



Energy density of age-0+ *Merluccius hubbsi* (Actinopterygii, Merlucciidae) as a food quality proxy for upper level predators

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Abstract. Assessing the energy density (ED) of forage fish provides key information for top predators bioenergetics' models and food web studies. In the Argentinean Continental Shelf (ACS), age-0+ year individuals of the Patagonian stock of *Merluccius hubbsi* concentrate in the San Jorge Gulf (45°-47°S, 65°30'W), where they constitute an important food source for demersal fish, seabirds and marine mammals species. Age-0+ *M. hubbsi* ED -deriving from proteins and lipids stored in muscle and liver- was determined as a food quality proxy, to gain insight into the amounts of energy they pass to predators. ED values ranged from 1.6 to 5.5 kJ g⁻¹ wet weight (3.4 ± 0.9) ($n = 40$), with muscle explaining most of its variation ($R^2 = 0.99$; $p < 0.001$). Muscle was dominated by proteins (92.9 ± 3.2%), while a similar contribution of both proteins (55.5 ± 14.1%) and lipids (44.5 ± 14.1%) was observed to the liver. These results provide novel information that was scarce for *M. hubbsi* in the ACS, particularly for the age-0+ stage. Data will be useful in the context of *M. hubbsi* predators' trophic ecology models, to understand how ecosystem shifts influence the structure of the San Jorge Gulf food web.

Key words: Argentine hake, Prerecruit stage, Nutritional quality, Argentinean Continental Shelf.

Resumen: Densidad energética de prereclutas de *Merluccius hubbsi* (Actinopterygii, Merlucciidae) como un indicador de calidad nutricional para sus predadores. Determinar la densidad energética (DE) de los peces brinda información clave para modelos bioenergéticos de predadores y estudios de tramas tróficas. En la plataforma continental argentina, los prereclutas del efectivo patagónico de *Merluccius hubbsi* se concentran en el Golfo San Jorge (45°-47°S, 65°30'W), donde son alimento de otros peces demersales, aves y mamíferos marinos. La DE de los prereclutas -derivada de las proteínas y los lípidos almacenados en músculo e hígado- se determinó como un indicador de calidad nutricional, para evaluar la cantidad de energía disponible para sus predadores. La DE ($n = 40$) varió entre 1,6 y 5,5 kJ g⁻¹ peso húmedo (3,4 ± 0,9), siendo el músculo el tejido que mejor explicó sus variaciones ($R^2 = 0,99$; $p < 0,001$). En el músculo dominaron las proteínas (92,9 ± 3,2%), mientras que en el hígado se observó un aporte similar de las proteínas (55,5 ± 14,1%) y los lípidos (44,5 ± 14,1%). Los resultados aportan información novedosa, que era escasa para *M. hubbsi* en la plataforma continental argentina, y son útiles en el marco de modelos de ecología trófica de sus predadores, permitiendo comprender el flujo de energía en la trama trófica del Golfo San Jorge.

Palabras clave: Merluza común, Edad 0, Calidad nutricional, Plataforma continental argentina.

Introduction

Adult, juvenile, and larval fish from many species provide the bulk of the diet for several predacious fishes, seabirds, and marine mammals; these so-called “forage fish species” occupy a key position in the food web, transferring energy between primary or secondary producers and higher trophic levels (Anthony *et al.* 2000). Piscivorous predators can experience multi-fold differences in energy intake rates based solely on the types of fishes consumed (Anthony *et al.* 2000). Foraging predators must integrate prey value variability in balancing costs and benefits to optimize survival and reproductive fitness (Stephens & Krebs 1986). In this context, they might be able to adjust their selection depending on prey quality to satisfy nutritional and energy requirements, which can potentially increase their own physiological condition and the productivity of the population.

Fish quality can be defined in terms of their energy density (ED, kJ g^{-1} wet weight), which derives directly from lipid, protein and carbohydrate amounts stored in the tissues (Anthony *et al.* 2000). Since the latter are usually negligible in fish, energy is normally stored partly as proteins by increasing muscle mass and partly as lipids embedded in the muscles, visceral cavity (e.g. clupeids) or stored separately in the liver (e.g. gadoids) (Jørgensen & Fiksen 2006). Knowledge of forage fish quality is relevant in the context of predators' trophic ecology, considering that low quality prey intake can lead to detrimental effects on populations (“junk food” hypothesis; Rosen & Trites 2000). ED can be seen as the basic currency in ecosystems that determines the energetic value of a trophic transfer (Lindeman 1942). Hence, it can be integrated in bioenergetics models with prey selection, predator/prey abundance and distribution, and predator metabolic requirements to understand how ecosystem shifts influence marine trophic structure (Anthony *et al.* 2000, Breck 2014). In this context, sets of field data are necessary for the calibration and validation of these models (Dubreil & Petitgas 2009). Moreover, in oceans subjected to climatic pressures and human impacts such as global warming or overfishing, subsequent shifts in prey quality could affect the fitness of predator species, affecting not only modeling but also fisheries management (Spitz *et al.* 2010).

Argentine hake *Merluccius hubbsi* supports the major demersal finfish fishery in the Argentinean Continental Shelf (ACS). The Patagonian stock (located between 41°-55°S) is the most abundant,

accounting for 85% of total hake biomass in the ACS (Aubone *et al.* 2000). Age-0+ individuals (prerecruits; total length 10-15 cm) of this stock nurse and settle in the San Jorge Gulf (SJG, 45°-47°S, 65°30'W), reaching an average of 300.000 ind nmi^{-2} (nautical miles) in summer, estimated by acoustic methods (Álvarez Colombo *et al.* 2014). This gulf has been identified as a priority strategic area by Argentina's scientific community within the framework of the political science and technology national program for marine conservation “Pampa Azul,” funded by the federal government, provided it is a spawning and breeding ground for important commercial fisheries (Góngora *et al.* 2012). Within this gulf, age-0+ *M. hubbsi* constitute an important food source for several demersal fish such as *Squalus acanthias*, *Raja flavirostris*, *Genypterus blacodes* y *G. brasiliensis* (Sánchez & Prenski 1996, García de la Rosa & Sánchez 1997). For instance, 68% of *S. acanthias* diet corresponded to prerecruits (6-14 cm). Intercohort cannibalism is also very common by age-1+ and age-2+ conspecifics, with a 47% occurring upon the size range 10-24 cm (Sánchez & García de la Rosa 1999, Sánchez 2009). In addition, several birds and marine mammal species prey upon age-0+ *M. hubbsi*. In the northern sector of the SJG, young hake represented 50% in biomass of the diet of the imperial cormorant *Phalacrocorax atriceps* (Yorio *et al.* 2010), while being a secondary prey of Magellanic penguins *Spheniscus magellanicus* (Yorio *et al.* 2017). With respect to marine mammals, 74% of the *M. hubbsi* consumed by the sea lion *Otaria flavescens* were less than 30 cm in total length (Koen Alonso *et al.* 2000), while the dusky dolphin *Lagenorhynchus obscurus* preys upon *M. hubbsi*, including age-0+ individuals, with 48% of occurrence in the stomachs of individuals captured in the SJG (Koen Alonso *et al.* 1998, Loizaga de Castro *et al.* 2016).

In this context, knowledge of age-0+ *M. hubbsi* quality as prey constitutes a central and lacking piece of information in the context of foraging behavior studies of several top predators in the ACS. Our main objective was to estimate the ED of age-0+ *M. hubbsi* from proteins and lipids stored in their tissues (muscle and liver) as a food quality proxy for upper trophic levels in the San Jorge Gulf. These data should aid in understanding changes in predator populations at higher trophic levels, being useful in models of marine energy dynamics within the SJG food web.

Materials and methods

Age-0+ individuals were collected during a *M. hubbsi* stock assessment survey carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) on board the R/V “Eduardo Holmberg” in the San Jorge Gulf in austral summer of 2014. Individuals were captured during daylight by using a bottom trawl net Engel (100 mm mesh at codend, intranet cover of 20 mm mesh size, headrope of 35 m and footrope of 50 m) in eight fishing trawls. Fish ($n = 40$) were individually stored in vacuum-sealed plastic bags and quickly frozen at -20°C following catch.

Once in the laboratory, individuals were thawed and total length (12.8 ± 1.2 cm), total weight (13.1 ± 3.8 g), somatic (= gutted) weight (10.8 ± 3.9 g) and liver weight (0.4 ± 0.2 g) were measured. Head and viscera were removed and not considered in the analyses. Muscle and liver dissected from each specimen were homogenized with a food blender and a glass potter, respectively, and the homogenates preserved frozen at -80°C . These tissues were analyzed for protein and lipid content (%), expressed as $\text{g } 100 \text{ g}^{-1}$ wet weight, WW). Carbohydrates were not determined, since their contribution to the energy content of marine species is near zero (Anthony *et al.* 2000, Eder & Lewis 2005, Breck 2014). Protein content was determined from 0.5 and 0.1 g of muscle and liver, respectively, following Lowry *et al.* (1951) (standard: bovine serum albumin 1 mg ml^{-1}). Lipid content was determined gravimetrically from 2-10 g of muscle and 0.1-0.5 g of liver of each individual, following Bligh & Dyer (1959). For each individual, protein and lipid content in muscle and liver were converted to energy density units (kJ g^{-1}) by means of energy equivalents available from the literature (20.1 and 36.4 kJ g^{-1} , respectively; Brett 1995). These equivalents are most appropriate for fish such as *M. hubbsi*, which tend to have relatively large proportions of unsaturated fat (Temperoni *et al.* 2018). Then, the energy densities deriving from proteins and lipids in muscle and liver were multiplied by the somatic and liver weight, respectively, and divided by the total weight. Finally, the energy densities of muscle and liver were sum to obtain the total energy density (ED) of each individual, which was expressed as kJ g^{-1} to avoid prerecruits size effect. Contribution of both tissues energy densities to the total ED, and of protein and lipid content to liver and muscle energy density were calculated and plotted. Significance ($\alpha = 0.01$) of these relationships was tested with Pearson's

correlations (r_s) and simple linear regressions. Analyses were performed with STATISTICA 8.0 (Statsoft Inc.).

Results

Energy density of age-0+ *M. hubbsi* ranged from 1.6 to 5.5 kJ g^{-1} WW (mean \pm standard deviation: 3.4 ± 0.9). Muscle tissue made a higher contribution ($93.2 \pm 3.4\%$) than liver ($6.8 \pm 3.4\%$) to the total ED of the individuals (Fig. 1). Accordingly, a strong and significant correlation was observed between total ED and muscle energy density ($r_s = 0.99$, $R^2 = 0.98$, $p < 0.001$), while the relationship with liver energy density was not significant. ED was also significantly correlated with somatic weight of the individuals ($r_s = 0.54$, $R^2 = 0.29$, $p < 0.01$), but weight explained only half of its variation. Protein content (Table I) was the primary determinant of muscle energy density ($92.9 \pm 3.2\%$; Fig. 2a) and explained most of its variation (Fig. 2b), while lipids represented only a minor fraction ($7.1 \pm 3.2\%$). On the other hand, contribution of protein and lipid content (Table I) to the energy density of the liver was somewhat similar (proteins: $55.5 \pm 14.1\%$; lipids: $44.5 \pm 14.1\%$; Figure 2a), but lipids explained most of its variation (Figure 2b).

Discussion

This research provides relevant new information about the nutritional value of age-0+ *M. hubbsi* available as prey to piscivorous predators in the San Jorge Gulf. Energy density of *M. hubbsi* in the ACS has been scarcely explored, with a few reports on juveniles from Patagonia ($\sim 41^{\circ}\text{--}53^{\circ}\text{S}$, $62^{\circ}\text{--}68^{\circ}\text{W}$) (Ciancio *et al.* 2007) and adults collected

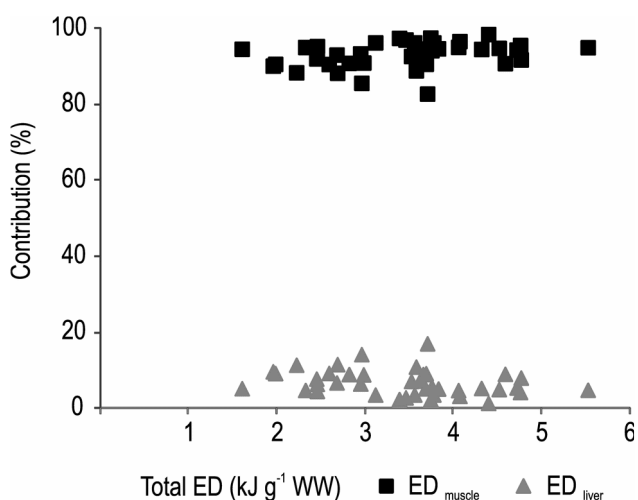


Figure 1. Contribution (%) of muscle (black squares) and liver (grey triangles) energy density (ED; kJ g^{-1} wet weight) to age-0+ *M. hubbsi* total energy density.

Table I. Range, mean and standard deviation (SD) values of protein and lipid content (% g 100 g⁻¹ wet weight) and energy density (ED; kJ g⁻¹ wet weight) in muscle and liver tissues of age-0+ *M. hubbsi*.

	Muscle			Liver		
	Range	Mean	SD	Range	Mean	SD
Protein content	10.04 - 27.04	18.02	3.62	13.42 - 26.43	20.30	3.32
Lipid content	0.18 - 1.37	0.73	0.30	1.34 - 24.64	10.15	5.38
ED_{protein}	1.38 - 4.98	2.97	0.83	0.05 - 0.23	0.11	0.04
ED_{lipid}	0.04 - 0.45	0.22	0.11	0.01 - 0.40	0.11	0.08
ED_{total}	1.52 - 5.25	3.20	0.88	0.06 - 0.63	0.22	0.12

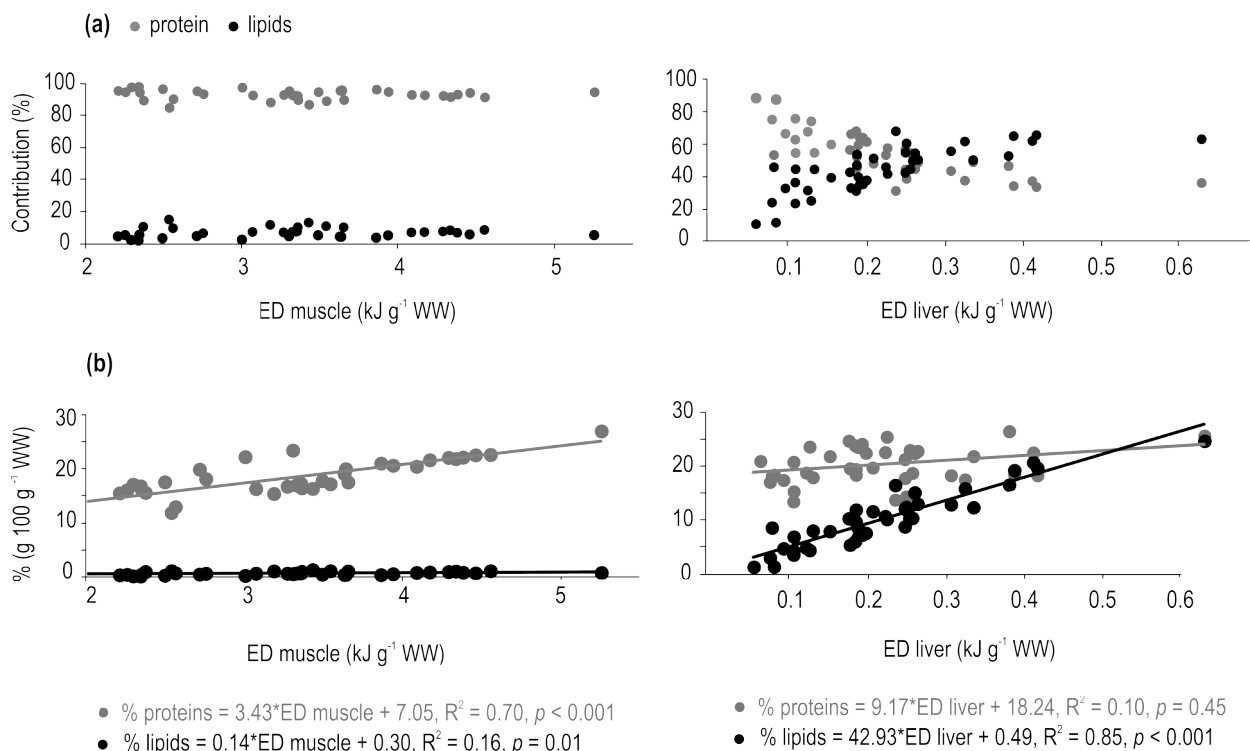


Figure 2. (a) Contribution (%) of proteins and lipids energy density to total energy density (ED, kJ g⁻¹ wet weight) in muscle and liver tissues of age-0+ *M. hubbsi*. (b) Relationships between protein and lipid content (% g 100 g⁻¹ wet weight) and the energy density of each tissue.

between 39°-51°S, 55°-65°W (Eder & Lewis 2005). Also, energy density of muscle, liver and gonads in adult individuals from the Argentinean shelf between 39°-53°S (Montecchia *et al.* 1990) and the Patagonian stock (Leonarduzzi *et al.* 2014) has been investigated. Our ED values, ranging between 1.6 and 5.5 kJ g⁻¹ WW (3.4 ± 0.9), are in agreement with those from Ciancio *et al.* (2007) and Eder & Lewis (2005), which reported mean values of 4.1 and 4.9 kJ g⁻¹, respectively. In addition, our values also resemble those found in age-0+ individuals of related gadoid species such as *Gadus macrocephalus* (Van Pelt *et al.* 1997), *Theragra chalcogramma* (Paul *et al.* 1998, Cianelli *et al.*

2002, Buchheister *et al.* 2006, Moss *et al.* 2009, Whitman 2010) and other members of the Gadidae family (Spitz *et al.* 2010), which varied between 2-4 kJ g⁻¹. In most of these works, bomb calorimetry or proximate composition analysis were the methodologies used to estimate ED, both of which consider the whole individual, rather than estimating it from protein and lipid content in muscle and liver, as in the present paper. However, our estimated age-0+ *M. hubbsi* ED values are comparable and within the same range as those previously recorded in the same and related species, providing support to our methodology.

When determining fish energy density, it is worth noting that, for the same species, values can vary considerable among seasons (Ciancio *et al.* 2007), ontogenetic stages (Breck 2014), spatial location and genders (Vollenweider *et al.* 2011). In this context, inaccurate estimates of ED can have significant implications for bioenergetic models, which are highly sensitive to fish condition inputs (Shelton *et al.* 1997). Estimates of ED that are developed specifically for the species and life stage of interest are preferable because extrapolating methods to different size-classes, life stages, or habitats is likely to introduce biases (Trudel *et al.* 2005). Hence, our data set provides life-stage-specific (for age-0+ individuals) energy data necessary to model energy flows in the San Jorge Gulf ecosystem during austral summer. Current efforts are being devoted to determine age-0+ *M. hubbsi* quality as prey in the San Jorge Gulf during winter and spring scenarios, to evaluate whether the energy they could provide to top predators fluctuates seasonally.

In age-0+ *M. hubbsi*, muscle tissue made a higher contribution (> 90%) to total energy density than liver tissue. This was expected, considering that muscle usually accounts for more than half of the fish's body mass (Houlihan *et al.* 1989). Within the muscle, most of the energy was derived from proteins, which were the dominant component in terms of percentage. This was also observed in *M. hubbsi* females (Leonarduzzi *et al.* 2014). On the other hand, within the liver, a fairly equal contribution of proteins and lipids to total energy density was observed. However, lipid content was higher in the liver than in the muscle. This confirms that liver is a lipid depot and muscle a protein depot in age-0+ *M. hubbsi*, as previously observed in adults of the species (Chiodi 1966, Montecchia *et al.* 1990, Méndez 1997, Leonarduzzi *et al.* 2014) and related gadoids (Lambert & Dutil 1997). However, it should be noticed that energy allocation strategies differ in juvenile and adult fish, provided that in the latter, gonads represent a third energy depot that is involved in reproduction and spawning. Particularly for rapidly growing age-0+ individuals, the energy allocation strategies reflect competing physiological demands of somatic growth versus lipid storage (Post & Parkinson 2001). Within the SJG, age-0+ *M. hubbsi* are known to prey upon lipid-rich crustacean prey (Temperoni & Derisio 2018) that probably provides them with sufficient metabolizable energy for maintenance. In this context, dietary protein can be allocated to tissue

synthesis and muscle growth (Roby 1991). The positive and significant correlation observed between total weight and total ED, which was mostly explained by protein content in the muscle, provides evidence for this fact. A rapid muscle growth could be advantageous in order to avoid predation and increase survival, as has been suggested for age-0+ walleye pollock (Cianelli *et al.* 1998).

Energy density values estimated for age-0+ *M. hubbsi* allow making a comparison with values available for other prey that are consumed by upper level predators (*S. acanthias*, *R. flavirostris*, *G. blacodes*, *G. brasiliensis*, *P. atriceps*, *S. magellanicus*, *O. flavescens* and *L. obscurus*) in the San Jorge Gulf. These predators, besides eating age-0+ *M. hubbsi*, also prey upon fish such as *Engraulis anchoita*, mollusks such as *Illex argentinus* and *Loligo gahi*, and crustaceans such as *Pleoticus muelleri*, *Munida gregaria*, and *Euphausia lucens*. ED values (kJ g^{-1} wet weight) for these prey species in the ACS are available from Ciancio *et al.* (2007), Eder & Lewis (2005) and Temperoni & Derisio (2018) (Table II). From these values, it is clear that prey profitability for predators assessed from ED can differ largely between species. In this sense, Spitz *et al.* (2010) proposed three functional groups based on ED values (wet weight basis): low ($\text{ED} < 4 \text{ kJ g}^{-1}$), moderate ($4 < \text{ED} < 6 \text{ kJ g}^{-1}$) and high quality species ($\text{ED} > 6 \text{ kJ g}^{-1}$). Considering this classification, age-0+ *M. hubbsi* could be considered a low or moderate quality prey, while *E. anchoita*, mollusks and some crustaceans would represent high-quality prey species. As stated by Spitz *et al.* (2010), all forage species, even when morphologically or taxonomically similar, cannot be considered as equivalent and interchangeable for the fulfillments of predator energy and food requirements. This information is key and should be considered when analyzing nutritional status of top predators and their energy allocation strategies in the ACS.

Predators can compensate for variation in prey availability through adjusted selection of prey in terms of their nutritional quality (Anthony *et al.* 2000), which has been demonstrated to have important effects on the performance of consumers. For instance, in the Gulf of Alaska and the Aleutians, the Steller sea lions population declines were related to the quality and diversity of fish prey available in the wild (Merrick *et al.* 1997, Rosen & Trites 2000, Österblom *et al.* 2008). In the North Sea, *Ammodytes marinus* quality appeared to be the

Table II. Mean energy density (ED, kJ g⁻¹ wet weight) values of prey species to top predators in the San Jorge Gulf. *dry-weight basis.

Prey species	Size range (cm)	ED (kJ g ⁻¹ WW)	Source
Fish			
<i>Merluccius hubbsi</i>	14.0-14.6	4.07	Ciancio <i>et al.</i> (2007)
	33.0-64.0	4.91	Eder & Lewis (2005)
	10.0-14.5	3.42	This study
<i>Engraulis anchoita</i>	11.0-15.5	5.55	Ciancio <i>et al.</i> (2007)
Mollusks			
<i>Illex argentinus</i>	21.0-41.5	5.01	Ciancio <i>et al.</i> (2007)
	16.5-33.0	6.42	Eder & Lewis (2005)
<i>Loligo gahi</i>	60.0-90.0	4.95	Ciancio <i>et al.</i> (2007)
Crustaceans			
<i>Munida gregaria</i>	5.0-7.0	11.01*	Ciancio <i>et al.</i> (2007)
	0.3-4.2	1.42	Temperoni & Derisio (2018)
<i>Euphausia</i> spp.	0.2-1.3	2.51	Ciancio <i>et al.</i> (2007)
	0.8-2.4	1.28	Temperoni & Derisio (2018)
<i>Pleoticus muelleri</i>	3.9-4.5	5.91	Ciancio <i>et al.</i> (2007)

proximate cause of seabird breeding failure in 2004, giving support to the ‘junk-food’ hypothesis (Wanless *et al.* 2005). For the South West Atlantic Ocean, it has been suggested that top predators populations are not declining, probably due to a broader spectrum of prey with high energetic value (Eder & Lewis 2005). However, within the Patagonia Large Marine Ecosystem, the ACS has shown significant increases in satellite chlorophyll *a* concentrations during the last ~20 years, with large potential implications for trophic relationships (Marrari *et al.* 2017). If this is the case, changes in prey species composition brought about by shifting ocean regimes may greatly affect the predators in the ecosystem, including commercially important fishes (e.g. Trites *et al.* 2007). This could be the case for age-0+ *M. hubbsi* in the SJG, whose energy reserves, particularly lipids, are known to be controlled by a bottom-up effect mediated by herbivorous euphausiids (Temperoni *et al.* 2018). In this context, information about age-0+ *M. hubbsi* quality is useful to understand future changes in trophic responses of predators as consequences of seasonal changes in food availability in a global change scenario.

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