Biochemical composition during the reproductive cycle of a novel gastropod resource from Atlantic Patagonia

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Abstract. Marine gastropods are a popular seafood, abundant along coastal shores and healthy for human consumption. We studied variations in nutritional components during the gonadal cycle of *Tegula patagonica*, a novel gastropod resource protected by a recent artisanal fishery regulation. Similar to other marine gastropods consumed worldwide, *T. patagonica* was found to have a high protein content (mean ± s.d., 28.8 ± 15.4%) and a low lipid (1.36 ± 0.43%) and carbohydrate (1.7 ± 0.8%) content. The spawning peak was registered during spring and summer, concordant with increases in temperature and photoperiod, as observed for other gastropods from Atlantic Patagonia. According to our results, the optimal quality of *T. patagonica* for consumption is during the austral autumn, after the spawning season and when the gastropods have a high bodyweight and best nutritional contribution. Thus, this resource could be captured when its quality is optimal and its conservation promoted if established minimum catch sizes are respected.

Introduction

Marine invertebrate fisheries have grown in recent years, partly in response to declining finfish catches (Anderson *et al.* 2012; Food and Agriculture Organization of the United Nations 2017). Invertebrates are an alternative source of protein, and generate job opportunities in preharvesting (e.g. shipyards, fishing gear manufacturing), harvesting and post-harvesting (e.g. processing, marketing) activities in an expanding market (Berkes *et al.* 2006; Anderson *et al.* 2012; Macho *et al.* 2013). However, although there are management and regulation processes in place for finfish fisheries and some more established invertebrate fisheries, most invertebrate resources have not received the same level of attention (Hilborn *et al.* 2005; Anderson *et al.* 2008). For example, in Argentina, biological studies of edible marine gastropods related to fisheries parameters were very useful in creating the first regulation of gastropod catches by the Secretary of Fisheries of Chubut Province in 2018 (Cumplido and Bigatti 2020).

Marine gastropods are a desirable seafood with healthy properties in the human diet, such as a high protein and carbohydrate content and essential polyunsaturated fatty acids (Manzano and Aranda 1998; Bigatti *et al.* 2018; Nieto-Vilela *et al.* 2019).

In Argentina, studies regarding the nutritional composition of marine gastropods are lacking for several species, even though they are widely consumed along the southwestern Atlantic coast (Bigatti *et al.* 2015; Cumplido *et al.* 2020). Over the 10 past years, Argentinean official records of marine gastropods landings have registered between 35 and 65 tonnes (Mg) of 'sea snail' resource (www.agroindustria.com.ar). In Atlantic Patagonia, marine gastropods are locally exploited and commercialised by artisanal fishermen (Bigatti and Ciocco 2008), with some intermittent exports registered in recent years without a consolidated market or official catch records (Bigatti *et al.* 2015; Nieto-Vilela *et al.* 2019).

Tegula patagonica (d'Orbigny, 1835) is a trochid gastropod endemic along the Atlantic Patagonian coast. This abundant species lives in low intertidal and shallow waters along rocky shores from Rio de Janeiro in Brazil to Tierra del Fuego in Argentina (Pastorino 1994; Aguirre *et al.* 2013; Miloslavich *et al.* 2013). *T. patagonica* is a broadcast spawner, but, to date, there is no information regarding its reproductive cycle, which is necessary for fisheries management (Underwood 1979; Bigatti *et al.* 2008; Zabala *et al.* 2013; Nieto-Vilela *et al.* 2019). The density of *T. patagonica* is greater along subtidal rocky shores than in the intertidal of Nuevo Gulf of North Patagonia. Penchaszadeh (1971) reported a density of 109 individuals m^{-2} in subtidal areas. Whereas the contribution in the intertidal area is ~6.6% during low tide, with absolute absence in the high and middle level tide (Rechimont *et al.* 2013). In Argentina, *T. patagonica* is a new resource with considerable artisanal fishing potential because of its high abundance along the Patagonian Atlantic coast, the low total fatty acid content in its edible tissues and its differential accumulation of toxic substances (e.g. trace metals, harmful algae; Bigatti *et al.* 2015, 2018). However, this species is still not consumed or captured in Argentina, although Chile registered artisanal catches of *Tegula* sp. resources of 31 and 20 Mg in 2018 and 2019 respectively (Servicio Nacional de Pesca y Acuicultura, see http://www.sernapesca.cl/, accessed 10 March 2020). Conversely, preliminary aquaculture trials were successful (Nieto-Vilela 2014), enhancing its culture potential.

The aim of this study was to document, for the first time, the reproductive cycle and seasonal variation in the biochemical composition of the novel gastropod resource *T. patagonica* from North Patagonia (Argentina). This study contributes to efforts to implement regulatory policies for marine gastropod fisheries in northern Patagonia (Zabala *et al.* 2013; Bigatti *et al.* 2018; Nieto-Vilela *et al.* 2019; Cumplido and Bigatti 2020; Cumplido *et al.* 2020). The results from this study regarding *T. patagonica* as a novel coastal resource can be used to strengthen the management policies recently enacted by government authorities.

Material and methods

Sampling

Forty *T. patagonica* specimens were collected manually monthly at low tide from January to December 2012 on the rocky intertidal shore of Punta Ninfas, Chubut (42°58′42″S, 64°18′33″W). Punta Ninfas is an open shore located 100 km from the city of Puerto Madryn. No individuals were collected during May, because the extreme weather conditions made it impossible to access the sampling site. The collected specimens were taken alive directly to the laboratory. Only snails greater than the size at maturity (based on gonad analysis; shell height 1.14 cm in females and 1.07 cm in males, following Nieto-Vilela 2014) were analysed in this study. Each month, 10 of the snails collected were used to evaluate the gonadal cycle, whereas the remaining 30 snails were used in biochemical analyses. The height and length of the sampled individuals were measured using callipers to the nearest 0.1 mm and recorded; similarly, total weight and wet bodyweight were measured using a digital balance (precision ±0.001 g) and recorded. Sex was determined on the basis of fresh gonadal *frotis* (histological smears of the gonads: male and female) under an optical microscope and related to gonad colour and confirmed with histological slides (See 'Gonadal cycle' section).

Environmental variables

During 2012, monthly mean values were recorded for five environmental variables potentially related to the lifecycle of the snails, namely sea surface temperature (SST), wind speed, salinity, chlorophyll (Chl)-*a* and photoperiod. The monthly mean for each variable was obtained from the GES-DISC Interactive Online Visualisation and Analysis Infrastructure (GIOVANNI) made available by NASA's Goddard Earth Sciences Data and Information Services Center (http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.swf8D.shtml).

Gonadal cycle

For each month, 10 individuals that had been collected were fixed in Bouin's fluid for 48 h and then stored in 70% (v/v) aqueous ethanol until they were used to determine the stage of the gonadal cycle following standard histological procedures as described previously (Ramón and Amor 2002; Horn *et al.* 2005). To study monthly gonad development and to measure oocyte diameter, the gonads were first embedded in paraffin, sectioned at 5–7 μm with a digital microtome (Leica), heated for 24 h at 60°C and then finally stained with haematoxylin and eosin (Gabe 1968). Histological slides were observed and photographed under a Zeiss Axiostar light microscope. Monthly size–frequency histograms were used to evaluate oocyte diameter using only gametes with a visible nucleolus, which ensures that the histological slide is taken through the middle, because the oocyte has a spherical shape ($n = 50$ oocytes). For both sexes, individuals were assigned to a gonadal stage. To facilitate understanding of the gonadal cycle, we divided it into four stages, namely developing, ripe, spawned and resorption (Table 1), with classification based on previous studies of Patagonian marine gastropods (Bigatti *et al.* 2008; Zabala *et al.* 2013; Nieto-Vilela *et al.* 2019).

Nutritional composition

Of the remaining 30 individuals sampled monthly, 15 were used in analyses of nutritional value and another 15 were used in ash determination. Considering that both sexes are collected altogether for consumption, these analyses were performed on pooled samples of males and females following the methodology of Nieto-Vilela *et al.* (2019). Snails were extracted from their shells to obtain total body mass, and each sample was then heated at 60°C to constant weight. Dried tissues were triturated to obtain a composite sample to determine a mean monthly value for the protein, lipid and carbohydrate content using colorimetry. Protein content was determined according to the method of Lowry *et al.* (1951) using bovine serum albumin as a standard; lipid content was determined according to the method of Zöllner and Kirsch (1962) using cholesterol as a standard; and the carbohydrate content was determined according to the method of Fraga (1956) using glucose as a standard. Measurements were made using a spectrophotometer, and the results are expressed as the percentage dry weight of tissues.

Table 1.   Gonadal cycle stages in *Tegula patagonica*
SC, spermatocytes

Stage	Females	Males
1. Developing	Gonads formed by tubules are supported by a germinal epithelium lying alongside (Fig. 1*a*). The oocytes attached to the wall proliferate inside the tubule. The basophilic oocytes (40–80 μm) are usually pyriform in shape. The oocytes also have a conspicuous external membrane and are found next to companion cells	The tubules are associated with multiple layers of spermatogonia (Fig. 1*e*). In this stage, the lumen of the tubules contains some empty space, along with some SC and spermatids
2. Ripe	Oocyte diameter increases (80–120 μm). There is a short distance between the mature acidophilic oocytes, producing rectangular shapes in the mature oocytes (120–140 μm; Fig. 2*b*)	Empty space in the tubules is at a minimum, while SC and spermatozoa are present (Fig. 2*f*)
3. Spawned	The tubule lumen is empty. Mature oocytes (≥140 μm) are attached to the lumen are very uncommon, while basophilic oocytes are more abundant (Fig. 2*c*). The lumen contains some atretic oocytes, and the trabeculae have become more enlarged	At this stage, spermatogonia are formed by two or three layers, whereas the spermatozoa become concentrated in the centre of the tubule (Fig. 2*g*). The epididymis is full of mature SC
4. Resorption	The oocytes have an irregular shape and size, and the follicle walls have became more conspicuous (Fig. 2*d*). Phagocytic-nutritive cells are present	The spermatozoa begin to withdraw from the tubules and become separated from each other while phagocytes are present in the centre of the tubules (Fig. 2h)

To determine total ash weight (AW), the soft bodies were placed in an oven at 60°C until the constant weight (CW) was reached. Then, samples were calcined in a muffle at 550°C for 12 h to obtain AW. The ash percentage was calculated by dividing AW by CW and then multiplying by 100.

Statistical analyses

The sex ratio was tested using the Chi-Square (χ^2) test; *t*-tests were used to evaluate the significance of differences in weight and length between males and females. Assumptions of normality and homogeneity were tested using the Shapiro–Wilk and Levene tests respectively. Generalised linear models (GLM) were used to analyse biochemical parameters (protein, lipid and carbohydrate percentages) in R (ver. 3.4.3, http://www.r-project.org). Assumptions of normality and homogeneity were tested as described above. Two-sided $P \leq 0.05$ was considered statistically significant. Models included the fixed effects of gonadal stage (spawning and non-spawning), seasons (summer, January–March; autumn, April–June; winter, July–September; and spring, October–December), and their interactions. The significance of differences in biochemical percentages between gonadal stages and seasons for *T. patagonica* was evaluated using analysis of variance (ANOVA), followed by Tukey's post hoc test. Finally, a general linear mixed model with Gaussian distribution analysis was used to describe the relationship between environmental factors and biochemical composition in R. In each case, biochemical values were log transformed to achieve homogeneity and normality assumptions. The dependent variable selected in each case was the biochemical value (protein, lipid and carbohydrate), whereas the predictor variables were the environmental factors of SST, wind speed, salinity, Chl-*a* and photoperiod. Collinear predictor variables were removed (Zuur *et al.* 2009) and the best model was determined using the Akaike information criterion (AIC) and the AIC corrected for small sample sizes (Akaike 1973; Hurvich and Tsai 1989). The process of examining several hypotheses simultaneously to identify the best set of models is called information theory (Grueber *et al.* 2011). The significance of each predictor variable and its relative importance were determined, as well as the adjusted R^2 and 95% confidence interval for the best-supported model (Grueber *et al.* 2011).

Results

In all, 330 *T. patagonica* were analysed: 171 females and 159 males. Throughout the study period, the sex ratio in the *T. patagonica* population of Punta Ninfas did not differ significantly from parity (1:1; $n = 330$; d.f. $= 1$, $P = 0.5$). There was also no significant difference in total weight (shell + soft tissues) between females and males, although the mean ($\pm$s.d.) bodyweight of females was significantly lower than that of males (0.6 ± 0.2 *v.* 0.8 ± 0.2 g respectively; $t = -5.4$; $P < 0.001$). During the autumn and winter, the bodyweight of males was higher than that of females. During spring, the bodyweight of females peaked and, during summer, the bodyweight of males and females was similar (Fig. 1). Finally, although the length of the shell did not differ between sexes, shell height was greater in males than females (mean $\pm$ s.d. 1.7 ± 0.3 *v.* 1.5 ± 0.3 cm respectively; $t = -3.4$; $P < 0.0007$).

Environmental variables

The MODIS Aqua satellite recorded an annual mean SST of 12.8°C (maximum 17.13°C, minimum 8.72°C) and an annual mean photoperiod of 13.0 h (maximum 16.3 h, minimum 10.06 h), with SST starting to increase in August and reaching a maximum (17°C) in January (Fig. 2). Throughout the year, SST and photoperiod values were higher in the summer and spring and lowest during winter and autumn. There was a tendency for wind speed and Chl-*a* to increase during autumn and decrease in spring and summer. Finally, salinity decreased during autumn and winter and increased to its highest value during spring.
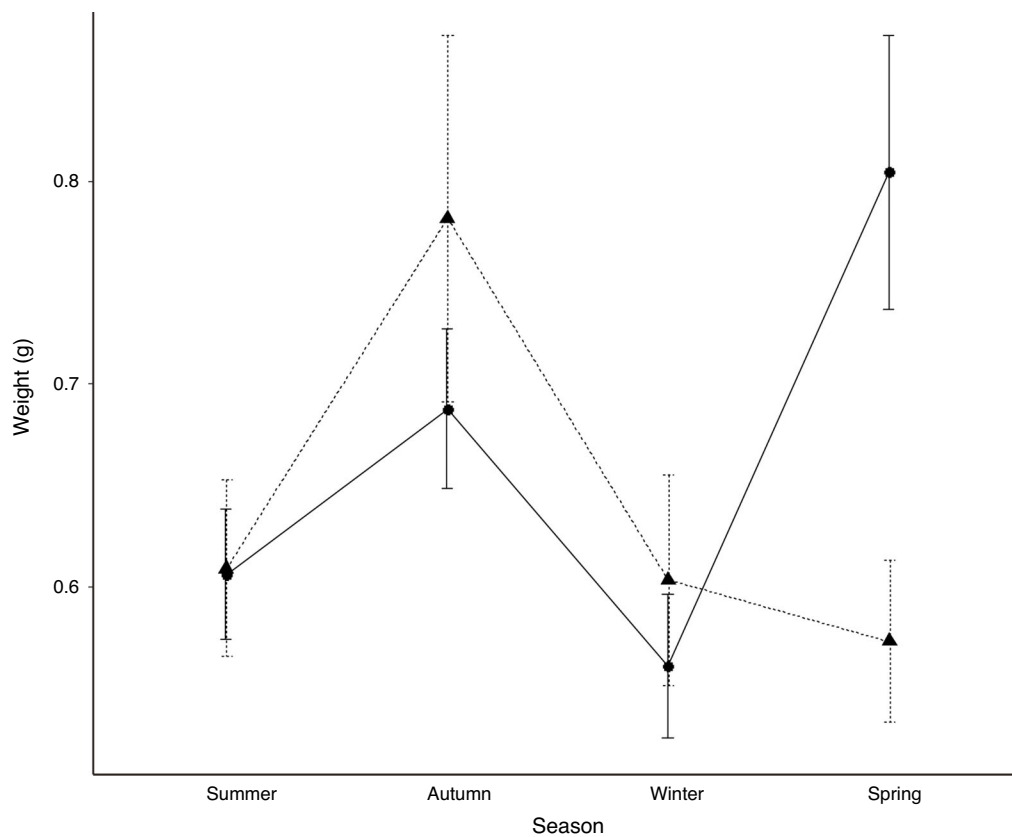
Fig. 1. Seasonal variations in soft body wet weight in females (circles) and males (triangles) of *Tegula patagonica* throughout 2012. Data are the mean ± s.d.

Gonadal cycle

The gonads exhibited a specific colouration pattern across the reproductive cycle in both sexes. In females, gonads were green during maturation and dark green in totally spawned specimens. Throughout the course of the year, different gonadal stages were present simultaneously (Fig. 3). Oocytes were spawned from April to November and during January, with high evacuation during October, November and January (Fig. 3). Resorption occurred all year round, primarily from June to December during and after the release of gametes. Females developed oocytes all year round, characterised by the presence of growing oogonia on the membrane trabeculae. As the developing phase advanced, the diameter of oocytes increased (Fig. 4). The ripe stage occurred from January to July, coinciding with the subsequent release of gametes. At this stage the nucleus and nucleolus of oocytes were visible and well developed (Fig. 4). The size of the oogonia and oocytes ranged from 9.05 μm in June to 166.11 μm in December (maximum recorded). Previtellogenic oocytes (<60 μm) were observed throughout the year. Mature oocytes (>140 μm) were present from April to January, coinciding with the spawning stage. Despite the observation of mature oocytes (>140 μm) ready to be released, a significant proportion were registered in the reabsorption stage, particularly from September to December. There was no correlation between oocyte size and any of the environmental variables analysed (Table 2).

In males, gonads were yellow upon maturing and in fully mature specimens and brown in individuals after gamete release. In contrast with females, males had fully active gonads and released gametes year round (Fig. 4, 5). In all cases, the spermatogenic tubules contained all cellular stages (spermatogonia, spermatocytes, spermatids and spermatozoa; Fig. 4). The release of mature spermatozoa was recorded during each month of sampling. After gamete release, the tubules remained almost empty. Resorption of gametes by nutritive phagocytes was observed (Fig. 4) from April to December (Fig. 5).

Nutritional composition

There were marked variations in the biochemical components analysed (protein, lipids and carbohydrates) throughout the reproductive cycle in *T. patagonica* (Fig. 6). The annual mean (±s.d.) content of proteins, lipids and carbohydrates was 28.8 ± 15.4% (range 2.9–78.5%), 1.36 ± 0.43% (range 0.7–2.3%) and 1.7 ± 0.8% (range 0.7–3.5%) respectively. The annual mean (±s.d.) ash content was 22.0 ± 5.3%. The pattern of variation in lipids and proteins was inverse to that of carbohydrates during the year (Fig. 6).

The protein content varied during the study period, with significantly higher values during autumn and winter than in summer (Fig. 6a). The lowest protein content was recorded in summer (mean ± s.d. 9.2 ± 5.4%, January) and the highest was recorded in late winter (mean ± s.d. 64.9 ± 14.9%, September).
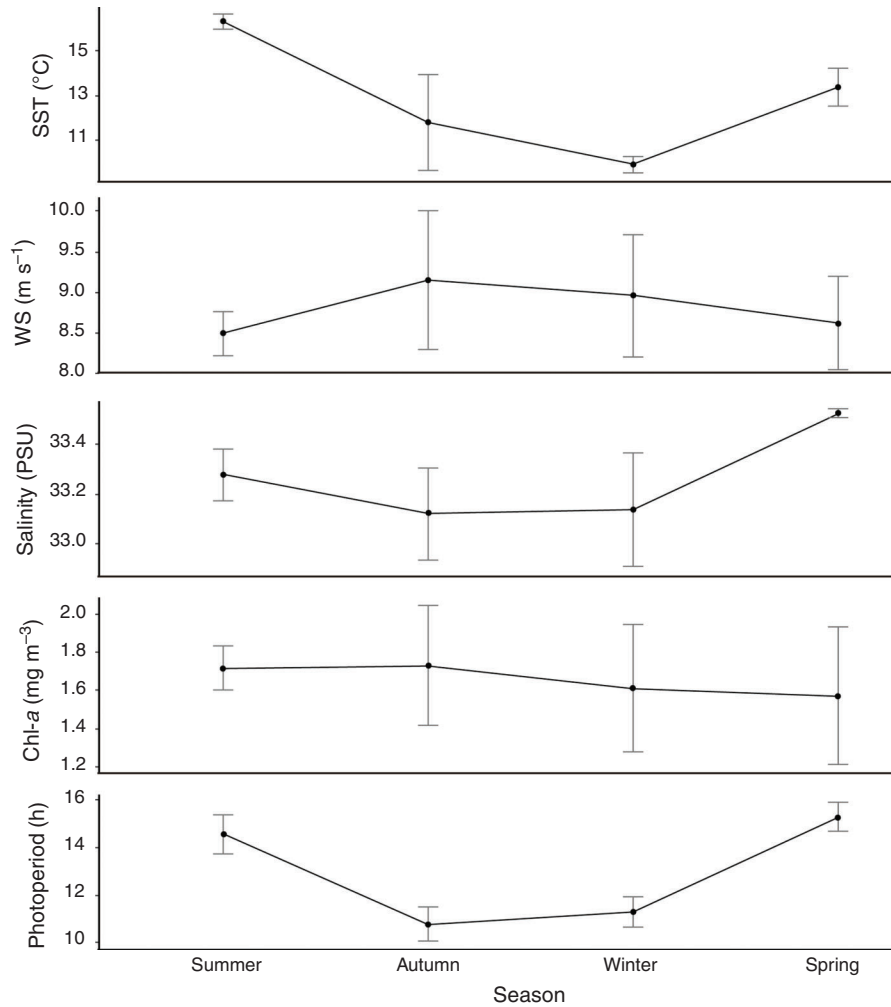
Fig. 2. Monthly mean (±s.d.) values for environmental variables based on remote sensor estimates and acquired from the GES-DISC Interactive Online Visualisation and Analysis Infrastructure (GIOVANNI), made available by NASA's GES Data and Information Services Center (http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.swf8D.shtml). SST, sea surface temperature; WS, wind speed.
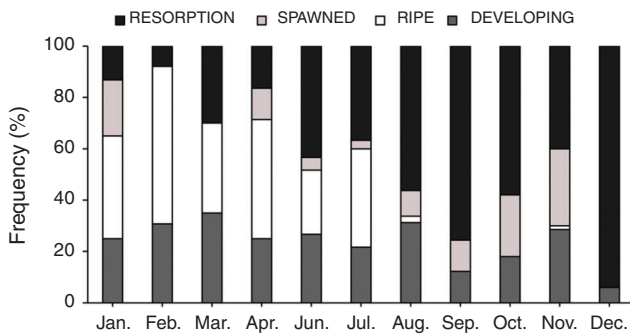

Fig. 3. Gonadal stages, as defined in Table 1, based on histological analysis of female *Tegula patagonica* collected monthly. Note, no individuals were collected in May because of extreme weather conditions that made it impossible to access the sampling site.

Multiple lineal regression analyses determined wind speed, salinity and photoperiod as predictor variables for total protein concentration. The effects of salinity and photoperiod on total protein concentration were significant ($F_{4,8} = 11$, $R^2 = 0.75$; $P = 0.001$ and $P = 0.002$ respectively), with salinity being the most important (Table 2). Lipid content was significantly higher during autumn and winter (Fig. 6b), with the highest lipid content found in autumn (mean ± s.d. 2.08 ± 0.21%, April) and the lowest in spring (mean ± s.d. 0.98 ± 0.05%, November). Photoperiod was a statistically significant predictor variable of total lipid content ($F_{4,8} = 6.9$, $R^2 = 0.37$, $P = 0.027$; Table 2). Carbohydrate contents was similar throughout the year (Fig. 6c), with a peak in summer (mean ± s.d. 3.4 ± 0.1%, March) and the lowest value in winter (mean ± s.d. 0.85 ± 0.08%, August). Although not statistically significant, SST, Chl-*a* and photoperiod were predictor variables of the total carbohydrate content ($F_{4,8} = 0.94$, $R^2 = 0.22$, $P > 0.05$), with the three variables having the same relative importance (Table 2).
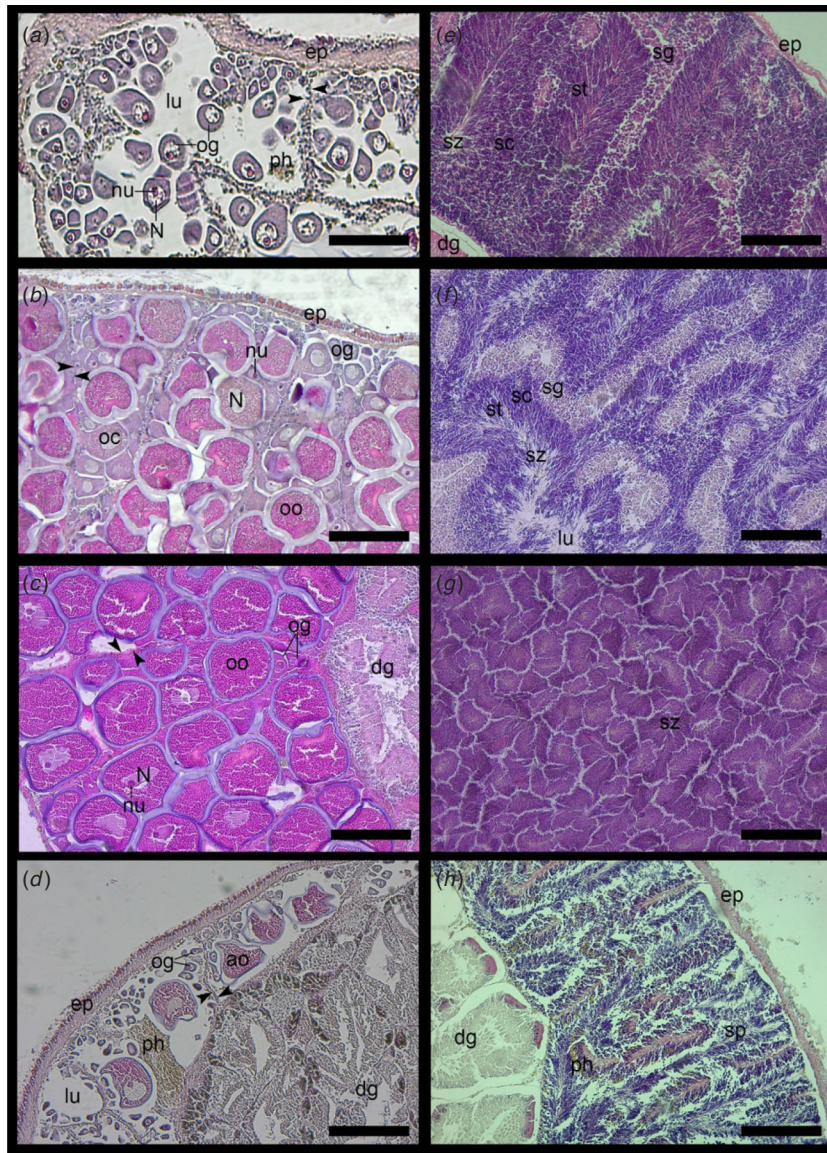
Fig. 4. Gonadal stages for (*a–d*) female and (*e–h*) male (right) *Tegula patagonica*. Developing; Ripe; Spawning; Resorption. ao, atretic oocytes; dg, digestive gland; ep, epithelium; lu, lumen; N, nucleus; nu, nucleolus; oc, primary oocyte; og, oogonia; Oo, oocytes, Ph, phagocytes; SC, spermatocytes; sg, spermatogonia; st, spermatids; sz, spermatozoa. Arrowheads indicate trabeculae. Scale bars: 100 μm (*a*, *b*, *e*); 120 μm (*c*, *h*, *f*); 150 μm (*d*, *g*).

Discussion

In this study, peak spawning of *T. patagonica* occurred during spring and summer, in accordance with increases in temperature and photoperiod, as has been reported for many Patagonian marine gastropods (Bigatti *et al.* 2008; Penchaszadeh *et al.* 2009; Averbuj *et al.* 2010; Cumplido *et al.* 2020). The biochemical composition of *T. patagonica* reported in this study is within the range of marine gastropods consumed worldwide (see Table S1 of the Supplementary material) and varied throughout the year, as did the gonadal cycle.

Despite the lower soft bodyweight in females, the total bodyweight of both sexes was similar, and this is probably related to the greater length, denoting a heavier shell, in males.

The low soft bodyweight recorded for both sexes during the winter could be related to the spawning and resorption period, as occurs in other marine gastropods from the region (e.g. *Buccinanops cochlidium* and *Odontocymbiola magellanica*; Bigatti *et al.* 2008; Averbuj *et al.* 2010). However, some authors have reported a linear relationship between bodyweight and food supply (Eisenberg 1970; Calow 1975; Underwood 1984), so the increase in bodyweight during the spring and summer could be due to an increase in the availability of food.

The gonadal cycle described in this study for *T. patagonica* coincides with cycles for other species of *Tegula* described for the Northern Hemisphere, in spawning events are related to seasonal temperature. For example, Vélez-Arellano *et al.* (2009)

Table 2.   Summary results for the best model selected: effects of each variable on the biochemical composition of *Tegula patagonica*
CI, confidence interval

Dependent variable	Predictor variable	Adjusted s.e.	95% CI	Relative importance
Protein content	Intercept	16.64538	−123.391, −44.671	−
	Wind speed	0.11168	−0.123, 0.405	0.05
	Salinity	0.49851	1.506, 3.863	0.6
	Photoperiod	0.05259	−0.373, −0.125	0.35
Lipid content	Intercept	0.44485	0.40966, 2.422287	−
	Photoperiod	0.03329	−0.16283, −0.01222	1
Carbohydrate content	Intercept	30.96071	−11.2345, 13.30601	−
	Chlorophyll-*a*	0.36166	−0.33091, 1.130957	0.329
	Photoperiod	0.13561	−0.25652, 0.119917	0.331
	SST	0.08204	−1.41514, 0.980883	0.33
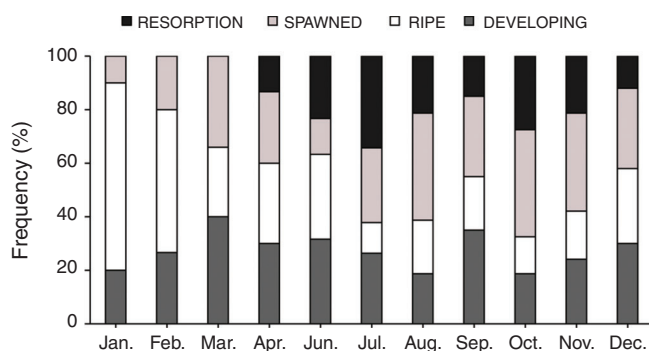
Fig. 5.   Gonadal stages, as defined in Table 1, based on histological analysis of male *Tegula patagonica* collected monthly. Note, no individuals were collected in May because of extreme weather conditions that made it impossible to access the sampling site.

described two spawning events for *Tegula eiseni* over the course of a year in Mexico, one in spring and the second in autumn. In the same area in Mexico, Vélez-Arellano *et al.* (2011) described a slightly different cycle for *Tegula aureotincta*, with two spawning events, one during autumn–winter and one in spring. Previous experimental studies in Chile described the start of the spawning period of *Tegula euryomphala* with an increase in water temperature (Romero Bastías 2014). Positive relationships between both photoperiod and water temperature and the development and release of oocytes has been described for many gastropods that inhabit the southern hemisphere (Bigatti *et al.* 2008; Penchaszadeh *et al.* 2009; Averbuj *et al.* 2010). Nevertheless, the absence of relationships between oocyte size and the environmental variables evaluated in this study raises questions as to the effects of environmental variables on the gonadal cycle of Patagonian gastropods.

The size of mature oocytes of *T. patagonica* (>140 μm) was similar to that reported in other congeners. For example, in Mexico, Ortíz-Ordoñez *et al.* (2009) reported that the diameter of mature oocytes in *T. eiseni*, *Tegula funebralis*, *T. aureotincta*, *Tegula gallina* and *Tegula regina* was 165 μm. In Pacific Patagonia, Moran (1997) reported that the diameter of mature oocytes was 160–165 μm in *T. funebralis*, whereas Kulikova and
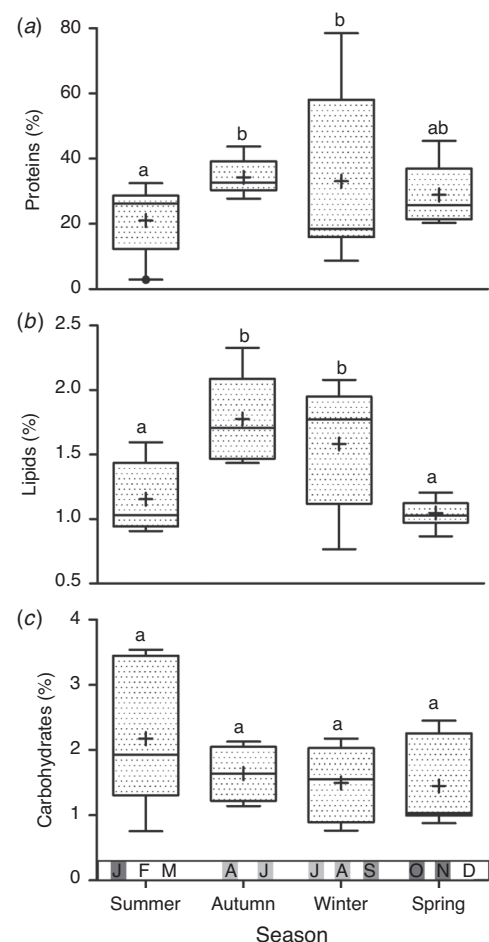
Fig. 6.   Biochemical composition of *Tegula patagonica* during the reproductive cycle. (*a*) Protein, (*b*) lipid and (*c*) carbohydrate content in different months and seasons. The boxes show the interquartile range, with the median value indicated by the horizontal line; crosses indicate mean values and whiskers show the 10th–90th percentiles. Dots indicate outliers. The female spawning season is indicated along the *x*-axis by grey shading, with darker shading indicating months with greater gamete release. Different letters indicate significant differences between seasonal means ($P < 0.05$, Tukey's test).

Omel'yanenko (2000) reported that the diameter of mature oocytes under experimental conditions in *T. rustica* was 145 μm. Oocyte size is useful for predicting larval life style, suggesting that species with small oocytes typically develop into planktotrophic larvae: *Tegula* species, as well as *Nacella* and *Patella* species, have high fecundity values with small oocyte sizes (diameter <180 μm), suggesting the production of planktonic larvae (Branch 1974; Morriconi 1999) for *T. patagonica.*

The biochemical composition of marine invertebrates is related to both internal conditions, such as the gonadal cycle, and external conditions, such as food supply (Ruiz *et al.* 1992). Protein content varies through the year associated with alimentation and metabolism (Najmudeen 2007); despite being the major structural material of cells, protein also serves as an energy reserve for costly process such as reproduction (Barber and Blake 1981; Mao *et al.* 2006). The high protein content of *T. patagonica* during winter could be related to the high abundance of algae (Teso *et al.* 2009) and phytoplankton in the regions during September and October (D'Agostino *et al.* 2018). In Nuevo Gulf (northern Patagonia), the seasonal distribution of phytoplankton is characterised by two peaks, one from March to May and the another higher peak from August to October (Gayoso and Fulco 2006; D'Agostino *et al.* 2018); this could explain the increase in the protein of *T. patagonica.*

Lipids are involved in the formation of gametes; therefore, an increase in the proportion of these compounds in the body is usually related to the period of gametogenesis (Manzano and Aranda 1998). Variations in lipid content have been found in bivalves during gamete development, with highest levels recorded during periods of maximum ripeness and the lowest levels recorded during periods of spawning (Barber and Blake 1981; Dridi *et al.* 2007; Acarli *et al.* 2015). Nevertheless, in *T. patagonica*, the lipid content was higher during the developing, ripe and resorption stages (during autumn and winter), coinciding with changes in lipid content found in *Nacella magellanica* in the same region (Nieto-Vilela *et al.* 2019). Possible reasons for difference in lipid content in *T. patagonica* are food intake during the summer and the occurrence of gametogenesis at that time, as found in other gastropods in the region (Cumplido *et al.* 2020). Conversely, an increase in the photoperiod could induce female gastropod spawning in Atlantic Patagonia (Bigatti and Ciocco 2008) and could thus be regulating the total lipid content, as we observed.

The lower carbohydrate content in *T. patagonica* during winter could be associated with the use of carbohydrates (Ren *et al.* 2003), given that they are the primary energy store in molluscs (Barber and Blake 1981; Carrasco *et al.* 2006) In addition, the decrease in the carbohydrate content from autumn to spring could be due to a transformation of carbohydrates to lipids to meet reproductive demands (Acarli *et al.* 2015).

Finally, *T. patagonica* was found to have a high ash content (22 ± 5.3%) compared with other marine gastropods widely consumed worldwide, such as *Haliotis varia*, which has been reported to have an ash content of 6.02–6.84% for females and 6.22–7.82% for males (Najmudeen 2007). Nevertheless, the ash content percentage of *T. patagonica* is similar to that of *Nacella magellanica* (mean ± s.d. 25 ± 2%), another Patagonian herbivorous snail (Nieto-Vilela *et al.* 2019). The high ash content of *T. patagonica* could be explained by the abundance

of inorganic sediment particles within their digestive system because they are benthic grazers.

To develop a sustainable fishery for a new resource it is necessary to perform biological studies of the species (Underwood 1979; Perry *et al.* 1999; Cumplido and Bigatti 2020). Considering the current scarcity of information on the biology of *T. patagonica*, this study makes a useful contribution to the knowledge of its reproductive cycle and biochemical composition in Atlantic Patagonia. The results reported here can be used to enhance and expand current efforts to protect and conscientiously exploit this new fishery resource. Taking into account the nutritional components and their contribution to the human diet, *T. patagonica* should be captured in the austral autumn when the species has a high protein content, high bodyweight and low lipid levels. This coincides with the recent official regulation that banned the capture of marine gastropods during the spawning period in winter–spring and adds to the conservation of this valuable marine resource, which could generate employment and be a new food source for healthy human nutrition.

Data availability

The data that support this study will be shared from the corresponding author upon request.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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