

## Pattern of energy allocation during the gametogenesis of the asteroid *Cosmasterias lurida* (Forcipulatida: Stichasteridae) from the Beagle Channel, Ushuaia, Argentina

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**Abstract:** Energy allocation patterns during the reproductive cycle of echinoderms may be determined by the different energy requirements of the organisms. In this study, we describe the energy reserves variation in the gonads, pyloric caeca and stomach among the gametogenic stages of a population of *Cosmasterias lurida* from the Beagle Channel, Argentina. Adult individuals of *C. lurida* were collected from the subtidal zone of Ushuaia Bay during four seasonal sampling periods (August 2010 to June 2011). Indices, energy density (kJ/g ash-free dry mass) and energy content (kJ) of gonads, pyloric caeca and stomach were determined. Oocytes number and diameter were evaluated. *Cosmasterias lurida* had a major peak of gonadal index (GI) in mature gonads (M), with a great decrease towards the spawning (PS/PSR) and remature (RM) periods. No variation was observed in the energy density of the gonads ( $ED_G$ ). The energy content of the gonads ( $EC_G$ ) presented a similar pattern to the GI. Thus, the gonadal storage cycle can be explained through the variation in gonad mass more than in its energy density. Females had higher  $EC_G$  and  $ED_G$  values than males, which suggest a greater energy contribution in females during the reproductive cycle. The stomach and the pyloric caeca indices, energy density and energy content remained unaltered among the stages. The energy density of pyloric caeca ( $ED_{PC}$ ) was higher in mature males than in mature females. Likewise, the energy density of the stomach ( $ED_S$ ) was overall higher in males than in females. This inverse pattern between sexes in relation to the  $ED_G$  may suggest a transference of energy from the pyloric caeca and stomach to gonads during mature stage playing a storage role for reproduction. Rev. Biol. Trop. 65(Suppl. 1): S197-S206. Epub 2017 November 01.

**Key words:** sea star; body indices; energetics; gametogenic stages; oocyte size distribution; reproductive biology.

Gonadal development in echinoderms is associated with the acquisition and accumulation of nutrients and, subsequently, their transference to gametogenic cells when needed (Lawrence, 1987a; Pearse & Cameron, 1991). This energy input is also devoted to other processes, such as growth and maintenance of the organisms (Lucas, 1996). Different echinoderms energy requirements may establish distinct energy allocation patterns throughout

the reproductive cycle and also between sexes (Lawrence & McClintock, 1994; Carey, 1999).

In asteroids, the pyloric caeca are important nutrient reserve organs, as they contain almost all energetic reserve substances (lipids, carbohydrates, proteins) of an individual (Jangoux & Van Impe, 1977; Ferguson, 1984; Lawrence, 1987b). The energy accumulated in the pyloric caeca can be transferred through the haemal system to the gonads during gametogenesis.

Many asteroids show an inverse relationship between gonad and pyloric caeca relative masses associated with stored nutrients carrying towards the developing gonads (Harrold & Pearse, 1980; Scheibling, 1981; Chia & Walker, 1991; among many others).

The subtidal asteroid *Cosmasterias lurida* (Philippi, 1858) has a continuous distribution range from the Argentinian shelf (38°00'S, 57°33'W) to the Chilean coast (29°56'S, 78°31'W), including South Georgia and Malvinas Islands (Madsen, 1956; Hernández & Tablado, 1985). *Cosmasterias lurida* is an important predator in the shallow subtidal communities where it inhabits and it is a generalist-opportunistic feeder (Garrido, 2012). In Tierra del Fuego, it feeds mainly on bivalves (*Mytilus chilensis*, *Aulacomya atra*) and gastropods (*Pareuthria plumbea*, *Trophon geversianus*) (Gordillo & Archuby, 2012; Curelovich pers com). *Cosmasterias lurida* has indirect development with planktotrophic larvae. There are few studies about the reproductive biology (Pastor de Ward et al., 2007; Cossi, Boy, Gimenez & Pérez, 2015) or ecology of this asteroid species (Vásquez & Castilla, 1984; Adams & Gordillo, 1999; Garrido, 2012).

Cossi et al. (2015) suggested an annual reproductive cycle with two maturing periods for *C. lurida* population from the Beagle Channel. Gametogenesis began in February (austral summer) and continued until June (austral autumn), and the spawning period occurred between August and December (austral winter-spring). Cossi et al. (2015) found that the stomach, the pyloric caeca and the body wall could act as energy reservoirs for the reproductive events in autumn-winter and early spring. In this study, we aimed to describe the pattern of energy allocation during gametogenesis, by comparing body indices, energetic content and density of different organs, of a population of *C. lurida* from the Beagle Channel.

## MATERIALS AND METHODS

**Study site:** *Cosmasterias lurida* was collected from the subtidal zone (2-4 m depth) of

Ushuaia Bay, Beagle Channel (54°50'06.08" S and 68°16'26.72" W) by SCUBA diving. Four seasonal sampling periods were performed from August 2010 to June 2011 (August, n = 30; December, n = 30; February, n = 28; June, n = 30). The sea stars were transported to the Laboratorio de Ecología, Fisiología y Evolución de Organismos Acuáticos and maintained in plastic tanks containing sea water at 7°C for 24 h. Asteroids were placed on a paper towel and the wet weight was recorded ( $\pm 0.01$  g).

**Somatic and gonadal indices:** All individuals were anesthetized by immersion in MS-222 (ethyl 3-aminobenzoate methanesulfonate acid salt, 98 %, Aldrich) 1 % in sea water, 45 min (O'Neill, 1994), and then the gonads, the pyloric caeca and the stomach were dissected and weighed ( $\pm 0.01$  g). The indices of each organ (gonad, pyloric caeca and stomach) were calculated as: [organ wet weight (g) / total wet weight (g)] x 100.

**Oocyte number, diameter and size distribution:** One gonad from each animal was immersed in Bouin's fixative for 12 h and dehydrated in a graded ethanol series. Tissue was embedded in paraffin (Paraplast®) and 5-7  $\mu\text{m}$  sections were cut and stained with hematoxylin-eosin (Pérez, 2009). Histological slides from 112 individuals (45 females, 67 males) were examined microscopically and a gametogenic stage was assigned to each one based on the criteria of Pastor de Ward et al. (2007) and Pérez, Boy, Morriconi & Calvo (2010). In addition, a quantitative analysis of oocytes was included in females to define the developmental stage of the gonads. Digital images of gonad sections were taken with a digital camera attached to an Olympus BX40 microscope and analyzed using Micrometrics SE Premium 4 software. Three microscopic fields were examined (100X; NA: 0.25; Area: 0.378  $\text{mm}^2$ ) per female slide. In each field, the number of oocytes and the oocyte diameter ( $\mu\text{m}$ , largest axis of oocytes with nucleus) were determined. The data are expressed as the mean oocyte diameter and oocyte number per female slide.

Five gametogenic stages were defined for both sexes: growth (G), premature (P), mature (M), partially spawned/partially spawned with recovery (PS/PSR) and remature (RM) according to Cossi et al. (2015).

**Gonad, stomach and pyloric caeca energy density and energy content:** Body organs (gonads, stomach and pyloric caeca) of each sea star were stored at  $-20^{\circ}\text{C}$  for calorimetric evaluation. They were dried to constant weight in an air circulating oven at  $60^{\circ}\text{C}$ . The dried samples were ground and pellets were made by compression with a press (Parr model 2812). The caloric content of the organs were determined by burning pellets inside a micro-bomb calorimeter (Parr model 1425) to complete combustion (Pérez, Morricóni, Boy & Calvo, 2008; Boy, Pérez, Fernández, Calvo & Morricóni, 2009). The values are expressed as kJ/g ash-free dry mass (energy density ED, kJ/g AFDM) and corrected for ash and acid content. The micro-bomb calorimeter was periodically calibrated with benzoic acid. The total energy content of the organs (EC) was calculated by multiplying the ED by the total dry weight of each organ (g).

Variations in GI, energy content of the gonads and energy density of the pyloric caeca ( $\text{EC}_G$  and  $\text{ED}_{PC}$ ) were analyzed using a non-parametric test (Kruskal-Wallis), given that the assumptions required by the parametric test (normality and/or homogeneity of variances) were not reached. Differences between sexes were tested using paired *t* test or non-parametric Mann-Whitney test when necessary. Variations in pyloric caeca and stomach indices (PCI and SI), energy density of stomach and energy content of both organs ( $\text{ED}_S$  and  $\text{EC}_{PC}$ ,  $\text{EC}_S$ ) were analyzed using a two-way ANOVA (gametogenic stage and sex as factors). Differences in the mean oocyte number and mean oocyte diameter per field were tested using a one-way ANOVA. The assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test) were tested and adjusted when necessary. Significant differences were analyzed by Tukey multiple

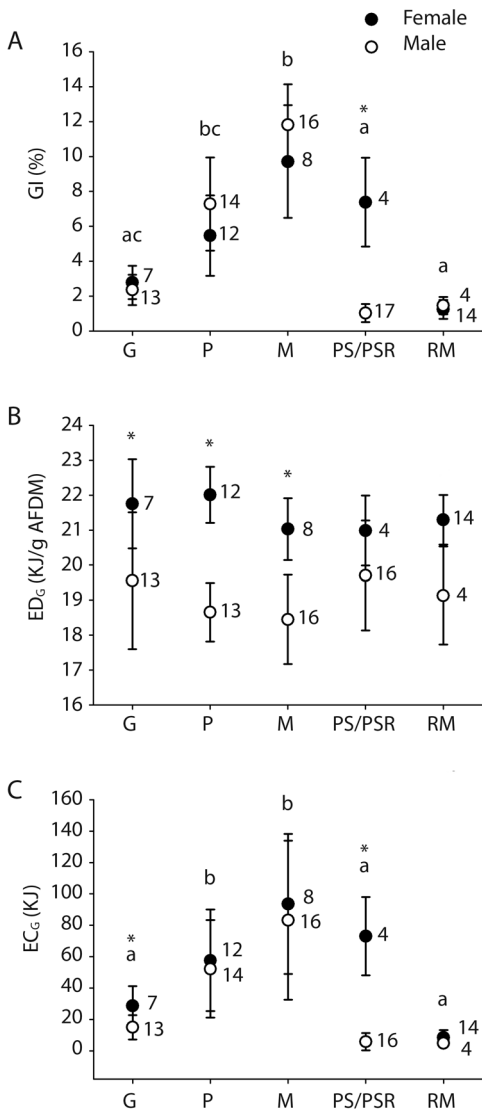
comparisons test. Statistical analyses were performed with Statistica 7.1 and GraphPad InStat 3.01.

## RESULTS

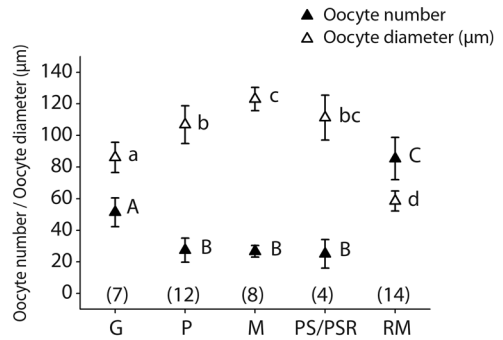
**Gonad:** The gonadal index (GI; Fig. 1A) varied significantly among gametogenic stages (Kruskal-Wallis,  $H = 76.59$ ,  $df = 4$ ,  $P < 0.0001$ ), with higher values registered in M and P individuals (Dunn's test,  $P < 0.001$ ). The female GI was significantly higher than the male GI in the PS/PSR stages (Mann-Whitney test,  $U = 0.00$ ,  $P < 0.05$ ). No differences between sexes were found in the other stages.

The energy density of gonads ( $\text{ED}_G$ ; Fig. 1B) showed no significant differences in the interaction between the sexes and the gametogenic stages (two-way ANOVA,  $F_{4,97} = 1.81$ ,  $P > 0.05$ ) and among gametogenic stages (two-way ANOVA,  $F_{4,97} = 1.60$ ,  $P > 0.05$ ). It varied significantly between sexes (two-way ANOVA,  $F_{1,97} = 75.74$ ,  $P < 0.05$ ), females had higher values than males in the G, P and M stages (Tukey test,  $P < 0.05$ ). A different scenario was observed in the energy content of gonads ( $\text{EC}_G$ ; Fig. 1C), which had a significant variation among gametogenic stages (Kruskal-Wallis,  $H = 64.50$ ,  $df = 4$ ,  $P < 0.0001$ ), with higher values in individuals from the P and M stages (Dunn's test,  $P < 0.001$ ). The  $\text{EC}_G$  for females was significantly higher than for males in the G and PS/PSR stages (*t* test,  $t = 3.03$ ,  $P < 0.05$  and Mann-Whitney test,  $U = 0.00$ ,  $P < 0.05$ , respectively).

**Oocyte number and diameter:** The mean oocyte number and diameter (per microscopic field; Fig. 2) had significant differences between the gametogenic stages (one-way ANOVA,  $F_{4,40} = 66.22$ ,  $P < 0.0001$  and  $F_{4,40} = 76.19$ ,  $P < 0.0001$ , respectively). Individuals from the RM stage had the highest number of oocytes while individuals from the P, M and PS/PSR stages showed the lowest number of oocytes (Tukey test,  $P < 0.05$ ). The oocytes reached their largest diameter in the M stage,



**Fig. 1.** A. Gonadal index [GI (%) mean  $\pm$  SD]; B. gonad energy density [ED<sub>G</sub> (kJ/g AFDM) mean  $\pm$  SD]; and C. gonad energy content [EC<sub>G</sub> (kJ) mean  $\pm$  SD] of the gametogenic stages of *C. lurida* from the Beagle Channel. *G* growth, *P* premature, *M* mature, *PS/PSR* partially spawned/partially spawned with recovery, *RM* remature, SD = standard deviation. Statistical differences between gametogenic stages are indicated with different letters above the bars and between sexes with asterisks. Numbers beside each dot correspond to the sample size of sea stars. **Fig. 1.** A. Índice gonadal [IG (%) media  $\pm$  DE]; B. densidad energética gonadal [DE<sub>G</sub> (kJ/g PSLC) media  $\pm$  DE]; y C. contenido energético gonadal [CE<sub>G</sub> (kJ) media  $\pm$  DE] de los estadios gametogénicos de *C. lurida* del Canal Beagle. *G* crecimiento, *P* premadurez, *M* madurez,



**Fig. 2.** Oocyte diameter ( $\mu\text{m}$ ) and oocyte number [mean  $\pm$  SD] of the gametogenic stages of *C. lurida* females from the Beagle Channel. Statistical differences between gametogenic stages are indicated with different letters. Numbers between parentheses correspond to the sample size of the female sea stars.

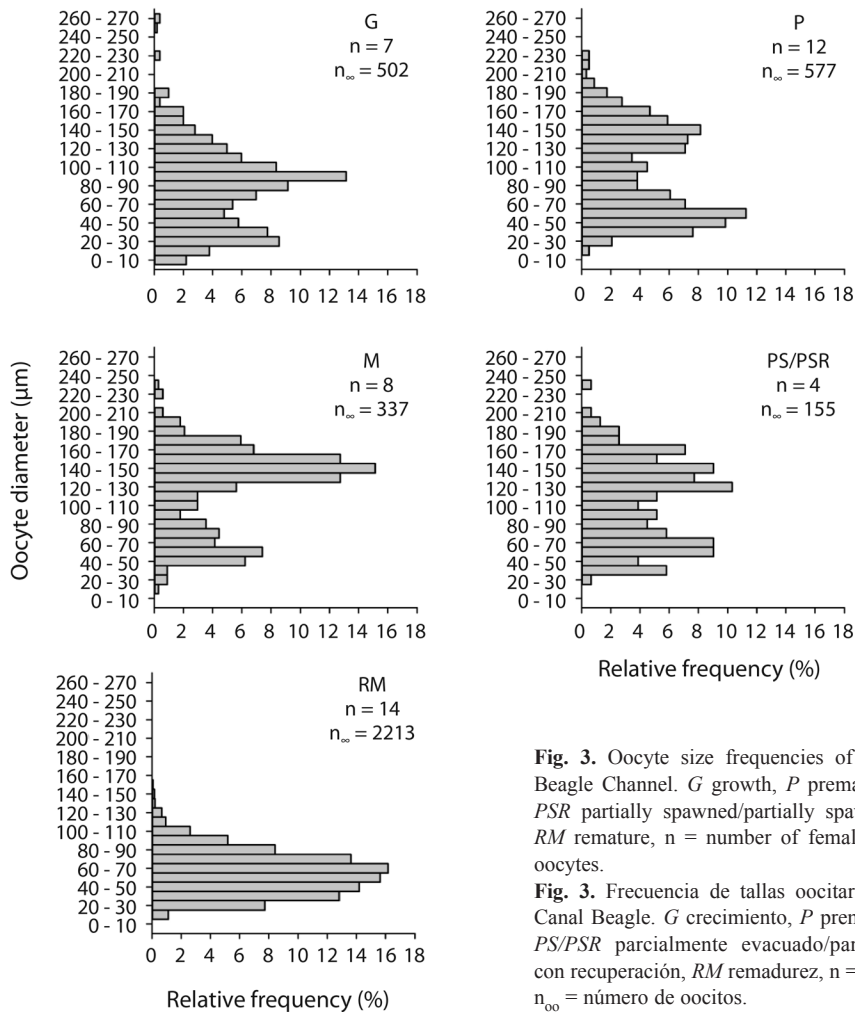
**Fig. 2.** Diámetro ( $\mu\text{m}$ ) y número de oocitos [media  $\pm$  DE] de los estadios gametogénicos de hembras de *C. lurida* del Canal Beagle. Las diferencias significativas entre estadios gametogénicos está indicada con letras distintas. Los números entre paréntesis corresponden a la cantidad de estrellas de mar hembras.

whereas they had the smallest diameter in the RM stage (Tukey test,  $P < 0.05$ ).

**Oocyte size distribution:** The oocyte diameter increased from the G stage (mode = 90 - 100  $\mu\text{m}$ ) to the M stage, where they reached their largest size (140 - 150  $\mu\text{m}$ ) (Fig. 3). In turn, the frequency and proportion of small oocytes decreased from the G stage towards the M stage. The RM stage had the smallest oocytes sizes (60 - 70  $\mu\text{m}$ ) together with the highest oocytes number.

**Stomach:** For the stomach index (SI; Table 1), there were no statistical differences in the interaction between sexes and gonadal stages (two-way ANOVA,  $F_{4,98} = 1.12$ ,  $P > 0.05$ ). Also, neither the main effects of sex

*PS/PSR* parcialmente evacuado/parcialmente evacuado con recuperación, *RM* remadurez, DE = desviación estándar. Las diferencias significativas entre estadios gametogénicos está indicada con letras distintas sobre las barras y entre sexos con asteriscos. Los números corresponden a la cantidad de replicas de estrellas de mar.



**Fig. 3.** Oocyte size frequencies of *C. lurida* from the Beagle Channel. *G* growth, *P* premature, *M* mature, *PS/PSR* partially spawned/partially spawned with recovery, *RM* remature, *n* = number of females, *n*<sub>oo</sub> = number of oocytes.

**Fig. 3.** Frecuencia de tallas oocitarias de *C. lurida* del Canal Beagle. *G* crecimiento, *P* premadurez, *M* madurez, *PS/PSR* parcialmente evacuado/parcialmente evacuado con recuperación, *RM* remadurez, *n* = número de hembras, *n*<sub>oo</sub> = número de oocitos.

(two-way ANOVA,  $F_{1,98} = 0.12$ ,  $P > 0.05$ ) nor gametogenic stage (two-way ANOVA,  $F_{4,98} = 1.92$ ,  $P > 0.05$ ) were significant.

The energy density of the stomach ( $ED_S$ ; Table 1) showed no significant differences in the interaction between sexes and gametogenic stages (two-way ANOVA,  $F_{4,99} = 0.89$ ,  $P > 0.05$ ) and also among gametogenic stages (two-way ANOVA,  $F_{4,99} = 0.88$ ,  $P > 0.05$ ). The males showed higher values of  $ED$  than the females (two-way ANOVA,  $F_{1,99} = 4.59$ ,  $P < 0.05$ ). Likewise, for the energy content of the stomach ( $EC_S$ ; Table 1) the interaction between both factors was not significant (two-way ANOVA,

$F_{4,99} = 0.40$ ,  $P > 0.05$ ) and there were neither main effects of sexes (two-way ANOVA,  $F_{1,99} = 0.50$ ,  $P > 0.05$ ) nor gametogenic stages (two-way ANOVA,  $F_{4,99} = 0.62$ ,  $P > 0.05$ ).

**Pyloric caeca:** The index and the energy content of the pyloric caeca ( $PCI$  and  $EC_{PC}$ ; Table 2) did not show a significant interaction between sexes and gametogenic stages (two-way ANOVA,  $F_{4,99} = 2.11$ ,  $P > 0.05$  and  $F_{4,98} = 0.79$ ,  $P > 0.05$ , respectively). Also, neither the main effects of sex (two-way ANOVA,  $F_{1,99} = 0.05$ ,  $P > 0.05$  and  $F_{1,98} = 1.71$ ,  $P > 0.05$ , respectively) nor gametogenic stage (two-way

TABLE 1  
Stomach index, energy density and content [Mean  $\pm$  SD] of the gametogenic stages  
of *C. lurida* from the Beagle Channel

CUADRO 1  
Índice, densidad y contenido energético de estómago [media  $\pm$  DE] de  
los estadios gametogénicos de *C. lurida* del Canal Beagle.

Gametogenic stage*		SI (%) <sup>1</sup>	ED <sub>s</sub> (kJ/g AFDM) <sup>2</sup>	EC <sub>s</sub> (kJ) <sup>3</sup>
G	Female (n = 7)	1.36 $\pm$ 0.28	20.27 $\pm$ 1.04	11.75 $\pm$ 3.84
	Male (n = 13)	1.41 $\pm$ 0.23	21.12 $\pm$ 1.13	12.81 $\pm$ 4.26
P	Female (n = 12)	1.49 $\pm$ 0.25	20.98 $\pm$ 0.61	13.37 $\pm$ 3.47
	Male (n = 14)	1.31 $\pm$ 0.27	20.75 $\pm$ 1.11	11.79 $\pm$ 5.76
M	Female (n = 8)	1.39 $\pm$ 0.23	20.54 $\pm$ 1.24	12.23 $\pm$ 3.59
	Male (n = 16)	1.42 $\pm$ 0.30	21.10 $\pm$ 1.28	12.84 $\pm$ 5.30
PS/PSR	Female (n = 4)	1.14 $\pm$ 0.16	20.05 $\pm$ 0.96	11.68 $\pm$ 4.94
	Male (n = 17)	1.29 $\pm$ 0.24	20.68 $\pm$ 0.75	9.49 $\pm$ 4.23
RM	Female (n = 14)	1.46 $\pm$ 0.29	20.02 $\pm$ 1.26	11.64 $\pm$ 6.72
	Male (n = 4)	1.50 $\pm$ 0.17	20.70 $\pm$ 0.57	9.96 $\pm$ 4.29

\* G = growth, P = premature, M = mature, PS/PSR = partially spawned/partially spawned with recovery, RM = remature.  
For males SI in G stage, n = 12.

<sup>1</sup> SI = stomach index.

<sup>2</sup> ED<sub>s</sub> = energy density of stomach.

<sup>3</sup> EC<sub>s</sub> = energy content of stomach.

TABLE 2  
Pyloric caeca index, energy density and content [Mean  $\pm$  SD] of the gametogenic stages  
of *C. lurida* from the Beagle Channel

CUADRO 2  
Índice, densidad y contenido energético de ciegos pilóricos [media  $\pm$  DE]  
de los estadios gametogénicos de *C. lurida* del Canal Beagle.

Gametogenic stage*		PCI (%) <sup>1</sup>	ED <sub>PC</sub> (kJ/g AFDM) <sup>2</sup>	EC <sub>PC</sub> (kJ) <sup>3</sup>
G	Female (n = 7)	13.02 $\pm$ 3.56	25.16 $\pm$ 1.20	243.02 $\pm$ 148.44
	Male (n = 13)	11.08 $\pm$ 2.31	25.44 $\pm$ 1.16	208.46 $\pm$ 115.01
P	Female (n = 12)	10.55 $\pm$ 2.60	25.67 $\pm$ 1.61	171.85 $\pm$ 45.33
	Male (n = 14)	11.85 $\pm$ 4.16	25.37 $\pm$ 1.42	181.88 $\pm$ 78.28
M	Female (n = 8)	14.76 $\pm$ 5.91	24.84 $\pm$ 0.92	235.51 $\pm$ 101.43
	Male (n = 16)	10.40 $\pm$ 2.89	26.52 $\pm$ 2.15	201.36 $\pm$ 114.25
PS/PSR	Female (n = 4)	14.79 $\pm$ 9.15	25.32 $\pm$ 0.38	344.83 $\pm$ 370.93
	Male (n = 16)	11.41 $\pm$ 3.64	25.26 $\pm$ 1.34	150.59 $\pm$ 72.41
RM	Female (n = 14)	9.75 $\pm$ 3.71	25.21 $\pm$ 1.10	178.57 $\pm$ 130.23
	Male (n = 4)	12.56 $\pm$ 3.29	24.87 $\pm$ 0.88	185.14 $\pm$ 108.57

\* G = growth, P = premature, M = mature, PS/PSR = partially spawned/partially spawned with recovery, RM = remature.  
For males PCI in PS/PSR stage, n = 17.

<sup>1</sup> PCI = pyloric caeca index.

<sup>2</sup> ED<sub>PC</sub> = energy density of pyloric caeca.

<sup>3</sup> EC<sub>PC</sub> = energy content of pyloric caeca.



ANOVA,  $F_{4,99} = 0.42$ ,  $P > 0.05$  and  $F_{4,98} = 0.81$ ,  $P > 0.05$ , respectively) were significant.

Despite the energy density of the pyloric caeca ( $ED_{PC}$ ; Table 2) not varying among the gametogenic stages (Kruskal-Wallis,  $H = 2.93$ ,  $df = 4$ ,  $P > 0.05$ ) it varied between the sexes. The  $ED_{PC}$  was significantly higher in males of the M stage than in females of the same stage (Mann-Whitney test,  $U = 29$ ,  $P < 0.05$ ).

## DISCUSSION

We observed an increase of the GI with gonadal maturation in both sexes, reaching its peak value in the mature stage. Cossi et al. (2015) reported gonadal maturation occurred during winter when seawater temperature decreased. Other echinoderms from the Beagle Channel also reached maturation at the same season (Orler, 1992; Pérez et al., 2008). Most gametogenic stages did not differ between sexes in the GI values. It has been reported that some asteroid species have higher GI values in females than in males (Carvalho & Ventura, 2002; Pastor de Ward et al., 2007; Bos, Gumanao, Alipoyo & Cardona, 2008; Benítez-Villalobos & Martínez-García, 2012) while others show higher values in males than in females (Benítez-Villalobos & Díaz-Martínez, 2010) or even no difference between the sexes (Georgiades, Temara & Holdway, 2006; Benítez-Villalobos, Díaz-Martínez & Tyler, 2007; Mariante, Lemos, Eutrópico, Castro & Gomes, 2010).

The  $ED_G$  remained constant among the gametogenic stages. However, the  $EC_G$  had a pattern of variation similar to that observed in the GI. An alternation of gametes and accessory cells could explain the lack of differences in the ED of the gonads between gametogenic stages. In females, accessory cells are usually found surrounding growing oocytes. These cells accompany the development of the oocytes by increasing in number (Pain, Tyler & Gage, 1982; Tyler, Pain, & Gage, 1982). Its function is mainly associated to phagocytosis of unspawned oocytes (Pain et al., 1982). In males, accessory cells are found

bunched together forming a central core, from which spermatogenic cell columns will develop (Walker 1980, 1982; Chia & Koss, 1994). Thus, these results indicate that the increase in the amount of energy stored in gonads of *C. lurida*, in relation to the degree of maturation, occurs due to the variation in gonad mass but not its energy density. The values of  $ED_G$  and  $EC_G$  were higher in females than males. These results can be attributed to the higher lipid or carbohydrate content in ovaries with respect to testes (Barker & Xu, 1991). Other Antarctic (McClintock & Pearse, 1987; McClintock, 1989) and Subantarctic (Pérez et al., 2010) echinoderms have similar relationships. These findings suggest a greater energy investment in female gonads than in male gonads during gonadal maturation.

The GI and  $EC_G$  in females were higher than in males in the partially spawned/partially spawned with recovery stages. This may be explained by the fact that female gonads at this stage contain gametes at very different stages of development (from early to mature oocytes).

The number and diameter of oocytes varied among the gametogenic stages. When gametogenesis begins, in the growth stage, the GI is low and many small oocytes are present. Then, GI increases towards premature stage and reaches its highest value in the mature stage. The gonads of mature females have a low number of oocytes with larger sizes than in other gametogenic stages. During spawning (partially spawned/partially spawned with recovery stage), some gonads still have a few large oocytes that have not been released and in some of them new small and medium sized oocytes appear. The remature stage has the lowest GI values, together with a significant increase of small oocytes. At this stage, gonads of both sexes are well developed and contain mature gametes, indicating a feasible second maturation period (remature) in spite of the lack of a GI relative maximum (Cossi et al., 2015). Multiplicity and intensity of maturation peaks in echinoids are associated with food quality and availability (Oyarzún, Marín, Valladares & Iriarte, 1999), minor environmental

variations in the sampling areas and inter annual variations in the environmental factors involved in the regulation of reproduction (Pearse & Cameron, 1991). Rematuring gonads had a greater number of smaller oocytes than mature gonads. There are several explanations for this phenomenon; 1) the studied rematuring females have not reached the maximum gonadal maturity, 2) as rematuration is the second event of gonadal maturation, the availability of energy could be lower and thus the capacity to accumulate yolk has decreased, reaching maturity with smaller oocytes instead of larger oocytes with abundant yolk.

The stomach and the pyloric caeca did not show a variation in their indices, energy density and energy content among the gametogenic stages. Nevertheless, the  $ED_{PC}$  was higher in males than females during maturation. Considering that the  $ED_G$  was higher in mature females than mature males, we can suggest a transfer of energy from pyloric caeca to female gonads (Jangoux & Van Impe, 1977; Scheibling, 1981; Chia & Walker, 1991) probably associated to the greater cost of reproduction for females than males (see above). Similarly, the  $ED_S$  was overall higher in males than in females. This can be also explained by the higher energy requirements of females for reproduction. These results could suggest a greater accumulation of energy in the pyloric caeca and stomach of females and thus a role as energy reservoir of this organ during mature stage. Cossi et al. (2015) proposed both organs (the pyloric caeca and the stomach) are energy reservoirs during gonadal maturation. They described the temporal variation of the energy content of both organs and found a maximum energy accumulation during autumn which could supply the demand of the sexual maturation. The integration of seasonal (Cossi et al., 2015) and gonadal stages (not only timing of reproduction) approaches allow a clearer overview of the internal energy transfer process of an organism.

The population of *C. lurida* from the Beagle Channel showed a significant variation of the GI and the  $EC_G$  among the gametogenic

stages. Both sexes had an increase in these parameters with the degree of gonadal maturation. The  $EC_G$  increase occurs mainly due to the variation in gonad mass. Females and males had different patterns of energy allocation to gonads, with a greater energy investment by females. The ED pyloric caeca and stomach variations between sexes suggest that these organs could play a role as energy reservoir for reproduction. This study provides information for understanding the latitudinal variation in the life history traits of *C. lurida* at the southernmost limit of its geographical distribution.

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#### RESUMEN

**Patrón de asignación energética durante la gametogénesis del asteroideo *Cosmasterias lurida* (Forcipulatida: Stichasteridae) del Canal Beagle, Ushuaia, Argentina.** Los patrones de asignación energética durante el ciclo reproductivo de equinodermos pueden estar determinados por distintos requerimientos energéticos de los organismos. En este estudio, describimos la variación de las reservas energéticas en gónadas, ciegos pilóricos y estómago entre los estadios gametogénicos de una población de *Cosmasterias lurida* del Canal Beagle, Argentina. Individuos adultos de *C. lurida* fueron colectados de la zona sub-mareal de Bahía Ushuaia durante cuatro muestreos estacionales (Agosto 2010 a Junio 2011). Los índices, la densidad energética (kJ/g peso seco de material libre de cenizas) y el contenido energético (kJ) gonadal, de ciegos pilóricos y estómago fueron determinados. El número y diámetro de oocitos fueron evaluados. El índice gonadal (IG) de *Cosmasterias lurida* fue máximo en gónadas maduras (M), con un importante decrecimiento hacia los períodos de desove (PD/PDR) y remadurez (RM). No se observó variación en la densidad energética gonadal ( $DE_G$ ). El contenido energético gonadal ( $CE_G$ ) presentó un patrón



similar al del IG. Por lo tanto, el ciclo de almacenamiento gonadal puede explicarse debido a la variación en la masa gonadal más que en su densidad energética. Las hembras tuvieron mayores valores de  $CE_G$  y  $DE_G$ , lo que sugiere una mayor contribución energética en hembras durante el ciclo reproductivo. Los índices, la densidad energética y el contenido energético de ciegos pilóricos y estómago no se vieron alterados entre los estadios. La densidad energética de ciegos pilóricos ( $ED_{PC}$ ) fue mayor en machos maduros que en hembras maduras. Asimismo, la densidad energética de estómago ( $ED_S$ ) fue globalmente mayor en machos que en hembras. Este patrón inverso entre sexos en relación a la  $DE_G$  podría sugerir una transferencia de energía desde los ciegos pilóricos y el estómago hacia las gónadas durante el estadio de madurez, actuando como reservorios energéticos para la reproducción.

**Palabras clave:** estrella de mar; índices corporales; energética; estadios gametogénicos; distribución de tallas oocitarias; biología reproductiva.

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