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Examination of female energy dynamics and larval quality in the southern king crab, *Lithodes santolla*: Annual and interannual variability

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Highlights

- Energy reserves in the ovary vary interannually and with female size.
- Depending on the year, multiparous females have better ovary quality than primiparous ones.
- Ovigerous and non-ovigerous females have a similar pattern of reserve accumulation.
- Energy reserves of larvae, eggs, or ovary do not influence larval survival.

- The survival of zoea I to zoea II larvae represents a bottleneck for recruitment.

Abstract

The southern king crab, *Lithodes santolla*, constitutes one of the most important fishery resources in the Beagle Channel. In this study, we considered that *Lithodes santolla* females showing better physiological conditions may produce larvae with higher survival rates. To determine whether this quality may be useful for the enhancement of natural crab stocks, in the present study, we aimed to evaluate several biochemical parameters considering the size and ovigerous condition of the female parent. Primiparous (<80 mm CL) and multiparous (>80 mm CL) females, as well as ovigerous and non-ovigerous females, were evaluated. The patterns of accumulation or use of several macromolecules (glycogen, lipids and proteins) in different organs and development stages (midgut gland, ovary, eggs, larval stages and first crabs) were also evaluated along two reproductive seasons. The possibility that some females could be producing larvae with high survival was evaluated through the relationship between the female midgut gland and ovarian quality and the larvae. The results obtained indicate that the energy content of L. *santolla* females is highly variable according to the year, season, and month, and between primiparous and multiparous females. We hypothesized that this variability in the energetic quality is explained by differences in the female's diet: food availability or food quality during ovary maturation. Most of the energy reserves of the ovary are transferred to the offspring. The only female parent-brood connection is through the energy reserves transferred to the eggs 10 months earlier, and we hypothesize that this depends on the previous environmental and female feeding conditions during ovarian development. Moreover, zoea I larvae showed high variability in survival, not influenced by their own energy reserves or by the reserves of the eggs or the ovary. The physiological variables here analyzed did not allow identifying better females that can produce larvae with higher survival.

Introduction

Over the last decades, king crab populations have fluctuated dramatically worldwide, and almost every fishery for this species is considered to be overfished (Otto, 2014). The South American fisheries for the southern king crab, *Lithodes santolla*, are not an exception, as it has been noted that the native populations are showing clear signs of reproductive failure, evidenced by a low abundance of ovigerous females [29% in the Beagle Channel, Argentina (Lovrich et al., 2017; Di Salvatore et al., 2021); 24% in the Chilean Pacific, (Molinet et al., 2020)], and alarming decreasing numbers of females with full clutches [<20% in the XII Region, Chile (Daza et al., 2016) and 40% in San Jorge Gulf, Argentina (Firpo et al., 2017)]. Therefore, scientists are looking for ways to restrain the declining abundance stocks by enhancing natural crab stocks through the release of cultured juveniles (Stevens, 2014). Thus, as a general principle, to improve the population status, there is a significant need for a large number of juveniles to be released into the ocean, and this must be supported by rearing large numbers of zoea in hatcheries (Sotelano et al., 2018). To reduce rearing costs, only females whose larvae present high survival should be used to produce juvenile crabs. However, whether there is a way to know beforehand how survival would be throughout larval development remains to be elucidated.

In crabs, the offspring quality depends mainly on the physiological state of the broodstock, which, in turn, is determined by the maternal body size/age, nutritional status, biochemical composition, number of successive spawnings, and inter-individual variability (genetic variability) (Racotta et al., 2003; Tropea et al., 2012; Tropea et al., 2015; Zhang et al., 2018; Di Salvatore et al., 2020). In endotrophic larvae, all the energy resources for their survival are provided by the female parent and hence the importance of the study of the different energy compartments of the female (midgut gland, ovary, eggs) (Anger, 2001). The midgut gland is the main organ for the synthesis and secretion of digestive enzymes and for the absorption and storage of biochemical reserves (Icely and Nott, 1992). During ovarian maturation, the biochemical reserves from the midgut gland are transferred to the ovary (Spaargaren and Haefner Jr, 1994; da Silva-Castiglioni et al., 2007; Subramoniam, 2011). Thus, the biochemical reserves transferred to the eggs play a central role in embryonic and larval development (Racotta et al., 2003). In addition, the larval biochemical profiles (Rotllant et al., 2014) and thus, larval quality (Bas et al., 2007; Verísimo et al., 2011) and juvenile growth (Giménez and Anger, 2003; Giménez, 2010), may show interannual differences due to changes in environmental conditions, such as temperature, photoperiod, or a combination of both.

The maximization of larval survival at a hatchery implies questions regarding the female parent. Some of these questions include: Are there better females that can provide larvae with higher survival? Can we predict larval survival from L. *santolla* female size or from the energy reserves of the ovary or eggs close to hatch? Is there any rapid proxy that can predict larval survival? The larval survival of massive larval cultures of L. *santolla* can sometimes be high or low, depending on the year (Tapella and Sotelano, CADIC, Ushuaia, Argentina, personal communication). In decapods, maternal size does not seem to be a reliable proxy of offspring quality, as some studies have found that both parameters correlate (Moland et al., 2010; Sato and Yoseda, 2010; Militelli et al., 2020), whereas others have found that they do not correlate (Sotelano, 2012; Swiney et al., 2013; Rey et al., 2017; Di Salvatore, 2019). Theory predicts that, if parental dietary compounds (e.g., amino acids, polyunsaturated fatty acids (PUFAs), and vitamin E) are unbalanced or insufficiently supplied in their diets, hatching success would decrease, and embryonic mortality and malformation would increase (Steinberg, 2018). In L. *santolla*, some females produce egg clutches with lower larval survival than others, and also the same female can produce eggs with different survival depending on the day of hatching, as previously observed in a study performed during three consecutive days (Di Salvatore, 2019). Similarly, in a multi-site-and-year analysis on the lobster *Homarus americanus*, the greatest single source of variance in offspring quality was the individual female, but not female size (Ouellet and Plante, 2004). Moreover, in brachyuran crabs, maternal nutrients and energy provisioning are affected by environmental factors, which eventually act as sources of variability in larval production (Sainte-Marie, 1993; Bryant and Hartnoll, 1995) and growth performance of juveniles (Giménez and Anger, 2003; Giménez, 2010; Rotllant et al., 2014).

In *L. santolla*, all larval stages are lecithotrophic (i.e. receive no nutrition other than the yolk), which implies that maternal investment per offspring is enhanced and, therefore, that larval energy resources are those previously accumulated in the female's ovaries (Lovrich et al., 2003). The reproductive cycle of this species is annual: mating and fertilization of eggs occur in December–January, embryos are carried by females for 9–10months, and hatching occurs in September–October (Vinuesa, 1984; Gowland-Sainz, 2018). Females that do not mate during the reproductive season extrude their eggs, and then lose them after a few weeks (Vinuesa, 1984; Gowland-Sainz, 2018). After egg hatching, females bear pleopods with dark setae and remnants of hatched eggs, which is evidence of having been in an ovigerous condition during the reproductive cycle of that year. This is in contrast to the "clean" setae (without remnants of hatched eggs) in females that are not ovigerous (Di Salvatore et al., 2021). The proliferation of oogonia and the beginning of growth in early oocytes begins in July, in the ovary proliferative zone, and it has thus been interpreted that oogenesis lasts two years (Vinuesa and Labal de Vinuesa, 1998). However, primary vitellogenesis –which is mainly a proteic phase- takes place toward the end of the first year, i.e. November–December, just previous to mating, and secondary vitellogenesis –which is mainly a lipidic phase- takes place during the following year (Vinuesa and Labal de Vinuesa, 1998). Annually and during the four months previous to their extrusion, oocytes grow and duplicate their size through the accumulation of yolk (Vinuesa and Labal de Vinuesa, 1998), which will nurture the embryos and larvae during the following ten and two months, respectively.

In the present work, the first objective was to study whether; there are L. *santolla* females with better ovarian quality, through the quantification of energy reserves in the ovary. Our second objective was to evaluate whether larval survival is influenced by the energy reserves from the ovary or eggs of the female parent, or by the larval energy reserves. To detect whether some of the females can produce larvae with better survival, we evaluated some proxies in females collected in the Beagle Channel (Argentina). First, we analyzed whether larval survival depends on the female parent size: since multiparous females probably produce larvae with higher survival, we tested multiparous vs. primiparous females. Furthermore, since 70% of the mature females of the Beagle Channel stock are non-ovigerous (i.e. do not bear eggs) due to reproductive failures, most likely caused by overfishing (Di Salvatore et al., 2021; Molinet et al., 2023), another source of variation in larval quality may be whether or not the female parent carried eggs during the previous reproductive season. Thus, we also compared ovigerous vs. non-ovigerous at the same time of the year. Secondly, we analyzed the reproductive season as a possible source of differences. As lecithotrophic larvae should be provided with enough energy to survive throughout larval development, which lasts approximately 60 days (Lovrich et al., 2003), energy can only come from the energy allocation into oocytes. Therefore, we tested the energy reserves in two different years (2016 and 2018). Finally, we analyzed whether larval energy quality depends on the energy allocation of the female parent into the oocytes that eventually become embryos, although this could be an indirect proxy, since there is no physiological connection between carried eggs and their female parent.

Section snippets

Animals

All animals were captured in the Beagle Channel, Argentina (54° 50′S; 68° 15′W) by using commercial traps baited with bovine fat. *Lithodes santolla* females were brought to the aquarium facilities of the Centro Austral de Investigaciones Científicas (CADIC), Ushuaia, Tierra del Fuego (Argentina), at ambient air temperature (0–6 °C). The transport of crabs never lasted more than three hours. We performed two studies. For study 1, primiparous and multiparous L. *santolla* females (ovigerous,…

Study 1: Annual and interannual energy variability in the ovary

The biochemical analyses of the samples collected in 2016 and 2018 showed significant variations in the content and dynamics of the energy reserves in the ovary of L. *santolla* (Fig. 2). In 2016, during ovarian development, the glycogen content decreased abruptly after April (73%), whereas lipid and protein contents increased gradually since February (~5.5 times) and April (~4 times), respectively (Fig. 2A-C). Lipids reached maximum levels between July and November (~390 mg/g tissue) (Fig. 2B),…

Discussion

Considering the physiological variables analyzed in this study, it was not possible to recognize better females that can provide larvae with higher survival. However, results demonstrated that the energy quality of L. *santolla* females has large variability between years, seasons, months, and crab sizes. In addition, our results suggest that lipids and proteins are converted into carbohydrates at the end of embryogenesis, previous to hatching. Also, during larval development, the zoea I stage…

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CRediT authorship contribution statement

Hernán Sacristán: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Pablo Di Salvatore:** Methodology, Writing – original draft, Writing – review & editing, Visualization. **Olga Florentín:** Methodology. **María Gowland-Sainz:** Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Laura López Greco:** Writing – original…

Declaration of Competing Interest

All the co-authors listed fully participated in and accept responsibility for the work. No part of this work is submitted or published elsewhere, and I have not any related articles, extended abstracts or reports sub-mitted or published elsewhere.…

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