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Research Article

Why are Brazilian deep-demersal fish resources valuable? An analysis of the size of edible flesh and its chemical composition

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ABSTRACT. Slope trawl fisheries of the southeastern and southern region off Brazil operate at 250-500 m depths, being basically sustained by three target-species: hake (*Merluccius hubbsi*), codling (*Urophycis mystacea*) and monkfish (*Lophius gastrophysus*), together with other high-priced species landed as incidental captures. These and all other species landed by the slope trawl fleet were sampled from commercial catches, differentiating between shelf/shelf-break species and slope species. Each species was characterized by ex-vessel price, carcass yield and chemical composition: water content and protein content as percentage of wet and dry mass. The differences found in the chemical composition of the slope species, relative to the shallower group, seemed to reflect adaptations for particular environmental factors; most likely low light levels in deeper areas. Their muscles were richer in water and lower in protein and lipids. Ex-vessel prices correlated better with these characteristics than with the edible fraction, revealing that slope fishes exploited off Brazil are appreciated more by their organoleptic characteristics, given by the chemical composition, than by the per-unit profit of the species.

Keywords: slope trawl fisheries, protein content, carcass yield, ex-vessel prices.

¿Por qué son valorados los recursos pesqueros demersales y de profundidad brasileños? Análisis del tamaño de los filetes y su composición bioquímica

RESUMEN. Las pesquerías de arrastre de talud de la región sudeste y sur de Brasil operan principalmente entre 250-500 m de profundidad, siendo básicamente sostenidas por sus especies objetivo: merluza (*Merluccius hubbsi*), brótola de profundidad (*Urophycis mystacea*) y rape (*Lophius gastrophysus*), junto con otras especies de elevado valor comercial desembarcadas como capturas incidentales. Éstas y todas las demás especies desembarcadas por la flota de arrastre de talud, fueron muestreadas a partir de las capturas comerciales, diferenciando entre especies de plataforma/borde de plataforma y especies de talud. Para cada especie se determinó el precio de primera venta, el rendimiento del cuerpo y la composición química: contenido en agua y contenido proteico como porcentaje de materia húmeda y seca. Las diferencias encontradas en la composición proximal de las especies de talud, en relación al grupo de menor profundidad, parecen reflejar adaptaciones a factores ambientales particulares; principalmente por la menor luminosidad en aguas más profundas. La musculatura fue más rica en agua y más pobre en proteínas y lípidos. Los precios de primera comercialización se correlacionaron con dichas características más que con la fracción comestible, revelando que las especies de talud explotadas en aguas brasileñas son más valoradas por sus características organolépticas, dadas por la composición química, que por su aprovechamiento individual.

Palabras clave: pesca de arrastre de talud, contenido proteico, rendimiento del cuerpo, precios de primera venta.

INTRODUCTION

Capture fisheries are responsible for two-thirds of the marine products consumed worldwide, directly contributing 10% of total animal protein destined for human nutrition (Tyedmers, 2004). Historically, this contribution has been sustained by intense harvesting of coastal, productive and accessible resources. However,

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because these resources have been exhaustively exploited and demands for marine products have increased by the world's growing population, fisheries globally expanded seaward, to remote deep areas (Pauly *et al.*, 2005; Morato *et al.*, 2006; Norse *et al.*, 2012). Such expansion was initially driven by the search for better catches of shelf demersal resources in the rim of the continental margin. Gradually, this process also led to the identification of concentrations of fish and shellfish species, usually dwelling on the slope and seamounts, that encouraged the development of specialized (most notably trawl) 'deep-water fisheries' (DWF) (Japp & Wilkinson, 2007). Because deep ecosystems are generally food-limited, deep water species were shown to be less productive and less resilient than shallow-water species, hence clearly not capable to replace economic losses at overfished continental shelves (Norse *et al.*, 2012). Nonetheless, important trawl fisheries have persisted in deep areas of the Pacific, Atlantic, Indian and Southern oceans as driven by aggregation patterns of some fish stocks, economic subsidies to the fishing industry and the high value sometimes attributed to commercial deep-water species (Koslow *et al.*, 2000; Gianni, 2004; Norse *et al.*, 2012).

Paralleling global trends, demersal fisheries off Brazil have also undergone a deep-water expansion process since the late 1990's. Landings of slope fish and shellfish species drastically increased between 2000 and 2007, being largely produced by a foreign fleet licensed to fish in Brazilian waters, as part of a fishery expansion government policy. Highly efficient and driven by export demands these vessels caused, in less than seven years, severe biomass reductions of most stocks, revealing their high susceptibility to overfishing (see Perez *et al.*, 2009). After 2007 activities of the foreign fleet came to an end, but slope fishing persisted mostly through a bottom trawling fishing regime established by national vessels (Dias & Perez, 2016). These trawlers have gradually spread their footprint to the slope areas of southeastern and southern sectors of Brazilian coast, between 100 and 500 m depth, exploiting multiple fish and crustacean species (Port *et al.*, 2016).

Recent studies have shown that a fraction of these trawlers gradually became 'specialized' in slope trawling and focused their effort on three target-species: hake (*Merluccius hubbsi*), codling (*Urophycis mystacea*) and monkfish (*Lophius gastrophysus*). Another fraction, however, adopted a 'generalist' behaviour in the slope areas producing lower catches of the former species, but retaining important amounts of other species including those available at the outer continental shelf and the shelf-break (Dias & Perez, 2016). These trawlers are led by fishermen that have learned to exploit opportunistically different species and areas in order to meet (or increase) their annual income demands. This strategy has proven economically successful in view of the excessive effort historically built upon the main shelf resources and competition for their reduced biomass (Pezzuto & Mastella-Benincá, 2015). Contrastingly, specialized trawlers have adapted to thrive exclusively on slope resources, suggesting that their abundance and/or value may compensate for (a) the economic advantages of generalist fishing and (b) the extra costs determined by the need to move longer distances and conduct lengthy deep trawling operations (Sethi *et al.*, 2010).

Fishing surveys and assessments conducted in the early 2000's concluded that most slope resources had reduced exploitation possibilities due to their generally low densities and limited sustainable harvesting rates, as inferred from specific life-history patterns (*e.g.*, growth and natural mortality rates) (Perez, 2006; Haimovici *et al.*, 2008). In Santa Catarina State, for example, that congregates a significant part of the trawl fishing industry, slope fish have represented no more than 15% of annual landings of all demersal resources (UNIVALI/ CTTMar, 2010). Value, on the other hand, as evidenced by prices attributed to some slope species in both domestic and international markets (*e.g.*, monkfish, Soares, 2008), is generally higher than that of shallow water species and may explain the sustained interest of trawlers that have fully relied on slope fish (Dias & Perez, 2016).

Value of fishing resources may be related with various indicators of per-unit profitability, including fish size, body shape and processing considerations (Sethi *et al.*, 2010). In addition, nutritional features, as determined by proximate composition, may contribute to the quality of food products and therefore to the profitability of different species to fishermen. This study explores the hypothesis that value of fish exploited by the trawl fisheries on the shelf-break and slope off southeastern and southern Brazil is related to the size of the edible fraction of fish targeted by trawlers and its protein and water content. We propose that these characteristics could have been elemental to make slope fish attractive to domestic and international markets and contribute to the development of a specialized slope trawl fisheries. Because fish chemical composition and physiological properties, as well as life-history traits, may reflect adaptations to habitat physical (temperature, light, depth, etc.) and biological conditions (type of food and quantity of them) (Childress, 1995; Drazen, 2007), we further explore the relationship between the value of slope fisheries and the selective pressures of deep demersal ecosystems off

Brazil. Information on chemical composition of Brazilian marine capture fish is scarce (Diniz *et al.*, 2013) making such aspects of Brazilian fisheries development largely overlooked.

MATERIALS AND METHODS

The selection of species to be included in the present analysis involved initially the consideration of previous studies that focused on the definition of fishing targets of the trawl fishery off southeastern and southern Brazil (Perez & Pezzuto, 2006, Perez *et al.*, 2009, Dias & Perez, 2016). Additionally, the species composition of 174 landings of trawlers that operated between 250 and 500 m depths were analysed from records obtained through interviews with skippers and logbooks between 2001 and 2015, as part of a routine industrial fishing sampling program conducted at the harbours of Santa Catarina State, Brazil (Perez *et al.*, 1998). The elected species were classified according to the known centre of their bathymetric distribution into (a) outer continental shelf/ shelf-break species (<250 m) and (b) slope species (>250 m). Samples of the selected species were obtained at the landing sites or at sea during commercial trips monitored by observers.

Seven to twelve individuals of each species were analysed for determination of carcass yields. Individuals had the total weight recorded (to 0.1 g) and were dismembered into five body parts: viscera, head (including gills), edible flesh, skin and scales, and the spine with the tail. These parts were weighed separately and expressed as proportions of total body weight (Britto *et al.*, 2014). Edible flesh comprised the trunk muscle, without bones and skin, and was regarded as the 'edible fraction' of each analysed species.

An approximate 12 g sample of the white muscle was extracted from each specimen and used for crude protein quantitation using the Kjeldahl method (AOAC 940.25, for fish and fish by-products) (AOAC, 2000). This method is based on the estimation of total nitrogen content in the muscle subsequently transformed into crude protein using Jones' factor (Jones, 1941) of N x 6.25, which assumes that most proteins contain around 16% of nitrogen (FAO, 1985; Regulation (EU) Nº1169/2011). It involved a digestion of the muscle sample with concentrated sulphuric acid, mediated by a copper catalyst, followed by a distillation and titration of the resulting solution. Through this process, all the organic nitrogen was transformed into ammonia, which is driven by steam through a boric acid solution and, finally, then titrated with hydrochloric acid. The volume of titration is used to calculate the protein values as showed in the equation 1, where *%Pwm* is the protein as percentage of wet mass; *V* is the volume of titration; *F* is the correction factor for the HCl solution; *N* is the normality of the HCl solution; 6.25 is Jones' factor; 0.014 is the nitrogen mEq; and *G* is the amount of sample used. Moisture was measured by drying 1.0 g of the muscle sample in infrared balance (Shimadzu MOC63U) and expressed as a percentage of the tissue mass; then the protein as percentage of dry mass *(%Pdm*) is calculated with the equation 2.

$$\%Pwm = \frac{V\ x\ F\ x\ N\ x\ 6.25\ x\ 0.014\ x\ 100}{G} \quad (1)$$

$$\%Pdm = \frac{\%Pwm}{\%\ dry\ mass} x100 \quad (2)$$

Commercial value of the selected species was represented by mean ex-vessel prices, here referred as the prices received by the fishermen after the first sale of the catch, which is what ultimately motivates them to go fishing (Sumaila *et al.*, 2007). These data were recorded in three consecutive years (2008-2010) in Santa Catarina State (Pezzuto & Mastella-Benincá, 2015). These mean prices were corrected to inflation to the reference date of July 2015, using the 'Producer Price Index' (*PPI*) (Fundação Getúlio Vargas, 2015), which records monthly prices of agriculture and industrial goods previous to final marketing (*e.g.*, at the producer level), according to the following equation 3:

$$V_{iy'} = \bar{V}_{iy}\ x\ \frac{PPI_{y'}}{PPI_y} \quad (3)$$

where ex-vessel price (*V*) of the species *i* in the period *y'* = July 2015 results from the mean price of this species in the period *y* = 2008-2010 (corrected for inflation to December 2010; Pezzuto & Mastella-Benincá, 2015) multiplied by the ratio between the PPIs in both periods (R$, converted to US$ 1 = R$ 3.13 in July 15th, 2015).

Data analysis

Ex-vessel prices of selected species (response variable) were plotted against the potential explanatory variables: edible fraction, protein as percentage of dry mass, protein as percentage of wet mass and water content. Linear regressions were fitted to these relationships and calculated slopes were tested for deviations from 0 (α = 0.05). In addition, protein in the wet mass and water were included in a multivariate Principal Component Analysis (PCA) to explore their correlation with biological and ecological features of the selected species (obtained from Haimovici *et al.*, 2008 and Visintin, 2015). The former included Von Bertalanffy's curve growth parameter (k), maximum length (LMAX), length-at-maturity (LMAT), maximum age (AMAX) and age-at-maturity (AMAT). The ecological features included mean landing per unit effort (LPUE) (kg h^{-1}) calculated between 2010 and 2011 as a proxy for the species density, trophic level (TL) and minimum depth of occurrence (MDO).The latter variable is defined as the depth below which 90% of a particular species were captured (Childress, 1995; Drazen & Seibel, 2007). Because accurate information about depth distribution was not available for all species, MDO was sometimes assumed as the mean depth of occurrence. All variables were standardized as a proportion of their mean. After building a correlation matrix, new axes (factors, or linear combinations of the original variables) were obtained in the direction of greatest variance, and variables were represented in a reduced two-dimension space. The argentine shortfin squid (*Illex argentinus*) was not included in this analysis as cephalopods have different structure and physiology (Seibel *et al.*, 1997).

RESULTS

Fourteen species were identified as most abundant and/or frequent in the slope trawl fishery. 'Slope species' comprised the main fishing targets (hake, codling, monkfish) together with the silver John dory (*Zenopsis conchifer*), pink cusk-eel (*Genypterus brasiliensis*), tilefish (*Lopholatylus villarii*), argentine shortfin squid (*Illex argentius*) and beardfish (*Polymixia lowei*) (Table 1). Those characteristically from shelf break area, usually included in the incidental captures, were the argentine goatfish (*Mullus argentinae*), grey triggerfish (*Balistes capriscus*), white-mouth croaker (*Micropogonias furnieri*), flounders (*Paralichthys* spp.), spiny dogfish (*Squalus* spp.) and bluewing searobin (*Prionotus punctatus*).

Carcass yields and chemical composition

The edible fraction was highest in the argentine shortfin squid (*I. argentinus*) (70%). This result was expected because, except for viscera and part of the head, squid body is all used for human consumption. Fish edible fractions oscillated around a mean value of 34% in both slope and shelf break groups. Highest edible fractions were shown by *U. mystacea* and *G. brasiliensis* (42.9% and 41.2%, respectively) (Fig. 1). This fraction was also elevated in *M. argentinae*, although that result may have been affected by handling difficulties (*e.g.* skin/scales fraction was computed with the edible one). Monkfish (*L. gastrophysus*) and silver John dory (*Z. conchifer*) exhibited remarkably low edible fractions due to the high proportions represented by head and spine fractions, respectively. Slope and outer shelf/shelf break species did not differ significantly in their edible fractions (Kruskal-Wallis Test, $P = 0.569$) (Fig. 2a).

Outer shelf/shelf break species exhibited slightly higher protein content (in the wet mass) than slope species (Fig. 2b), although no significant difference was found (Kruskal-Wallis Test; $P = 0.302$). Spiny dogfish (*Squalus* spp.) revealed the highest value (23.9%), followed by codling, grey triggerfish and bluewing searobin, all oscillating around 22%. In contrast, the argentine shortfin squid, monkfish, flounder and tilefish presented the lowest levels of muscle protein (13.1, 17.6 and 17.6%, respectively). On the other hand, almost the entire edible fraction of codling, hake, monkfish and the pink cusk-eel was composed of crude protein (96.2-91.9% of dry matter; Table 1) as opposed to beardfish and argentine goatfish, which exhibited the lowest protein contents in their edible fractions (64.4-64.7% of dry matter). Generally, slope species showed more protein content, as percentage of dry mass, than the shallower species (Fig. 2c); however, no statistical difference was found (Kruskal-Wallis Test (KW); $P = 0.245$). Highest levels of water were found in the flesh of the argentine shortfin squid and monkfish (82.9-80.9%), contributing for the mean value of 76.6% for the slope species (Fig. 2d). Once again, this difference between the groups was not statistically different (KW; $P = 0.053$).

Value analysis

Ex-vessel prices (US\$ kg^{-1}) of the selected species are listed in Table 1. Mean values of slope and outer shelf/shelf break species did not differ significantly (KW; $P = 0.796$) but the slope species, pink cusk-eel, monkfish and codling were the most valuable among the selected species (US\$ 1.02, 0.97 and 0.87 kg^{-1}, respectively). Protein content, as % of dry mass, was found to positively affect ex-vessel prices of the elected species (slope = 0.018; $P = 0.001$) (Fig. 3a). A similar, yet not significant, effect was shown by the water content (slope = 0.023; $P = 0.095$) (Fig. 3b). Edible fraction and protein content, as % of wet mass, had no effect on the species values (slope = -0.003; $P = 0.637$ and slope = 0.007; $P = 0.8$, respectively) (Figs. 3c-3d). Such effects remained unchanged when only fish data were analysed (the Argentine short finned squid removed), except for the water content which turned to affect significantly ex-vessel prices (slope = 0.033; $P = 0.024$).

Protein (% wet mass) and water contents were included in a multivariate exploratory approach to assess potential associations with ecological and biological characteristics of the selected species. In this analysis the argentine squid was not included because of the essential differences that cephalopods display when compared to fish, that could introduce errors in general interpretations. The first two PCA extracted factors explained together 69.88% of the total variance (Factor 1: 47.5%; Factor 2: 22.4%). Trophic level, length-at-maturity, maximum length and water content were highly correlated, as were protein content and

Table 1. Selected species separated by bathymetrical distribution. Chemical composition expressed as percentages of the total muscle mass. Value correspond to ex-vessel prices (US$/kg). Biological (k (growth rate), maximum length, length at maturity, maximum age) and ecological (LPUE, minimum depth of occurrence (MDO), trophic level) variables used for Principal Components Analysis (PCA). *Averages excluding *I. argentinus*. **Mean depth of occurrence.

Name	Scientific name	Chemical composition			Value ($US\$ kg^{-1}$)	PCA						
		Water content (%)	Protein-dry mass (%)	Protein-wet mass (%)		K	Length max. (cm)	Length maturity (cm)	Age max. (years)	LPUE ($kg\ hour^{-1}$)	MDO (m)	Trophic level
Slope (≥ 250 m)												
Argentine hake	*Merluccius hubbsi*	78.56	94.69	20.30	0.55	0.230	60	35	12	23.58	375	4.3
Brazilian codling	*Urophycis mystacea*	77.27	96.19	21.86	0.87	0.108	65	43	14	57.34	405**	4.7
Monkfish	*Lophius gastrophysus*	80.9	91.93	17.56	0.97	0.125	95	52	18	9.93	510	4.7
Silver John dory	*Zenopsis conchifer*	74.06	73.70	19.12	0.15	0.142	63	29	15	1.04	300	3.8
Pink cusk-eel	*Genypterus brasiliensis*	79.29	94.03	19.47	1.02	0.099	145	53	29	2.20	300	4.7
Tilefish	*Lopholatylus villarii*	79.63	86.47	17.61	0.58	0.040	107	42	35	1.06	270**	4.6
Argentine squid	*Illex argentinus*	82.87	76.72	13.14	0.35							
Beardfish	*Polymixia lowei*	66.38	64.57	21.71	0.18	0.130	30		20	1.89	400	3.5
	Average	76.58*	85.94*	19.66*	0.58							
Shelf break (≤ 250 m)												
Argentine goatfish	*Mullus argentinae*	68.84	64.74	20.17	0.38	0.220	25	13	8	0.06	150	3.5
Grey triggerfish	*Balistes capriscus*	73.89	83.54	21.81	0.49	0.180	60	20	14	0.05	50**	3.6
Whitemouth croaker	*Micropogonias furnieri*	77.13	83.66	19.33	0.63	0.255	75	35	40	0.02	50**	3.3
Flounder	*Paralichthys* spp.	77.99	79.99	17.61	0.62		38			0.72	150	4.0
Spiny dogfish	*Squalus* spp.	72.63	87.34	23.90	0.69	0.050	89	59	35	0.02	170**	4.3
Bluewing searobin	*Prionotus punctatus*	66.41	67.65	21.65	0.56	0.130	46	26	15	0.50	180**	3.8
	Average	72.82	77.82	20.75	0.56							

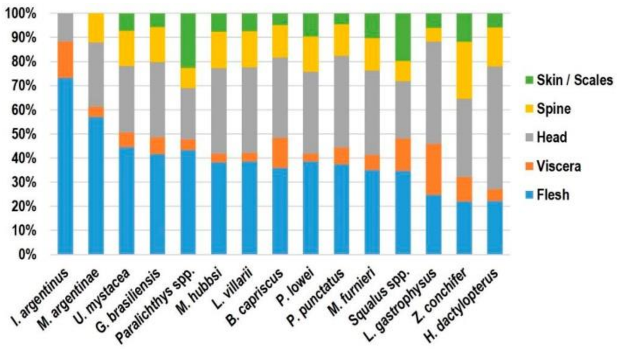

Figure 1. Carcass yield of target-species and main incidental species of the slope-trawl fishery fleet off southeastern and southern Brazil.

growth rate (Fig. 4). Highest loadings in Factor 1 were attributed to trophic level, length-at-maturity, maximum length and water (positive) and growth (k) (negative). Factor 2 was largely influenced by LPUE, depth (positive) and maximum age (negative).

In the bi-dimensional space produced by factors 1 and 2 (Fig. 4), slope species tended to appear in the right-hand hemiplane, as determined by their high scores in factor 1; (*i.e*. species with lower growth rates, larger sizes, higher trophic levels and higher water contents). Hake and silver John dory were the exceptions of the group due to the high growth rate of the former, and the relative high protein content and low trophic level of the latter. The upper-right position of the codling was a result of its high abundance (LPUE) and the depth reached.

Species that are generally captured in outer shelf and/or shelf break concentrated in the left hemiplane as scored by their faster growth, smaller sizes, trophic levels and water contents and higher protein. For this group the anomaly in the distribution was spiny dogfish due to its lower growth rate and higher length at maturity and maximum age. Their scores by factor 2 were also generally low due to their less abundant biomass (incidental species) and shallower catches.

DISCUSSION

Fishermen pursue fish and shellfish species in different marine environments expecting profits; *i.e.*, that total incomes exceed fishing costs (Sethi *et al.*, 2010). In deep and remote areas of the continental margins, operating costs are generally high and only valuable concentrations (and/or economic subsidies) should drive specialized fishing. Off southeastern and southern Brazil, developing slope trawl fishing has been sustained by three top-valued fish species (hake, codling and monkfish) along with high-priced components of the incidental catch, most notably the pink cusk-eel. The present study associates their value, as perceived by fishermen, with the proximate composition of their edible fractions, regardless of the size of that fraction (*i.e*., their carcass yields).

Fish products have generally been regarded as important sources of animal protein for human societies (World Bank, 2013). The edible fraction of fish, the muscle, is composed of water (mostly), protein and lipid, and a very small fraction, about 1-2%, comprising carbohydrates, nucleic acids, and inorganic salts (Childress & Nygaard, 1973; Diniz *et al.*, 2013). Aside from water, fish muscle is basically made of protein and lipids in an inverse relationship. In general, proteins concentrated in fish muscle, along with some fatty acids, provide benefits to human nutrition and seem good reasons to consume fish products and motivate fishing enterprises.

On that base, it was revealed that slope species tend to present higher water content and lower protein content in their muscle than the species that live in shallower areas of the outer shelf/shelf break. Slope species may also be poor in lipids, as inferred by the remarkably high content of proteins in the dry muscle. Interpretation of these results demands caution owned to the fact that the Kjeldahl method, here applied, measures both protein and non-protein nitrogen, overestimating to some extent the results obtained for all the species. In the case of elasmobranchs, such as the spiny dogfish (23.9%), the apparently high protein content can in fact be affected by the elevated levels of urea and TMAO (trimethylamine oxide), used for the osmoregulation (Bone, 1988; Lakshmanan, 2000). For teleost species it was found an increase in TMAO with depth (Samerotte *et al.*, 2007); however, the mean value obtained by these authors for several species from different families, was only about 0.7% of the total composition. Although the concentration and trends in these non-protein nitrogen compounds in fishes may be relevant they are limited to about 6-14% of the total nitrogen contained in the muscle (Puwastien *et al.*, 1999; Diniz *et al.*, 2013).

Fish chemical composition and physiological features are determined by environmental surrounding conditions, both biotic and abiotic. The exploratory multivariate analysis revealed that both the low protein (% wet mass) and the high water contents were generally associated with features attributed to slope fishes such as large size, slow growth, late maturity and high trophic level. These features agree with similar studies focusing on deep pelagic and benthopelagic species (Childress & Nygaard, 1973; Childress, 1995; Drazen, 2007; Drazen & Seibel, 2007), which generally propose that such chemical adjustments may constitute

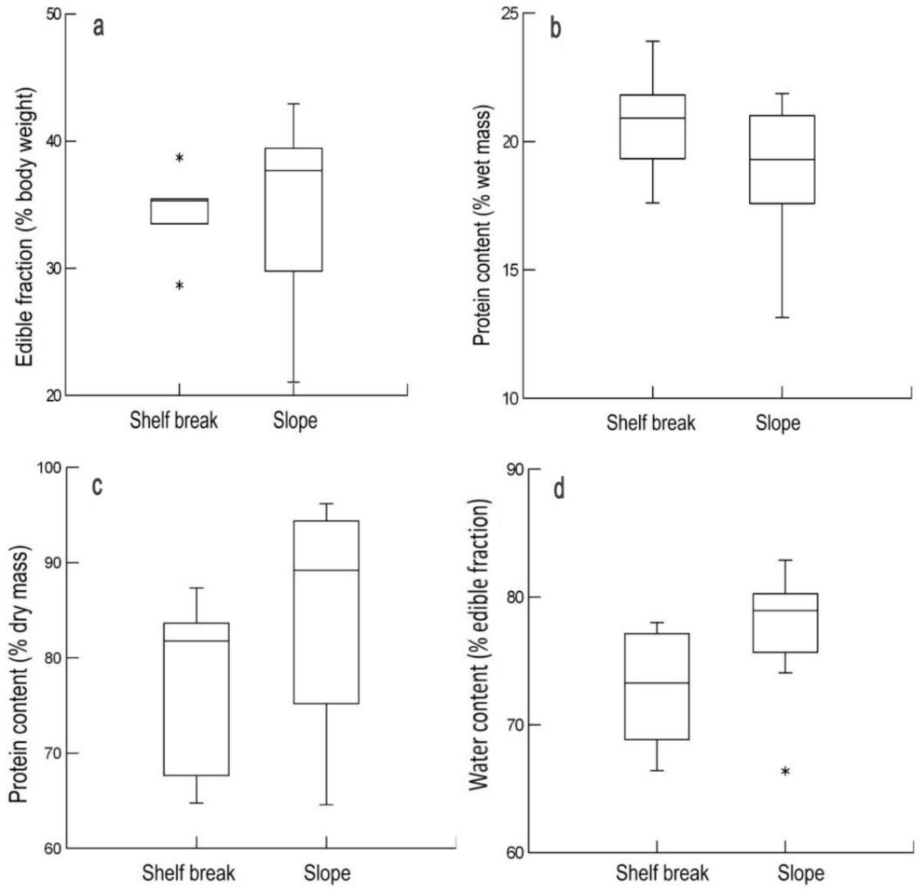

Figure 2. Comparison between outer shelf/shelf break and slope species for the principal body features analysed. a) Edible fraction; b) protein content, % wet mass; c) protein content, % dry mass; d) water content. The differences between the groups of species for all the variables were not statistically significant (KW; $P > 0.05$). In the graphics, the box includes 50% of the data for each variable and each group of species; the inner line of the box indicates the median; the whiskers extend to the 5^{th} and 95^{th} percentiles.

a suite of adaptations to deep ecosystem conditions. Specifically, lower light levels at slope depths could be a determinant factor since in an environment with reduced visual interaction distances, predator-prey visual relations are relaxed and so the necessity of great locomotor capacity (Childress, 1995; Drazen, 2007; Drazen & Seibel, 2007), which subdue a major purpose that is energetic economy (Drazen *et al.*, 2007). The result is a watery composition with low caloric demand per unit of muscle, which enables larger body sizes, helpful to decrease potential predators and increase access to bigger preys in food poor environments. Contrastingly, outer shelf/shelf break species contained more protein in the muscle, necessary in a more brightly lit environment where visual interactions occur over longer distances and higher proportion of lipids as a primarily form of energy store.

Differences in the biochemical composition between both groups of species here analysed may result in divergent sensorial characteristics of the edible flesh because "for humans, flavour and nutrition are inseparable" (Mahboob *et al.*, 2009). Ex-vessel prices increased with water and protein content as percentage in the dry mass, which indirectly reflects low lipid proportion. Fish muscle lipids include, among other components, short-chain fatty acids associated with volatile organic compounds that are responsible for the fish aroma, usually more important to humans than taste (Gabr & Gab-Alla, 2007). Such particularities in muscle composition suggest that high-priced slope species present more attractive organoleptic features than fish from the shallower group, given by an odourless, leaner smooth flesh (Gabr & Gab-Alla, 2007; Mahboob *et al.*, 2009), found for instance in the pink cusk-eel, monkfish or Brazilian codling.

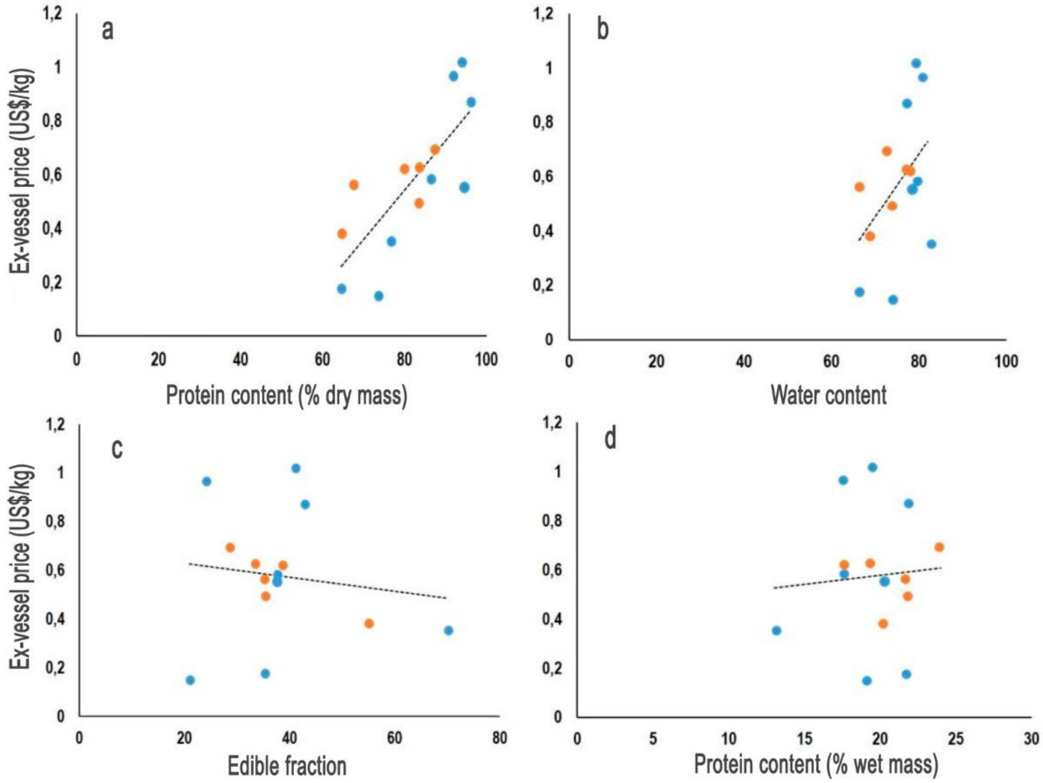

Figure 3. Relationship between ex-vessel price (US$ kg^{-1}) of the species and (a) protein content (as percentage of dry mass), (b) water content, (c) edible fraction and (d) protein content (% wet mass). Blue dots represent slope species; orange dots represent outer shelf/shelf break species.

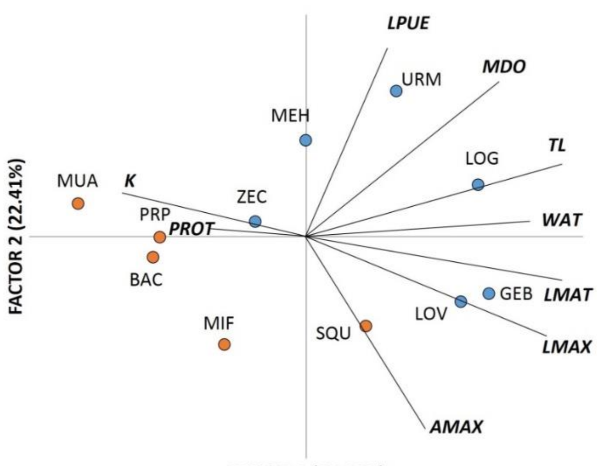

Figure 4. Spatial Principal Component Analysis (PCA) representation of the relationship between species based on their ecological and biological characteristics. Loadings of biological and ecological factors are represented by sticks. Species are distributed accordingly to their characteristics, orange dots represent outer shelf/shelf break species, and blue dots correspond to slope species.

The reduced number of species analysed and limitations of methods employed made it uncertain to assess to what extent such food qualities could drive the development of specialized slope trawling off Brazil. It is important to note, however, that whatever role these qualities play, they seem to reflect adaptation to selective pressures of deep slope areas, as do life-history traits (*i.e.*, large body sizes, late maturity and low growth rates) generally associated with the low resilience of slope fish populations to fishing mortality (Perez, 2006; Visintin, 2015). The same low-energy deep environment that selected for a biochemical composition attractive to humans as food, also selected for biological features that make slope stocks more vulnerable to overfishing than shallow-water ones (Perez *et al.*, 2009). Such a paradox was also proposed by Koslow (1997) with regards to seamount fishes (*e.g.*, orange roughy) that contrast with most deep-water fishes by exhibiting firm-textured flesh, as determined by the high protein and low water contents of their muscles. These fish may be adapted to use enhanced food supply mechanisms, associated with topographically-induced current regime, requiring strong swimming capacity to persist near highly dynamic seamount habitats. Such increased activity tends to consume a considerable fraction of food energy and compromise somatic growth and reproduction, typically low and inefficient among seamount fish. In a sense, seamount fishers, while selecting firm-textured flesh fishes, are taking advantage of particular deep seamount selective pressures, which in turn also favour life-history features that limit opportunities for productive and sustainable catches (Norse *et al*., 2012).

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