Marine and Fishery Sciences 38 (4): xxx-xxx (2025)
https://doi.org/10.47193/mafis.3842025011002

ORIGINAL RESEARCH

Condition and energy allocation during the reproductive cycle of the Patagonian redfish *Sebastes oculatus* from the Argentine continental shelf

Karina A. Rodrigues[1, *], Ezequiel Leonarduzzi[1], María I. Militelli[1] and Gustavo J. Macchi[1, 2]

[1]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo Nº 1, Escollera Norte, B7602HSA - Mar del Plata, Argentina. [2]Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Mar del Plata (UNMdP), Juan B. Justo 2550, B7608FBY - Mar del Plata, Argentina.
ORCID *Karina A. Rodrigues* https://orcid.org/0000-0003-4407-3474, *Ezequiel Leonarduzzi* https://orcid.org/0000-0002-6232-0478, *María I. Militelli* https://orcid.org/0000-0002-1189-3380, *Gustavo J. Macchi* https://orcid.org/0000-0003-1821-5491

*Correspondence:
krodrigues@inidep.edu.ar

Received: 19 March 2025
Accepted: 29 May 2025

ISSN 2683-7595 (print)
ISSN 2683-7951 (online)

https://ojs.inidep.edu.ar

Journal of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)

ABSTRACT. The Patagonian redfish (*Sebastes oculatus* Valenciennes 1833) is a viviparous species inhabiting the mid and outer shelf waters, as well as the rocky reefs along the Patagonian coast of Argentina. At present, the energy allocation strategy of this species during reproduction remains unknown. Thus, in this study, we analyzed the variations in biochemical and bioenergetic condition indices of adult females over a seasonal cycle. A total of 157 specimens were collected by onboard observers in commercial vessels between November 2016 and September 2017. The gonadosomatic index (GSI), morphophysiological condition (hepatosomatic index HSI and relative condition factor Kn), and the proximate composition (lipids, proteins, and moisture) along with energy density in muscle, liver, and gonads, were evaluated. Results showed an increase in lipid and protein reserves in the muscle and gonads during winter, coinciding with the onset of maturation. It was also observed that the energy density (kJ g^{-1}) in the liver and muscle decreases in spring, coinciding with the greatest gonadal development (GSI). The highest energy density values in muscle were recorded during winter, which coincides with increased feeding activity of the species, suggesting a reproductive strategy closer to a 'capital breeder', with energy storage prior to the beginning of spawning.

Key words: Reproduction, viviparity, body condition, energy density.

Condición y asignación de energía durante el ciclo reproductivo de la cabrilla patagónica *Sebastes oculatus* de la plataforma continental argentina

RESUMEN. La cabrilla patagónica (*Sebastes oculatus* Valenciennes 1833) es una especie vivípara que habita las aguas de la plataforma media y exterior, así como los arrecifes rocosos a lo largo de la costa patagónica de Argentina. En la actualidad, la estrategia de asignación de energía de esta especie durante la reproducción sigue siendo desconocida. Por lo tanto, en este estudio, analizamos las variaciones en los índices de condición bioquímica y bioenergética de hembras adultas a lo largo de un ciclo estacional. Un total de 157 especímenes fueron colectados por observadores a bordo de buques comerciales entre noviembre de 2016 y septiembre de 2017. Se evaluaron el índice gonadosomático (GSI), la condición morfofisiológica (índice hepatosomático HSI y factor de condición relativa Kn) y la composición proximal (lípidos, proteínas y humedad), junto con la densidad energética en músculo, hígado y gónadas. Los resultados mostraron un aumento en las reservas de lípidos y proteínas en el músculo y las gónadas durante el invierno, coincidiendo con el inicio de la maduración. También se observó que la densidad energética (kJ g^{-1}) en el hígado y el músculo disminuye en primavera, coincidiendo con el mayor desarrollo gonadal (GSI). Los valores más altos de densidad energética en el músculo se registraron durante el invierno, lo que coincide con una mayor actividad alimentaria de la especie, lo que sugiere una estrategia reproductiva más cercana a un *capital breeder*, con almacenamiento de energía antes del inicio del desove.

Palabras clave: Reproducción, viviparidad, condición del cuerpo, densidad energética.

INTRODUCTION

Body condition indexes have been commonly used to describe both the general health status of an animal and its nutritional or energy reserves (Schulte-Hostedde et al. 2005). The ability of an organism to acquire and manage energy resources, which are subsequently used to meet its energy demands, directly influences its overall body condition and associated indices (Jakob et al. 1996). This energy is distributed among three essential functions: maintenance metabolism, somatic growth, and reproduction (Calow 1985; Sibly and Calow 1986). In immature female fish, most of the energy is allocated for growth and metabolism, but part of it is redirected towards egg production and reproductive behavior once the gonad maturation begins. During the spawning season, these energy reserves often fluctuate significantly (Eliassen and Vahl 1982; Lucas 1996), and individuals in better body condition not only have a higher chance of survival as well as future reproductive success.

Maternal attributes and condition affect fish maturity (Marteinsdottir and Begg 2002; Morgan and Lilly 2006; Grift et al. 2007), fecundity, and egg production (Kjesbu et al. 1991; Rijnsdorp et al. 1991; Lambert and Dutil 2000; Marshall et al. 2006), as well as offspring viability (Brooks et al. 1997; Heyer et al. 2001; Berkeley et al. 2004). In summary, these factors influence the reproductive potential of the stock and should therefore be incorporated into assessment models (Morgan 2008). Fish condition can be assessed using a variety of criteria, ranging from simple morphometric measures (length-weight ratio or condition factor K) to physiological indicators (hepatosomatic index) and biochemical measures (proximal composition), which consist of measuring tissue concentrations of lipids, proteins, and other components (Jakob et al. 1996; Domínguez-Petit et al. 2010).

The Patagonian redfish (*Sebastes oculatus*) has been described as a species exhibiting internal fertilization, a single parturition, and ovoviviparity (Sánchez and Acha 1988). This species is distributed in waters of South America, from the San Matías Gulf (Argentina) in the Atlantic Ocean to the coasts of Peru and Chile in the Pacific Ocean (Rocha-Olivares et al. 1999; Galván et al. 2009). Two morphotypes have been identified in the Argentine Sea: the ‘dark or shallow’, inhabiting coastal waters less than 40-50 m (usually < 30 m), and the ‘light or deep’, inhabiting depths between 80 and 100 m. Venerus et al. (2013) analyzed both morphotypes caught in Argentina and found limited gene flow between them, which could facilitate an incipient speciation process.

Rodrigues et al. (2024) determined that the oocyte development pattern of *S. oculatus* is group-synchronous, with gonadal development starting in late austral winter and continuing into spring, and larvae being released in spring and early summer. Males mature earlier than females, suggesting that copulation may occur in autumn, with females retaining sperm in the ovary until oocyte fertilization. The evidence provided by these authors suggests that viviparity in this species is lecithotrophic, and a positive relationship between relative fecundity and maternal size was observed, indicating that larger and older females have greater reproductive potential, producing more eggs per unit of weight than younger individuals.

Marine species differ in their energy allocation strategies for reproduction, which can be placed along a continuum between two extremes: capital and income breeding. Capital breeders acquire energy previous to the beginning of the spawning season, and this stored energy constitutes the main source for egg production (Pavlov et al. 2009; Stephens et al. 2009). This strategy is typical of species inhabiting high latitudes and cold waters, often exhibiting marked seasonality, short spawning period, and synchronous oocyte development (Saborido-Rey and Macchi 2021). In contrast, income breeders acquire and mobilize energy during reproduction, without the need for prior storage. This pattern is common in species from tropical, subtropical, or highly productive temperate regions, which usually show prolonged spawning seasons and asynchronous oocyte development (Stephens et al. 2009). It remains unknown whether the Patagonian redfish stores energy prior to the onset of reproductive activity or whether it has the capacity to acquire energy by active feeding during reproduction. Therefore, the objective of the present study was to analyze variations in condition, proximate composition, energy density, and trophic activity throughout an annual cycle in order to examine the energy allocation strategy in relation to the sexual development of *S. oculatus* females.

MATERIALS AND METHODS

Sample collection

Specimens of *S. oculatus* were collected by onboard observers in commercial vessels along the Argentine continental shelf between 39° S and 51° S, from 62 to 230 m depth (Figure 1). A total of 157 adult females were analyzed from November 2016 to September 2017. The collection and handling of fish were conducted in accordance with ethical and legal standards established by the relevant authorities in the country.

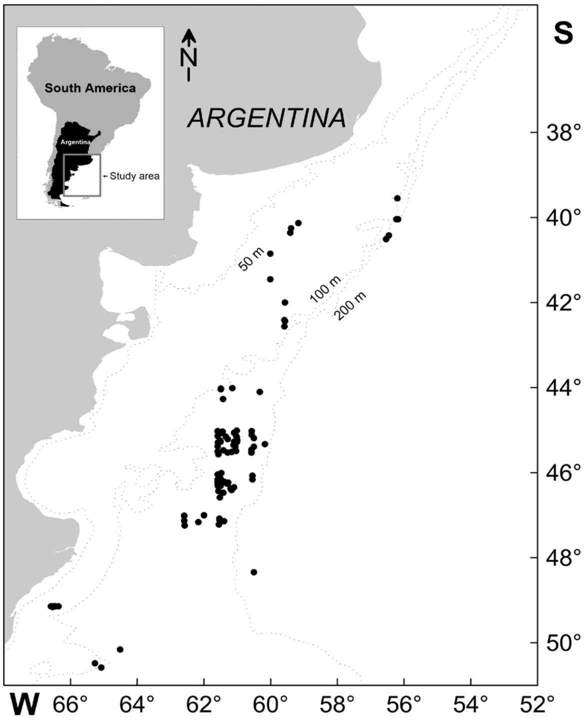

Figure 1. Locations where specimens of *Sebastes oculatus* were captured by onboard observers between November 2016 and September 2017.

Total length (TL), total weight (TW), gutted weight (GW), gonad weight (GoW), liver weight (LW), and macroscopic maturity phase of each specimen were recorded. For histological analysis, the ovaries were fixed in 10% formalin, and small samples from each were dehydrated using ethanol, cleared in xylene, and embedded in paraffin (García del Moral 1993). Sections of approximately 4 μm thick were cut using a microtome Sakura (model RH-12DM), and subsequent staining was performed using the hematoxylin-eosin technique. The histological classification of maturity phases followed the criteria proposed by Gunderson et al. (1980) for four species of genus *Sebastes*. We also used a macroscopic maturity key of 5 phases developed for bony fishes (Macchi and Pájaro 2003; Brown-Peterson et al. 2011): I. Immature; II. Developing; III. Spawning capable (in the case of females with embryos or larvae); IV. Regressing; V. Regenerating.

Proximate composition analysis and feeding activity

The proximate composition, determined from the proportion of lipids, proteins, and water content (moisture) was measured in gonads, liver, and muscle of *S. oculatus*. The relative amount of biochemical components within each tissue were analyzed with the goal of relating them to the gonadosomatic index and morphophysiological condition factors (hepatosomatic index and condition factor), as well as correlating the biochemical composition of the different tissues analyzed. Additionally, the seasonal variation of the proximate composition among tissues during an annual cycle was evaluated.

The gonadosomatic index (GSI), hepatosomatic index (HSI) and relative condition factor (Kn) were estimated. The Kn was expressed as a ratio between the observed GW and the GW determined by the total TL-GW relationship estimated for the analyzed period (Le Cren 1951). These indices were defined by the following equations:

$$\mathrm{GSI} = \left(\frac{\mathrm{GoW}}{\mathrm{GW}}\right) \times 100$$

$$\mathrm{HSI} = \left(\frac{\mathrm{LW}}{\mathrm{GW}}\right) \times 100$$

$$\mathrm{Kn} = \left(\frac{\mathrm{GW}}{0.017 \times \mathrm{TL}^{2.971}}\right) \times 100$$

Samples of liver, ovaries, and muscle (skinless fillet) were extracted from all specimens and stored in vacuum-sealed polypropylene bags at -22 °C until laboratory processing. Lipid and protein quantification was performed for all tissue, and when the sample size allowed, moisture content was also calculated.

Lipid content was obtained by using tissue subsamples of approximately 1.0 g. Lipid extraction followed the method of Bligh and Dyer (1959) in Undeland et al. (1998), with solvent proportions adjusted according to available tissue. Subsequently, total lipids were quantified using the gravimetric method of Herbes and Hallen (1983), which involves transferring 2 ml of lipid extract to a pre-weighed Eppendorf tube. The tube was then evaporated at 60 °C, and the post-evaporation weight was recorded using a precision balance. The difference in weight before and after evaporation determined the lipid content of the extract. Results were expressed as g 100 g^{-1} wet tissue or percentage.

For protein analysis, 1.0 g of each tissue was diluted in 50 ml of 0.1 N NaOH. Protein content was determined using the colorimetric method of Lowry et al. (1951), based on the reaction of proteins with the Folin-Ciocalteu reagent, forming a colored complex whose intensity depends on protein concentration. Bovine serum albumin (BSA) at a concentration of 1 mg ml^{-1} was used as a standard solution to create a calibration curve. The concentration of the 'unknown' samples was determined by interpolating absorbance values on the calibration curve.

To determine water content (moisture), subsamples of up to 10 g of each tissue, depending on tissue size, were taken and placed in pre-weighed Petri dishes. The wet weight of the tissue was recorded and samples were then dried in an oven at 105 °C for 24 h. After cooling to room temperature, they were weighed again.

Energy density (kJ g^{-1}) for each tissue (ovary, liver, muscle) was estimated by multiplying the lipid and protein content (mg g^{-1} of wet mass) by their respective energy equivalents (lipid = 39.5 kJ g^{-1}, protein = 23.6 kJ g^{-1} (Kleiber 1975).

Finally, given that the stomach content was not available, a visceral weight index (VWI) was calculated to obtain an estimator of the trophic activity of specimens. This index was determined by subtracting the eviscerated weight and weights of organs (gonads and liver) from the total weight, meaning that the remaining weight value would correspond mainly to the intestine and stomach (visceral weight-VW):

$$\mathrm{VWI} = \left(\frac{\mathrm{VW}}{\mathrm{TW}}\right) \times 100$$

Statistical analysis

Due to the small number of specimens collected in some months, data were grouped by season to analyze the mean monthly values of female morphological characteristics (total length, eviscerated weight, liver weight, and gonad weight), as well as the IGS, IHS, and Kn indices, and biochemical components.

To determine potential differences between the means of biochemical components analyzed in each tissue, energy density, condition indices and trophic activity by season, an ANOVA or Kruskal-Wallis tests were applied, depending on whether the assumptions of normality and homoscedasticity of variances were met. When significant differences were detected, *post-hoc* analyses were performed using Tukey's test after ANOVA or Dunn's test after Kruskal-Wallis. All statistical analyses were performed using InfoStat version 2017.1.2 (Di Rienzo et al. 2017).

RESULTS

A total of 157 adult females of *S. oculatus* were analyzed between November 2016 and September 2017, with sample sizes varying monthly (Table 1). The highest number of individuals was recorded in November 2016 (N = 39) and August 2017 (N = 47). Total length (TL) ranged from 23 to 43 cm, and total weight (TW) from 190 to 1888 g, with the largest individuals observed in November. Gutted weight (GW) showed a similar pattern, ranging from 150 to 1,349 g. Liver weight (LW) varied between 3.8 and 42.2 g, while gonad weight (GoW) ranged from 1.0 to 175.4 g.

The distribution of gonadal maturity phases during a seasonal cycle showed that developing females were predominant during autumn and spring, and ovaries with larvae were observed in spring and summer (Figure 2). The highest proportion of regressing females was recorded in spring, while the regenerating phase was predominantly observed in summer. Mean values of the GSI (Figure 2; Table 2) showed significant differences between

Table 1. Number of adult females (N) analyzed each month. Minimum and maximum values are provided for total length (TL), total weight (TW), gutted weight (GW), liver weight (LW), and gonad weight (GoW).

Year	Month	N	TL (cm)	TW (g)	GW (g)	LW (g)	GoW (g)
2016	November	39	23-43	190-1,888	150-1,349	4.7-42.2	2.9-175.4
2017	January	8	31-39	461-972	425-849	6.0-12.4	3.6-45.2
2017	March	6	28-39	452-1,095	413-1,015	5.8-26.8	2.8-10.2
2017	April	4	27-35	358-755	332-706	5.7-9.8	2.3-28.3
2017	May	4	30-38	487-870	454-828	6.4-23.3	4.1-14.6
2017	June	12	26-35	298-717	279-653	4.3-18.7	1.0-12.6
2017	July	6	27-36	333-1,014	312-848	3.8-26.5	1.4-24.7
2017	August	47	25-37	302-954	280-850	5.8-20.5	1.7-121.9
2017	September	31	26-39	323-1,196	299-1,040	4.5-22.6	2.6-83.2
Total		157					

seasons ($p < 0.001$, Kruskal-Wallis test), with maximum gonadal development in spring and a decline at the end of the reproductive period (summer and autumn) ($p < 0.05$; Dunn's test). Similarly, the seasonal variation of the HSI and Kn was analyzed, which showed no significant differences ($p > 0.05$, Kruskal-Wallis test) (Table 2).

The mean lipid content across the analyzed tissues was 1.70% in muscle, 16.37% in the liver, and 7.54% in the gonads (Table 3). Significant differences were observed between seasons in all three tissues ($p < 0.01$, ANOVA test). In muscle, the highest values were recorded in winter, with significant differences compared to spring and autumn ($p < 0.05$, Tukey-Kramer test). In the liver, lipid content was significantly lower in spring compared to the other seasons ($p < 0.05$, Tukey-Kramer test). As for the ovary, lipid percentages were statistically higher in winter ($p < 0.05$, Tukey-Kramer test), starting to deplete in spring, with the lowest values observed in summer and autumn (Table 3).

Similar to lipids, protein content showed significant seasonal differences across all three analyzed tissues. In muscle, protein content was significantly higher in winter compared to spring and summer ($p < 0.001$, ANOVA test; $p < 0.01$, Tukey-Kramer test) (Table 4). Proteins in the ovaries and liver showed almost opposite patterns. Protein levels

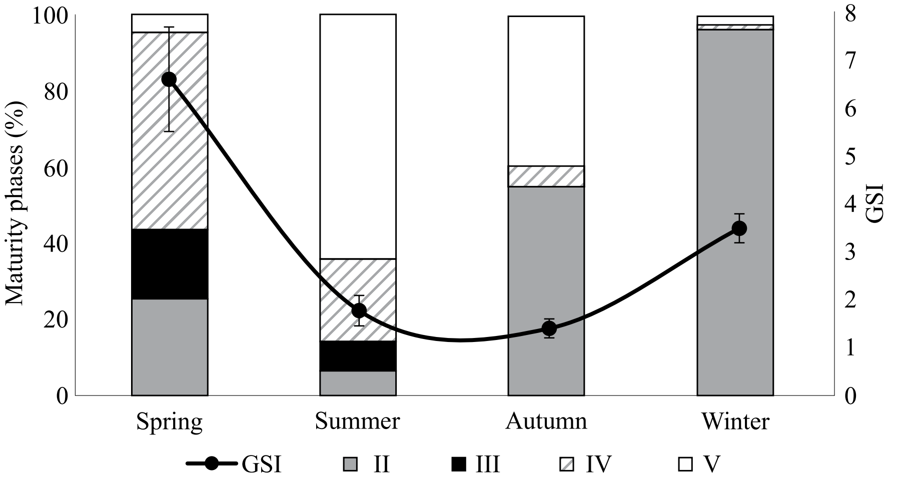

Figure 2. Seasonal distribution of the mean and standard error (bars) of gonadosomatic index (GSI) and percentage of *Sebastes oculatus* females at different maturity phases. II: developing; III: spawning capable (with embryos or larvae); IV: regressing; V: regenerating.

Table 2. Mean and standard deviation (in brackets) of condition indices by season. N: number of specimens. GSI: gonadosomatic index. HSI: hepatosomatic index. Kn: relative K. VWI: visceral weight index. Values with different superscript letters differ significantly ($p < 0.05$).

	N	GSI	HSI	Kn	VWI
Spring	39	6.58 (± 6.83)^{a}	2.35 (± 0.59)^{a}	1.03 (± 0.10)^{a}	3.87 (± 2.47)^{a}
Summer	14	1.66 (± 0.95)^{b}	1.95 (± 0.48)^{a}	1.04 (± 0.09)^{a}	4.52 (± 1.41)^{ab}
Autumn	20	1.42 (± 1.00)^{b}	2.04 (± 0.89)^{a}	1.03 (± 0.08)^{a}	3.72 (± 2.03)^{a}
Winter	84	3.08 (± 2.32)^{ab}	2.22 (± 0.65)^{a}	1.06 (± 0.09)^{a}	5.40 (± 2.21)^{b}

in the liver were significantly lower in spring compared to summer and winter, and there were also significant differences between summer and autumn ($p < 0.001$, Kruskal-Wallis test; $p < 0.05$, Dunn's test). In the ovaries, protein values were highest at the onset of gonadal development (winter) and remained high during the reproductive period (spring), declining in summer and autumn (end of the reproductive period and beginning of gonad resting) (Table 4) ($p < 0.001$, ANOVA test; $p < 0.05$, Tukey-Kramer test).

Seasonal variations in muscle water content were not significant ($p > 0.01$, ANOVA), with an average of 77.86% (Table 5). The liver exhibited its highest water concentration in spring (70.21%), which was significantly different from winter, when it reached a minimum of 59.60% ($p < 0.001$, Kruskal-Wallis test; $p < 0.01$, Dunn's test). Winter moisture content in ovaries, was significantly lower (63.27%) than in other seasons ($p < 0.001$, Kruskal-Wallis test; $p < 0.001$, Dunn's test) with an opposite trend to lipids and proteins.

In muscle, it was observed that energy per gram of tissue was significantly higher in winter (10.37 kJ g^{-1}) than in other seasons ($p < 0.001$, ANOVA test; $p < 0.01$, Tukey-Kramer test) (Table 6; Figure 3). The energy density in the liver was statistically lower in spring (8.16 kJ g^{-1}) compared

Table 3. Mean lipid percentage (%) in each tissue of adult female *Sebastes oculatus* across seasons. N: number of specimens. Values with different superscript letters differ significantly ($p < 0.05$; *post-hoc* test).

	Muscle		Liver		Gonads	
	N	%	N	%	N	%
Spring	35	1.40^{a}	39	12.14^{a}	29	5.94^{a}
Summer	14	1.58^{ab}	14	17.45^{b}	11	3.33^{b}
Autumn	20	1.24^{a}	20	15.55^{ab}	10	5.01^{ab}
Winter	76	1.90^{b}	77	18.53^{b}	72	9.18^{c}
Mean		1.70		16.37		7.54

Table 4. Mean protein percentage (%) in each tissue of adult female *Sebastes oculatus* across seasons. N: number of specimens. Values with different superscript letters differ significantly ($p < 0.05$; *post hoc* test).

	Muscle		Liver		Gonads	
	N	%	N	%	N	%
Spring	39	18.18^{a}	37	14.12^{a}	24	20.01^{a}
Summer	14	18.21^{a}	13	17.28^{b}	6	16.93^{a}
Autumn	20	19.24^{ab}	19	15.12^{ab}	4	19.24^{ab}
Winter	84	20.78^{b}	75	16.61^{b}	61	26.82^{b}
Mean		19.71		15.84		24.47

to summer and winter ($p < 0.001$, Kruskal-Wallis test; $p < 0.01$, Dunn's test). In autumn, it was also low, but in this case, differences were not significant ($p > 0.05$, Dunn's test) (Table 6; Figure 3). The energy density in the ovaries was significantly higher during winter ($p < 0.001$, ANOVA test; $p < 0.01$, Tukey-Kramer test), prior to the peak of reproductive activity (Table 6; Figure 3).

The VWI, used as an approximation of the trophic activity of females, was significantly higher in winter (Table 2) ($p < 0.001$, ANOVA test; $p < 0.05$, Tukey-Kramer test) and coincided with the previously mentioned highest energy density values in muscle (Figure 4).

DISCUSSION

This study set out to investigate the seasonal variation in energy allocation and body condition in adult females of *S. oculatus*, aiming to assess its reproductive strategy within the capital-income breeding continuum. Results showed a significant increase in lipid and protein content in muscle and gonads during winter, coinciding with the onset of gonadal development, while liver reserves declined in spring, when gonadal investment peaked. Additionally, an increasing feeding activity was

Table 5. Mean moisture percentage (%) in each tissue of adult female *Sebastes oculatus* across seasons. N: number of specimens. Values with different superscript letters differ significantly ($p < 0.05$; *post-hoc* test).

	Muscle		Liver		Gonads	
	N	%	N	%	N	%
Spring	39	78.22^{a}	39	70.21^{a}	30	77.83^{a}
Summer	14	78.42^{a}	14	64.69^{ab}	11	81.53^{a}
Autumn	20	78.33^{a}	20	66.18^{a}	4	78.98^{a}
Winter	82	77.48^{a}	84	59.60^{b}	70	63.27^{b}
Mean		77.86		63.53		69.36

Table 6. Mean energy density (kJ g^{-1}) in each tissue of adult female *Sebastes oculatus* across seasons. N: number of specimens. Values with different superscript letters differ significantly ($p < 0.05$; *post hoc* test).

	Muscle		Liver		Gonads	
	N	kJ g^{-1}	N	kJ g^{-1}	N	kJ g^{-1}
Spring	35	4.88^{a}	39	8.16^{a}	19	6.89^{a}
Summer	14	4.92^{a}	13	10.97^{b}	6	5.29^{a}
Autumn	20	5.03^{a}	19	9.58^{ab}	4	6.65^{a}
Winter	76	5.65^{b}	70	11.00^{b}	52	10.37^{b}
Mean		5.31		10.05		8.99

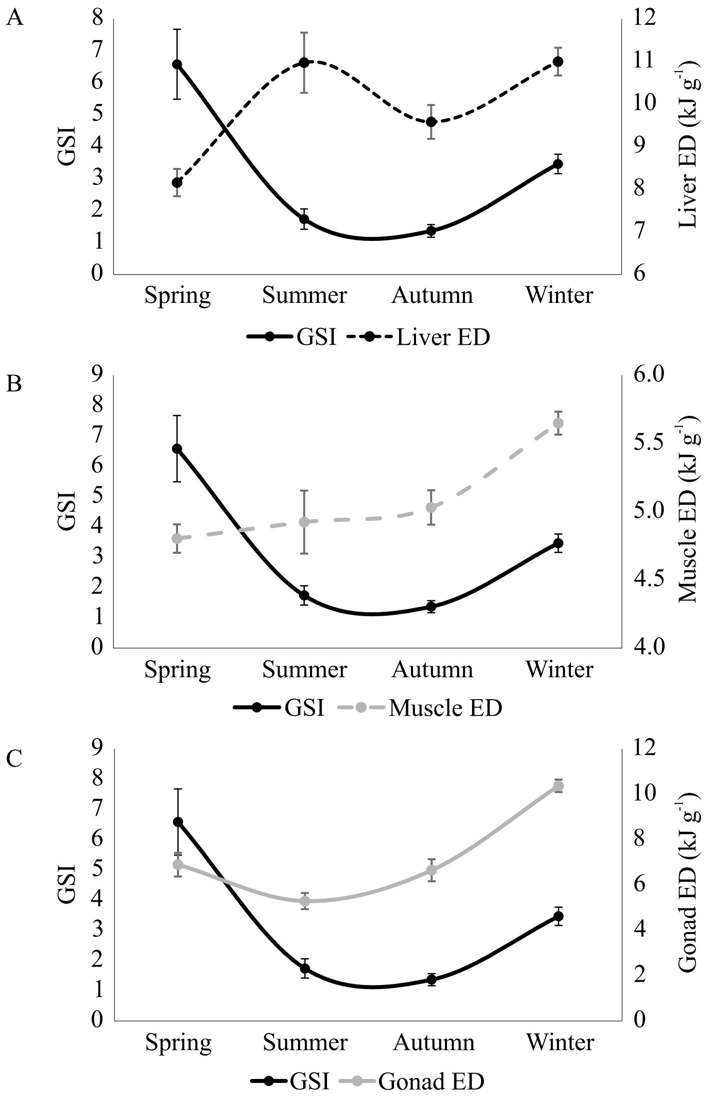

Figure 3. Seasonal variation of the mean and standard error (bars) of energy density (ED) in liver (A), muscle (B) and gonad (C), and gonadosomatic index (GSI) of *Sebastes oculatus*.

recorded in winter, just prior to the reproductive period. These findings support the hypothesis that *S. oculatus* relies on energy reserves accumulated before the spawning season, consistent with a capital breeding strategy.

The distribution of gonadal maturity phases in *S. oculatus* females during a seasonal cycle showed that ovary development begins in autumn and extended into spring, indicating a period of significant gonadal growth and maturation. The presence of ovaries with larvae was recorded during spring and summer and regression-regeneration females were mainly observed at the end this period. The mean GSI values in *S. oculatus* increased during winter and peaked in spring, consistent with the period of active gonadal development and spawning capability observed in the maturity phases analysis. The timing of spawning, coinciding with the

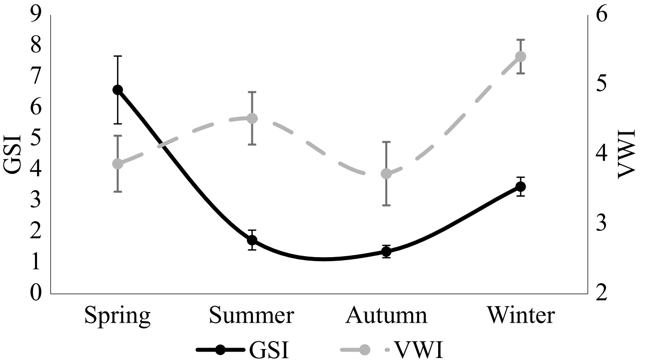

Figure 4. Seasonal variation of the mean and standard error (bars) of gonadosomatic index (GSI) and visceral weight index (VWI) of *Sebastes oculatus*.

productive cycle of temperate waters (spring-summer), is crucial for the development and survival of offspring, aiming to maximize reproductive success (Cushing 1990). Individuals must allocate their energy resources to ensure that their offspring develop under suitable environmental conditions. Spawning events during spring-summer in the Southern Hemisphere are also common among other abundant marine fish species in the Patagonian region, such as *Merluccius hubbsi* (Macchi et al. 2018) and *Engraulis anchoita* (Pájaro et al. 2009), as well as some rocky reef fish like *Pagrus pagrus* and *Pseudopercis semifasciata* (López 2022).

In most species with seasonal spawning, the gonadosomatic index (GSI) changes significantly throughout the reproductive cycle and is a very useful tool for delineating the spawning period. A marked increase in GSI generally indicates a rapid rate of yolk deposition in oocytes (Alonso Fernández 2011). Conversely, the hepatosomatic index (HSI) reflects changes in liver weight primarily due to lipid accumulation associated with vitellogenin synthesis, and is often used as an indicator of energy reserves in fish (Marteinsdottir and Begg 2002; Leonarduzzi et al. 2014; Rodrigues et al. 2018). Similarly, the relative condition factor (Kn or K) is used to estimate the somatic energy status of fish. In *S. oculatus*, both the HSI and Kn did not differ significantly across seasons, while Kn tended to be higher in winter prior to the reproductive peak. A similar pattern has been observed in *Percophis brasiliensis*, where HSI showed no seasonal variation and K increased during winter (Rodrigues et al. 2013).

The chemical composition of different tissues, which reflects the condition of organisms more accurately than the HSI and K indices, can vary considerably, particularly in lipid and water content (Haug 1990). During periods of high intake, lipids may be stored in somatic tissue, liver, and around the viscera (Collins and Anderson 1995; Hoque et al. 1998;), making lipids useful markers of condition, as they reflect annual cycles associated with changes in physiological state (Shulman and Love 1999). Seasonal variations in lipid content were recorded in *S. oculatus*, ranging from 0.4% to 4.6% in muscle, 5.5% to 31.8% in the liver, and 1.6% to 13.5% in the gonads. Lipids decreased markedly in the liver during the reproductive period (spring), but increased in gonads and muscle during winter. These patterns suggest the mobilization of liver energy reserves for reproduction; however, this was not reflected in the HSI, possibly due to an increase in moisture that increased the weight of the organ. Records of the proximal composition of this species have not been found, but total lipid determinations have been conducted in Pacific *S. flavidus* (MacFarlane et al. 1993). These authors found lipid values between 1% and 4% in muscle, 4% and 40% in liver, and 1% and 10% in gonads, suggesting that lipids accumulated in the mesentery and liver during summer and autumn would be transferred to developing ovaries during winter. The Argentine hake (*M. hubbsi*), although is an income breeder species, exhibit a comparable energetic pattern, with the highest lipid concentrations recorded in the liver of regenerating females, indicating the onset of energy reserve accumulation during this phase of the reproductive cycle (Leonarduzzi et al. 2010).

During different seasons of the year, the mean protein content of females varied between 18.2% and 20.8% in muscle, from 16.9% to 26.8% in gonads, and from 14.1% to 17.3% in liver. No significant differences were recorded in muscle among seasons. Protein levels in the liver were significantly lower in spring compared to summer and winter. Regarding gonads, protein concentration peaked in winter when oocytes begin to mature and then slightly decreased toward spring (maximum gonadal development), reaching its lowest values at the end of the reproductive period (summer and autumn), similar to the GSI.

According to MacFarlane et al. (1993), the protein content in ovaries of *S. flavidus* decreases by approximately 21% between fertilization and larval release, indicating that the species exhibits primarily lecithotrophic viviparity. However, it was observed that during gestation, levels of phospholipids and calcium in serum (indicators of vitellogenin) were significantly elevated compared to those in males, suggesting a matrotrophic contribution. In *S. oculatus*, the mean ovarian protein content decreased by 15.4% from spring (20.01%) to summer (16.93%), calculated as a relative difference using the spring value as the baseline. This period corresponds to the time of larval release. Although serum studies are lacking in our case, Rodrigues et al. (2024) found no significant differences in the dry weight of ovulated oocytes and free larvae in the ovary, suggesting that the embryo develops completely at the expense of the yolk before expulsion, indicating that the viviparity of this species is lecithotrophic.

The mean water content varied between 77.5% and 78.4% in muscle, between 63.3% and 81.5% in gonads, and 59.6% and 70.2% in the liver. No differences were recorded in muscle across seasons, while the moisture content in the liver and gonads exhibited an inverse trend to that of lipids and proteins in these tissues. In general, the water content in different tissues tends to follow an opposite trend to the content of organic components, as the proportion of water increases when energy is consumed, and is often considered an indicator of the individuals' condition (Lambert and Dutil 2000; Dutil et al. 2003; Alonso Fernández and Saborido Rey 2011).

All variability in proximal composition can be summarized as the variation in the energetic content of tissues (Domínguez-Petit 2006). In this study, energy density in muscle and gonads increased significantly in winter, coinciding with the onset of gonadal growth. Energy density in the liver was lower during spring when the greatest gonadal growth occurs, suggesting that hepatic reserves are utilized for reproduction. In *S. oculatus*, the liver begins to accumulate energy in summer, coinciding with the highest combined percentage of females in the regression and regeneration phases, similar to what has been observed in other species from the Argentine Sea, such as *P. brasiliensis* (Rodrigues et al. 2013) and *M. hubbsi* (Leonarduzzi et al. 2010). The energy storage in ovaries of Patagonian redfish begins after reproduction and peaks just before the next spawning period, in winter. During this season, higher values of the VWI were recorded, indicating increased trophic activity, which coincided with a marked rise in yolk deposition in the ovaries. The increase in VWI also coincided with the highest energy density values in the muscle, suggesting the accumulation of energy reserves prior to the spawning period.

In conclusion, it was established that the composition of lipids and proteins in the liver of *S. oculatus* decreases markedly in spring, during peak gonadal development (presence of advanced vitellogenic oocytes or larvae in the ovary), indicating a mobilization of these reserves for reproduction. Then, during regression and developing phases (from summer to winter), these components increase. In muscle, lipids and proteins significantly increase as winter approaches (maturation). These results together with the increase of the VWI in winter, suggests an incorporation of energy from food, prior to the onset of reproduction. Thus, the Patagonian redfish exhibits an energy accumulation strategy during reproduction closer to that of a 'capital breeder'. Nevertheless, these results should be considered preliminary due to the low number of specimens analyzed in some months. Future studies analyzing the influence of energy acquisition based on food quality and quantity will be essential to evaluate how dependent this species is on energy uptake during the reproductive stage. This will help confirm whether the Patagonian redfish is a capital breeder or it adopts a mixed breeder strategy, utilizing both accumulated body reserves and energy obtained through feeding (McBride et al. 2015).

ACKNOWLEDGEMENTS

We would like to thank the on-board observers of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) for the collection of the samples used in this work. We also thank the technicians Marta Estrada and Hugo Brachetta for their help in processing the tissues. This is INIDEP contribution no. 2500.

Author contributions

Karina A. Rodrigues: conceptualization; methodology; formal analysis; investigation; writing-original draft; writing-review and editing; visualization. Ezequiel Leonarduzzi: investigation; methodology; writing-review and editing; validation. María I. Militelli: resources; writing-review and editing; validation. Gustavo J. Macchi: resources; writing-review and editing, supervision; validation.

REFERENCES

Alonso Fernández A. 2011. Bioenergetics approach to fish reproductive potential: case of *Trisopterus luscus* (Teleostei) on the Galician Shelf (NW Iberian Peninsula) [PhD thesis]. Vigo: Departamento de Ecología y Biología Animal, Universidad de Vigo. 280 p.

Berkeley SA, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology. 85: 1258-1264. DOI: http://doi.org/10.1890/03-0706

Bligh EG, Dyer WJ. 1959. A rapid method of total lipid extraction and purification. Can J Biochem Physiol. 37: 911-917.

Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK. 2011. A standardized terminology for describing reproductive development in fishes. Mar Coast Fish. 3 (1): 52-70. DOI: https://doi.org/10.1080/19425120.2011.555724

Brooks S, Tyler CR, Sumpter JP. 1997. Egg quality in fish: what makes a good egg? Rev Fish Biol Fish. 7 (4): 387-416.

Calow P. 1985. Adaptive aspects of energy allocation. In: Tytler P, Calow P, editors. Fish energetics: new perspectives. London: Croom Helm. p. 13-31.

Collins AL, Anderson TA. 1995. The regulation of endogenous energy stores during starvation and refeeding in the somatic tissues of the golden perch. J Fish Biol. 47: 1004-1015.

Cushing DH. 1990. Plankton production and yearclass strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol. 26: 249-293.

Di Rienzo JA, Casánoves F, Balzarini MG, González L, Tablada M, Robledo CW. 2017. InfoStat versión 2017. Grupo InfoStat. Universidad Nacional de Córdoba. https://www.infostat.com.ar.

Domínguez-Petit R. 2006. Study of the reproductive potential of the *Merluccius merluccius* in the Galician shelf [PhD thesis]. Vigo: Instituto de Investigaciones Marinas, Universidad de Vigo. 253 p.

Domínguez-Petit R, Saborido-Rey F. 2010. New bioenergetic perspective of European hake (*Merluccius merluccius* L.) reproductive ecology. Fish Res. 104: 83-88.

Domínguez-Petit R, Saborido-Rey F, Medina I. 2010. Changes of proximate composition, energy storage and condition of European hake (*Merluccius merluccius*, L. 1758) through the spawning season. Fish Res. 104: 73-82.

Dutil JD, Gauthier J, Lambert Y, Fréchet A, Chabot D. 2003. Stock rebuilding and fish bioenergetics: low productivity hypothesis. Canadian Science Advisory Secretariat Research Document 2003/60. 39 p.

Eigenmann CH. 1892. The fishes of San Diego, California. Proc US Natl Mus. 15: 123-178.

Eliassen JE, Vahl O. 1982. Seasonal variations in biochemical composition and energy content of liver, gonad and muscle of mature and immature cod, *Gadus morhua*, from Balsfjorden, northern Norway. J Fish Biol. 20: 707-716.

Galván DE, Venerus LA, Irigoyen AJ. 2009. The reef-fish fauna of the Northern Patagonian gulfs of Argentina, Southwestern Atlantic. Open Fish Sci J. 2: 90-98.

García del Moral R. 1993. Laboratorio de anatomía patológica. McGraw-Hill Interamericana. 659 p.

Grift RE, Heino M, Rijnsdorp AD, Kraak SBM, Dieckmann U. 2007. Three-dimensional maturation reaction norms for North Sea plaice. Mar Ecol Prog Ser. 334: 213-224.

Haug T. 1990. Biology of the Atlantic halibut *Hippoglossus hippoglossus* (L., 1758). Adv Mar Biol. 26: 1-70.

Herbes S, Allen C. 1983. Lipid quantification of freshwater invertebrates: method modification for microquantitation. Can J Fish Aquat Sci. 14: 1315-1317.

Heyer CJ, Miller TJ, Binkowski FP, Caldarone EM, Rice JA. 2001. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can J Fish Aquat Sci. 58: 1477-1487.

Hoque MT, Yusoff FM, Law AT, Syed MA. 1998. Effect of hydrogen sulphide on liver somatic index and Fulton's condition factor in *Mystus nemurus*. J Fish Biol. 52: 23-30.

Hunter JR, Macewicz BJ, Lo NCH, Kimbrell CA. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish Bull US. 90: 101-128.

Jakob EM, Marshall SD, Uetz GW. 1996. Estimating fitness: a comparison of body condition indices. Oikos. 77: 61-67.

Jobling M. 1995. Environmental biology of fishes. Fish and Fisheries Series 16. London: Chapman and Hall. 455 p.

Jørgensen C, Fiksen O. 2006. State-dependent energy allocation in cod (*Gadus morhua*). Can J Fish Aquat Sci. 63: 186-199.

Kjesbu OS, Klungsoyr J, Kryvi H, Witthames PR, Greer Walker M. 1991. Fecundity, atresia and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can J Fish Aquat Sci. 48: 2333-2343.

Kleiber M. 1975. The fire of life: an introduction to animal energetics. New York: Krieger Publishing Company. 453 p.

Lambert Y, Dutil J. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? Can J Fish Aquat Sci. 54 (1): 104-112.

Lambert Y, Dutil J. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Can J Fish Aquat Sci. 57 (4): 815-825.

LEONARDUZZI E. 2018. Bioenergética y condición nutricional de la merluza común, *Merluccius hubbsi*, del efectivo Patagónico y sus implicancias en el potencial reproductivo de la especie [PhD thesis]. Mar del Plata: Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. 197 p.

LEONARDUZZI E, MASSA A, MANCA E. 2010. Variación de la composición bioquímica en hembras de merluza común (*Merluccius hubbsi*) durante el ciclo reproductivo. Inf Invest INIDEP Nº 42/2010. 16 p.

LEONARDUZZI E, RODRIGUES KA, MACCHI GJ. 2014. Proximate composition and energy density in relation to Argentine hake females (*Merluccius hubbsi*) morphometrics and condition indices. Fish Res. 160: 33-40.

LÓPEZ S. 2022. Ecología reproductiva de peces óseos en arrecifes rocosos bonaerenses [PhD thesis]. Mar del Plata: Universidad Nacional de Mar del Plata. 174 p.

LOWERRE-BARBIERI SK, BROWN-PETERSON NJ, MURUA H, TOMKIEWICZ J, WYANSKI D, SABORIDO-REY F. 2011. Emerging issues and methodological advances in fisheries reproductive biology. Mar Coast Fish. 3: 32-51.

LOWRY OH, ROSBROUGH NJ, FARR AL, RANDALL RJ. 1951. Protein measurement with the folin phenol reagent. J Biol Chem. 193: 265-275.

LUCAS A. 1996. Bioenergetics of aquatic animals. London: Taylor and Francis.

MACFARLANE R, NORTON E, BOWERS M. 1993. Lipid dynamics in relation to the annual reproductive cycle in yellowtail rockfish (*Sebastes flavidus*). Can J Fish Aquat Sci. 50: 391-401. DOI: https://doi.org/10.1139/f93-044

MCBRIDE RS, SOMARAKIS S, FITZHUGH GR, ALBERT A, YARAGINA NA, WUENSCHEL MJ, ALONSO-FERNANDEZ A, BASILONE G. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish. 16 (1): 23-57.

MACCHI GJ, PÁJARO M. 2003. Comparative reproductive biology of some commercial marine fishes from Argentina. Fisk Havet. 12: 67-76.

MACCHI GJ, RODRIGUES KA, LEONARDUZZI E, DÍAZ MV. 2018. Is the spawning frequency of Argentine hake, *Merluccius hubbsi*, affected by maternal attributes or physical variables? Fish Res. 204: 147-155.

MADDOCK DM, BURTON MPM. 1999. Gross and histological observations of ovarian development and related condition changes in American plaice. J Fish Biol. 53 (5): 928-944.

MARSHALL CT, NEEDLE CL, THORSEN A, KJESBU OS, YARAGINA NA. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock-recruit theory and management. Can J Fish Aquat Sci. 63: 980-994.

MARTEINSDOTTIR G, BEGG GA. 2002. Essential relationships incorporating the influence of age, size, and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser. 235: 235-256.

MELLO LGS, ROSE GA. 2005. Seasonal growth of Atlantic cod: effects of temperature, feeding, and reproduction. J Fish Biol. 67: 149-170.

MORGAN MJ 2008. Integrating reproductive biology into scientific advice for fisheries management. J Northwest Atl Fish Sci. 41: 37-51.

MORGAN MJ, LILLY GR. 2006. The impact of condition on reproduction in Flemish Cap cod. J Northwest Atl Fish Sci. 37: 81-86.

MOSER HG, AHLSTROM EH, SANDKNOP EM. 1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the Eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. NOAA Tech Rep NMFS. 402.

PÁJARO M, MACCHI GJ, LEONARDUZZI E, HANSEN J. 2009. Spawning biomass of Argentine anchovy (*Engraulis anchoita*) from 1996 to 2004 using the daily egg production method. J Mar Biol Assoc UK. 89: 829-837.

PAVLOV DA, EMEL'YANOVA NG, NOVIKOV GG. 2009. Reproductive dynamics. In: JAKOBSEN T, FOGarty MJ, Megrey BA, Moksness E, editors. Fish reproductive biology. Chichester: Wiley-Blackwell. p. 48-69.

Potts G, Wootton R. 1989. Fish reproduction: strategies and tactics. 3rd ed. London: Academic Press Limited.

Rocha-Olivares A, Rosenblatt RH, Vetter RD. 1999. Molecular evolution, systematics, and zoogeography of the rockfish subgenus *Sebastomus* (*Sebastes*, Scorpaenidae) based on mitochondrial cytochrome *b* and control region sequences. Mol Phylogenet Evol. 11: 441-458.

Rätz HJ, Lloret J. 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. Fish Res. 60: 369-380.

Rijnsdorp AD, Daan N, Van Beek FA, Heesen HJL. 1991. Reproductive variability in North Sea plaice, sole and cod. ICES J Mar Sci. 47: 352-375.

Rodrigues KA, Macchi GJ, Massa A. 2013. Seasonal analysis of condition, biochemical and bioenergetic indices of females of Brazilian flathead, *Percophis brasiliensis*. Neotrop Ichthyol. 11 (1): 153-162.

Rodrigues KA, Leonarduzzi E, Macchi GJ, Militelli MI. 2018. Maternal condition, fecundity and oocyte quality of Argentine hake (*Merluccius hubbsi*) from the Northern stock. Fish Res. 197: 105-112. DOI: https://doi.org/10.1016/j.fishres.2017.09.005

Rodrigues KA, Militelli MI, Macchi G. 2024. Reproductive cycle, spawning and fecundity of *Sebastes oculatus* (Patagonian redfish) in the Argentine continental shelf. Ichthyol Herpetol. 112 (3): 353-364.

Saborido-Rey F, Macchi GJ. 2021. Introducción. Ecología reproductiva y pesquerías en el contexto Iberoamericano. Vigo: Red Iberoamericana de Investigación para el Uso Sostenible de los Recursos Pesqueros (RED INVIPESCA). p. 6-31.

Sánchez RP, Acha M. 1988. Development and occurrence of embryos, larvae and juveniles of *Sebastes oculatus* with reference to two Southwest Atlantic Scorpaenids: *Helicolenus dactylopterus lahillei* and *Pontinus rathbuni*. Meeresforsch. 32: 107-133.

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology. 86: 155-163.

Shulman G, Love R, editors. 1999. The biochemical ecology of marine fishes. Advances in marine biology. 36. San Diego: Academic Press. 351 p.

Sibly RM, Calow P. 1986. Physiological ecology of animals: an evolutionary approach. Oxford: Blackwell Scientific.

Stephens PA, Boyd IL, McNamara JM, Houston AI. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology. 90: 2057-2067. DOI: https://doi.org/10.1890/08-1369.1

Tyler AV, Dunn RS. 1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. J Fish Res Board Can. 33: 63-75.

Undeland I, Harrod M, Lingnert H. 1998. Comparison between methods using low-toxicity solvents for the extraction of lipids from herring (*Clupea harengus*). Food Chem. 61: 355-365.

Venerus LA, Ciancio JE, Riva-Rossi C, Gilbert-Horvath EA, Gosztonyi AE, Garza JC. 2013. Genetic structure and different color morphotypes suggest the occurrence and bathymetric segregation of two incipient species of *Sebastes* off Argentina. Naturwissenschaften. 100: 645-658.

Wourms JP. 1991. Reproduction and development of *Sebastes* in the context of evolution of piscine viviparity. Environ Biol Fishes. 30: 111-126.