Trophic ecology of the demersal predator Brazilian flathead *Percophis brasiliensis* (Percophidae) in a coastal upwelling ecosystem, SW Atlantic

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Upwellings are important oceanographic processes that induce several changes in marine ecosystems, including in the benthic-pelagic coupling (BPC) that plays a major role in coastal areas. However, there is little available information about the possible effects of coastal upwellings on the trophic role of predators and in the BPC. Thus, here we investigate possible seasonal and ontogenetic changes in the trophic interaction of a demersal predator, the Brazilian flathead *Percophis brasiliensis*, from an upwelling ecosystem. Sampling was carried out for one year during two coastal upwelling events. Based on stomach content analysis (SCA) were recorded seasonal diet shifts, probably driven by coastal upwellings, leading to an increase in pelagic prey and changing the trophic coupling pathways. Stable isotope analysis revealed that isotopic niche decreased with the body size, as well as the values of the Levins' index. Also, significant, and positive relationships were observed between $\delta^{13}C$ and $\delta^{15}N$ *versus* total length. Our results showed that the demersal predator has a relevant trophic role in the BPC which is probably influenced by coastal upwellings.

Keywords: Benthic-pelagic coupling, Feeding habit, Marine ecology, Stable isotopes, Stomach content.

Ressurgências são importantes processos oceanográficos que induzem diversas mudanças nos ecossistemas marinhos, inclusive no acoplamento bento-pelágico (ABP) que desempenha um papel importante nas áreas costeiras. No entanto, existem poucas informações sobre os possíveis efeitos das ressurgências costeiras no papel trófico de predadores e no ABP. Em vista disso, aqui investigamos as possíveis mudanças sazonais e ontogenéticas nas interações tróficas de um predador demersal, o tira-vira *Percophis brasiliensis*, em um ecossistema com ressurgência. A amostragem foi realizada ao longo de um ano durante dois eventos de ressurgências costeiras. Baseado nas análises de conteúdos estomacais (ACE) foram registradas mudanças sazonais na dieta provavelmente impulsionadas pelas ressurgências costeiras, levando a um aumento de presas pelágicas e alterando as vias de acoplamento trófico. As análises de isótopos estáveis revelaram que o nicho isotópico diminuiu com o tamanho do corpo, assim como os valores do índice de Levin. Além disso, relações significativas e positivas foram observadas entre δ¹³C e δ¹⁵N *versus* comprimento total. Nossos resultados mostraram que o predador demersal tem um papel trófico relevante no ABP que provavelmente é influenciado por ressurgências costeiras.

Palavras-chave: Acoplamento bento-pelágico, Conteúdo estomacal, Ecologia marinha, Hábito alimentar, Isótopos estáveis.

INTRODUCTION

Studies on trophic interactions are important to understand several ecological aspects, such as resource partitioning, ecosystem function, and the transfer of nutrients and energy in the different ecosystem compartments (Paine, 1966; Schoener, 1974; Coll *et al.*, 2009). There are several methods to study different aspects of feeding ecology (Braga *et al.*, 2012; Pethybridge *et al.*, 2018). One of the most traditional and effective methods is the stomach content analysis (SCA). This method allows to identify the prey with high taxonomic precision and quantifies the biomass, number, and frequency of the ingested items (Hyslop, 1980; Cortés, 1997). The approach requires a large number of samples and it provides a snapshot of diet (Baker *et al.*, 2014). More recently, ecologists have used other methods, such as stable isotope analysis (SIA), to overcome some of the SCA limitations (Layman *et al.*, 2012). The stable isotope ratios of nitrogen and carbon in an organism's tissue reflect the isotopic ratio of the prey and also the environment (Bearhop *et al.*, 2004). Stable isotope values of tissues reflect the diet assimilated over the period that the tissue was synthesized (Bearhop *et al.*, 2002, 2004). For fishes, tissue turnover rates of muscle tissue can range from two to four weeks (Mont'Alverne *et al.*, 2016) to several months (Hussey *et al.*, 2012). Consequently, the use of both SCA and SIA provides a powerful tool to better elucidate diet, feeding behavior, and trophic ecology (Layman, Post, 2008).

In marine environments, variations in feeding habits and, consequently, in the trophic role of fishes are widely observed. Such diet variations are commonly related to ontogenetic development (*e.g.*, Graham *et al.*, 2007; Russo *et al.*, 2007; Andrades *et al.*,

2019), and seasonal fluctuations in prey availability (*e.g.*, Wellenreuther, Connell, 2002; Beukers-Stewart, Jones, 2004; Mendoza-Carranza, Vieira, 2008). Seasonal changes in the diet of marine species are frequently caused by changes in prey availability, often due to oceanographic processes such as coastal upwellings (Boje, Tomczak, 1978; Giralt *et al.*, 2020).

In coastal ecosystems, upwellings are important oceanographic processes that induce several changes in the marine environment (Margalef, 1978). Upwellings transport nutrients from deep waters to the euphotic layer, leading to an increase in primary productivity and usually increasing the biomass of all trophic levels in a cascade effect (Boje, Tomczak, 1978; Cury *et al.*, 2000; Fernandes *et al.*, 2017). Consequently, it also changes the prey availability and induces seasonal shifts in the predators' diet (Cury *et al.*, 2000; Miller *et al.*, 2010). Such upwelling events also modify the benthic-pelagic coupling that regulates the nutrient cycling and energy transfer between the benthic and pelagic domains (Navarrete *et al.*, 2005; Dale *et al.*, 2017). Upwellings may change the trophic role of a species, for example, if it shifts its primary diet from benthic to pelagic prey (and vice versa), thereby changing the dynamics and intensity of the benthic-pelagic coupling. Griffiths *et al.* (2017), in a review on benthic-pelagic coupling, point out that one of the important aspects little understood or quantified is the relative importance of fish predation in the benthic-pelagic coupling dynamics. The benthic-pelagic coupling plays a major role in marine ecosystems but there is little available information about the effects of upwelling-driven shifts on the trophic role of predators (Griffiths *et al.*, 2017).

The coastal region of the SW Atlantic between the Cabo de São Tomé (~22°S) and Cabo Frio (~23°S), Brazil, is particularly known for the periodic coastal upwellings, more frequent (or intense) during the austral summer and winter-spring (Valentin *et al.*, 1987; Campos *et al.*, 2000; Silveira *et al.*, 2000; Acha *et al.*, 2004). These events induce the replacement of the oligotrophic and warm Tropical Water by the nutrient-rich and cold South Atlantic Central Water (SACW) (Valentin *et al.*, 1987; Acha *et al.*, 2004). In this system, changes in the composition and abundance of organisms (*e.g.*, phytoplankton, zooplankton, and pelagic squids) associated with upwellings were also detected (Costa, Fernandes, 1993; Valentin, Monteiro-Ribas, 1993; Sumida *et al.*, 2005). This region is also considered one of the most productive areas for small and large-scale fisheries on the Brazilian coast (Costa *et al.*, 2017), where the Brazilian flathead *Percophis brasiliensis* Quoy & Gaimard, 1825 (Percophidae) is one of the most commonly caught as bycatch in bottom trawl fisheries (FIPERJ, 2021).

Percophis brasiliensis is a demersal fish endemic to the coastal waters of SW Atlantic, occurring along 5,000 km of coastline, between Rio de Janeiro State, Brazil (22°S) to Santa Cruz Province, Argentina (47°S) (Bernardes *et al.*, 2005; Cousseau, Perrotta, 2013). *Percophis brasiliensis* is a generalist predator that feeds mainly on Teleostei at the southernmost limit of its distribution (Milessi, Mari, 2012), but information concerning its trophic ecology is still lacking along the Brazilian coast, which covers most of the species distribution. Therefore, in the present study, we investigate possible seasonal and ontogenetic changes in the trophic interaction of *P. brasiliensis* from the upwelling ecosystem between the Cabo de São Tomé (~22°S) and Cabo Frio (~23°S), Brazil. As previously shown, upwelling ecosystems are highly dynamic, and biological communities are influenced by environmental changes, thus we expect to detect seasonal variations

in the *P. brasiliensis* diet, and for that we use SCA. Also, we expect to find ontogenetic differences in the *P. brasiliensis* diet since there is evidence of ontogenetic migration where large-sized specimens are found in deeper waters than smaller ones (Barretto, 2007; Rodrigues *et al.*, 2013), for this hypothesis, both SCA and SIA were used.

MATERIAL AND METHODS

Study area and sampling procedure. *Percophis brasiliensis* specimens were collected monthly between February 2017 and January 2018 from landings of small-scale bottom trawlers. Voucher specimens, as well as tissue samples for molecular studies, were deposited at the fish collection of the Instituto de Biodiversidade e Sustentabilidade – NUPEM, Universidade Federal do Rio de Janeiro (see Catelani *et al.*, 2019), catalog numbers: NPM 2588, NPM 3813, and NPM 5642. The fisheries took place between 20 to 50 m depth in the coastal area between 21°50'S to 22°50'S (Fig. 1). The sampled region is characterized by the strong northeast winds, which combined with the coastal morphology, produce strong and seasonal upwelling events, mainly during the summer and spring (Valentin *et al.*, 1987; Campos *et al.*, 2000; Silveira *et al.*, 2000; Acha *et al.*, 2004). To infer coastal upwelling events during the sampling period, the sea surface temperature (SST) was recorded at 2 to 4 h intervals with a data logger (HOBO Tidbit UTBI-001) fixed at 1 m deep in the rocky shores of Praia Grande, Arraial do Cabo, Rio de Janeiro, within the same upwelling ecosystem.
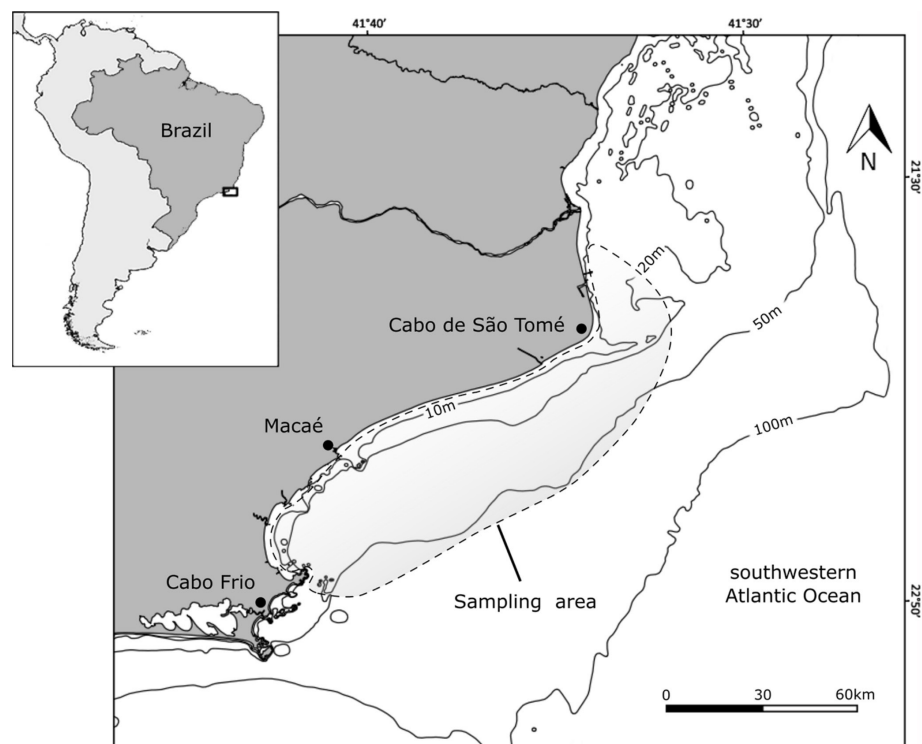
FIGURE 1 | Location of the study area (in gray bordered by the dashed line), an upwelling ecosystem, SW Atlantic. The continuous line represents the isobaths of 10, 20, 50, and 100 meters deep.

Stomach content analysis. The 1016 collected specimens were stored in ice and transported to the laboratory immediately after landing and kept frozen until the processing. The total weight (TW, 0.1 g), total length (TL, 1.0 mm), and sex were recorded for each specimen. The stomachs were removed, fixed in buffered formalin solution (10%) for at least 24 h, and preserved in 70% alcohol solution. Prey items were identified to the lowest possible taxonomic level using a stereomicroscope, counted, and weighed (wet weight 0.001 g). Identification guides, taxonomic keys, and original descriptions were used to achieve a precise taxonomic identification (see Figueiredo, Menezes, 1978, 2000; Menezes, Figueiredo, 1980a,b, 1985; Melo, 1996; Costa *et al.*, 2003; Fischer *et al.*, 2011; Rossi-Wongtschowski *et al.*, 2014; Brenha-Nunes *et al.*, 2016; Marceniuk *et al.*, 2016; Conversani *et al.*, 2017; Giaretta *et al.*, 2017; Santificetur *et al.*, 2017). Diet was represented as the percent of the total ingested weight (%W), number (%N), and frequency of occurrence (%F). The stomach fullness index was estimated using the percentage of the stomach content weight in the predator body weight (% BW), by the equation: BW = 100 X SW/(TW-SW), where SW (g) is the stomach content weight and TW (g) the consumer total weight (Hyslop, 1980; Cortés, 1997). To investigate ontogenetic changes, reproduction information was combined with the number of specimens collected with non-empty stomachs. *Percophis brasiliensis* reach their first sexual maturity (*i.e.*, L50) with 250 mm TL for males and 380 mm TL for females (Militelli, Macchi, 2001). Herein, specimens were classified into three ontogenetic groups: juveniles (200 – 359 mm TL), young adults (360 – 434 mm TL), and adults (435 – 615 mm TL).

Stable isotope analysis. Muscle tissue from *P. brasiliensis* (n = 41) was collected inside the study area during the austral summer, between December 2017 and January 2018. All samples were freeze-dried, powdered, and weighed (~1 mg) into tin capsules. Stable isotopes of nitrogen and carbon were analyzed using an Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometer (Europa Hydra 20/20). Abundances of stable isotopes are expressed in delta (δ) values in parts per thousand (‰), as determined by the equation:

$$\delta X = [(R_{sample}/ R_{standard} - 1] \times 1000$$

where R_{sample} and $R_{standard}$ represent the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the experimental and control (standards), respectively. The analytical precision of both $\delta^{15}N$ and $\delta^{13}C$ was < 0.06‰ based on three internal laboratory standards: Amaranth flour with $\delta^{15}N$ and $\delta^{13}C$ values of 2.55‰ and – 12.98‰; Bovine liver with $\delta^{15}N$ and $\delta^{13}C$ values of 7.61‰ and – 21.63‰; Keratin with $\delta^{15}N$ and $\delta^{13}C$ values of 4.74‰ and – 24.38‰. Lipid extractions and mathematical normalization were not performed as any of the C:N ratio values exceeded 3.5 (mean = 3.3) (Post *et al.*, 2007).

Statistical analyses. Factorial PERMANOVA permutation-based multivariate variance analysis was used to investigate the diet changes among ontogenetic groups (three levels: juveniles, young adults, and adults, as a random factor), seasons (four levels: Summer, Autumn, Winter, and Spring, as a fixed factor) and their interaction effects. Then, post-hoc pairwise PERMANOVA tests were used to reveal possible

differences among groups. A factorial PERMANOVA was applied to investigate possible diet differences between sex (two levels: female and male, as a fixed factor), ontogenetic groups, and their interactions. Non-metric multidimensional scaling (nMDS) ordination plots were used to illustrate the similarity and potential overlap of the groups (ontogenetic groups and seasons) with the factor (prey items weight). The PERMANOVA and nMDS were based on Bray-Curtis similarity matrices built with the square root of prey masses. The prey mass data was chosen because we believe it better reflects the energy consumed by the predator and also because it has been used in most studies on trophic relationships (Baker *et al*., 2014). For stomach content analysis (SCA), preys were categorized into six groups based on taxon and habitat use: Pelagic crustaceans, Benthic crustaceans, Demersal fishes, Pelagic fishes, Non-identified fishes, and Demerso-pelagic cephalopods. All PERMANOVA tests were based on 9,999 permutations, and p-values < 0.05 were considered significant. To estimate the niche breadth, the standardized Levins' index based on prey masses was used (Levins, 1968; Hulbert, 1978). Levins' index was calculated using the package *spaa* (Zhang, Ma, 2014). The standardization was carried out based on the formula: $B_{std}=B-1/n-1$, where B is the calculated Levins' index and n is the number of ingested prey items.

To further evaluate possible ontogenetic shifts for *P. brasiliensis*, linear regression was carried out on δ^{13}C and δ^{15}N values *versus* TL, then the normality of the residuals was tested. The isotopic niche size and overlap of each ontogenetic group were estimated from δ^{15}N and δ^{13}C values using the standard ellipse area (95%) corrected for small samples (SEAc) using package *SIBER* (Jackson *et al*., 2011; Syväranta *et al*., 2013). The statistical procedures with stomach content and stable isotope data were run in PRIMER v. 7 (Anderson, 2001; Anderson *et al*., 2008) and R 3.3.2 (R Development Core Team, 2021).

RESULTS

Sea surface temperature (SST) data recorded by the data logger confirmed the presence of upwelling events throughout the sampling period (Fig. **S1**). The events occurred with greater intensity mainly in February, September and October with average temperatures close to 16°C.

Diet description. The non-empty stomachs corresponded to 49% (n = 496) of the total specimens collected and dissected (n = 1016) (Tab. 1). *Percophis brasiliensis*' diet was composed of 37 prey taxa, of which 27 were identified at the species level (Tab. 2). Teleostei was the most consumed prey group in %W for all ontogenetic groups, mainly composed of small pelagic fishes (Clupeiformes). The juveniles showed a higher percentage of Teleostei prey, 79.7%W, mainly composed by Engraulidae. For juveniles, crustaceans (mostly shrimps) and Cephalopoda (squids) represented 20.3%W of the prey. The importance of Teleostei is similar between young adults and adults (54.6 and 53.9%W, respectively), with an increase in crustaceans (27.0 and 15.5%W) and cephalopods (17.5 and 29.6%W).

TABLE 1 | The total number of stomachs and the percentage of non-empty stomachs (in parentheses) of each ontogenetic group by season of Brazilian flathead *Percophis brasiliensis*.

Ontogenetic groups / Seasons	Summer	Autumn	Winter	Spring
Juveniles	86 (38.4)	68 (54.4)	74 (33.8)	56 (51.8)
Young adults	94 (44.7)	113 (49.56)	100 (43.0)	109 (49.5)
Adults	75 (37.3)	105 (53.3)	93 (52.2)	62 (74.2)

TABLE 2 | Diet composition of ontogenetic groups of Brazilian flathead *Percophis brasiliensis*. SL = Average standard length (mm), and TW = Average weight of predators (g), %N = Percentage in number, %W = Percentage in weight, %F = Frequency of occurrence. NI = Not identified.

Prey Items	Juveniles n = 124, SL = 292, TW = 137			Young adults n = 195, SL = 353, TW = 265			Adults n = 177, SL = 437, TW = 520		
	%W	%F	%N	%W	%F	%N	%W	%F	%N
Pelagic prey	**42.06**	**38.71**	**62.67**	**54.02**	**38.95**	**74.78**	**63.48**	**46.33**	**88.96**
Crustaceans	**6.85**	**4.84**	**44.45**	**15.64**	**10.26**	**69.04**	**11.67**	**11.3**	**84.9**
Peisos petrunkevitchi Burkenroad, 1945	6.57	3.23	43.83	15.64	10.26	69.04	10.89	10.17	79.83
Sergestidae NI	0.28	1.61	0.62	0	0	0	0.78	1.13	5.07
Fishes	**27.8**	**25.8**	**15.13**	**20.9**	**18.97**	**4.16**	**22.24**	**18.06**	**2.28**
Anchoa sp.	1.34	1.61	0.62	1.45	2.05	0.26	0.06	0.56	0.05
Anchovia clupeoides (Swainson, 1839)	0	0	0	0.29	0.51	0.07	0	0	0
Carangidae NI	0	0	0	0.65	0.51	0.07	1.1	1.13	0.09
Chirocentrodon bleekerianus (Poey, 1867)	1.71	1.61	0.62	8.54	4.62	0.72	0.58	1.13	0.09
Clupeidae NI	0	0	0	0	0	0	1.39	0.56	0.05
Clupeiformes NI	7.54	4.84	3.09	0.6	0.51	0.07	2.76	2.82	0.23
Engraulidae NI	17.21	17.74	10.8	8.5	9.23	2.64	1.87	6.78	1.23
Engraulis anchoita Hubbs & Marini, 1935	0	0	0	0.59	1.03	0.26	0.11	1.13	0.09
Harengula clupeola (Cuvier, 1829)	0	0	0	0	0	0	5.29	0.56	0.09
Lycengraulis grossidens (Spix & Agassiz, 1829)	0	0	0	0.28	0.51	0.07	0	0	0
Sardinella aurita Valenciennes, 1847	0	0	0	0	0	0	7.5	2.26	0.27
Trachurus lathami Nichols, 1920	0	0	0	0	0	0	1.58	1.13	0.09
Cephalopoda	**7.41**	**7.26**	**3.09**	**17.49**	**11.28**	**1.58**	**29.57**	**20.33**	**1.78**
Doryteuthis pleii (Blainville, 1823)	0.26	1.61	0.93	15.22	4.62	0.66	24.27	14.12	1.14
Doryteuthis sp.	6.85	2.42	0.93	1.33	2.05	0.26	3.94	2.82	0.23
Lolliguncula brevis (Blainville, 1823)	0	0	0	0.39	3.08	0.46	0.1	1.13	0.09
Teuthida NI	0.3	3.23	1.23	0.54	1.54	0.2	1.26	2.26	0.32
Benthic/Demersal prey	**16.81**	**27.45**	**14.22**	**31.19**	**37.97**	**18.06**	**24.15**	**53.59**	**7.47**
Crustaceans	**6.07**	**16.13**	**7.41**	**11.36**	**19.99**	**9.03**	**3.82**	**17.49**	**4.12**
Artemesia longinaris Bate, 1888	0	0	0	0.35	1.54	0.2	0.32	1.69	0.37
Brachyura NI	0	0	0	0.01	0.51	0.07	0	0	0
Dendrobranchiata NI	2.93	10.48	4.94	2.22	5.64	7.18	0.73	4.52	2.78
Farfantepenaeus sp.	0	0	0	1.15	1.03	0.13	1.19	1.13	0.09

TABLE 2 | (Continued)

Prey Items	Juveniles n = 124, SL = 292, TW = 137			Young adults n = 195, SL = 353, TW = 265			Adults n = 177, SL = 437, TW = 520		
	%W	%F	%N	%W	%F	%N	%W	%F	%N
Hemisquilla braziliensis (Moreira, 1903)	2.23	1.61	0.62	3.27	5.64	0.72	0.64	3.39	0.32
Hemisquillidae NI	0.55	3.23	1.23	0.4	2.56	0.33	0.37	3.95	0.32
Isopoda NI	0	0	0	0.05	0.51	0.07	0.01	0.56	0.05
Pleoticus muelleri (Bate, 1888)	0	0	0	3.68	2.05	0.26	0.32	1.13	0.09
Portunus spinicarpus (Stimpson, 1871)	0	0	0	0.23	0.51	0.07	0.18	0.56	0.05
Sicyonia sp.	0	0	0	0	0	0	0.06	0.56	0.05
Sicyonia dorsalis Kingsley, 1878	0.36	0.81	0.62	0	0	0	0	0	0
Fishes	**10.74**	**11.32**	**6.81**	**19.73**	**17.47**	**8.96**	**20.31**	**35.54**	**3.3**
Anguilliformes NI	0	0	0	0.86	1.03	0.13	1.02	1.69	0.14
Ctenosciaena gracilicirrhus (Metzelaar, 1919)	0.91	1.61	0.62	1.2	2.05	0.26	1.35	2.26	0.23
Cynoscion guatucupa (Cuvier, 1830)	0.14	0.81	0.31	0	0	0	0.02	0.56	0.05
Cynoscion jamaicensis (Vaillant & Bocourt, 1883)	1.43	0.81	0.31	0.45	1.54	0.2	0.88	1.69	0.18
Cynoscion sp.	2.48	2.42	1.23	0.98	2.05	0.26	0.15	1.13	0.09
Dactylopterus volitans (Linnaeus, 1758)	0	0	0	0	0	0	1.6	1.69	0.18
Dules auriga Cuvier, 1829	1.7	0.81	0.62	5.61	3.08	0.4	2.03	3.39	0.32
Etropus longimanus Norman, 1933	0	0	0	1.57	3.08	0.4	0.8	4.52	0.41
Isopisthus parvipinnis (Cuvier, 1830)	0	0	0	0	0	0	0.21	0.56	0.05
Ophichthus gomesii (Castelnau, 1855)	0	0	0	0.45	0.51	0.07	0	0	0
Paralonchurus brasiliensis (Steindachner, 1875)	0.07	0.81	0.93	0.86	2.05	0.46	1.65	1.69	0.27
Pleuronectiformes NI	0	0	0	0	0	0	0.22	0.56	0.05
Porichthys porosissimus (Cuvier, 1829)	1.1	0.81	0.31	1.76	1.03	5.93	0.98	2.26	0.18
Prionotus punctatus (Bloch, 1793)	0	0	0	0	0	0	0	0.56	0.05
Prionotus sp.	1.13	0.81	0.93	0.49	0.51	0.13	1.01	1.69	0.14
Raneya brasiliensis (Kaup, 1856)	0.09	0.81	0.31	4.86	0.03	0.46	6.33	9.04	0.77
Saurida sp.	0.43	0.81	0.62	0.4	0.51	0.13	0	0	0
Sciaenidae NI	0	0	0	0.24	0	0.13	0.45	0.56	0.05
Stellifer sp.	1.26	0.81	0.62	0	0	0	0	0	0
Symphurus sp.	0	0	0	0	0	0	1.61	1.69	0.14
Gastropoda	**0**	**0**	**0**	**0.05**	**0.51**	**0.07**	**0.02**	**0.56**	**0.05**
Philine sp.	0	0	0	0.05	0.51	0.07	0.02	0.56	0.05
Fishes NI	**41.13**	**49.19**	**22.84**	**14.92**	**40**	**6.65**	**12.27**	**35.59**	**3.29**
Total	**325.13 g**		**n = 323**	**1112.73 g**		**n = 1510**	**2585.24 g**		**n = 2185**

We found significant differences among ontogenetic groups, seasons, and the interaction between these factors (PERMANOVA; $p \leq 0.03$) (Tab. 3). Dietary ontogenetic shifts have been detected but these changes vary according to the season. During Autumn and Winter, juveniles differed from young adults and adults (pairwise PERMANOVA; $p \leq 0.02$). Only adults showed differences from the other two ontogenetic groups in the Summer ($p \leq 0.04$). Juveniles and adults are different during Spring ($p = 0.004$), but we found no differences between juveniles and young adults, and young adults and adults ($p = 0.10$ and $p = 0.49$, respectively). Females (n = 348, 433.1 mm ± 69.2) were larger than males (n = 144, 365.2 mm ± 40.5; PERMANOVA, $p = 0.001$). However, no differences in diet were observed between males and females (Pseudo–F = 1.36, $p = 0.33$).

In juveniles, there was no significant differences in the diet throughout the year ($p \geq 0.081$), while young adults' diet differed among all seasons ($p < 0.01$), except between winter and summer ($p = 0.57$) when similar %W of demersal fishes and non-identified fish were ingested (Fig. 2). During the autumn, *P. brasiliensis* fed on the small pelagic shrimp *Peisos petrunkevitchi* Burkenroad, 1945, while in the spring demersal-pelagic cephalopods were the main prey group. The diet of adults during autumn was significantly different from all other seasons ($p < 0.01$). Adults and young adults consumed a high proportion (%W) of *P. petrunkevitchi* during the autumn (Figs. 2–3). Besides, during the autumn, the ingested prey number was four to 29 times higher than in other seasons for juveniles and adults (Tab. S2). Despite the increase in prey number intake mainly between March and April, this pattern is not reflected in the %BW values (Fig. S3). In all other seasons, larger fish have a more diverse diet (Tab. S2).

Niche breadth of young adults and adults was smaller during Autumn, probably due to the large ingestion of a single species (Tab. S2). For juveniles, the lowest calculated niche breadth was observed in Spring. In general, the niche breadth slightly decreases with growth, with mean values of standardized Levins' index = 0.29, 0.27, and 0.26 in juveniles, young adults, and adults, respectively (Tab. S2).

Stable Isotope Analysis. *Percophis brasiliensis* $\delta^{13}C$ values ranged between –18.36 and –16.77 ‰, with a mean of –17.58 ± 0.26 ‰, while $\delta^{15}N$ ranged between 11.91 and 14.29 ‰, with a mean of 13.52 ± 0.41 ‰ (Tab. 4). Significant relationships were observed between $\delta^{13}C$ ($r^2 = 0.092$, $p = 0.030$) and $\delta^{15}N$ ($r^2 = 0.645$, $p < 0.001$) *versus* total length (Fig. 4).

TABLE 3 | PERMANOVA results of the main effects between the factors ontogenetic groups and seasons of Brazilian flathead *Percophis brasiliensis*, estimated from Bray-Curtis similarity matrix based on %W. Significantly differences ($p < 0.05$) are presented in bold.

Source	df	MS	Pseudo-F	P(perm)	Perm. (n)
Ontogenetic groups	2	16716	2.832	**0.0288**	9940
Season	3	19204	3.2602	**0.0085**	9941
Ontogenetic groups *vs.* Season	6	5946	1.5593	**0.0176**	9864
Residual	481	3813.3			
Total	492				
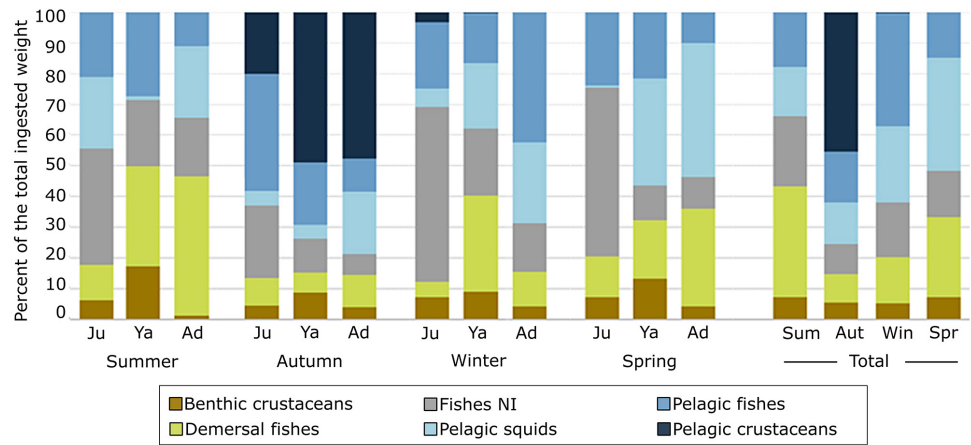
FIGURE 2 | Seasonal variation in dietary composition (%W) for each ontogenetic group of Brazilian flathead *Percophis brasiliensis*. Seasons: Summer, Sum; Autumn, Aut; Winter, Win; Spring, Spr. Ontogenetic groups: Juvenile, Ju; Young adults, Ya; Adults, Ad.
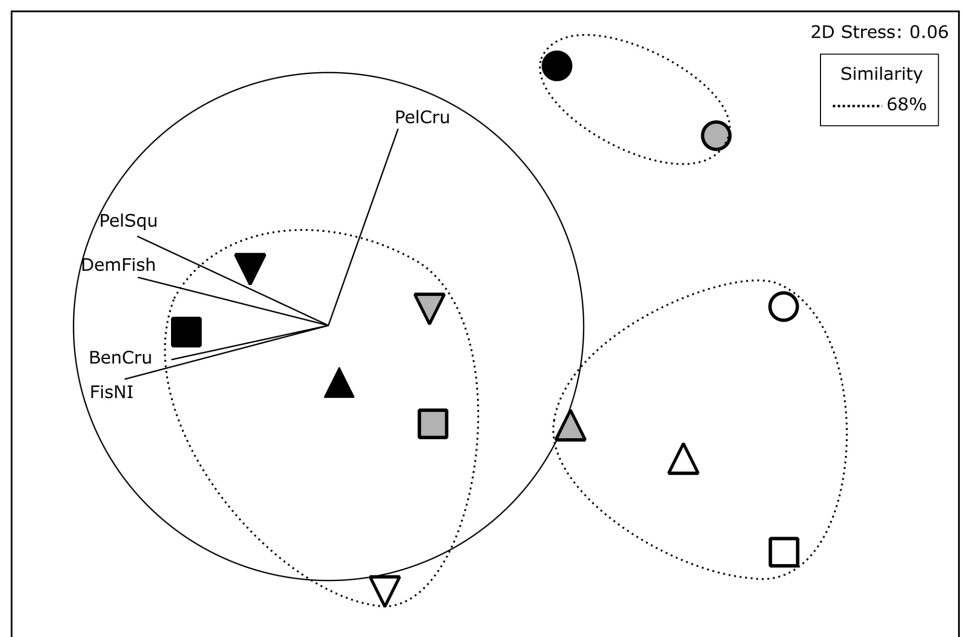

FIGURE 3 | nMDS ordination plot of the Bray-Curtis similarity matrix based on the %W of prey groups of Brazilian flathead *Percophis brasiliensis*. Juveniles = white, young adults = gray, adults = black. Summer = triangle, Autumn = circle, Winter = square, Spring = inverted triangle. The main prey categories are represented by Spearman's correlation vectors. The length of each vector provides the strength of the correlation coefficient, where the radius of the circle represents the maximum correlation (=1). Prey categories: PelCru = pelagic crustaceans, BenCru = benthic crustaceans, DemFish = demersal fishes, FisNI = non-identified fishes, and PelSqu = pelagic squids. Dotted lines represent the Bray-Curtis similarity of 68%.

Based on the measured standard ellipse corrected for small sample size (SEAc), the isotopic niche width decreases with the increase in fish size. Juveniles showed the broader niche (0.37), followed by young adults (0.34) and adults (0.28). The overlap area between juveniles and young adults was 37%, between young adults and adults was 53%, and between juveniles and adults was 28% (Fig. 5).

TABLE 4 | Sample size (n), mean and standard deviation (SD) of the stable isotope values (δ^{15}N and δ^{13}C) of Brazilian flathead *Percophis brasiliensis*.

Ontogenetic groups	n	δ^{15}N ± SD	δ^{13}C ± SD
Juveniles	13	13.0±0.5	-17.8±0.4
Young adults	11	13.6±0.3	-17.5±0.4
Adults	17	13.9±0.3	-17.4±0.3
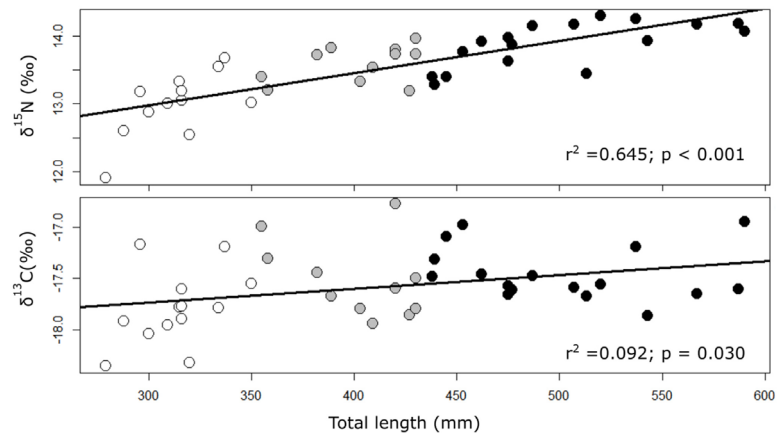
FIGURE 4 | Relationships between total length (mm TL) *versus* δ^{15}N values (‰; above) and total length *versus* δ^{13}C values (‰; below) for Brazilian flathead *Percophis brasiliensis*. Juveniles (white circles), young adults (gray circles) and adults (black circles).
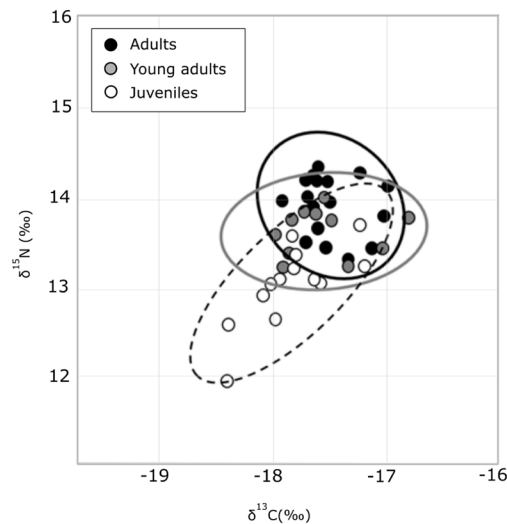
FIGURE 5 | Isotopic niche width and overlap of Brazilian flathead *Percophis brasiliensis*.

DISCUSSION

Coastal upwellings are important oceanographic processes that can induce several changes in trophic interactions in marine ecosystems. The studied area is influenced by coastal upwellings which are more intense in two periods of the year, reportedly summer/autumn and spring (Valentin *et al.*, 1987; Castelao, Barth, 2006). The first coastal upwellings event occurred in late summer to early autumn and the second in late winter to early spring. In the current study, we identified changes in the demersal predator's diet, the Brazilian flathead *P. brasiliensis*, during the two recorded upwelling events.

In the summer, *P. brasiliensis* was more connected to the benthic trophic pathways since half of the diet of young adults and adults were composed of benthic prey (Fig. 2). The benthic pathway depends largely on the sinking of particulate organic matter being ingested by benthic detritivore organisms, which in turn are prey to benthic and demersal fish (secondary consumers), which are then preyed upon by the studied predator (tertiary consumer) (Mann, 1988; Gooday, Turley, 1990). In the late summer (February), intense coastal upwellings occurred. In the following autumn months (March and April), the pelagic shrimp *P. petrunkevitchi* was the main prey species consumed by both young adults and adults, completely altering the diet and the trophic coupling pathways from benthic to pelagic environment. A study conducted by Simões *et al.* (2013) in a vicinity area showed that *P. petrunkevitchi* has a rapid density increase due to the fertilization effects of SACW upwelling. In our study, *P. petrunkevitchi* was also responsible for a large increase in the ingested prey number found in March and April, probably due to coastal upwellings that occurred in late summer.

The second upwelling event occurred in the late winter to the early spring, probably inducing changes in the predator's diet. *Percophis brasiliensis* used mainly the pelagic trophic pathway, preying on small squids and pelagic fish. Pelagic squids represented a large part of the diet (20–45%W) of *P. brasiliensis* adults throughout the year, young adults (in winter and spring), and juveniles (in summer). The most consumed squid, *Doryteuthis plei* (Blainville, 1823), inhabits coastal waters and has a short life cycle and very fast growth (five months lifespan, Jackson, Forsythe, 2002). Spawning populations of *D. plei* were observed during winter, spring, and summer (Rodrigues, Gasalla, 2008), being more abundant during spring-summer in the region (Costa, Fernandes, 1993). During spring–summer, adult *D. plei* aggregate in shallower waters for spawning, showing increasing feeding activity and taking advantage of the greater prey availability provided by upwellings (Rodrigues, Gasalla, 2008; Gasalla *et al.*, 2010). Seasonal increases in prey availability and consumption provided by intense coastal upwellings, as observed here, may have a positive effect on the physiological condition of fish of different trophic levels (Rosa *et al.*, 2010; Pulgar *et al.*, 2013). These positive effects include improved fitness and reproductive capacity, with direct implications for stock management and conservation (Stevenson, Woods, 2006; Rosa *et al.*, 2010).

Despite being a bottom dweller, *P. brasiliensis* probably performs short vertical migrations in the water column to capture small pelagic fishes (*e.g.*, *Anchoa* sp. and *Chirocentrodon bleekerianus* (Poey, 1867)), squids (*Doryteuthis* sp.), and shrimps (*P. petrunkevitchi*). Such foraging behavior may contribute to the benthic-pelagic coupling that links the nutrients and energy produced by planktonic organisms (pelagic pathway), and the energy and nutrients derived from benthic production and detrital recycling

(benthic pathway) (Marcus, Boera, 1998; Woodland, Secor, 2013; Van Denderen *et al.*, 2018). The pelagic organisms that sink to the bottom due to bycatch must also be considered because there are small to medium-scale fisheries operating in the study area. Understanding the benthic-pelagic coupling processes is important because it affects the benthic/demersal species diversity, productivity, stability (Townsend, Cammen, 1988; Moodley *et al.*, 1998; Gray, 2002) and the marine ecosystem functioning in general (Griffiths *et al.*, 2017). The benthic-pelagic coupling is regulated by different factors such as water column deep, physical mixing, primary production, community composition, and organism life cycles (Marcus, Boera, 1998). Consumers that can use both pelagic and benthic resources, such as *P. brasiliensis*, have the potential to generate food web stability (Rooney *et al.*, 2006; Van Denderen *et al.*, 2018).

The assessment of the source of organisms' food has implications for a better understanding of marine food webs. Most of the benthic and/or demersal organisms depend directly or indirectly on the input of organic matter, mainly in the form of debris, which is linked to the productivity of the superficial layers (Mann, 1988; Gooday, Turley, 1990). By feeding directly on pelagic organisms, the population dynamics of these demersal species are linked to the rapid fluctuations in energy pulses provided by oceanographic processes, and to possible changes caused by climatic changes. The sampling period of the current study was characterized by weak La Niña anomalies (NOAA, 2021). El Niño/La Niña–Southern Oscillation anomalies are known to change local climate and precipitation, sea surface temperature, and to intensify or weaken upwellings (Colberg *et al.*, 2004; Middleton *et al.*, 2007; Jacox *et al.*, 2015). Thus, interannual anomalies, as well as global climate changes, have great potential to change the trophic role of species and the dynamics of bento-pelagic coupling.

The stomach content analysis revealed *P. brasiliensis* as a generalist predator with a broad prey spectrum. With a total of 27 taxa identified at the species level, the species number observed is 56% higher than previously recorded (n = 17) for this species in the Argentine-Uruguayan Coastal Ecosystem (34°S to 41°S; AUCE) based on 657 non-empty stomachs analyzed (Milessi, Mari, 2012). Also, in the AUCE, bony fishes were the most important prey group for *P. brasiliensis* (%W = 93.1), feeding mainly on the small pelagic fishes *Trachurus lathami* Nichols, 1920 (%W=58.0) and *Engraulis anchoita* Hubbs & Marini, 1935 (%W = 24.4%). In the present study, bony fishes were less consumed by *P. brasiliensis* (%W = 53.9–79.7), depending on the ontogenetic groups.

Ontogenetic diet shifts were detected by both SCA and SIA. A factor that can help to understand such feeding pattern is that juveniles and young adults are commonly found in shallow waters with high temperatures and low salinities, while the larger individuals move to deeper regions in the continental shelf with higher salinity and lower temperatures (Barretto, 2007; Rodrigues *et al.*, 2013). Such changes in habitat use may expose juveniles and adults to different prey availability. Pelagic prey is more important for juveniles, throughout the year they feed mostly on engraulids. Engraulids are often associated with the coastal ecosystem, such as sand beaches, bays, and estuaries (Araújo *et al.*, 2008). Although fish highly contributes to the diet of *P. brasiliensis*, squids and crustaceans increase their importance from juveniles to adults. The increase of squids (*e.g.*, *D. plei*) and crustaceans (*e.g.*, *P. petrunkevitchi*, *Artemesia longinaris* Bate, 1888, and *Pleoticus muelleri* (Bate, 1888)) abundances in the studied area are strongly related to the upwellings of cold SACW (Costa, Fernandes, 1993; Simões *et al.*, 2013; Silva *et al.*, 2014; Costa *et al.*, 2017).

As *P. brasiliensis* grows, there is a significant increase in δ^{15}N and δ^{13}C values, with a decrease in isotopic niche width. The observed variation of δ^{15}N and δ^{13}C values in relation to *P. brasiliensis* size may be related to the changes in the major components of its diet. Engraulids are small pelagic fishes, that occupy a relatively low trophic position, and feed primarily on zooplankton (Sergipense *et al.*, 1999; Pizarro *et al.*, 2019) that are δ^{15}N and δ^{13}C depleted, 8.4 ± 3.3 and –17.7 ± 0.3 respectively, in the study area (Gatts *et al.*, 2021). This probably explains, at least in part, the lower δ^{15}N and δ^{13}C values observed in juveniles. Larger *P. brasiliensis* ingested greater amounts of small demersal fish (*e.g.*, *Dules auriga* Cuvier, 1829) and squid (*D. plei*) that presented higher δ^{15}N and δ^{13}C values, with δ^{15}N = 11.7 and δ^{13}C = –16.6 and δ^{15}N = 12.1 and δ^{13}C = –16.9, respectively (Gatts *et al.*, 2021). Changes in δ^{15}N and/or δ^{13}C values of demersal predator about size have been reported in the scientific literature, including with Argentine hake *Merluccius hubbsi* Marini, 1933 and *Trichiurus lepturus* Linnaeus, 1758 from the continental shelf of southeastern Brazil (Muto, Soares, 2011; Di Beneditto *et al.*, 2013). The SIA data presented in this study are interesting as it corroborates, at least in part, the results of traditional SCA. However, these data must be interpreted with some caution due to limitations related to the number of samples (41 in total) and the sampling period (austral summer). New studies with a greater number of samples for SIA and temporal range could better elucidate the temporal trophic dynamics of the *P. brasiliensis* under coastal upwellings influence.

Our results showed shifts in the trophic pathways used by the demersal predator, altering the dynamics and the trophic role of the benthic–pelagic coupling. The changes in the *P. brasiliensis*' diet are probably influenced by coastal upwelling events in a period characterized by weak La Niña anomalies. This oceanographic process provided fast increases in the availability of pelagic prey, such as small fish, shrimps and squids (Matsuura *et al.*, 1992; Costa, Fernandes, 1993; Gasalla *et al.*, 2010; Simões *et al.*, 2013; Silva *et al.*, 2014; Costa *et al.*, 2017), altering the *P. brasiliensis* diet and the trophic coupling pathways from benthic to pelagic. By feeding directly on pelagic organisms, the population dynamics of this demersal species is connected with the rapid fluctuations in energy pulses provided by coastal upwellings events. Nonetheless, in this study, specimens were collected over one year, without annual replications. Upwelling ecosystems are strongly influenced by climate change (Bograd *et al.*, 2023) and their temporal effects on the trophic dynamics of *P. brasiliensis* and other demersal predators are still poorly understood. Long-term studies are needed to better understand natural processes in upwelling ecosystems such as the intensity and frequency of upwelling as well as the biological responses to environmental changes. Furthermore, human interference, such as fishing and climate change, may influence ecological processes in upwelling ecosystems.

ACKNOWLEDGMENTS

REFERENCES

- **Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J.** Marine fronts at the continental shelves of austral South America: Physical and ecological processes. J Mar Syst. 2004; 44(1–2):83–105. https://doi.org/10.1016/j.jmarsys.2003.09.005

- **Anderson MJ.** A new method for non-parametric multivariate analysis of variance. Austral Ecol. 2001; 26(1):32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

- **Anderson MJ, Gorley RN, Clarke KR.** PERMANOVA + for PRIMER: Guide to software and statistical methods. Plymouth, UK: PRIMER-E Ltd; 2008.

- **Andrades R, Andrade JM, Jesus-junior PS, Macieira RM, Bernardino AF, Giarrizzo T *et al*.** Multiple niche-based analyses reveal the dual life of an intertidal reef predator. MEPS. 2019; 624:131–41. https://doi.org/10.3354/meps13027

- **Araújo FG, Silva MA, Santos JNS, Vasconcellos RM.** Habitat selection by anchovies (Clupeiformes: Engraulidae) in a tropical bay at Southeastern Brazil. Neotrop Ichthyol. 2008; 6(4):583–90. https://doi.org/10.1590/S1679-62252008000400006

- **Baker R, Buckland A, Sheaves M.** Fish gut content analysis: robust measures of diet composition. Fish Fish. 2014; 15(1):170–77. https://doi.org/10.1111/faf.12026

- **Barretto AC.** Influencia ambiental en la distribución espacial de las clases de edad de pez palo (*Percophis brasiliensis*) en el Sistema Costero del Atlántico Sudoccidental (34°- 41° S). Buenos Aires: Universidad de Buenos Aires; 2007. Available from: http://hdl.handle.net/1834/3017

- **Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H.** Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol. 2004; 73(5):1007–12. https://doi.org/10.1111/j.0021-8790.2004.00861.x

- **Bearhop S, Waldron S, Votier SC, Furness RW.** Factors that influence assimilation rates and fractionation of Nitrogen and Carbon Stable Isotopes in avian blood and feathers. Physiol Biochem Zool. 2002; 75(5):451–58. https://doi.org/10.1086/342800

- **Di Beneditto APM, Bittar VT, Rezende CE, Camargo PB, Kehrig HA.** Mercury and stable isotopes (δ^{15}N and δ^{13}C) as tracers during the ontogeny of *Trichiurus lepturus.* Neotrop Ichthyol. 2013; 11(1):211–16. https://doi.org/10.1590/s1679-62252013000100024

- **Bernardes RA, Rossi-Wongtschowski CLB, Wahrlich R, Vieira RC, Santos AP, Rodrigues AR.** Prospecção pesqueira de recursos demersais com armadilhas e pargueiras na Zona Econômica Exclusiva da região Sudeste-Sul do Brasil. 1st ed. São Paulo: Instituto Oceonográfico (USP); 2005.

- **Beukers-Stewart BD, Jones GP.** The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. J Exp Mar Bio Ecol. 2004; 299(2):155–84. https://doi.org/10.1016/j.jembe.2003.08.015

- **Boje R, Tomczak M.** Upwelling ecosystems. vol. 1. 1st ed. Berlin: Springer-Verlag Berlin Heidelberg; 1978. https://doi.org/10.1007/978-3-642-66985-9

- **Braga RR, Bornatowski H, Vitule JRS.** Feeding ecology of fishes: an overview of worldwide publications. Rev Fish Biol Fish. 2012; 22:915–29. https://doi.org/10.1007/s11160-012-9273-7

- **Brenha-Nunes MR, Santificetur C, Conversani VRM, Giaretta MB, Rossi-Wongtschowski CLB, Siliprandi CC.** Atlas of marine bony fish otoliths (sagittae) of Southeastern-Southern Part IV: Perciformes (Centropomidae, Acropomatidae, Serranidae, Priacanthidae, Malacanthidae, Pomatomidae, Carangidae, Lutjanidae, Gerreidae and Haemulidae). Braz J Oceanogr. 2016; 64(1):23–75. https://doi.org/10.1590/S1679-875920161100064(sp1)

- **Bograd SJ, Jacox MG, Hazen EL, Lovecchio E, Montes I, Buil MP *et al*.** Climate change impacts on eastern boundary upwelling systems. Annu Rev Mar Sci. 2023; 15(1): 303–28. https://doi.org/10.1146/annurev-marine-032122-021945

- **Campos EJD, Velhote D, Silveira ICA.** Shelf break upwelling driven by Brazil current cyclonic meanders. Geophys Res Lett. 2000; 27(6):751–54. https://doi.org/10.1029/1999GL010502

- **Castelao RM, Barth JA.** Upwelling around Cabo Frio, Brazil: The importance of wind stress curl. Geophys Res Lett. 2006; 33(3):1–04. https://doi.org/10.1029/2005GL025182

- **Catelani PA, Bauer AB, Agostinho LS, Villarins BT, Pozzobon APB, Carvalho PH *et al*.** The fish collection of the Instituto de Biodiversidade e Sustentabilidade - NUPEM/UFRJ, Universidade Federal do Rio de Janeiro (UFRJ), Brazil. Bol Soc Bras Ictiol. 2019; 129:109–13. Available from: https://www.sbi.bio.br/images/sbi/boletim-docs/2019/outubro_129.pdf

- **Colberg F, Reason CJC, Rodgers K.** South Atlantic response to El Niño-Southern Oscillation induced climate variability in an ocean general circulation model. J Geophys Res. 2004; 109:12015. https://doi.org/10.1029/2004JC002301

- **Coll M, Bundy A, Shannon LJ.** Ecosystem modelling using the ecopath with ecosim approach. In: Bernard AM, Moksness E, editors. Comput Fish Res. Second Ed. Nehterlands: Springer Netherlands; 2009. p.225–91. https://doi.org/10.1007/978-1-4020-8636-6

- **Conversani VRM, Brenha-Nunes MR, Santificetur C, Giaretta MB, Siliprandi CC, Rossi-Wongtschowski CLB.** Atlas of marine bony fish otoliths (sagittae) of Southeastern-Southern Brazil Part VII: Atheriniformes, Beloniformes, Beryciformes, Zeiformes, Syngnathiformes, Scorpaeniformes and Tetraodontiformes. Braz J Oceanogr. 2017; 65(3):400–47. https://doi.org/10.1590/s1679-87592017134306503

- **Cortés E.** A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci. 1997; 54(3):726–38. https://doi.org/10.1139/f96-316

- **Costa PAS, Braga AC, Martins AS, Haimovici M, Mincarone MM.** Padrões de distribuição das assembleias de peixes e cefalópodes demersais na plataforma e talude continental da Bacia de Campos. In: Curbelo-Fernandez MP, Braga, AC. Comunidades Demersais e Bioconstrutores. Rio de Janeiro: Elsevier Ltd.; 2017. p.87–110. https://doi.org/10.1016/b978-85-352-7295-6.50004-x

- **Costa PAS, Fernandes FC.** Seasonal and spatial changes of cephalopods caught in the Cabo Frio (Brazil) upwelling ecosystem. Bull Mar Sci. 1993; 52(2):751–59.

- **Costa RC, Fransozo A, Melo GSA, Freire FAM.** Chave ilustrada para identificação dos camarões Dendrobranchiata do litoral norte do Estado de São Paulo, Brasil. Biota Neotrop. 2003; 3(1):1–12. https://doi.org/10.1590/S1676-06032003000100011

- **Cousseau MB, Perrotta RG.** Peces marinos de Argentina: Biología, distribución, pesca. 4th ed. Mar Del Plata; 2013.

- **Cury P, Bakun A, Crawford RJM, Jarre A, Quin RA, Shannon LJ** *et al*. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J Mar Sci. 2000; 57(3):603–18. https://doi.org/10.1006/jmsc.2000.0712

- **Dale AW, Graco M, Wallmann K.** Strong and dynamic benthic-pelagic coupling and feedbacks in a coastal upwelling system (Peruvian Shelf). Front Mar Sci. 2017; 4(2):29. https://doi.org/10.3389/fmars.2017.00029

- **Fernandes LDA, Fagundes Netto EB, Coutinho R.** Inter-annual cascade effect on marine food web: A benthic pathway lagging nutrient supply to pelagic fish stock. PLoS ONE. 2017; 12(9):e0184512. https://doi.org/10.1371/journal.pone.0184512

- **Figueiredo JL, Menezes NA.** Manual de peixes marinhos do Sudeste do Brasil. VI. Teleostei (5). São Paulo: Museu de Zoologia da USP; 2000.

- **Figueiredo JL, Menezes NA.** Manual de peixes marinhos do Sudeste do Brasil. II. Teleostei (1). 1st ed. São Paulo: Museu de Zoologia da USP; 1978.

- **Fundação Instituto de Pesca do Estado do Rio de Janeiro (FIPERJ).** Projeto de monitoramento da atividade pesqueira no estado do Rio de Janeiro: Relatório Técnico Semestral - Agosto de 2021. Rio e Janeiro; 2021.

- **Fischer LG, Pereira LED, Vieira JP.** Peixes estuarinos e costeiros. 2nd ed. Rio Grande; 2011.

- **Gasalla MA, Rodrigues AR, Postuma FA.** The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem. ICES J Mar Sci. 2010; 67(7):1413–24. https://doi.org/10.1093/icesjms/fsq106

- **Gatts PV, Franco MAL, Almeida MG, Rezende CE, Costa PAS.** Isotopic niche of coastal fish and cephalopods off the Campos Basin, southeastern Brazil. Estuar Coast Shelf Sci. 2021; 261:107563. https://doi.org/10.1016/J.ECSS.2021.107563

- **Giaretta MB, Siliprandi CC, Santificetur C, Brenha-nunes R, Conversani VRM, Rossi-Wongtschowski CLB.** Atlas of marine bony fish otoliths (sagittae) of Southeastern-Southern Brazil Part VI: Albuliformes, Anguiliformes, Osmeriformes, Stomiiformes, Aulopiformes, Myctophiformes, Ophidiiformes, Polimixiiformes, Batrachoidiformes and Lophiformes. Braz J Oceanogr. 2017; 65(2):258–308. https://doi.org/10.1590/s1679-87592017133806502

- **Gooday AJ, Turley CM.** Responses by benthic organisms to inputs of organic material to the ocean floor: A review. Philos Trans R Soc London. 1990; 331(1616):119–38. https://doi.org/10.1098/rsta.1990.0060

- **Graham BS, Grubbs D, Holland K, Popp BN.** A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. Mar Biol. 2007; 150(4):647–58. https://doi.org/10.1007/s00227-006-0360-y

- **Gray JS.** Species richness of marine soft sediments. MEPS. 2002; 244:285–97. https://doi.org/10.3354/meps244285

- **Griffiths JR, Kadin M, Nascimento FJA, Tamalander T, Tornroos A, Bonaglia S** *et al*. The importance of benthic – pelagic coupling for marine ecosystem functioning in a changing world. Glob Chang Biol. 2017; 23(6):2179–96. https://doi.org/10.1111/gcb.13642

- **Hulbert SH.** The measurement of niche overlap and some relatives. Ecology. 1978; 59(1):67–77. https://doi.org/10.2307/1936632

- **Hussey NE, MacNeil MA, Olin JA, McMeans BC, Kinney MJ, Chapman DD** *et al*. Stable isotopes and elasmobranchs: Tissue types, methods, applications and assumptions. J Fish Biol. 2012; 80(5):1449–84. https://doi.org/10.1111/j.1095-8649.2012.03251.x

- **Hyslop EJ.** Stomach contents analysis-a review of methods and their application. J Fish Biol. 1980; 17(4):411–29. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

- **Jackson AL, Inger R, Parnell AC, Bearhop S.** Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J Anim Ecol. 2011; 80(3):595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

- **Jackson GD, Forsythe JW.** Statolith age validation and growth of *Loligo plei* (Cephalopoda: Loliginidae) in the north-west Gulf of Mexico during spring/summer. J Mar Biol Assoc UK. 2002; 82(4):677–78. https://doi.org/10.1017/S0025315402006069

- **Jacox MG, Fiechter J, Moore AM, Edwards CA.** ENSO and the California Current coastal upwelling response. J Geophys Res Ocean. 2015; 120(3):1691–702. https://doi.org/10.1002/2014JC010650

- **Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR et al.** Applying stable isotopes to examine food-web structure: An overview of analytical tools. Biol Rev. 2012; 87(3):545–62. https://doi.org/10.1111/j.1469-185X.2011.00208.x

- **Layman CA, Post DM.** Can stable isotope ratios provide for community-wide measures of trophic structure? Reply. Ecology. 2008; 89(8):2358–59. https://doi.org/10.1890/08-0167.1

- **Levins R.** Evolution in changing environments. Princeton: Princeton University Press; 1968.

- **Mann KH.** Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnol Oceanogr. 1988; 33(4, part 2):910–30. https://doi.org/10.4319/lo.1988.33.4part2.0910

- **Marceniuk AP, Caires R, Siccha-Ramirez R, Oliveira C.** Review of the harvestfishes, genus *Peprilus* (Perciformes: Stromateidae), of the Atlantic coast of South America. Zootaxa. 2016; 4098(2):311–32. https://doi.org/10.11646/zootaxa.4098.2.6

- **Marcus NH, Boera F.** Minireview: The importance of benthic-pelagic life cycles in coastal aquatic systems. Limnol Oceanogr. 1998; 43(5):763–68. https://doi.org/10.4319/lo.1998.43.5.0763

- **Margalef R.** What is an upwelling ecosystem? In: Boje R, Tomczak M, editors. Upwelling Ecosyst. 1st ed. Berlin: Springer Berlin Heidelberg; 1978. p.306. https://doi.org/10.1007/978-3-642-66985-9_2

- **Matsuura Y, Spach HL, Katsuragawa M.** Comparison of spawning patterns of the Brazilian sardine (*Sardinella brasiliensis*) and anchoita (*Engrautis anchoita*) in Ubatuba region, southern Brazil during 1985 through 1988. Bol Inst Ocean. 1992; 40(1–2):101–15. https://doi.org/10.1590/s0373-55241992000100009

- **Melo GSA.** Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. 1st ed. São Paulo: Plêiadr; 1996.

- **Mendoza-Carranza M, Vieira J.** Whitemouth croaker *Micropogonias furnieri* (Desmarest, 1823) feeding strategies across four southern Brazilian estuaries. Aquat Ecol. 2008; 42:83–93. https://doi.org/10.1007/s10452-007-9084-4

- **Menezes NA, Figueiredo JL.** Manual de peixes marinhos do Sudeste do Brasil. V. Teleostei (4). São Paulo: Museu de Zoologia da USP; 1985.

- **Menezes NA, Figueiredo JL.** Manual de peixes marinhos do Sudeste do Brasil. IV. Teleostei (3). São Paulo: Museu de Zoologia da USP; 1980a.

- **Menezes NA, Figueiredo JL.** Manual de peixes marinhos do Sudeste do Brasil. III. Teleostei (2). São Paulo: Museu de Zoologia da USP; 1980b.

- **Middleton JF, Arthur C, Van Ruth P, Ward TM, McClean JL, Maltrud ME et al.** El Niño effects and upwelling off South Australia. J Phys Oceanogr. 2007; 37(10):2458–77. https://doi.org/10.1175/jpo3119.1

- **Milessi AC, Mari NR.** Ecología trófica del pez palo, *Percophis brasiliensis* (Quoy & Gaimard, 1825) en el ecosistema costero Argentino-Uruguayo (34° S-41° S). Rev Invest Desarr Pesq. 2012; 21:61–72. http://hdl.handle.net/1834/4905

- **Militelli MI, Macchi GJ.** Reprodución del pez palo (*Percophis brasiliensis*) en aguas costeras de la provincia de Buenos Aires. Rev Invest Desarr Pesq. 2001; 14:5–21. http://hdl.handle.net/1834/1864

- **Miller TW, Brodeur RD, Rau G, Omori K.** Prey dominance shapes trophic structure of the northern California Current pelagic food web: Evidence from stable isotopes and diet analysis. MEPS. 2010; 420:15–26. https://doi.org/10.3354/meps08876

- **Mont'Alverne R, Jardine TD, Pereyra PER, Oliveira MCLM, Medeiros RS, Sampaio LA et al.** Elemental turnover rates and isotopic discrimination in a euryhaline fish reared under different salinities: Implications for movement studies. J Exp Mar Bio Ecol. 2016; 480:36–44. https://doi.org/10.1016/j.jembe.2016.03.021

- **Moodley L, Heip CHR, Middelburg JJ.** Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics. J Sea Res. 1998; 40(3–4):263–80. https://doi.org/10.1016/S1385-1101(98)00026-4

- **Muto EY, Soares LSH.** Spatio-temporal variations in the diet and stable isotope composition of the Argentine hake *Merluccius hubbsi* Marini, 1933 of the continental shelf of southeastern Brazil. Mar Biol. 2011; 158:1619–30. https://doi.org/10.1007/s00227-011-1674-y

- **Navarrete SA, Wieters EA, Broitman BR, Castilla JC.** Scales of benthic-pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. PNAS. 2005; 102(50):18046–51. https://doi.org/10.1073/pnas.0509119102

- **National Oceanic and Atmospheric Administration (NOAA).** Multivariate ENSO index version 2. Boulder: Natl Ocean Atmos Adm.; 2021. Available from: https://psl.noaa.gov/enso/mei/

- **Paine RT.** Food web complexity and species diversity. Am Nat. 1966; 100(910):65–75. https://doi.org/10.1086/282400

- **Pethybridge HR, Choy CA, Polovina JJ, Fulton EA.** Improving marine ecosystem models with biochemical tracers. Ann Rev Mar Sci. 2018; 10:199–228. https://doi.org/10.1146/annurev-marine-121916-063256

- **Pielou EC.** Species-diversity and pattern-diversity in the study of ecological succession. J Theor Biol. 1966; 10(2):370–83. https://doi.org/10.1016/0022-5193(66)90133-0

- **Pizarro J, Docmac F, Harrod C.** Clarifying a trophic black box: stable isotope analysis reveals unexpected dietary variation in the Peruvian anchovy *Engraulis ringens*. PeerJ. 2019; 7:e6968. https://doi.org/10.7717/peerj.6968

- **Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG.** Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia. 2007; 152(1):179–89. https://doi.org/10.1007/s00442-006-0630-x

- **Pulgar J, Poblete E, Alvarez M, Morales JP, Aranda B, Aldana M et al.** Can upwelling signals be detected in intertidal fishes of different trophic levels? J Fish Biol. 2013; 83(5):1407–15. https://doi.org/10.1111/jfb.12220

- **R Development Core Team.** R: A language and environment for statistical computing. R Foundation for Statistical Computing. Viena: 2021. Available from: https://www.R-project.org/

- **Rodrigues AR, Gasalla MA.** Spatial and temporal patterns in size and maturation of *Loligo plei* and *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in southeastern Brazilian waters, between 23°S and 27°S. Sci Mar. 2008; 72(4):631–43. https://doi.org/10.3989/scimar.2008.72n4631

- **Rodrigues KA, Jaureguizar AJ, Guerrero RA.** Environmental factors that define the spawning and nursery areas for *Percophis brasiliensis* (Teleostei: Percophididae) in a multispecific reproductive coastal zone, El Rincón (39°–41°S), Argentina. Hydrobiologia. 2013; 709(1):1–10. https://doi.org/10.1007/s10750-013-1479-8

- **Rooney N, Mccann K, Gellner G, Moore JC.** Structural asymmetry and the stability of diverse food webs. Nature. 2006; 442(6):265–69. https://doi.org/10.1038/nature04887

- **Rosa R, Gonzalez L, Broitman BR, Garrido S, Santos AMP, Nunes ML.** Bioenergetics of small pelagic fishes in upwelling systems: relationship between fish condition, coastal ecosystem dynamics and fisheries. MEPS. 2010; 410:205–18. https://doi.org/10.3354/meps08635

- **Rossi-Wongtschowski CLB, Siliprandi CC, Brenha MR, Gonsales SA, Santificetur C, Vaz-dos-Santos AM.** Atlas of marine bony fishotoliths (Sagittae) of Southern Brazil Part I: Gadiformes (Macrouridae, Moridae, Bregmacerotidae, Phycidae and Merlucciidae); Part II: Perciformes (Carangidae, Sciaenidae, Scombridae and Serranidae). Braz J Oceanogr. 2014; 62:1–103. https://doi.org/10.1590/S1679-875920140637062sp1

- **Russo T, Costa C, Cataudella S.** Correspondence between shape and feeding habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758. J Fish Biol. 2007; 71(3):629–56. https://doi.org/10.1111/j.1095-8649.2007.01528.x

- **Santificetur C, Giaretta MB, Conversani VRM, Brenha-Nunes MR, Siliprandi CC, Rossi-Wongtschowski CLB.** Atlas of marine bony fish otoliths of Southeastern-Southern Brazil Part VIII: Siluriformes (Ariidae) and Pleuronectiformes (Achiridae, Paralichthyidae, Cynoglossidae). Braz J Oceanogr. 2017; 65(3):448–94. https://doi.org/10.1590/s1679-87592017143106503

- **Schoener TW.** Resouce partitioning in ecological communities: Research on how similar species divide resources helps. Science. 1974; 185(4145):27–39. https://doi.org/10.1126/science.185.4145.27

- **Sergipense S, Caramaschi EP, Sazima I.** Morphology and feeding habits of two engraulid fish (Teleostei, Clupeiformes) in the Baía de Sepetiba, Rio de Janeiro. Rev Bras Oceanogr. 1999; 47(2):173–88. https://doi.org/10.1590/S1413-77391999000200006

- **Silva ER, Sancinetti GS, Fransozo A, Azevedo A, Costa RC.** Biodiversity , distribution and abundance of shrimps Penaeoidea and Caridea communities in a region the vicinity of upwelling in Southeastern of Brazil. Nauplius. 2014; 22(1):1–11. https://doi.org/10.1590/S0104-64972014000100001

- **Silveira ICA, Schmidt ACK, Campos EJD, Godoi SS, Ikeda Y.** The Brazil current off the Eastern Brazilian Coast. Rev Bras Oceanogr. 2000; 48(2):171–83. https://doi.org/10.1590/S1413-77392000000200008

- **Simões SM, Castilho AL, Fransozo A, Negreiros-Fransozo ML, Costa RC.** Distribution related to temperature and salinity of the shrimps *Acetes americanus* and *Peisos petrunkevitchi* (Crustacea: Sergestoidea) in the south-eastern Brazilian littoral zone. J Mar Biol Assoc UK. 2013; 93(3):753–59. https://doi.org/10.1017/S0025315412000902

- **Stevenson RD, Woods WA.** Condition indices for conservation: New uses for evolving tools. Integr Comp Biol. 2006; 46:1169–90. https://doi.org/10.1093/icb/icl052

- **Sumida PYG, Yoshinaga MY, Ciotti ÁM, Gaeta SA.** Benthic response to upwelling events off the SE Brazilian coast. MEPS. 2005; 291:35–42. https://doi.org/10.3354/meps291035

- **Syväranta J, Lensu A, Marjomäki TJ, Oksanen S, Jones RI.** An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. PLoS ONE. 2013; 8(2):e56094. https://doi.org/10.1371/journal.pone.0056094

- **Townsend DW, Cammen LM.** Potential importance of the timing of spring plankton blooms to benthic-pelagic coupling and recruitment of juvenile demersal fishes. Biol Oceanogr. 1988; 5(3):215–28. https://doi.org/10.1080/01965581.1987.10749514

- **Valentin JL, Andre DL, Jacob SA.** Hydrobiology in the Cabo Frio (Brazil) upwelling: two-dimensional structure and variability during a wind cycle. Cont Shelf Res. 1987; 7(1):77–88. https://doi.org/10.1016/0278-4343(87)90065-3

- **Valentin JL, Monteiro-Ribas WM.** Zooplankton community structure on the east-southeast Brazilian continental shelf (18-23°S latitude). Cont Shelf Res. 1993; 13(4):407–24. https://doi.org/10.1016/0278-4343(93)90058-6

- **Van Denderen PD, Lindegren M, MacKenzie BR, Watson RA, Andersen KH.** Global patterns in marine predatory fish. Nat Ecol Evol. 2018; 2(1):65–70. https://doi.org/10.1038/s41559-017-0388-z

- **Wellenreuther M, Connell SD.** Response of predators to prey abundance: separating the effects of prey density and patch size. J Exp Mar Bio Ecol. 2002; 273(1):61–71. https://doi.org/10.1016/S0022-0981(02)00145-4

- **Woodland RJ, Secor DH.** Benthic-pelagic coupling in a temperate inner continental shelf fish assemblage. Limnol Oceanogr. 2013; 58(3):966–76. https://doi.org/10.4319/lo.2013.58.3.0966

- **Zhang JL, Ma KP.** spaa: An R package for computing species association and niche overlap. Res Prog of Bio Con CN. 2014; 10:165–174.

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Arthur de Barros Bauer: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing–original draft.

Luciano Gomes Fischer: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing–review and editing.

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The collection and transport of specimens were authorized by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio License N° 44025).

COMPETING INTERESTS

The author declares no competing interests.

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