 114	441±67µm	$R^2 = 0.47$	np	no
	Libidoclaea granaria	Schejter & Spivak 2005	between 36° & 39°40'S	160 to 480 (CW)	1 200 to 9 300	np	np	np	пр
	Libinia emarginata	Hartnoll 2006	np	np	np	np	пр	4.7%	np
	Libinia spinosa	Present study	Cracker Bay, Argentina	41.9 to 62.7	29 164 ±9 787	54.45±6.48 μg/egg	$R^2 = 0.16$	4.9%	No
			(42°56'S, 64°21'W)	(CW)	-				
	Loxorhynchus crispatus	Hartnoll 2006	пр	пр	пр	пр	пр	8.7%	np
	Loxorhynchus grad&is	Hartnoll 2006	пр	пр	пр	пр	пр	5.2%	np
	Mimulus foliatus	Hartnoll 2006	пр	np	np	np	np	5.2%	пр
	Pugettia producta	Hartnoll 2006	пр	пр	np	np	пр	8.1%	пр
	Puggettia richii	Hartnoll 2006	пр	пр	пр	пр	пр	8.1%	np

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	Scyra acutifrons	Hartnoll 2006	np	np	np	np	np	5.6%	np
Hymenosomatidae	Halicarcinus cookii	Van den Brink 2006	Kaikoura Peninsula, New Zeald.	5.4 to 11.4 (CW)	306 to 2 438	np	$R^2 = 0.69$	np	yes
	Halicarcinus planatus	Diez & Lovrich 2009	Bahía Brown,	6.9 to 11.6	692 to 1 226	np	np	2.1%	yes
			Beagle Channel (54°51´S- 67°30´W)	(CW)	-				
Inachidae	Inachus	Bryant &	Irish sea	пр	пр	47.2±0.31	$R^2 = 0.40$ to	пр	yes
	dorsettensis	Hartnoll 1995		-	-	µg/egg	$R^2 = 0.49$	-	·
		Hartnoll 2006	np	np	пр	np	Np	8.9%	np
	Stenorhynchus	Okamori &	Ubatuba	9.24 ±1.52	621.1±339.6	_480±100μm	$R^2 = 0.43$	пр	no
	seticornis	Cobo (2003)	region Brazil	(CW)	69 to 1 850				
Inachoididae	Leurocyclus	Present study	Cracker Bay,	40.3 to 68.7	35 199 ±16	29.36±1.21	$R^2 = 0.19$	4.96%	Yes
	tuberculosus		Argentina		735	µg/egg			
			(42°56'S, 64°21'W)	(CW)	6				
Majidae	Maiopsis panamensis	Villalejo- Fuerte et al. 1998	Gulf of California	120 to162 (CW)	351.5 to 1162.6	np	Np	np	np
	Maja	Verísimo <i>et</i>	Ría de	132.5 to 191.3	300 192±92	89.5±8.0	$R^2 = 0.21$ to	8.2%	пр
	brachydactyla	al. 2011	Arousa		912	_µg/egg	$R^2 = 0.46$		•
			(Galicia,Spai	(CL)	125 181 to		IX -0.70		
	Maia orienata	Carmona	<u>n).</u> Isobio Itoly	108 to 716	530 309 11 473±4 797	318+24 2	Nn	ип	ир
	maja crispaia	Califiona- Suárez 2003	iscilla-italy	470 W / IV	114/3±4/0/	510+24.2 μm	1 · <i>p</i>	np	np
		Suai (2 2003	(40°42′N;13° 55′W)		4 866 to 19 800	_			
	Microphrys	López-Greco	Isla	16.7±0.2	1	36.91±1.21	Np	0.88%	пр
	bicornutus	et al. 2000	Margarita,		_207.55±6422	µg/egg			
			Venezuela	(CL)					

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	Mithraculus forceps	Cobo & Okamori	Couves Isl& (23°25'25"S,	940 to	402.8 ± 240.1	пр	Np	np	no
		(2008)	44°52'03"W)	1 400 (CW)	60 to 1 123	-			
	Stenocionops ovata	Villalejo- Fuerte <i>et al</i> . 1999	Gulf of California	65.6 to 88.5	35 187 to 170 057	пр	$R^2 = 0.61$	пр	пр
Oregoniidae	Chionoecetes bairdi	Somerton & Meyers 1983	Alaska – (57°N- 170°W)	68 to110 (CW)	50 000 to 330 000	np	пр	пр	no
		Paul 1984	Kodiak Isl& & Resurrection Bay, Alaska	80 to 119 (CW)	215 000 ± 75 000	np	np	np	пр
		Webb 2009	Glacier bay, Alaska	<u>91.0 ± 8.7</u> (CW)	143 000 ± 51 700	np	пр	np	пр
	Chionoecetes opilio	Sainte-Marie 1993	Baie Sainte- Marguerite (50°06 N- 66°35 W	40 to 77 (CW)	81 630 to 83 143 (at the end of development, near hatching)	np	R ² =0.7	пр	пр
		Comeau <i>et al</i> . 1999	Bonne Bay, Newfoundl&	67 (CW)	54 000 (at the end of development, near hatching)	_np	$R^2 = 0.96$	np	yes
	Hyas coarctatus	Bryant & Hartnoll 1995	Irish sea	пр	пр	56.9± 0.35 μg/egg	$R^2 = 0.78$	np	пр
		Hartnoll 2006	пр	пр	пр	np	пр	9.6%	пр

np = *not provided*.

Table 2. Fecundity, relative fecundity, reproductive effort and dry weight per egg for all females of *Leurocyclus tuberculosus* (N: 85) and *Libinia spinosa* (N = 95).

* Significant differences (p < 0.05) between species.

	L. tuberculosus	L. spinosa
Fecun	dity (F) (N° of eggs per female	e)
Mean ± standard deviation	35 199 ± 16 735	29 164 ± 9 787
Range	1 175 – 75 922	8 613 - 55 342
Relativ	e fecundity (RF) (F/mm of CV	W)
Mean ± standard deviation	661 ± 300*	547 ± 172*
Range	103 – 1 383	188 – 1 098
Re	eproductive effort (RE) (%)	
Mean ± standard deviation	4.96 ± 2.25*	6.90 ± 2.59 *
Range	1.08 - 12.44	2.51 - 18.42
Dry v	weight per egg (DWE) (µg/egg	
Mean ± standard deviation	29.36 ± 1.21*	$54.45 \pm 6.48*$
Range	19.02 - 29.83	35.21 - 74.25

viation 19.02 - 29.85