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ORIGINAL RESEARCH

Energy allocation strategy during the reproductive cycle of Patagonian grouper (*Acanthistius patachonicus*) from the southwestern Atlantic Ocean

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ABSTRACT. The term 'condition' is used to describe the overall health status of an animal and to describe its energy reserves. The storage and use of energy reserves are fundamental components of a species' life strategy, and these processes directly influence the balance between current and future reproductive success. Understanding the energy allocation strategy adopted by a species is an important aspect in assessing possible variations in reproductive potential. The aim of this work was to analyse the seasonal variations of condition indices, biochemical composition, and energy density of different tissues in order to determine the strategy of energy allocation during the reproductive cycle of females *Acanthistius patachonicus*. Mature females were collected between April 2016 and March 2017 from commercial landings. Biochemical components such as lipids, proteins, and water content were measured in liver, gonad and muscle. The gonadosomatic index was highest during winter, at the beginning of the reproductive period, while the hepatosomatic index and condition factor did not differ among seasons. The study of the proximal composition of tissues revealed that the liver was the primary source of energy reserves. Highest values of these reserves in the liver were found before the onset of gonadal maturation (autumn). As the reproductive period progresses (winter and spring), these energy reserves decreased significantly, suggesting they were mobilized to support reproductive processes. This suggests that *A. patachonicus* primarily adopts a capital breeding strategy, but females possibly incorporate energy by feeding during the spawning period.

Key words: Condition factors, proximal composition, reproductive biology, energetic strategies.

Estrategia de asignación de energía durante el ciclo reproductivo del mero patagónico (*Acanthistius patachonicus*) del Océano Atlántico Sudoccidental

RESUMEN. El término "condición" se utiliza para describir el estado general de salud de un animal y sus reservas energéticas. El almacenamiento y uso de las reservas energéticas son componentes fundamentales de la estrategia vital de una especie, y estos procesos influyen directamente en el equilibrio entre el éxito reproductivo actual y futuro. Comprender la estrategia de asignación energética adoptada por una especie es un aspecto importante para evaluar las posibles variaciones en el potencial reproductivo. El objetivo de este trabajo fue analizar las variaciones estacionales de los índices de condición, la composición bioquímica y la densidad energética de diferentes tejidos para determinar la estrategia de utilización energética durante el ciclo reproductivo de las hembras de *Acanthistius patachonicus.* Se recolectaron hembras maduras entre abril de 2016 y marzo de 2017 en desembarques comerciales. Se midieron componentes bioquímicos como lípidos, proteínas, y contenido de agua en el hígado, las gónadas y el músculo. El índice gonadosomático alcanzó su máximo

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durante el invierno, al inicio del período reproductivo, mientras que el índice hepatosomático y el factor de condición no difirieron entre estaciones. El estudio de la composición proximal de los tejidos reveló que el hígado era la principal fuente de reservas energéticas. Los valores más altos de estas reservas en el hígado se observaron antes del inicio de la maduración gonadal (otoño). A medida que avanza el período reproductivo (invierno y primavera), estas reservas energéticas disminuyen significativamente, lo que sugiere que se movilizaron para apoyar los procesos reproductivos. Esto sugiere que *A. patachonicus* adopta principalmente una estrategia de reproducción de capital, pero las hembras posiblemente incorporen energía alimentándose durante el período de desove.

Palabras clave: Factor de condición, composición proximal, biología reproductiva, estrategias energéticas.

INTRODUCTION

Seasonal variations in temperature and productivity, characteristic of temperate environments (Clarke 1983), have a profound effect on the availability and quality of food for fish (Wotton 1990; Beamish and Bouillon 1995). The energy incorporated by organisms must be distributed between maintenance, somatic growth and reproduction (Calow 1985; Sibly and Calow 1986). This allocation varies across life stages to optimise egg production. Some species require efficient energy storage well before the spawning season. This strategy is crucial when reproduction occurs under unfavourable conditions, such as limited availability of food and temperature variability, among other factors (Pavlov et al. 2009). The stored energy can later be mobilised for reproduction, making it the main resource for egg production (Stephens et al. 2009). This strategy also enables a temporal and spatial separation between feeding and spawning grounds, allowing adults to accumulate energy in one location and time for use in another (MacKinnon 1972; Reznick and Braun 1987; Jönsson 1997). Species that follow this strategy are known as capital breeders and are typically found at high latitudes and in cold-water environments characterised by marked seasonality and short spawning periods (Saborido-Rey et al. 2010). Conversely, income breeders reproduce under more favourable conditions in productive environments, using recently acquired energy for egg production and reducing the need for energy storage (Stephens et al. 2009). This strategy creates a closer spatial and temporal coupling between energy intake and reproduction (Aristizabal 2007). Income breeders are characteristic of low-latitude regions (tropical and subtropical zones), often exhibiting extended spawning seasons. In these species, spawning may depend on daily foraging success by adults. However, reproductive strategies may not always fall strictly into the categories of capital or income breeding. Instead, a continuum likely exists, with species exhibiting intermediate strategies along this spectrum (McBride et al. 2015).

The term ‘condition’ is commonly employed to denote the overall health status of an animal, and more frequently, to describe the stored nutrient or energy reserves (Schulte-Hostedde et al. 2005). This parameter has been correlated with changes in the energy density of various organs (Jobling 1995; Lucas 1996). Maternal characteristics and condition have an impact on fish maturity (Marteinsdottir and Begg 2002; Morgan and Lilly 2006; Grift et al. 2007) and egg production (Kjesbu et al. 1991; Rijnsdorp et al. 1991; Lambert and Dutil 2000; Marshall et al. 2006). Notably, the condition of parent organisms plays a significant role in determining the viability of offspring (Brooks et al. 1997; Heyer et al. 2001; Berkeley et al. 2004). The evaluation of fish condition comprises a spectrum of criteria, ranging from simple morphometric measures such as the length-weight ratio (K factor) to morpho-physiological indicators such as hepatosomatic and gonadosomatic indices (Schulte-Hostedde et al. 2005). Additionally, biochemical measures, including proximate composition analysis covering lipids, proteins and other tissues constituents provide valuable insights. It is widely accepted that the form, storage and utilisation of energy reserves are fundamental components of the life strategy of a species. These processes directly influence the balance between current and future reproductive success (Stearns 1992; Roff 1993). Consequently, understanding the energy allocation strategy adopted by a species or population emerges as a critical aspect for interpreting possible variations in reproductive potential.

The Patagonian grouper (*Acanthistius patachonicus*) is a demersal rocky-reef fish inhabiting coastal waters of the southwest Atlantic (23° S-48° S), at depths of up to 100 m. This species is known for its longevity and can reach a maximum total length of approximately 65 cm. It is considered a multiple spawner with indeterminate annual fecundity and is characterized by the formation of reproductive aggregations between September and December (Ciechomski and Cassia 1976; Dell'Arciprete et al. 1987; Irigoyen et al. 2020). The number of annual spawning events is likely influenced by environmental factors such as food availability and temperature (Wotton 1990). In northern Patagonia, *A. patachonicus* is a target species supporting commercial, recreational, and sporting activities, including scuba diving, hook-and-line and spearfishing. It is also caught by both coastal and high-seas fleets, as well as bycatch in fisheries targeting Argentine hake (*Merluccius hubbsi*) and Argentine red shrimp (*Pleoticus muelleri*) (Villanueva Gomila et al. 2015).

At present, it is unknown whether this species stores energy in the period prior to the onset of reproductive activity ('capital breeding') or whether it has the capacity to acquire energy through active feeding during reproduction ('income breeding'). Therefore, the aim of the present study was to analyse variations in condition, proximal composition, and energy density throughout the annual cycle of *A. patachonicus*. This investigation aimed to elucidate the strategy of accumulation and energy allocation of this species in relation to sexual maturity and spawning.

MATERIALS AND METHODS

A total of 37 female specimens of *A. patachonicus* were obtained from commercial landings at the Necochea port (38° 34′ S, 58° 42′ W) from April 2016 to March 2017 (Table 1). To minimise possible size-dependent variations in the biochemical composition of females, only mature specimens within a specific length range (35-45 cm TL) were used to analyse seasonal patterns.

Total length (TL) was recorded to the nearest cm and total weight (TW), gutted weight (GuW), gonad weight (GW) and liver weight (LW) were recorded to the nearest gram. Maturity phases were determined through macroscopic examination following the criteria established by Macchi and Acha (1998) for coastal species, and the general description provided by Brown-Peterson et al. (2011) as developing, spawning capable, regressing, and regenerating. To further characterise the specimens, three condition indices were estimated across all samples: gonadosomatic index (GSI), hepatosomatic index (HSI), and relative condition factor (Kn), which were calculated using the following equations:

$$GSI = (GW/GuW) \times 100$$

$$HIS = (LW/GuW) \times 100$$

$$Kn = (GuW/(0.0328 \times TL^{2.7861})) \times 100$$

The Kn is expressed as the ratio of the observed GuW to the GuW determined by the relationship between TL and GuW of the fish sampled (Le Cren 1951).

To establish the proximal composition of tissues of the Patagonian grouper, samples of liver, gonads and muscle (skinless fillet) were carefully taken from all specimens and immediately feezed in plastic bags. Samples were then first homogenised, and biochemical components (water, protein, and lipid)

Table 1. Mean values and standard error of morphometric variables of *Acanthistius patachonicus* by season. N: Number of specimens. TL: total length. GuE: gutted weight. LW: liver weight. GW: gonad weight.

Season	N	TL (cm)	GuW(g)	LW(g)	GW(g)
Spring	13	39.7 ± 2.9	896.7 ± 250.9	19.6 ± 10.1	34.91 ± 23.8
Summer	5	37.33 ± 2.08	779.7 ± 86.8	14.93 ± 3.7	9.41 ± 3.5
Autumn	7	39.9 ± 3.18	975.6 ± 249.2	11.35 ± 2.61	12.24 ± 5.89
Winter	12	39.9 ± 3.12	997.08 ± 202.1	17.89 ± 6.79	91.1 ± 50.62

were systematically determined. To measure lipid content, 1 g was taken from each tissue. Lipids were extracted using the method of Bligh and Dyer (1959) modified by Undeland et al. (1998), and quantified gravimetrically following the procedure outlined by Herbes and Allen (1983). Protein content was determined from frozen tissues (2 g) using bovine serum albumin (BSA) concentrated at 1 mg ml^{-1} as standard. The protocol established by Lowry et al. (1951) was followed for protein quantification. For the determination of water content, subsamples of varying sizes were taken depending on the tissue: liver (2 g), gonads (2 g), and muscle (2 to 5 g). Samples were dried at 105 °C for 24 h before being weighed at ambient temperature. All determinations were expressed as g 100 g^{-1} wet tissue.

Finally, the energy density (ED, KJ g^{-1}) of the analysed tissue was determined as follows:

$$ED = \frac{L \times L' + P \times P'}{100}$$

Energy equivalents for lipids (L) L': 39.5 KJ g^{-1}, and proteins (P) P': 23.6 KJ g^{-1} were used (Brett and Groves 1979).

Relationships between condition indices, biochemical compositions and energy density obtained from each season were examined using an analysis of variance (ANOVA). Homogeneity of variance and normality were previously assayed using Levene's and Shapiro-Wilk's tests, respectively. Despite the limited sample size, both assumptions were met. In cases of significant differences, Tukey's test was used. All statistical analyses were conducted using the R statistical programme (version 3.6.1) (R Core Team 2023).

RESULTS

Condition indices and maturity stages

Of the condition indices analysed, only the GSI showed significant differences between seasons ($F = 13.53$, $p < 0.001$) (Figure 1). Notably, when maturity stages of *A. patachonicus* were grouped by season (Figure 2), the mean GSI was highest in winter (9.12), coinciding with the period prior to the onset of reproduction. In contrast, the GSI showed a decrease in spring (3.80) due to increased spawning activity. Subsequently, GSI values were significantly lower during summer and autumn (1.18 and 1.33, respectively), coinciding with the highest proportions of females in the regenerating stage (Figure 2). Although the HSI showed no significant differences between seasons, highest values of this index were observed in spring, during spawning activity (Figure 1).

Lipids seasonal variation

No significant differences were observed in the lipid content of muscle between seasons, with a

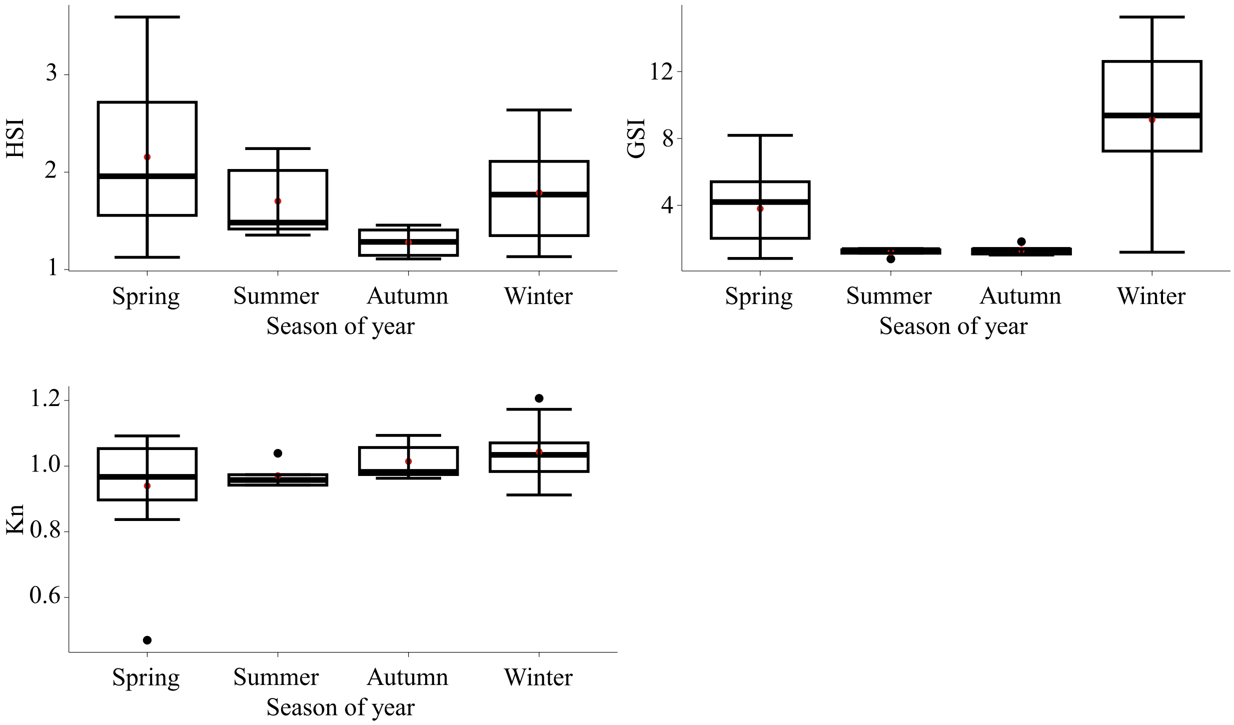

Figure 1. Boxplot showing the seasonal variation of hepatosomatic index (HIS), gonadosomatic index (GSI) and relative condition factor (Kn) of *Acanthistius patachonicus*. Each box shows the range between the first and third quartiles (Q1-Q3). Horizontal line inside the box indicates the median. Red circles define the mean values. Black circles represent outliers.

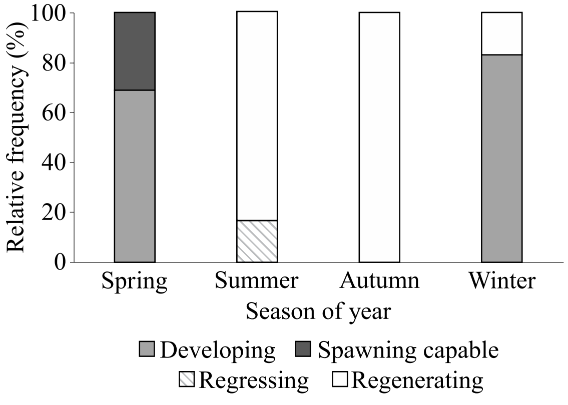

Figure 2. Seasonal evolution of gonad stage proportions in mature females *Acanthistius patachonicus*.

consistent mean value of 1.45 g 100 g^{-1}. Compared to other tissues, muscle always had the lowest values. Notably, significant differences in lipid content between seasons were found in gonads and liver, showing opposite patterns (Table 2; Figure 3). Highest values were observed in the gonads immediately before and during the reproductive season (6.7 g 100 g^{-1} in winter and 5.2 g 100 g^{-1} in spring), while liver lipid content were higher during gonadal regeneration (11.35 g 100 g^{-1} in summer and 15.9 g 100 g^{-1} in autumn).

Proteins seasonal variation

Protein content in muscle and liver did not differ significantly between seasons, with mean values of 19.06 g 100 g^{-1} and 16.5 g 100 g^{-1}, respectively (Table 2; Figure 4). Protein levels were elevated in the gonads before and during the reproductive season (winter-spring), but decreased during the resting stage (summer-autumn). However, statistical significance was only observed for winter, where the gonadal protein content was significantly higher

Table 2. ANOVA results of seasonal changes of all biochemical components and energy density in the tissues of *Acanthistius patachonicus*.

	Muscle		Gonad		Liver	
	F	p	F	p	F	p
Lipids	0.809	0.498	22.45	< 0.0010	8.099	< 0.001
Proteins	1.246	0.31	6.35	0.0016	2.703	0.061
Water	3.116	0.0402	4.584	0.0086	8.934	< 0.001
Energy density	0.325	0.814	15.87	< 0.0010	8.519	< 0.001

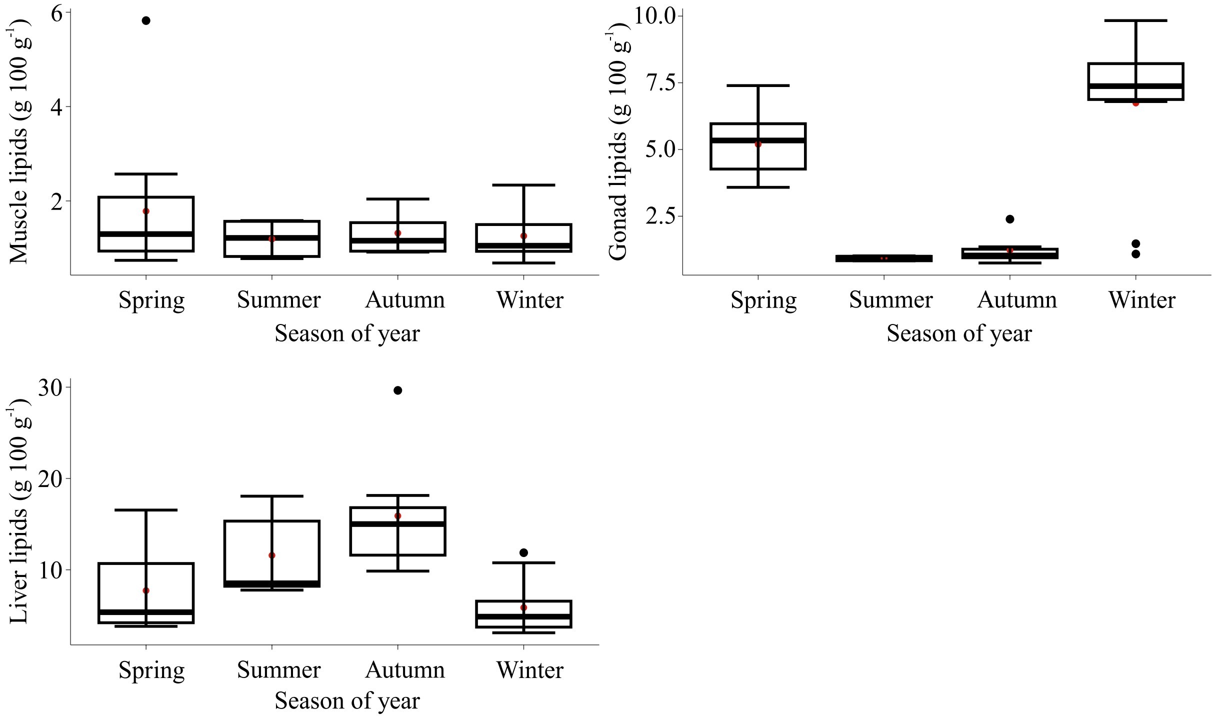

Figure 3. Boxplot showing the seasonal variation of lipids content of muscle, gonad and liver of *Acanthistius patachonicus*. Each box shows the range between the first and third quartiles (Q1-Q3). Horizontal line inside the box indicates the median. Red circles define the mean values. Black circles are outliers.

than that recorded in autumn and summer (Table 2; Figure 4).

Water content seasonal variation

The water content of the three tissues analysed showed seasonal variation (Table 2; Figure 5). During the predominance of the resting stage (autumn) and immediately before the spawning season (winter), significant differences in water content values were observed in both muscle and gonad. The gonad had the highest water content in autumn, while

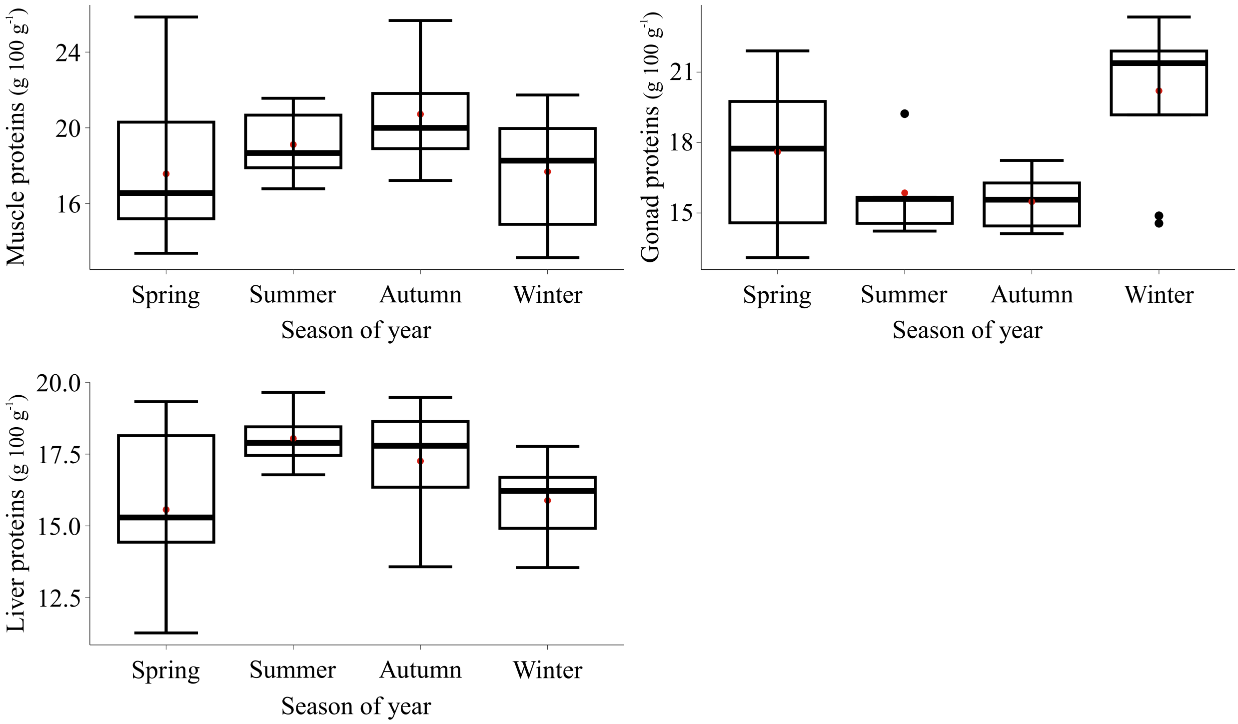

Figure 4. Boxplot showing the seasonal variation in protein content of muscle, gonad and liver tissues of *Acanthistius patachonicus*. Each box shows the range between the first and third quartiles (Q1-Q3). Horizontal line inside the box indicates the median. Red circles define the mean values. Black circles are outliers.

the muscle had the lowest. Conversely, gonads had the lowest water content in winter, while the muscle had the highest. The liver had the highest water content in winter and spring (74.1 and 72.3, respectively), and the lowest in autumn and summer (66.65 and 64.6, respectively).

Energy density seasonal variation

No significant differences between seasons were observed in the mean energy density estimated for muscle, with values around 4.81 KJ g^{-1} (Table 2; Figure 6). The energy density of gonads decreased significantly during the resting period (4.13 KJ g^{-1} in autumn and 4.25 KJ g^{-1} in summer). In contrast, the liver showed the highest energy density during that period (10.35 KJ g^{-1} in autumn and 8.6 KJ g^{-1}, in summer), while the lowest values were observed during the reproductive activity.

DISCUSSION

The reproductive biology of the Patagonian grouper has been analysed during the last decades in various studies (Ciechomski and Cassia 1976; Dell'Arciprete et al. 1987; Militelli et al. 2013; López et al. 2015). However, the existing literature on energetic analysis is relatively scarce and outdated (Cabral and Kopatschek 1942; Moreno et al. 1982; Nielsen and Escribano 1997). Understanding the dynamics of endogenous energy use is crucial, and such insights can be partially understood by monitoring morphological indices such as the hepatosomatic index (HSI), the gonadosomatic index (GSI) and the relative condition factor (Kn) (Collins and Anderson 1995). These indices play a key role in assessing the

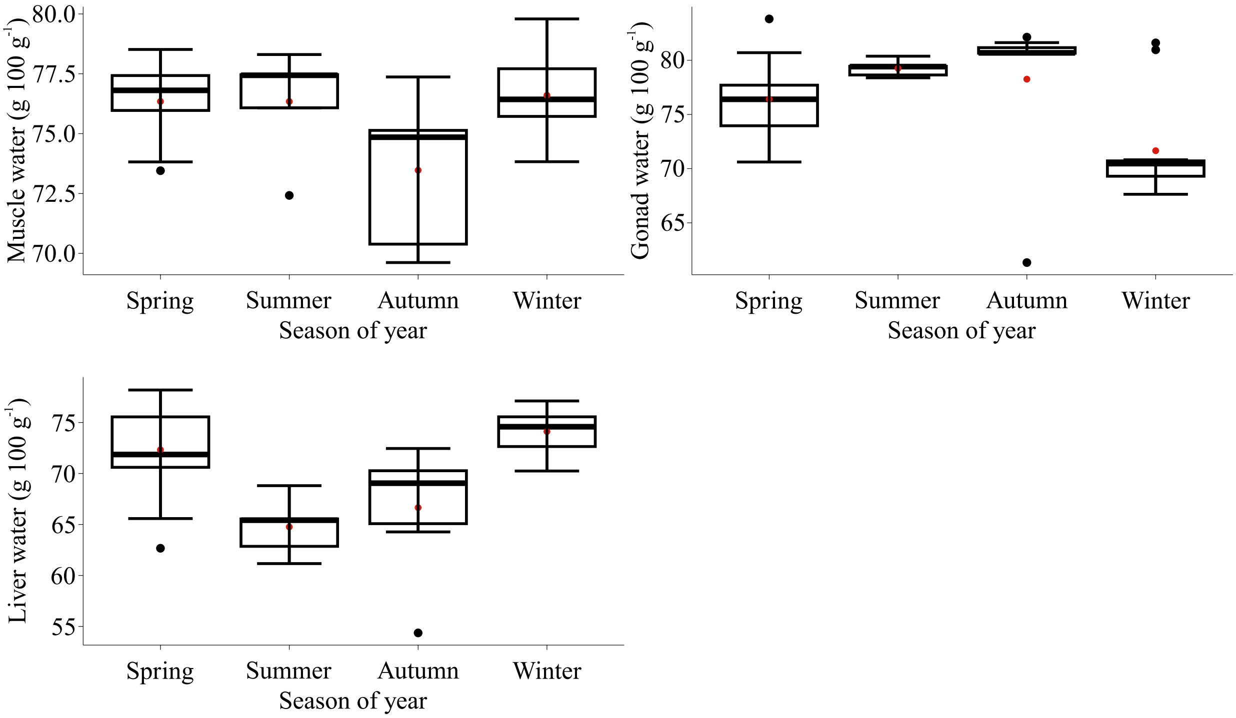

Figure 5. Boxplot showing the seasonal variation in water content of muscle, gonad and liver tissues of *Acanthistius patachonicus*. Each box shows the range between the first and third quartiles (Q1-Q3). Horizontal line inside the box indicates the median. Red circles define the mean values. Black circles are outliers.

reproductive potential of the stock, complementing the analysis of energy reserves and proximal composition of females (Domínguez Petit 2006). The temporal analysis carried out on samples of Patagonian grouper showed that the GSI was the only index that varied significantly between seasons, reaching its highest values immediately before and during the reproductive period (winter-spring). Although the HSI of this species did not show significant seasonal differences, a discernible temporal pattern with higher values during spring and winter was observed, coinciding with that of GSI. Changes in Kn are attributed in other species to the mobilisation of somatic energy reserves essential for gonad development and spawning activity (Maddock and Burton 1999; Rätz and Lloret 2003). However, in this case, Kn did not show significant differences throughout the year.

Considerable variation in the biochemical composition were well documented in different tissues, especially in lipid and water content (Haug 1990). Lipids stored during high feeding periods accumulate in somatic tissues, liver and around the viscera (Hoque et al. 1998; Collins and Anderson 1995), making them valuable markers of condition. In general, the proportion of these lipids showed annual variations associated with changes in fish condition (Shulman and Love 1999). Throughout the annual cycle, the recorded variation in lipid content of Patagonian grouper ranged from 0.68 to 2.57% in muscle, 3.11 to 29.64% in liver, and 0.75 to 9.83% in gonads. These values are very similar to those obtained for the striped weakfish (*Cynoscion guatucupa*) from Buenos Aires waters, where the minimum and maximum concentrations were 1.50-5.90% in muscle, 3.8-27.50% in liver, and 1-8.7% in gonads (Chiodi 1962). They are also

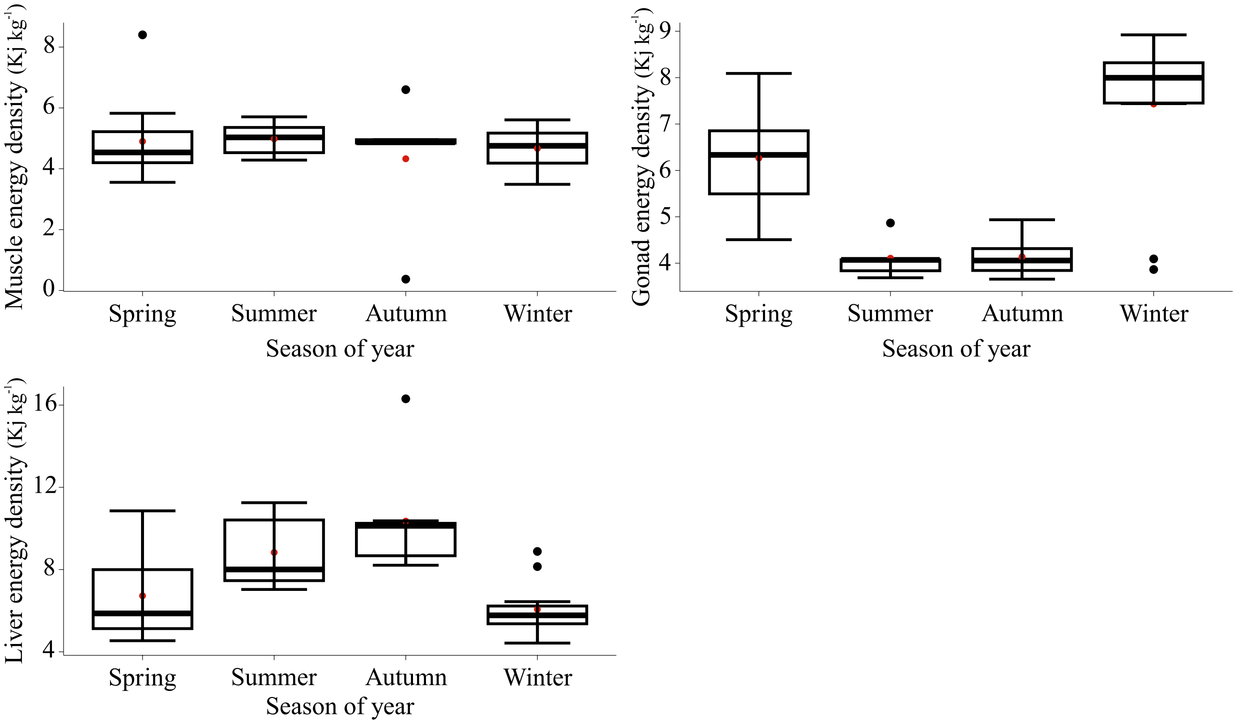

Figure 6. Boxplot showing the seasonal variation in energy density content of muscle, gonad and liver tissues of *Acanthistius patachonicus*. Each box shows the range between the first and third quartiles (Q1-Q3). Horizontal line inside the box indicates the median. Red circles define the mean values. Black circles are outliers.

similar to those obtained for the Brazilian flathead, *Percophis brasiliensis*, with a variation of 0.25-2.05% in muscle, 3.6-24% in liver, and 1.22-10% in gonads (Rodrigues et al. 2013). The seasonal trend observed in Patagonian grouper showed that liver lipids increased during the non-reproductive period (summer and autumn) and decreased during the reproductive activity. In contrast, gonadal lipids increase in winter and spring, during the spawning season of the species, indicating a mobilization of energy from the liver to the gonads. Seasonal variations in muscle lipid content were not significant, suggesting that this species accumulates lipid reserves for reproduction primarily in the liver. This pattern, characterised by the highest lipid concentration in the liver during the non-spawning season, is consistent with previous observations in *A. patachonicus* (Moreno et al. 1982) and other species, such as *Pseudopercis semifasciata* (López et al. 2018), *P. brasiliensis* (Rodrigues et al. 2013), *M. hubbsi* (Leonarduzzi et al. 2012) and *M. merluccius* (Lloret et al. 2008).

The protein content obtained for Patagonian grouper females showed seasonal variations ranging from 13.14% to 25.85% in muscle, 11.27% to 19.65% in liver, and 13.10% to 23.35% in gonads. Notably, significant differences were observed only in the gonadal protein content, with lower levels during the non-spawning season and higher concentrations during spawning. This is similar to what was seen for lipids and is consistent with the expected protein mobilisation during oocyte maturation. Although no significant seasonal differences were found in the liver, the highest protein concentration was recorded at the end of the reproductive period (summer). This temporal pattern is consistent with observations in *P. brasiliensis* (Rodrigues et al. 2013).

In general, the water content of different tissues follows an inverse trend to the content of organic matter, increasing as the energy is consumed. This phenomenon is often considered as an indicator of the condition of individuals (Lambert and Dutil 2000; Dutil et al. 2003; Alonso- Fernandez and Saborido-Rey 2011). In Patagonian grouper, the water content of tissues ranged from 69.62% to 79.79% in muscle, 54.37 to 78.26% in the liver, and 61.33 to 83.81% in gonads. These values are similar to those reported by Rodrigues et al (2013) for *P. brasiliensis*. Water content showed an inverse pattern with respect to lipids, especially in the gonad and liver, but, with respect to protein content, this trend was only observed in the gonad. These observations suggest that water content could be useful as a rapid indicator of lipid reserves (for gonads and liver), as demonstrated in other species such as *P. semifasciata* (López et al. 2018) and *M. hubbsi* (Leonarduzzi et al. 2012).

The energy density estimated for the muscle of Patagonian grouper remained relatively constant throughout different seasons. In contrast, liver and gonads showed an opposing seasonal pattern. The liver accumulates reserves during months of gonadal resting, but the energy decreases during the reproductive period. In contrast, the gonads showed maximum energy concentrations during the reproductive period, consistent with observations reported for other species, such as *P. brasiliensis* (Rodrigues et al. 2013), *M. hubbsi* (Leonarduzzi et al. 2012) and *P. semifasciata* (López et al. 2018). Analysis of stomach contents of Patagonian grouper revealed feeding activity in all seasons (Riestra 2019). Highest proportions of stomachs with contents were recorded during autumn, winter, and spring (Goldstein and Cousseau 1987; Sánchez and Prenski 1996; Riestra 2019). However, there are no reports in the literature on dietary analysis by sex and gonadal development stage. In conclusion, the analysis of tissue composition suggests that the primary source of energy for reproduction in the Patagonian grouper is the liver. Maximum energy reserves in this organ were recorded during oocyte growing and gonadal development (autumn) and decreased during the spawning season (spring). After reproduction, a recovery of energy levels was observed in summer, which was probably influenced by late summer samples. These fluctuations in energy levels correspond to the mobilisation of lipids, with a smaller contribution from proteins stored in the liver. This pattern indicates that *A. patachonicus* predominantly follows a capital breeding strategy, relying on stored energy for reproduction. In line with this conclusion, López et al (2023) found in this species that the relative fecundity, as well as the size and dry weight of hydrated oocytes, were lower during December. This supports the idea that energy reserves may be depleted by the end of the reproductive season. However, the possibility of concurrent energy intake through feeding during the spawning season cannot be ruled out. According to the categories proposed by McBride et al. (2015), this species may be classified as a mixed capital-income breeder, provided that females primarily rely on stored energy. These findings not only increase our understanding of the biology of *A. patachonicus* but also highlight the need to understand the energetic strategies employed by the fish. This information is essential for the effective population management and conservation of the species within the marine ecosystem. Observed seasonal variations in energy reserves in this species suggest a strong reliance on stored energy for reproduction, which could make the species more vulnerable to environmental fluctuations or anthropogenic pressures, such as fishing, particularly during the pre-spawning period. Therefore, protecting individuals during this time could be crucial to maintaining reproductive success and sustaining population productivity. Although this study provides a comprehensive overview, it is important to recognise that a thorough understanding of the energetic biology will require further detailed research, including temporal and spatial replication and larger sample sizes, to better inform conservation and management strategies.

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Conflict of interest

The authors declare no conflicts of interest.

Author contributions

Sofía López: conceptualization; methodology; formal analysis; investigation; data curation; writing-original draft; writing-review and editing; visualization; validation. María I. Militelli: resources; writing-review and editing; supervision; validation. Cecilia M. Riestra: investigation; writing- eview and editing; validation. Gustavo J. Macchi: resources; writing-review and editing, supervision; validation.

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