

Feeding habits of the cockfish, *Callorhynchus callorhynchus* (Holocephali: Callorhinchidae) from off northern Argentina



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The feeding habits of *Callorhynchus callorhynchus* were investigated in coastal waters off northern Argentina. The effect of body size, seasons and regions was evaluated on female diet composition using a multiple-hypothesis modelling approach. *Callorhynchus callorhynchus* fed mainly on bivalves (55.61% PSIRI), followed by brachyuran crabs (10.62% PSIRI) and isopods (10.13% PSIRI). *Callorhynchus callorhynchus* females showed changes in the diet composition with increasing body size and also between seasons and regions. Further, this species is able to consume larger bivalves as it grows. Trophic level was 3.15, characterizing it as a secondary consumer. We conclude that *C. callorhynchus* showed a behavior of crushing hard prey, mainly on bivalves, brachyuran, gastropods and anomuran crabs. Females of this species shift their diet with increasing body size and in response to seasonal and regional changes in prey abundance or distribution.

Keywords: Chondrichthyes, Diet, Ontogenetic shifts, Southwest Atlantic, Trophic level.

Submitted September 21, 2018

Accepted December 5, 2019

by Lisa Whitenack

Published April 20, 2020

Online version ISSN 1982-0224

Print version ISSN 1679-6225

Neotrop. Ichthyol.

vol. 18, no. 1, Maringá 2020

Epub, Apr 17, 2020

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Los hábitos alimentarios de *Callorhynchus callorynchus* fueron investigados en las aguas costeras del norte de Argentina. Se evaluó el efecto del tamaño del cuerpo, la temporada y la región sobre la composición de la dieta de las hembras mediante un enfoque de modelado de múltiples hipótesis. *Callorhynchus callorynchus* se alimentó principalmente de bivalvos (55,61% PSIRI), seguido de cangrejos brachyuras (10,62% PSIRI) y de isópodos (10,13% PSIRI). Las hembras de *C. callorynchus* presentaron cambios en la dieta con incremento del tamaño del cuerpo, la temporada y la región. Además, esta especie es capaz de consumir bivalvos de mayor tamaño a medida que incrementa el tamaño del cuerpo. El nivel trófico fue calculado en 3,15, caracterizando a esta especie como un consumidor secundario. Concluimos que *C. callorynchus* presentó un comportamiento de triturador de presas duras, principalmente bivalvos, cangrejos y gasterópodos. Las hembras de esta especie cambian su dieta con el incremento del tamaño del cuerpo y en respuesta a cambios temporales y regionales en la abundancia y distribución de sus presas.

Palabras clave: Atlántico Sudoccidental, Cambios ontogenéticos, Condrictios, Dieta, Nivel trófico.

INTRODUCTION

The cockfish, *Callorhynchus callorynchus* (Linnaeus, 1758) (Callorhynchidae), is an endemic holocephalan from South America, occurring from 23°S in the Southwestern Atlantic to 18°S in the Southeastern Pacific (López *et al.*, 2000; Didier, 2004; Cousseau, Perrotta, 2013). This species inhabits depths ranging from the shoreline to 200 m (Cousseau, Perrotta, 2013). It is captured year-round as part of commercial bottom trawl fisheries in Argentina, Chile and Peru (Dagit *et al.*, 2007; Consejo Federal Pesquero, 2009). In northern Argentina, the area with the highest catch and landings of chondrichthyans, *C. callorynchus* represents an important resource for recreational and artisanal fisheries (Massa *et al.*, 2004; Consejo Federal Pesquero, 2009; Cedrola *et al.*, 2011; Lucifora *et al.*, 2012; Cousseau, Perrotta, 2013). In this area the abundance of this species has declined by nearly 50% between 1994 to 1999, but today this information is unknown (Massa *et al.*, 2004; Consejo Federal Pesquero, 2009). However, the International Union for Conservation of Nature (IUCN) categorized *C. callorynchus* in South America as least concern (Dagit *et al.*, 2007).

Distribution and reproductive biology of *C. callorynchus* have been studied from individuals collected in different marine regions, such as in San Matías Gulf, northern Patagonia waters, Argentina (41°30'S 64°15'W) (Di Giacomo, 1990; 1992; Di Giacomo, Perier, 1994; Bernasconi *et al.*, 2015a, b), in coastal waters off northern Argentina (36°–38°S 56°–57°W) (Chierichetti *et al.*, 2017), and off Coquimbo, Chile (30°15'S 70°30'W) (Alarcón *et al.*, 2011). Additionally, reproductive observations in coastal waters off northern Argentina, indicate that this area is not a nursery ground for *C. callorynchus* (Cousseau, Perrotta, 2013; Chierichetti *et al.*, 2017). In contrast, little has

been studied regarding the diet and feeding habits of the cockfish in waters of South America (Di Giacomo *et al.*, 1994; Di Giacomo, Perier, 1996; Cousseau, Perrotta, 2013).

Off the north coast off Argentina, the feeding habits of several species of chondrichthyans have been well documented. These species exhibited sexual, ontogenetic, regional and/or seasonal changes in their dietary composition (*e.g.*, sharks, Lucifora *et al.*, 2006; 2009; Belleggia *et al.*, 2012; skates, Barbini, Lucifora, 2011; 2012; 2016; apron ray, Spath *et al.*, 2012; and mylibatoid rays Ruocco, Lucifora, 2016). Previous studies of the feeding habits of *C. callorynchus* in coastal waters of the San Matías Gulf (northern Patagonia) indicated that the diet composition was dominated by bivalve molluscs, mainly scallops, and that diet composition changed in relation to ontogeny (Di Giacomo *et al.*, 1994; Di Giacomo, Perier, 1996). Conversely, feeding habits of this species in northern Argentina coastal waters are poorly known: scarce data are provided by Rios, Pereira (1986) concerning only qualitative aspects of its diet. Despite advances in our understanding of the biology of *C. callorynchus*, there are major gaps in our knowledge on feeding habits and some questions arise: are bivalves the main prey item in coastal waters off northern Argentina?; do ontogenetic, regional and seasonal differences exist in the dietary composition of *C. callorynchus*? Therefore, the purpose of this study was to determine the feeding habits of *C. callorynchus* in northern Argentinean coastal waters. Our specific aims were to: (1) describe diet composition; (2) identify changes in diet with maturity stage, body size, region and season; (3) examine relationships between predator size and prey size; and (4) determine the trophic level of *C. callorynchus*. Evaluating the effects of specific characteristics (maturity stage, body size, region and season) on the feeding habits of this species, will allow us insights into ways in which the cockfish exploits food resources and to understand how this species influences the dynamics of predator-prey interactions in this area. Basic ecological data, such as diet composition, constitutes one of so many necessary tools to develop a suitable plan of marine ecosystem conservation (Cochrane, 2002; Thrush, Dayton, 2010).

MATERIAL AND METHODS

Study area and sampling. The study area is located between 36° and 40° S (Fig. 1) and consists of two coastal systems. A stratified coastal zone (north of 37° S) influenced by the discharge of the Río de la Plata and a homogeneous coastal zone (south of 37° S), that comprises an estuarine system called El Rincón, characterized by the discharge of the Río Negro and Río Colorado and discharges of high salinity waters of the San Matías Gulf (Guerrero, Piola, 1997; Lucas *et al.*, 2005) (Fig. 1).

Individuals of *C. callorynchus* were obtained from June to December between 2011 and 2014, by small-scale artisanal fishermen using longlines or commercial bottom trawlers. For each individual captured, precaudal length (PCL, mm), total body mass (in g), sex and maturity stage (immature or mature) were recorded. Maturity stage was determined according to the degree of calcification of the claspers and the development of testes and reproductive ducts in males, and to the observation of the uteri, oviductal glands and ovarian follicles in females (Chierichetti *et al.*, 2017). The guts were removed and frozen at -20° C for subsequent analyses in the laboratory.

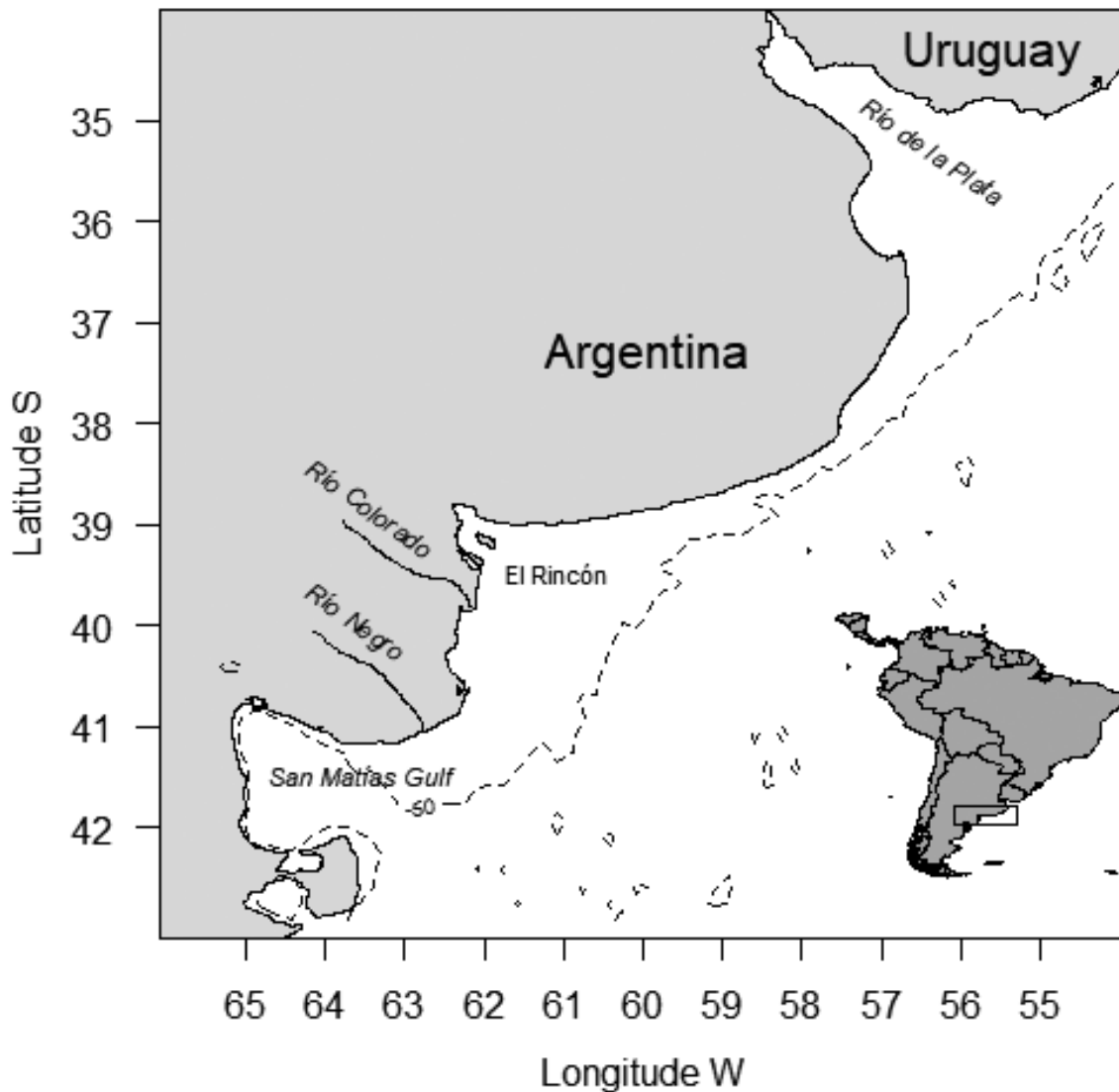


FIGURE 1 | Study area showing where individuals of *Callorhynchus callorhynchus* were captured off northern Argentina. The rectangle in the inset shows the location of the study area in South America.

Diet composition and analysis. Gut contents were sorted and identified to the lowest possible taxonomic level, using reference collections and published catalogues. Prey were counted and their wet weights recorded (± 0.01 g). When possible, carapace width (CW) of brachyuran crabs and valve width (VW) of bivalves were measured. To assess the importance of each prey and allow comparisons with other studies, the composition of the diet was established by the prey-specific index of relative importance (%PSIRI) (Brown *et al.*, 2012), by using the equation:

$$PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

where $\%FO_i$ is the number of guts containing prey category i , divided by the number of guts n , $\%PN_i$, and $\%PW_i$ are prey-specific abundance in terms of percent number and percent weight, respectively. The prey-specific abundance ($\%PA_i$) was calculated following Brown *et al.* (2012):

$$\%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n_i}$$

where $\%A_{ij}$ is the abundance by counts ($\%PN_i$) or weight ($\%PW_i$) of the prey category i in gut sample j and n_i is the number of gut contents containing prey i .

To determine whether a sufficient number of individuals was sampled to conduct statistical analyses, the order of guts was randomised 100 times and the accumulation prey curve was plotted as a function of sample size. Sample size was considered sufficient to describe diet if the cumulation prey curve reached an asymptote (Ferry, Cailliet, 1996).

For the statistical analyses, prey were grouped into seven zoological categories: bivalves, gastropods, brachyuran crabs, anomuran crabs, isopods, amphipods and cumaceans. These categories were chosen because they reflected the ecological variability of the diet of *C. callorynchus*. To identify changes in the diet with maturity stage (immature or mature), body size (PCL), region (north, center and south) and season (warm = October–December; cold = June–September), generalized linear models (GLM) were fitted (Venables, Ripley, 2002). Due to the low number of individuals from the southern region, and the low overall number of males in the total sample, the generalized linear models were adjusted only for females of the north and center region.

For each prey category, models were built where the response variable was the number of prey consumed and the independent variables were maturity stage, PCL, region and season. Also, models with combinations between PCL + region, PCL + season, maturity stage + region, maturity stage + season, season + region as independent variables were fitted. A model without any of the independent variables (*i.e.*, null model) was fitted to assess whether none of the tested variables had an effect on the consumption of prey categories (Lucifora *et al.*, 2009; Barbini, Lucifora, 2011). All models had a negative binomial error distribution because response variables had a high number of zero-values and variance much greater than the mean, and a log link (Crawley, 2005). A multiple-hypothesis model approach was used to identify the best model explaining the consumption of a given prey (Anderson *et al.*, 2000; Franklin *et al.*, 2001) (Tab. 1).

For each model, the Akaike information criterion (AIC) and the Akaike's weight (w) were calculated. The AIC value for a given model represents the information lost, so the model with the lowest AIC was selected as the best model among the set of models proposed. The w value was calculated to obtain the likelihood of each competing model given the data (Franklin *et al.*, 2001; Johnson, Omland, 2004). If w did not provide strong support for any model fitted, we used model averaging to estimate the parameters of the variables included in the best model (Symonds, Moussalli, 2011).

To examine relationships between predator size and prey size, we used PCL of *C. callorynchus* and CW of crabs and VW of bivalves. Regressions on the 5, 50 and 95% quantiles were fitted in order to test an increase in minimum, medium and maximum

prey size with increasing PCL, respectively (Scharf *et al.*, 1998).

The trophic level of *C. callorhynchus* was calculated using the trophic index (TL_k), to determine its position within the food web applying the method proposed by Cortés (1999) as:

$$TL_k = 1 + \left(\sum_{j=1}^n P_j \times TL_j \right)$$

where TL_j is the trophic level of each prey category j and P_j is the proportion of each prey category j (using %W) in the diet, and n is the total number of prey categories.

Seven prey categories were used to calculate this trophic level of *C. callorhynchus*: bivalves, gastropods, brachyuran crabs, anomuran crabs, isopods, amphipods and cumaceans. Trophic level of each prey category was obtained from Ebert, Bizarro (2007). The observations were randomly sampled 100 times with replacement in order to obtain the frequency distribution of TL_k and to get mean and standard deviation values. All statistical analyses were performed using the R statistical software, version 3.1.0 (R Development Core Team, 2019).

RESULTS

Overall diet. A total of 210 individuals, 180 females and 30 males, were sampled and 83.8% (176) of them contained food. Of the individuals containing food, 152 were females ranged from 390–630 mm PCL and weighing between 825–3330 g, and 24 were males ranged from 350–480 mm PCL and weighing between 640–1630 g (Fig. 2).

Overall, 9642 prey with a total weight of 2230 g were found in the guts. The accumulation prey curves reached an asymptote for all the groups considered, indicating that sample sizes were sufficient (Fig. 3).

In total, 64 different prey taxa were identified: 25 molluscs, 19 decapods, six isopods,

TABLE 1 | Models fitted between the number of consumed prey (N) by females of *Callorhynchus callorhynchus* and the independent variables. The categorical variables were maturity stage (immature and mature), region (north and center) and season (warm and cold) (PCL: precaudal length; *: null model).

Numbers	Models
1	$N \sim \text{PCL}$
2	$N \sim \text{maturity stage}$
3	$N \sim \text{season}$
4	$N \sim \text{region}$
5	$N \sim \text{PCL} + \text{season}$
6	$N \sim \text{PCL} + \text{region}$
7	$N \sim \text{maturity stage} + \text{season}$
8	$N \sim \text{maturity stage} + \text{region}$
9	$N \sim \text{season} + \text{region}$
10*	$N \sim 1$

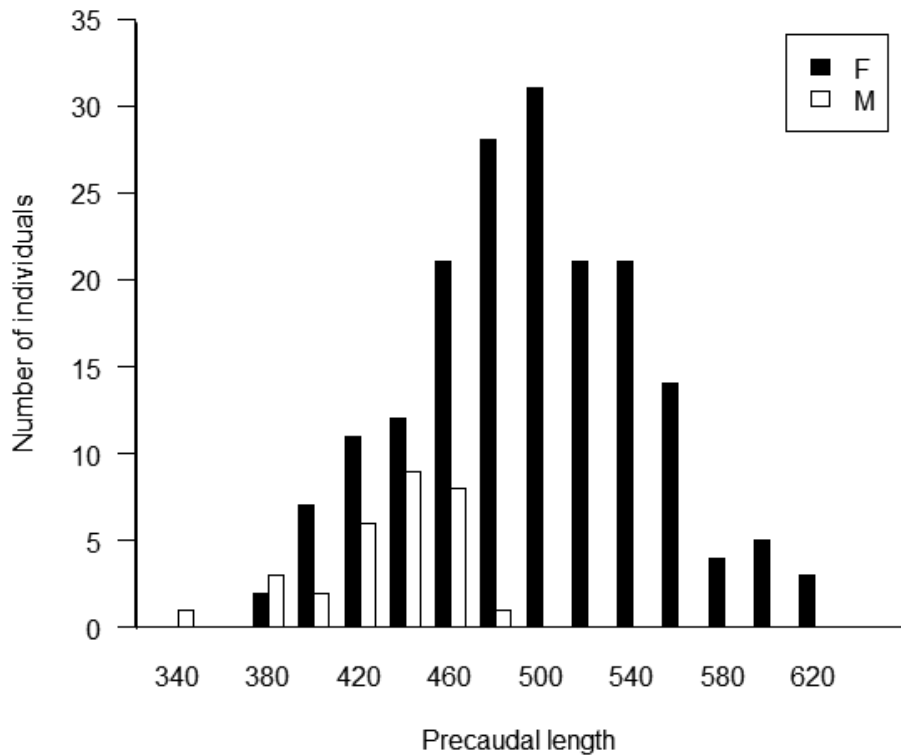


FIGURE 2 | Length-frequency distributions of *Callorhynchus callorynchus* for females (F) and males (M) off northern Argentina.

three polychaetes, three amphipods, three cumaceans, one teleost, one echinoderm, one bryozoan and one sipunculid (Tab. 2). In terms of %PSIRI the diet of *C. callorynchus* was dominated mainly by bivalves. Brachyuran crabs, isopods, gastropods, anomuran crabs, amphipods and cumaceans were also consumed but in lower proportion. The most frequent prey category was bivalves. Gastropods and isopods showed the same frequency of occurrence in the diet of *C. callorynchus*. The most important prey categories according to prey-specific abundance by number and weight were bivalves and unidentified Teleostei, followed by isopods and brachyuran crabs in term of the %PN and %PW. Among bivalves, *Amiantis purpurata* was the most consumed prey species in terms of %PN, %PW, %FO and %PSIRI. *Mytilus edulis* was the second most important in terms of %PSIRI, followed by *Corbula patagonica* and *Mactra marplatensis*. Unidentified gastropods were the most frequent prey species in the diet of the *C. callorynchus*. The crab *Libinia spinosa* was the most important prey species among crustaceans in terms of %PN and %PW. Amphipods belonging to the Ampeliscidae family and the crab *Blepharipoda doelloi*, were the second most important in terms of the %PN and %PW among crustaceans.

The diet composition of both sexes was composed mainly by bivalves. Females preyed more heavily on anomuran crabs and isopods than males. Brachyuran crabs was the second prey item more consumed by males (Tab. 3)

Changes in the diet. Several patterns were found in the relationships between number of prey consumed with PCL, maturity stage, season and region for females (Tab. 4). The consumption of isopods and amphipods decreased with increasing PCL (Fig.

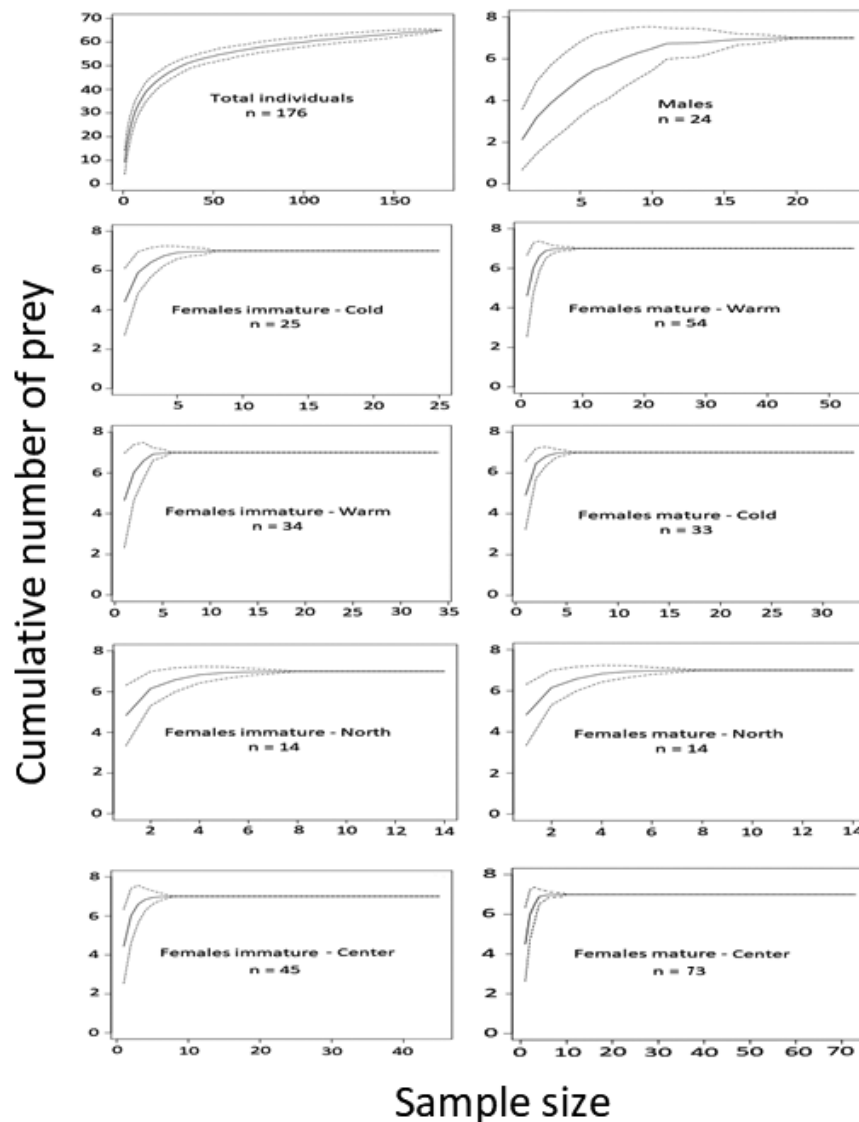


FIGURE 3 | Cumulative prey curves as a function of sample size of *Callorhynchus callorynchus* for total individuals, males and for each group of females considered in the dietary analysis. Mean (continuous lines) \pm SD (dashed lines) are plotted.

4). On the other hand, the consumption of gastropods and anomuran crabs increased with increasing PCL (Fig. 4). Mature females preyed more heavily on brachyuran crabs than did immature females (Fig. 5). The consumption of brachyuran crabs and gastropods was higher in the cold season than in the warm season, and cumaceans were more consumed in the warm season than the cold season. The consumption of bivalves, anomuran crabs and cumaceans was affected by the region. *C. callorynchus* preyed more heavily on bivalves in the center region (38° S) than in the north region (36° – 38° S). The number of anomuran crabs and cumaceans consumed was higher in the north region than in the center region (Figs. 4, 5).

Models for bivalves, isopods and amphipods had a low w , therefore model averaging was computed. The averaged coefficient for bivalves was -0.248 (s.e. = 0.31) for the north

TABLE 2 | Diet composition of *Callorhynchus callorynchus* off northern Argentina. %N, percent number; %PN, percent prey-specific number; %W, percent weight; %PW, percent prey-specific weight; %FO, percent frequency of occurrence; %PSIRI, the prey-specific index of relative importance.

PREY		%N	%PN	%W	%PW	%FO	%PSIRI
MOLLUSCA							
BIVALVIA		49.44	53.05	61.79	66.32	93.18	55.61
Unidentified Bivalvia		2.29	5.10	1.97	4.39	44.89	2.13
Veneridae	<i>Amiantis purpurata</i>	16.73	33.46	18.19	36.38	50	17.46
	<i>Tivela dentata</i>	1.16	14.57	1.88	23.64	7.95	1.52
	<i>Transeptar americana</i>	0.97	28.37	1	29.28	3.41	0.98
Mytilidae	<i>Mytilus edulis</i>	8.09	52.73	9.10	59.34	15.34	8.60
	<i>Brachidontes rodriguezii</i>	2.36	14.87	5.40	33.96	15.91	3.88
Nuculanidae	<i>Adrana electa</i>	1.46	8.02	2.03	11.19	18.18	1.75
Nuculidae	<i>Ennucula puelcha</i>	1.38	24.22	1.09	19.28	5.68	1.23
Mactridae	<i>Mactra isabelleana</i>	1.96	7.66	4.34	16.99	25.57	3.15
	<i>Mactra marplatensis</i>	4.25	9.12	7.05	15.13	46.59	5.65
	<i>Raeta plicatella</i>	0.01	1.82	0.03	4.52	0.57	0.02
Solenidae	<i>Solen tehuelchus</i>	1.10	5.87	1.81	9.67	18.75	1.46
Corbulidae	<i>Corbula patagonica</i>	5.94	23.23	6.88	26.92	25.56	6.41
Semelidae	<i>Semelle</i> spp.	0.52	18.45	0.38	13.48	2.84	0.45
Cardiidae	<i>Trachycardium muricatum</i>	0.09	1.75	0.08	1.55	5.11	0.08
Montacutidae		0.82	14.43	0.26	4.57	5.68	0.54
Glycymerididae	<i>Glycymerididae longior</i>	0.06	2.02	0.17	6.01	2.84	0.11
Tellinidae	<i>Ardeamya pettitiana</i>	0.26	6.61	0.05	1.36	3.98	0.16
	<i>Macoma brevifrons</i>	0.01	1.82	0.02	4.02	0.57	0.02
Pholadidae	<i>Cyrtopleura lanceolata</i>	0.01	1.00	<0.01	0.12	0.57	<0.01
Pinnidae	<i>Atriana seminuda</i>	<0.01	0.67	<0.01	0.15	0.57	<0.01
Mesodesmatidae	<i>Mesodesma mactroides</i>	0.01	1.33	<0.01	0.04	0.57	<0.01
GASTEROPODA		5.16	8.19	7.50	11.89	63.07	6.33
Unidentified Gasteropoda		3.02	4.92	5.28	8.60	61.36	4.15
Calliostomatidae	<i>Photinulla</i> spp.	1.88	27.51	2.17	31.86	6.82	2.02
Crepidulidae	<i>Crepidula argentina</i>	0.27	2.60	0.04	0.43	10.23	0.15
CRUSTACEA							
BRACHYURA		8.15	13.04	13.10	20.96	62.5	10.63
Unidentified Brachyura		1.73	10.88	2.05	12.86	15.91	1.89
Acteocyclusidae	<i>Peltarion spinosulum</i>	1.75	44.05	1.84	46.22	3.98	1.79
Majidae	<i>Libinia spinosa</i>	2.09	7.90	5.12	19.58	26.14	3.60
	<i>Pyromaia</i> spp.	0.21	3.76	0.33	5.88	5.68	0.27
	<i>Leurocyclus tuberculata</i>	0.11	2.36	0.48	10.66	4.54	0.29
Epialtidae	<i>Leucippa pentagona</i>	0.15	3.81	0.22	5.74	3.97	0.19
Belliidae	<i>Corystoides chilensis</i>	0.68	4.01	1.81	10.62	17.04	1.25
Varunidae	<i>Cyrtograpsus altimanus</i>	0.72	5.48	0.89	6.84	13.07	0.80
Platyxantidae	<i>Platyxantidae crenulatus</i>	0.02	1.73	<0.01	0.23	1.14	0.01
Pinnotheridae	<i>Austinixa patagonensis</i>	0.58	6.42	0.17	1.92	9.09	0.38
	<i>Pinnixa brevipollex</i>	0.01	1.37	<0.01	0.06	0.57	<0.01
	<i>Pinnotheres garthi</i>	0.06	3.41	0.16	9.64	1.70	0.11
	<i>Tumidotheres maculatus</i>	0.04	3.27	0.01	0.73	1.14	0.02
ANOMURA		7.29	13.50	5.15	9.53	53.98	6.22
Unidentified Anomura		0.80	4.14	0.22	1.16	19.32	0.51
Paguridae	<i>Pagurus exilis</i>	3.93	12.13	3.07	9.47	32.39	3.50
	<i>Pagurus criniticornis</i>	2.09	11.86	0.67	3.79	17.61	1.38
Diagonidae	<i>Loxopagurus loxochelis</i>	0.45	6.66	0.94	13.76	6.82	0.70
Porcellanidae	<i>Pachycheles laevidactylus</i>	0.01	2.04	0.05	8.33	0.57	0.03
Albuneidae	<i>Blepharipoda doelloi</i>	<0.01	0.67	0.20	35.44	0.57	0.10
ISOPODA		14.40	22.83	5.88	9.32	63.07	10.14
Unidentified Isopoda		0.34	2.30	0.03	0.22	14.77	0.18
Serolidae	<i>Serolis marplatensis</i>	7.73	15.46	4.41	8.82	50	6.07
	<i>Serolis bonaerensis</i>	0.13	2.92	0.01	0.23	4.54	0.07
Sphaeromatidae	<i>Sphaeroma serratum</i>	5.83	13.32	1.37	3.14	43.75	3.60
Idoteidae	<i>Idotea</i> spp.	0.36	3.18	0.05	0.41	11.36	0.20
	<i>Jaeropsis dubia</i>	<0.01	1	<0.01	0.44	0.56	<0.01
AMPHIPODA		7.28	15.83	1.84	4.00	46.02	4.56
Unidentified Amphipoda		0.30	2.95	0.03	0.29	10.23	0.16
Ampeliscaidae	<i>Ampelisca</i> spp.	6.69	18.68	1.79	5.01	35.79	4.24
Caprellidae		0.30	4.74	0.02	0.31	6.25	0.16
CUMACEA		4.27	9.39	1.24	2.74	45.45	2.76
Unidentified Cumacea		0.18	2.45	0.14	1.88	7.39	0.16
Diastylidae		2.48	7.38	0.39	1.15	33.52	1.43
Bodotriidae		1.61	8.10	0.72	3.61	19.89	1.16
CIRRIPEDIA		0.60	3.20	0.55	2.93	18.75	0.57
Balanidae	<i>Balanus</i> spp.	0.60	3.20	0.55	2.93	18.75	0.57
TELEOSTEI		1.30	38.05	1.16	34.19	3.41	1.23
Unidentified Teleostei		1.30	38.05	1.16	34.19	3.41	1.23
POLYCHAETA		1.74	5.48	1.60	5.03	31.82	1.67
Lumbrineridae		0.91	4.34	0.73	3.51	21.02	0.82
Opheliidae	<i>Travisia</i> spp.	0.54	19.32	0.83	29.33	2.84	0.69
Maldanidae		0.03	2.96	<0.01	0.22	1.14	0.02
Tubos de poliquetos		0.25	2.31	0.03	0.25	10.79	0.14
ECHINODERMATA		0.03	4.76	0.01	1.78	0.57	0.02
Ophiuridae		0.03	4.76	0.01	1.78	0.57	0.02
BRYOZOA		0.07	1.42	0.01	0.13	5.11	0.04
SIPUNCULIDA		0.27	7.84	0.16	4.79	3.41	0.21

TABLE 3 | Diet composition for females and males of *Callorhynchus callorhynchus* off northern Argentina. %PN: percent prey-specific number; %PW: percent prey-specific weight; %FO: percent frequency of occurrence; %PSIRI: the prey-specific index of relative importance. A dash indicates that some categories of prey were not consumed by males.

Prey	%PN		%PW		%FO		%PSIRI	
	Females	Males	Females	Males	Females	Males	Females	Males
Bivalvia	50.94	67.44	65.29	73.31	94.08	87.5	54.67	61.58
Gasteropoda	8.28	6.25	12.21	5.12	69.74	20.83	7.14	1.18
Brachyura	11.12	28.74	18.74	39.10	64.47	50	9.62	16.96
Anomura	12.93	23.75	9.73	5.88	59.21	20.83	6.71	3.09
Isopoda	22.24	38.49	9.02	17.42	70.39	16.67	11.00	4.66
Amphipoda	15.92	14.09	4.14	1.41	50.66	16.67	5.08	1.29
Cumacea	9.41	8.56	2.80	0.31	51.31	8.33	3.13	0.37
Cirripedia	3.24	2.04	3.01	0.11	21.05	4.17	0.65	0.04
Teleostei	20.00	41.67	32.67	34.50	0.66	20.83	0.17	7.93
Polychaeta	4.74	25.5	3.59	43.78	35.53	8.33	1.48	2.89
Equinodermata	4.76		1.78		0.66		0.02	
Bryozoa	1.42		0.13		5.92		0.04	
Sipunculida	7.84		4.79		3.95		0.04	

TABLE 4 | Best models explaining the consumption in number of the main prey categories of *Callorhynchus callorhynchus* off northern Argentina. PCL: precaudal length; AIC: Akaike Information criterion; w: Akaike weights. The coefficients of the models are relative to immature individuals, center region and warm season. Standard error in parentheses.

Prey categories	Intercept	Coefficient	AIC	w
Bivalvia	3.56 (0.12)	- 0.49 (0.28) north	1286.1	0.21
Gasteropoda	- 4.55 (1.13)	0.01 (<0.01) PCL + 0.76 (0.22) cold	499.8	0.88
Brachyura	0.19 (0.22)	0.59 (0.24) mature + 0.58 (0.23) cold	585.4	0.56
Anomura	- 3.68 (1.36)	0.01 (<0.01) PCL + 0.91 (0.34) north	633.5	0.57
Isopoda	5.02 (1.26)	- 0.01 (0.002) PCL	925.6	0.34
Amphipoda	7.07 (1.87)	- 0.01 (0.004) PCL	696.9	0.42
Cumacea	1.17 (0.19)	-1.36 (0,32) cold + 1.59 (0.37) north	599.08	0.97

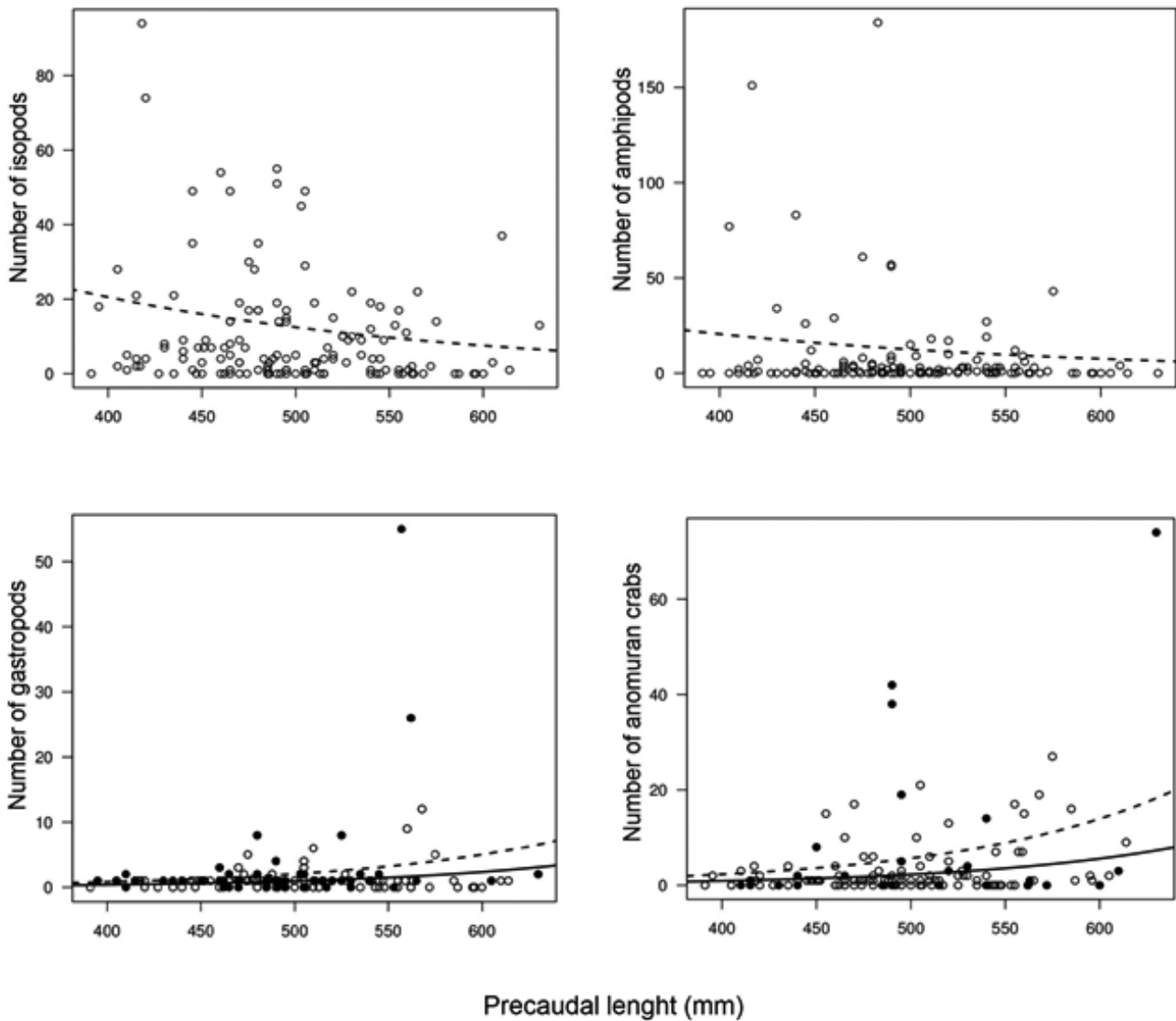


FIGURE 4 | Changes in consumption of isopods, amphipods, gastropods and anomuran crabs with body size, season and region of *Callorhynchus callorynchus* females estimated by generalized linear models. In gastropods: cold season with dashed lines and open circles; warm season with solid lines and solid circles. In anomuran crabs: north region with dashed lines and open circles; center region with solid lines and solid circles.

region ($w = 0.52$). For isopods and amphipods the averaged coefficients were -0.003 (s.e. = 0.003) and -0.001 (s.e. = 0.004) for PCL with a w of 0.60 and 0.88 , respectively.

No relationship between PCL of *C. callorynchus* and CW of brachyuran crabs was found. However, as significant relationship between predator size and size of bivalves was found. As PCL of *C. callorynchus* increased, minimum, medium and maximum VW of bivalves increased (slopes of 5, 50 and 95% quantile regressions = 0.010 , 0.022 , 0.019 , respectively; $p < 0.01$) (Fig. 6).

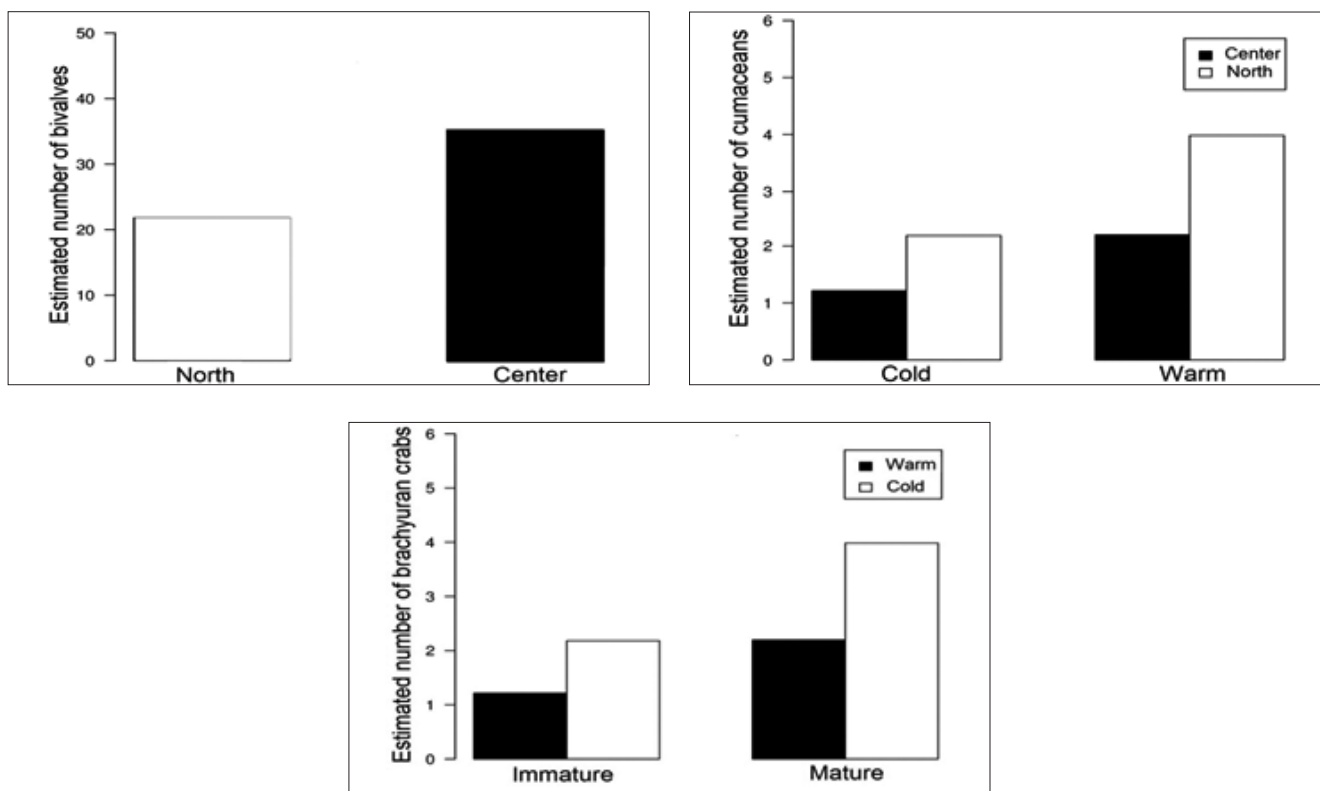


FIGURE 5 | Changes in consumption of bivalves, cumaceans and brachyuran crabs with region, season and maturity stage of *Callorhynchus callorynchus* females estimated by generalized linear models.

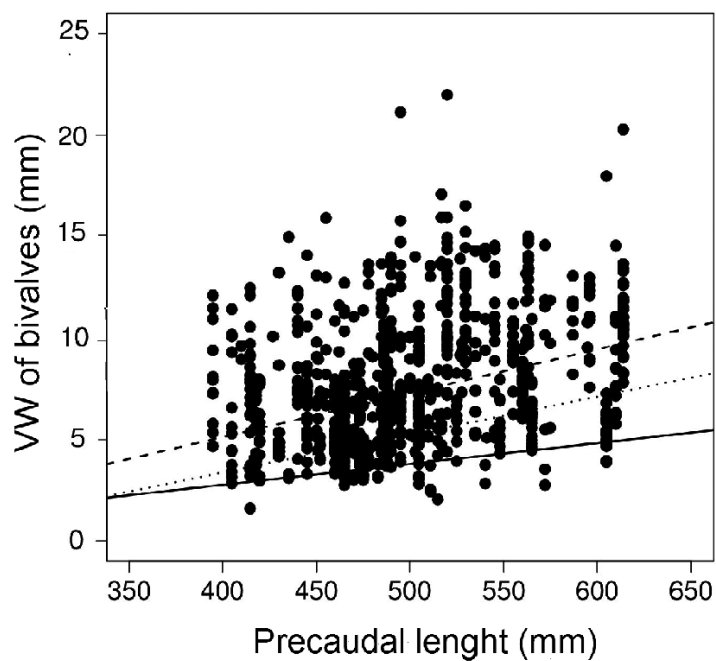


FIGURE 6 | Relationship between valve width (VW) of bivalves and precaudal length of *Callorhynchus callorynchus*. The solid, dashed and dotted lines are 5%, 50% and 95% quantile regressions, respectively.

Trophic level. The mean trophic position was 3.19 (standard deviation = 0.01), indicating that *C. callorynchus* is a secondary consumer throughout the entire study area.

DISCUSSION

The diet of *C. callorynchus* consists mainly of bivalves, followed by brachyuran crabs, isopods, and other benthic invertebrates, which implies that this species has benthic feeding habits. Further, *C. callorynchus* females showed changes in the diet composition with increasing body size and also between seasons and regions.

A previous study conducted in the San Matías Gulf, northern Patagonia (41°30'S 64°15'W), found that bivalves were the main prey consumed by *C. callorynchus*, followed by polychaetes, decapods and stomatopods (Di Giacomo, Perier, 1996). However, the main species of bivalve consumed were different between studies. The most important species of bivalves observed by Di Giacomo, Perier (1996) were the scallop *Zygochlamys patagonica*, and the clams *Ennucula puelcha* and *Pitar rostratus*. In our study, the clams *Amiantis purpurata*, *Mytilus edulis*, *Corbula patagonica* and *Mactra marplatensis* were the most consumed bivalves. This difference in consumption of bivalves may be associated with regional and bathymetric differences in prey availability, because the results of Di Giacomo, Perier (1996) reflected the diet of samples taken in the San Matías Gulf in depths between 20 m and 130 m, whereas the samples in our study were obtained exclusively in coastal areas (<50 m depths). Our results also agree with Rios, Pereira (1986); they observed that in individuals captured off Uruguay and northern Argentina (34°38'S–54°53'W 34°36'S–57°53'W) between 10 and 80 m depth the most important prey were bivalves.

In Atlantic waters the diet of *C. callorynchus* is mainly dominated by bivalves, however, this observation is not consistent in Pacific localities. For example, in coastal waters off San Antonio (Molina *et al.*, 1980) and off Puerto Montt (Bahamonde, 1950), Chile, the diet composition of *C. callorynchus* was dominated mainly by decapod crustaceans. These differences in the overall observation of diet composition between Atlantic and Pacific waters may be due possibly to several reasons: different prey availability in benthic communities, different regional interaction between potential competitors in each marine community, period of time in which these studies were conducted, and that the two Pacific studies were conducted off central Chile.

Callorhynchus callorynchus, in Atlantic waters, showed a diet similar to another Callorhynchidae species. *Callorhynchus capensis* off Velddrif Harbour, South Africa, has a high frequency of bivalves in its diet (*e.g.*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*) (Nibam, 2011). On the other hand, in the northeastern Atlantic, other chimaeroid species of the families Chimaeridae (*Chimaera monstrosa* and *Hydrolagus mirabilis*) and Rhinochimaeridae (*Harriotta raleighana*) have a diverse diet based on benthic invertebrates. These species feed mainly on crustaceans, polychaetes, echinoderms and anemones (Mauchline, Gordon, 1983). In the same way, on the continental slope off southern Portugal and in the Eastern Mediterranean, the rabbitfish *C. monstrosa* presents a diet composed mainly by crustaceans (*i.e.*, amphipods and crabs), followed by polychaetes and molluscs (Moura *et al.*, 2005; Eronat, 2016). The biomass and distribution of the benthic fauna varies with depth (Witman, Roy, 2009). Therefore,

these differences in the diet among chimaeroid families could be related to differences in the depth distribution range: *Callorhynchidae* species occurs in coastal regions, whereas *Chimaeridae* and *Rhinochimaeridae* species occur mainly in deep waters.

Off northern Argentina *C. callorhynchus* consumes a wide variety of benthic organisms, however, its diet was composed mostly by hard prey (e.g., bivalves, gastropods, brachyuran and anomuran crabs). This feeding habit may be related to the development of tooth plates of the mouth apparatus which could be the most relevant characteristic associated with the crushing of the hard prey, favoring feeding habits suited for durophagy (Di Giacomo, Perier, 1996; Summers, 2000; Summers *et al.*, 2003). Furthermore, the consumption of the infaunal prey suggests that *C. callorhynchus* could dig into the bottom in search of prey. An important result to note is the high consumption of the purple clam *Amiantis purpurata*. This infaunal bivalve is common in the coastal sandy bottom of the Southwest Atlantic (Penchaszadeh *et al.*, 2006). There is evidence that this species is an important food source for a number of chondrichthyan species in shallow coastal waters (e.g., *Discopyge tshudii*, Spath *et al.*, 2012; *Myliobatis* spp., Molina, López Cazorla, 2015). However, the extent of its contribution to the food web is still unknown.

Predator roles in marine communities can be influenced by many factors, such as prey abundance, body size and reproductive condition (Wetherbee, Cortés, 2004). As a result, ontogenetic, regional and/or seasonal changes in the dietary composition can occur. Ontogenetic diet shifts are a phenomenon widely observed in many chondrichthyan species off northern Argentina (Lucifora *et al.*, 2009; Barbini, Lucifora, 2011; 2012; Belleggia *et al.*, 2012; Spath *et al.*, 2012; Ruocco, Lucifora, 2016). In the same way, *C. callorhynchus* females showed shifts in its diet composition: small individuals consumed amphipods and isopods, but large individuals preyed on gastropods and brachyuran and anomuran crabs. A possible explanation for these dietary shifts can be a combination of an improved ability to capture larger prey and a change in the reproductive condition of large individuals. As body size increases, individuals can modify their abilities associated with the feeding, such as gape size, bite force, handling and suction force (Tanaka, 1973; Capapé, 1976; Hernandez, Motta, 1997; Scharf *et al.*, 2000; Carrol *et al.*, 2004; Huber, Motta, 2004; Lowry, Motta, 2008; El Kamel-Moutalibi *et al.*, 2013). On the other hand, an increase in the metabolic requirements of mature females may also contribute to generate ontogenetic dietary shifts. A similar observation was found in San Matías Gulf, where mature individuals of *C. callorhynchus* preyed more heavily on crabs than immature individuals (Di Giacomo, Perier, 1996).

The diet composition of *C. callorhynchus* females varied seasonally and regionally. *Callorhynchus callorhynchus* consumed more brachyuran crabs and gastropods in the cold season, and feed on cumaceans in the warm season. Information on seasonal variability of the abundance of benthic invertebrates consumed by *C. callorhynchus* in the study area is not available and further studies are needed. However, the seasonal variability could be attributed to fluctuations in the distribution and abundance of the prey (Muto *et al.*, 2001). This finding for females of *C. callorhynchus* has been suggested for other species of chondrichthyans in the same area (e.g., *Psammobatis extenta*, Braccini, Perez, 2005; *P. bergi*, San Martín *et al.*, 2007; *Zapteryx brevirostris*, Barbini, Lucifora, 2011; Barbini *et al.*, 2011; *Rioraja agassizii*, *Atlantoraja castelnaui*, Barbini, Lucifora, 2012).

The regional variability is characterized by a higher consumption of bivalves in the center region and a higher consumption of anomuran crabs and cumaceans in

the north region. Differences in richness and abundance of the benthic community between regions could explain this variability. The north area is strongly influenced by the Río de la Plata estuary: bottom type, salinity and the presence of a turbidity front are considered the main variables structuring the benthic community of this area (Giberto *et al.*, 2004). Consequently, the spectrum of available prey could be different between these regions. These results indicate that *C. callorynchus* is a plastic and versatile predator, adapting its feeding habits in response to seasonal and regional changes.

Our results show that as the size of *C. callorynchus* increases, the size of consumed bivalves does too. An increase of prey size consumed is generally attributed to ontogenic mouth size increase (Karachle, Stergiou, 2011). The selection of small prey by small individuals may be the results of morphological constraints, as mouth gape or the development of the structures involved in the feeding (*i.e.*, tooth plates of the upper and lower jaws) (Di Giacomo, Perier, 1996; Scharf *et al.*, 2000; Karpouzi, Stergiou, 2003). The pattern found here may be related to the crushing power of the mouth of large individuals, which could be higher than of the mouth of small individuals (Juanes *et al.*, 2002). Bivalve shell's strength is typically correlated with its size (Zuschin *et al.*, 2003; Lowry, Motta, 2007; Kolman, Huber, 2009). Thus, small individuals of *C. callorynchus* may be unable to both handle and crush hard-shelled prey.

The trophic level of *C. callorynchus* indicates that it is a secondary consumer in the northern Argentina coastal ecosystems. This constitutes the first trophic level estimation for a member of the family Callorhynchidae. Eronat (2016) estimated the trophic levels of *Chimaera monstrosa* off Sigacik Bay, Eastern Mediterranean, with values similar to those reported in this study. The Shortose eagle ray *Myliobatis ridens* (Myliobatiformes) is a chondrichthyans with feeding habits similar to *C. callorynchus* in the same area of study (Ruocco, Lucifora, 2016). It is known that some benthic Myliobatiformes affect the species turnover of benthic communities by disrupting the structure of the bottom and preying on benthic invertebrates (VanBlaricom, 1982; Thrush *et al.*, 1994). Hence, *C. callorynchus* being a secondary consumer that feeds on benthic prey, could play an important role structuring benthic communities.

In conclusion, this study provides valuable information on the feeding habits of an important predator in the coastal waters from off northern Argentina. Our results show that this holocephalan has a strong predatory interaction with the benthic community, since its diet was composed mainly of benthic prey (*i.e.*, bivalves, brachyuran crabs and isopods). In addition, this study fills gaps in our knowledge about his biology in this area. However, to deepen understanding of the feeding habits of *C. callorynchus* in this area, future research should consider a greater number of juvenile individuals (< 300 mm, PCL) and adult males (> 500 mm, PCL).

ACKNOWLEDGMENTS

We are grateful to artisanal fishermen (Martín, Julio, Jose and Hector) for sample collection. We thank C. Bass and L. Ferrero for help in the identification of prey, C. Estupiñán-Montaña and S. A. Briones-Hernández for their suggestions in the calculation of the prey-specific index of relative importance, and L. O. Lucifora and E. E. Di Giacomo for critical reading of the manuscript. We also wish to extend our thanks

to the anonymous reviewers for comments that greatly improved the manuscript. J. M. Roman and M. A. Chierichetti were supported by scholarships from CIC and CONICET (Argentina), respectively.

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Official Journal of the
Sociedade Brasileira de Ictiologia

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ETHICAL STATEMENTS

Not applicable.

HOW TO CITE THIS ARTICLE

- Roman JM, Chierichetti MA, Barbini SA, Scenna LB. Feeding habits of the cockfish, *Callorhynchus callorynchus* (Holocephali: Callorhynchidae) from off northern Argentina. Neotrop Ichthyol. 2020; 18(1):e180126. <https://doi.org/10.1590/1982-0224-2018-0126>