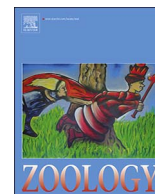




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## Dynamics of energy reserves and the cost of reproduction in female and male fiddler crabs

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### ABSTRACT

The physiological costs of reproduction can be measured as the energy allocated to reproductive activities. In fiddler crabs, females allocate energy to vitellogenesis and brooding, whereas males perform expensive courtship behaviors. We evaluated in a large-scale study the reproduction cost of females and males of *Leptuca uruguayensis* in a temperate estuary, where their reproductive efforts are synchronized in a short reproductive season. The reproductive investments (vitellogenesis, spermatophore production, and male reproductive behaviors) were measured and related to the dynamics of storage and expenditure of energy reserves (glycogen, total lipids, and total protein) in the hepatopancreas, ovary, and muscle of the enlarged cheliped, throughout one annual cycle. Maximum energy storage occurred in winter, a period of low activity, whereas minimum energy storage occurred during the reproductive period, characterized by expensive activities. The glycogen reserves of the hepatopancreas decreased about 66% in females and 61% in males, suggesting high and similar physiological costs of reproduction between sexes, despite their different reproductive strategies to maximize their fitness.

### 1. Introduction

The resources destined to growth, maintenance, and reproduction depend on a balance between the availability and demand of these resources, which can vary according to the life stage, life strategy, and environmental conditions (Reznick, 1985; Barnes and Partridge, 2003). Reproduction is an expensive process, and the physiological costs of reproduction can cause conflicting demands for resources with other life history traits (trade-offs between reproduction, growth, and maintenance) (Reznick et al., 2000; Kotiaho, 2001; Ramirez-Llodra, 2002; Reedy et al., 2016). Reproduction also has ecological costs, in which interactions with the environment during reproductive activities expose the organism to risks as disease, injury or predation (Reznick, 1992). Assessing the trade-offs between costs of reproduction and costs of other life variables, as well as their consequences on parental survival and future reproductive performance can contribute to a better understanding of the life history evolution of species (Calow, 1979; Reznick, 1985; Ellers and van Alphen, 1997; Candolin, 1998; Ramirez-Llodra, 2002; Hoy et al., 2016; Kindsvater et al., 2016).

The physiological costs of reproduction can be measured as energy allocated to reproductive activities (Calow, 1979; Kotiaho, 2001; Scharf et al., 2013). Usually, females allocate resources mainly to ensure

embryo development and many species show some level of maternal care, whereas males attempt to increase their mating opportunities. Old concepts supposed that female reproductive costs were greater than those of males, since males show an inexpensive and considered unlimited sperm production (Scharf et al., 2013). However, males of many species show sexually selected ornaments and complex behaviors (mate searching, courtship, combat, and territory defense) that maximize their reproductive success, but also increase the costs of reproduction (Matsumasa and Murai, 2005; Mowles, 2014; Greenspan et al., 2016). In these cases, although females and males have different strategies to maximize their fitness, the reproductive costs can be similar between sexes (Maklakov and Lummaa, 2013; Reedy et al., 2016).

In crabs, most of the knowledge about reproductive investment is based on female effort, probably because the reproductive traits ordinarily measured are those usually used as indicators of costs of reproduction (e.g. gamete production, fecundity, brooding time) (Hartnoll, 2006; Baeza et al., 2015; Bert et al., 2016). Reproductive female crabs load oocytes with yolk proteins (vitellogenesis) and, after fecundation, they brood the egg mass up to eclosion (maternal care). In female crabs, both vitellogenesis and brooding demand high energy expenditure (Eastman-Reks and Fingerman, 1985; Harrison, 1990; Fernández et al., 2000; Tsukimura, 2001; Brante et al., 2003;

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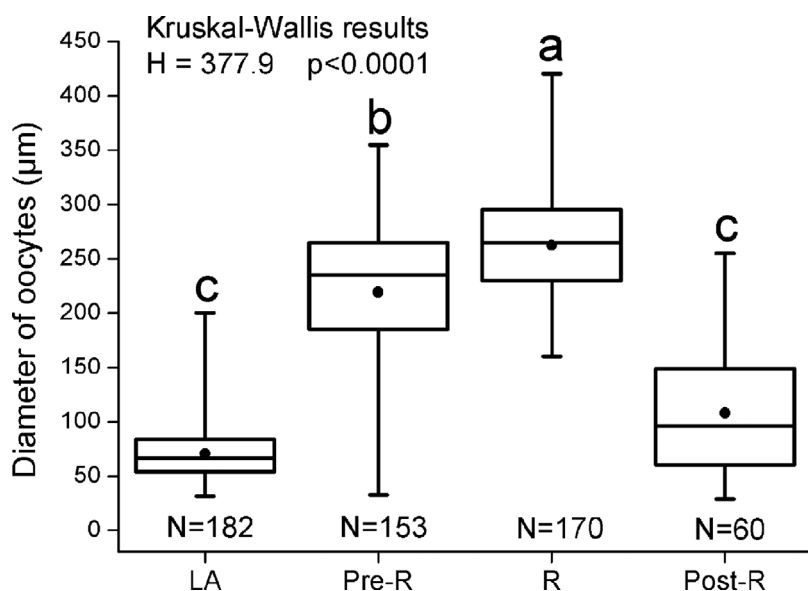


Fig. 1. Comparison of oocyte size (point = mean, line = median, box = 25–75%, whiskers = min–max) found in female gonads of *Leptuca uruguayensis* in each period of the reproductive cycle (LA, low-activity period; Pre-R, pre-reproductive period; R, reproductive period; Post-R, post-reproductive period). N, number of oocytes measured in each period. Different letters indicate statistically significant differences between medians ( $p < 0.05$ ).

Guadagnoli et al., 2005; Zmora et al., 2007; Jimenez and Kinsey, 2015). In crabs, the hepatopancreas is the principal energy storage organ and plays an important role in reproductive activities, since it supplies energy and synthesizes yolk components (Harrison, 1990; Zmora et al., 2007; Girish et al., 2014; Thongda et al., 2015; Sacristán et al., 2017). Unlike females, male crabs allocate a low amount of energy to gamete production (Wu et al., 2010), but show several mating behaviors (Christy, 1987; McLay and Becker, 2015). Besides this behavioral diversity, little is known on the energetic requirements of males for reproduction. Only the glucose and lactate concentrations in the blood of male fiddler crabs have been evaluated as indicators of the metabolic demands of their reproductive behaviors (Matsumasa and Murai, 2005; Matsumasa et al., 2013).

The fiddler crabs are interesting models to evaluate the cost of reproduction, because males have one of the chelipeds enlarged. This large cheliped is a sexually selected ornament, which is displayed vigorously to attract females, and used as a weapon in fights with other males to protect the mating burrow (Crane, 1975). This ornament increases the reproductive success of males, but the use of this enlarged appendage impacts on physiological costs, since it demands high energy expenditure (Matsumasa and Murai, 2005; Allen and Levinton, 2007; Gerald and Thiesen, 2014), and ecological costs, because it increases male vulnerability to predation (Bildstein et al., 1989; Koga et al., 2001; Cummings et al., 2008).

Among fiddler crabs, *Leptuca uruguayensis* is a eurythermal species that inhabits the temperate estuaries of the southwestern Atlantic coast (Argentina, 37°S). In these areas, the low winter temperatures prevent their activities and the gonad development in females, limiting the reproductive period to the warmer months (Colpo and López-Greco, 2017). Therefore, in temperate populations of *L. uruguayensis*, the reproductive efforts of females (vitellogenesis and brooding) and males (courtship behaviors) are synchronized in a short reproductive season. This feature makes the Argentine population of *L. uruguayensis* a suitable model to analyze the physiological costs of reproduction in females and males separately, considering their different strategies to maximize fitness. Throughout one annual cycle, we evaluated in this study the investment in reproduction and the dynamics of energy reserves in females and males of a temperate population of *L. uruguayensis*. For this, we measured throughout the year, the energy invested in vitellogenesis (female direct/gamete investment in reproduction), spermatophore production and accumulation in the vas deferens (male direct/gamete investment in reproduction), and the time spent in reproductive behaviors (male indirect/behavioral

investment in reproduction). We also assessed the physiological costs of these reproductive investments by surveying the dynamics of storage and expenditure of energy reserves (glycogen, total lipids, and total protein) in the hepatopancreas, ovary, and muscle, throughout the year. This way, we can estimate in a large temporal scale the costs of reproduction in a temperate fiddler crab. Moreover, knowledge on the energy invested in reproduction allows understanding the trade-offs among other life history traits throughout the year.

## 2. Material and methods

The study was performed in the Samborombón Bay, Río de la Plata estuary, Argentina. The field works were performed during low tide, from February 2014 to January 2015, in a muddy sand area of approximately 3,500 m<sup>2</sup> in the intertidal zone of the Saladero canal (36°25'0.3"S–65°57'11"W), in the locality of General Lavalle, Buenos Aires province. *Leptuca uruguayensis* is distributed from tropical estuaries in Rio de Janeiro, Brazil (22°S) to temperate salt marshes in Buenos Aires, Argentina (37°S) (Melo, 1996; Bezerra, 2012). In temperate estuaries, *L. uruguayensis* shows a conspicuous annual reproductive cycle affected by temperature, involving four periods: the low-activity period (LA, May–July), the pre-reproductive period (Pre-R, August–October), the reproductive period (R, November–January), and the post-reproductive period (Post-R, February–March) (more details about definition of the periods in Colpo and López-Greco, 2017). In each period, the fiddler crabs were sampled at three different time spans, to ensure appropriate temporal replication based on Underwood and Chapman (2013).

### 2.1. Cost of female and male gametes production

During vitellogenesis, the size of oocytes increases due to yolk accumulation (Castiglioni et al., 2007; Antunes et al., 2010). Therefore, to determine the temporal variations in energy expenditure in gamete production in *L. uruguayensis* females, the size of oocytes was measured in each period of their annual reproductive cycle. For this, the gonads of six random adult non ovigerous females (> 10 mm of maximum carapace width) by period were histologically examined. Ovaries were dissected and fixed in Bouin's solution for 4 h at 20 °C. Then, the gonads were dehydrated in ascending ethanol series, cleared in n-Butanol, embedded in Paraplast® and sectioned (6 µm thick) with a microtome. Slides were stained with Masson's trichrome (Subarna et al., 2012). Under a microscope, all oocytes with visible nucleus were measured

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