

Trophic niche partitioning of five skate species of genus *Bathyraja* in northern and central Patagonia, Argentina

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ABSTRACT

Overexploitation of marine communities can lead to modifications in the structure of the food web, and can force organisms like elasmobranchs, for example, to change their feeding habits. In order to evaluate the impact that fisheries have on food webs and on the interactions between species, it is necessary to describe and quantify the diet of the species involved and follow it through time. This study compares the diet of five skate species, by means of the data obtained from the bycatch of the Argentine hake (*Merluccius hubbsi*) fishery in north and central Patagonia, Argentina. Diet composition was assessed by analysing digestive tract contents and trophic overlapping between species of the genus *Bathyraja*: *B. albomaculata*, *B. brachyurops*, *B. macloviana*, *B. magellanica* and *B. multispinnis*. A total of 184 stomachs were analysed. The *B. albomaculata* and *B. macloviana* diets were mainly comprised annelids, while the *B. brachyurops* diet primarily comprised fish, including hake heads discarded by the fishery. *B. magellanica* and *B. multispinnis* diets were largely based on crustaceans. Despite the morphological similarities and their shared preference for benthic habitats, no complete diet overlaps were found between the different species. These results suggest that these skate species have undergone a process of diet specialisation. This is a common feeding strategy that occurs in order to successfully eliminate competition when resources are limited, which corresponds to the conditions found in an environment being affected by the pressures of overfishing.

KEYWORDS

Diet, *Bathyraja*, niche partitioning, Patagonian continental shelf waters

INTRODUCTION

The composition of marine communities tends to change over time depending on the exploitation levels to which they are subjected (Dulvy *et al.*, 2000). There is evidence of the direct impact fisheries have on ecosystems: reduction of biological diversity, decrease in abundance, changes in the size of harvested individuals and the composition of the assemblage of species, an increase in the dominance of low trophic level species, and changes in life history parameters of target and bycatch species (Gislason *et al.*, 2000; Cury & Palomares, 2005). Bottom-trawl fisheries, in particular, cause high mortality rates in non-target species like sea birds, marine mammals, elasmobranchs, non-commercial bony fishes and many benthic invertebrate species (Crespo *et al.*, 1997; Clark *et al.*, 2015). Studying the mechanisms that regulate community structure is crucial for understanding the impact that commercial fishing exploitation has on populations (Bax, 1998). The study of diet and food-web structures is the first step towards increasing baseline knowledge on species affected by fisheries, and for marine ecosystems being affected by overfishing (Koen Alonso & Yodzis, 2005). These studies provide a better understanding of niche use, and trophic interactions, as well as the potential regulatory effects of these ecosystems (Braccini, 2008).

Elasmobranchs play an important ecological role in marine ecosystems (Crespi-Abril *et al.*, 2013). As predators, they can regulate interactions between the trophic levels within a community (Navia *et al.*, 2010). Elasmobranch populations have undergone rapid and widespread declines, due to the direct and indirect consequences of fishing (Dulvy *et al.*, 2008; Ferretti *et al.*, 2008). However, fishing pressure can lead to different indirect impacts depending on the skate species. One of these, is the competition release process (Walker & Hislop, 1998; Dulvy *et al.*, 2000). For example, while larger species can become locally extinct as a result of overfishing, other species with smaller body sizes, in contrast, may increase in abundance (Graham *et al.*, 2001; Devine *et al.*, 2006). Overfishing causes modifications in the trophic webs that can lead to changes in the feeding habits of the affected species (Ruocco *et al.*, 2012). For example,

the ontogenetic shift in the diet of the beaked skate *Dipturus chilensis* (Guichenot 1848) and the spiny dogfish *Squalus acanthias* L. 1758 changed as a consequence of fishing exploitation (Koen Alonso *et al.*, 2001; Buren, 2004; Herrera *et al.*, 2012).

In Argentine waters, the fishing industry has had a dramatic increase in fishing effort since the late 1980s and mid-1990s. The *Rajidae* family is a common by-catch in the Argentine hake *Merluccius hubbsi* Marinni 1933 bottom-trawl fishery (Consejo Federal Pesquero Argentino, 2009). In Argentina, the family is represented by eight genus (Cousseau *et al.*, 2007), *Bathyraja* being the most diverse, represented by eight species: *B. albomaculata* (Norman 1937), *B. brachyurops* (Fowler 1910), *B. macloviana* (Norman 1937), *B. magellanica* (Philippi 1902), *B. multispinis* (Norman 1937), *B. griseocauda* (Norman 1937), *B. scaphiops* (Norman 1937) and *B. cousseauae* Díaz de Astarloa & Mabragaña 2004 (Menni & Stehmann, 2000; Cousseau *et al.*, 2007; Ebert & Compagno, 2007; Ruocco *et al.*, 2007; Menni *et al.*, 2010). Its distribution encompasses the Argentinian continental shelf, which ranges from 36°S to 55° S (Cousseau *et al.*, 2007; Ruocco *et al.*, 2007) with higher values of relative abundances from 36° S to 44° S (Ruocco *et al.*, 2007). Even so, captures of *B. albomaculata*, *B. brachyurops*, *B. macloviana*, *B. magellanica* and *B. multispinis* are associated with the presence of Argentine hake (Ruocco *et al.*, 2007).

Given that elasmobranchs have such an important impact on the trophic network, describing and quantifying their diet is crucial in order to understand the effects that the fishing industry has on them. Furthermore, as many of these species share morphological similarities (Crespi-Abril *et al.*, 2013), this could provide evidence that they belong to a trophic assembly (*i.e.*, a group of species that exploit similar trophic resources) (Cohen, 1989). All of this information is crucial to build multispecies food-web models, which can be used as a tool for evaluating the dynamics of an ecosystem, as well as the fisheries impacts and the use of trophic resources in an impacted marine ecosystem (Pauly *et al.*, 2000; Bai & Cai, 2015). In this scenario, the goal of the present study was to compare the feeding habits and analyse the trophic overlap

of five *Bathyraja* species in Argentine Patagonian Shelf waters: *B. macloviana*, *B. brachyurops*, *B. albomaculata*, *B. magellanica* and *B. multispinis*.

MATERIALS AND METHODS

Study area and data collection

Samples were taken in northern and central Patagonian waters, between 41° S and 48° S, ranging from 60 to 180 m in depth (Figure 1), between November 2000 and July 2007. These samples were taken from by-caught skates from commercial bottom trawls that were targeting *M. hubbsi*. By-caught skates were preserved on ice until dissection. A total of 184 stomach contents were analysed, these belonged to the following five skate species (order Rajiformes, family Rajidae): *B. albomaculata* (n=15), *B. brachyurops* (n=115), *B. macloviana* (n=16), *B. magellanica* (n=28) and *B. multispinnis* (n=10).

Stomach content analysis

For each individual skate the sex, total body length (L_T , cm), mass (M , kg), and disc width (D_w , cm) were recorded to the nearest mm. Additionally, the diet composition was studied using the digestive tract contents (stomach and spiral valve). Digestive tracts were frozen at -20 °C until they were analysed. The contents were then separated through the use of water fleshing, a column of sieves, and 0.5, 1, and 2.5 mm decantation trays.

Prey species were identified at the lowest possible taxonomic level from the available remains, including complete specimens, and hard remains like squid beaks, fish otoliths, and crustacean exoskeletons. Local species reference collections at the Marine Mammals Laboratory¹ and published catalogues were used as references for the identification process (Menni *et al.*, 1984; Roper *et al.*, 1984; Toschi *et al.*, 1992; Gosztonyi & Kuba, 1996; Volpedo & Echeverría, 2000; Cousseau *et al.*, 2007; Nelson

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et al., 2016).

The minimum number of individuals (NI) of each fish species found in a given stomach was estimated as: $NI = LO + 0.5 NA$ (if $LO > RO$) or

$$NI = RO + 0.5 NA \text{ (if } RO > LO\text{),}$$

where LO, RO, and NA are the numbers corresponding to the left, right and unassigned otoliths, respectively (Koen Alonso *et al.*, 1998).

The minimum number of cephalopods in a given stomach was estimated using the amount of upper or lower beaks (jaws) found for each particular species. The minimum number of crustaceans in a given stomach was estimated using the number of complete skeletons present or, when it was not possible, we used the number of right and/or left propodus found. The minimum number of annelids was estimated using the amount of jaws pieces present.

Total body length of fish, length of dorsal mantle of squids, maximum length of crustacean shells, and the wet weight were estimated from the hard remains found in the digestive tracts, using allometric regressions (Clarke, 1986; Santos, 1994; Koen Alonso *et al.*, 1998; Koen Alonso, 1999; Koen Alonso *et al.*, 2000; Buren, 2004). For those species where the allometric regression was not available, parameters were estimated using the allometric regressions of closely related or similar species.

Cumulative prey curves were constructed for each skate species to determine if an adequate number of stomachs was analysed to accurately describe their diets (Cortés, 1997; Kovács & Török, 1997). Stomachs analysed were randomised 100 times (*i.e.* 100 permutations) and the cumulative number of new prey items were counted for each randomisation. Afterwards, the number of analysed stomachs was plotted against the mean \pm standard deviation number of prey item encountered in the stomachs. Cumulative prey curves were performed using the *specaccum* function (*rarefaction* method) in the *vegan* package (Oksanen *et al.*, 2019) in R statistical software, version 3.5.0 (Development Core, 2018). Prey - stomach curves that reached

a stable asymptote and displayed a reduction in variability were considered sufficient to describe their diet (Hurtubia, 1973; Cortés, 1997). Adequacy of sample size was statistically assessed using the linear regression method of Bizzarro *et al.* (2007). A linear regression was performed on the final 4 points of the curve to determine if the slope (or regression coefficient, b) was significantly different from 0. If slope was not significantly different ($P > 0.05$), then the curve reached an asymptote (Bizzarro *et al.*, 2007).

Diet Analysis

Diet composition was evaluated using the prey-specific index of relative importance, relativised to 100% ($\%I_{PSRI}$) (Brown *et al.*, 2012). The $\%I_{PSRI}$ was estimated as: $\%I_{PSRI} = [\%F_{O_i} (\%N_{P_i} + \%W_{P_i})] * 0.5$, where $\%F_{O_i}$ is the percent frequency of occurrence (the number of stomachs containing prey category i divided by the total number of stomachs) (Hyslop, 1980), $\%N_{P_i}$ and $\%W_{P_i}$ is the percent prey-specific abundance (counts and masses, respectively, of prey category i in stomach sample j divided by the number of stomachs containing prey i) (Brown *et al.*, 2012). Furthermore, $\%N_{P_i}$ and $\%W_{P_i}$ also can be estimated as the percent abundance ($\%N_i$ and $\%W_i$) over $\%F_{O_i}$ (Brown *et al.*, 2012). $\%I_{PSRI}$ was estimated by species and major zoological groups (Fish, Crustaceans, Molluscs, and Annelids). Finally, to allow comparisons with previous diet studies, $\%I_{RI}$ and its indicators also was reported (Table S1, Supporting information). However, only $\%I_{PSRI}$ data was used to discuss the obtained results.

$\%I_{PSRI}$ was used instead of the traditional $\%I_{RI}$ (Cortés, 1997) because the former one is an additive index with respect to taxonomic levels (*i.e.* $\%I_{PSRI\ CLASS} = \sum \%I_{PSRI\ FAMILY}$ within rounding errors), which allows comparisons between studies (Brown *et al.*, 2012). Furthermore, $\%I_{PSRI}$ allows a robust estimate since it does not overestimate dominant prey (Ortiz *et al.*, 2006; Brown *et al.*, 2012).

Trophic overlap

A hierarchical cluster analysis was used as an exploratory method to identify relations between diet

patterns across the different species. The algorithm UPGMA (Unweighted Pair Group Method using Arithmetic Averages) was used to define the distances between two or more groups as the average of all the distances of pairs between elements from both groups (Cuadras, 1981). The prey species with % $I_{PSRI} > 1\%$ were used to estimate the Euclidean distances.

Finally, the general overlap (I_{GO}) and specific overlap (I_{SO}) indices were used to evaluate diet similarities between skate species (Petraitis, 1979; Ludwig & Reynolds, 1988). The I_{GO} evaluates the probability of obtaining the species i utilisation curve from a common utilisation curve with all of the species. I_{GO} varies between 0 and 1, in which $I_{GO} = 1$ means a complete overlap. The null hypothesis of a complete overlap between all predator species can be statistically tested by using the V statistic (Ludwig & Reynolds, 1988).

The I_{SO} index evaluates the probability of obtaining the utilization curve of species i from the curve of utilisation of species k . I_{SO} varies between 0 and 1, where $I_{SO} = 1$ means a complete overlap. The null hypothesis of a complete overlap can be tested using the U statistic (Ludwig and Reynolds, 1988).

Both indices were estimated for prey species and major zoological groups (Fish, Crustaceans, Molluscs, and Annelids). The prey species with % $I_{PSRI} > 1\%$ were then used to estimate both indices (Koen Alonso, 1999).

Ethical Statement

An ethical statement is not applicable because experimental animals were not used for our research. The samples were taken from by-caught skates from commercial bottom trawls that were targeting the *Merluccius hubbsi*.

RESULTS

Database

A total of 184 skates were analysed. *B. brachyrops* (n=115) was the most abundant species, and *B.*

multispinnis (n=10) was the least represented. The total body length varied between 26.31 cm and 85.54 cm. The disc width varied between 15.52 cm and 62.85 cm, and the mass varied between 0.13 kg, and 4.58 kg. The largest species was *B. multispinnis*, while the smallest was *B. magellanica* (Table 1).

Stomach content analysis

The cumulative prey curves generated reached an asymptote for *B. albomaculata* (b: regression coefficient = 0.01, $P = 0.05$), *B. brachyurops* (b = 1.11E-9, $P > 0.05$), and *B. macloviana* (b = 5.67E-5, $P > 0.05$) indicating adequate sample size for each skate species (Figure 2). On the other hand, cumulative prey curves for *B. magellanica* (b = 0.24, $P < 0.001$) and *B. multispinnis* (b = 0.11, $P < 0.001$) did not approach an asymptote. This would indicate representation of the diet could not be as accurate, and more stomachs should be provided. All of the stomach contents analysed, with the exception of four *B. brachyurops* individuals, one *B. magellanica* and one *B. albomaculata* individual, contained food sources at different stages of digestion, which varied from complete organisms to small fragments. Only the stomachs containing prey were analysed further. A total of 1282 prey were identified. 192 were fish 553 crustaceans, 501 annelids, 20 molluscs and 16 *M. hubbsi* heads from fishery discard.

The most commonly consumed species of fish were the southern cod *Patagonotothen ramsayi* (Regan 1913), and the *M. hubbsi*. Additional hake remains (*M. hubbsi* heads) from fishery activities were found. These were identified by the markings imprinted on the skulls of the fish that had been made with circular saws, indicating that those individuals were processed on board. Among the crustaceans, only three individuals could not be assigned to any group. The spider crab *Libinia spinosa* Edwards 1834 was the most consumed species. As for the annelids, the species could not be determined for the majority of the samples found. However, three different species were identified from these samples. Out of these three species, the sea mouse *Aphroditella alta* (Kinberg 1856) was the most common. Lastly, the Argentinian squid *Illex argentinus* (Catellanos 1960) was the most abundant mollusc (Table 2).

A total of 27 prey items presented a %*I*_{PSRI} greater than 1%, but only 11 prey items presented a %*I*_{PSRI} greater than 10%. For *B. albomaculata*, an unidentified errant polychaete (%*I*_{PSRI} = 24.51%) and *A. alta* (%*I*_{PSRI} = 23.70%) were the main prey species. For *B. brachyurops*, the most important prey were the *M. hubbsi* (%*I*_{PSRI} = 28.04%) and the *P. ramsayi* (%*I*_{PSRI} = 26.26%) both of which were also found in *B. magellanica*, but in lower relative importance (%*I*_{PSRI} = 1.22 and 1.36%, respectively). The *M. hubbsi* head (%*I*_{PSRI} = 10.26%) was also found as part of the food remains of *B. brachyurops*. In the case of *B. macloviana*, *A. alta* (%*I*_{PSRI} = 53.83%) was the most important prey, followed by an unidentified isopod (%*I*_{PSRI} = 20.24%). Meanwhile for *B. magellanica*, the main prey species were the *D. patagonicus* crab (%*I*_{PSRI} = 25.2%), followed by the *A. alta* annelid (%*I*_{PSRI} = 16.69%). Similarly, for *B. multispinnis*, the crustacean species *P. spinosulum* (%*I*_{PSRI} = 33.82%), and followed by *L. spinosa* (%*I*_{PSRI} = 27.80%) were the most important food items (Table 2).

Crustaceans were the only prey found in all of the studied species. However, they were more predominant in *B. magellanica* and *B. multispinnis* (%*I*_{PSRI} = 60.84 and 90.29%, respectively). For the rest of skate species, it displayed a predominance of 25%*I*_{PSRI}. *B. brachyurops* was the only species in which fish %*I*_{PSRI} was highest (%*I*_{PSRI} = 55.82%). Annelids were the most important prey for *B. macloviana* and *B. albomaculata*, with high values of %*I*_{PSRI} (77.69% and 64.46%, respectively) (Table 2)

Hierarchical clustering analysis

Using %*I*_{PSRI} of the prey consumed and taking into account a UPGMA method and a Euclidean distance (cophenetic correlation factor: 0.938), the five skate species were clustered in three trophic groups. Group A consisted of *B. brachyurops*. Group B comprised *B. magellanica*, and *B. multispinnis*; and finally, group C consisted of *macloviana* and *B. albomaculata* (Figure 3).

The A trophic group was the only group characterised by a piscivore diet, which consists of *B. brachyurops*. The B trophic group, which correspond to *B. magellanica* and *B. multispinnis*, showed a

marked preference for different crustacean species; therefore, their diet could be classified as being crustacean-dominant. Lastly, group C possesses an annelid dominated diet, due to the presence of a wide variety of polychaetes as well as small crustaceans, such as isopods. (Table 2).

Trophic overlap analysis

The trophic overlap between the predator species was studied using the General Overlap (I_{GO}) and the Specific Overlap (I_{SO}) indices. The I_{GO} estimates indicated that there was not a complete overlap between skate species analysed ($I_{GO} = 0.42$; $V = 2037.68$; $X^2_{108\text{ df}; \alpha=0.05} = 133.25$; $p < 0.001$; $I_{GO\text{min}} = 1.14E-13$; $I_{GO\text{adj}} = 0.42$). This indicates that skates are consuming prey in different ways across species.

When the specific overlap between any given pair of species was calculated, I_{SO} was generally near zero, with the exception of *B. macloviana* and *B. albomaculata* ($I_{SO\text{mac-alb}} = 0.19$, $U_{\text{mac-alb}} = 715.70$). Similarly, all $U_{i,m}$ were significant ($p < 0.01$) for all of the compared paired relations, including I_{SO} between *B. macloviana* and *B. albomaculata* (Table S2, Supporting information).

When taking the zoological groups into account, the I_{GO} value was higher than I_{GO} by prey species ($I_{GO\text{group}} = 0.69$; $I_{GO\text{min}} = 1.14E-13$; $I_{GO\text{adj}} = 0.69$). The null hypothesis was also rejected ($V = 891.35$; $X^2_{12\text{ df}; \alpha=0.05} = 21.02$; $p < 0.001$).

All of the $U_{i,m}$ were significant ($p < 0.001$) for all of the comparisons between pairs of predator species. Thus, the complete overlap hypothesis was rejected for all paired species. Yet, the overlap between *B. albomaculata* and *B. macloviana* and vice-versa was higher ($I_{SO\text{alb-mac}} = 0.86$; $I_{SO\text{mac-alb}} = 0.96$), which may indicate similar diets for this particular pair of species. The rest of the pairs presented values under $I_{SO} = 0.65$, with exception of the *B. multispinnis*-*B. magellanica* and *B. magellanica*-*B. brachyurops* pairs, with $I_{SO} = 0.85$ and $I_{SO} = 0.69$, respectively (Table S3, Supporting information).

DISCUSSION

This study compares the diet of five of *Bathyraja* species captured as by-catch in the Argentinian

hake fishery along the Patagonian Shelf in the South Atlantic Ocean (Wohler *et al.*, 2011). Although the skates were morphologically similar, their diets differ from one species to another. Even though the sample size for three of the species precludes us making strong statements, the results are consistent, indicating trophic niche partition (Ross, 1986).

Diet data derived from stomach contents has typically been restricted by sample size obtained in the studied area, which could be associated with the fact that samples were taken as by-catch from commercial bottom trawls fishing for *M. hubbsi*. There is not a directed *Bathyraja* species fishery, with the exception of the multispecies skate fishery around Malvinas/Falkland Islands, which target mixed rajid species assemblages (Wakeford *et al.*, 2005; Silva *et al.*, 2012). As the data on abundance are scarce, it is also possible that the greatest abundance of *Bathyraja* species is restricted to certain areas. In particular *B. albomaculata*, *B. brachyurops*, and *B. macloviana* are most abundant ($> 2.5 \text{ t/ mn}^2$, respectively) between 36° and 44° while *B. magellanica* is most abundant near 50° . While on the other hand, *B. multispinnis* shows in general low values for its distribution range ($<0.5 \text{ t/mn}^2$) (Ruocco *et al.*, 2007). Even so, the five skate species mainly fed on crustaceans, annelids, fish and molluscs. The results obtained from this study concur with other previously published works related to the feeding habits of the Rajidae (Belleggia *et al.*, 2014). This family has been characterised as having generalist and opportunistic predatory behaviours (Sánchez & Mabrugaña, 2002; Mabrugaña & Giberto, 2007; Ruocco *et al.*, 2009; Belleggia *et al.*, 2014). A generalist and opportunistic predator feeds on prey in relation to its relative abundance, while in a selective predator, the predator chooses the prey regardless of its relative abundance in the habitat (Wetherbee *et al.*, 1990). For example, while a wide variety of prey can be found in the stomach contents of opportunistic predators, individuals with selective feeding habits commonly have a predominant type or species of prey, despite the possibility that it might have a low abundance within the habitat. However, if a predator feeds on prey that is highly abundant within the habitat, it would be difficult to accurately differentiate between

opportunistic and selective feeding (Wetherbee *et al.*, 1990).

In this study, a wide variety of prey was found in the stomach contents of the skates, therefore their diet could be classified as a generalist. However, having the relative abundances and the distribution of all prey species is necessary in order to determine under which of the two dietary classifications a specific predator falls. The spectrum of available prey was assumed to be the same for all of the predators in accordance with what Petraitis (1979) proposes in terms of species overlap. Schoener (1974), and Hurlbert (1978) suggest taking the availability of each resource into account. However, in marine environments this information can be difficult to obtain, and even then, the perception of availability of the resource could differ markedly from that of the predator's perception (Petraitis, 1979).

Changes in the diet of skates may depend on intrinsic (*i.e.*: ontogenetic) or extrinsic (*i.e.*: anthropogenic activities) factors (Barbini *et al.*, 2013). Significant intraspecific differences have been found between the feeding habits of mature and immature individuals, suggesting that consumption is conditioned by the size of the individual and the habitat that it occupies in depending on stage of maturity (Koen Alonso *et al.*, 2001; Bizzarro *et al.*, 2007; Belleggia *et al.*, 2008; Sommerville *et al.*, 2011).

The diet can also vary depending on the availability, temporal fluctuations (*e.g.*: seasons), and the geographic distribution of the prey populations; these variations must be taken into account in order to understand the results (Lima *et al.*, 2017). Additionally, some species may undergo both trophic, and reproductive migrations (Lucifora, 2003). Due to the effect that these variables have on the feeding habits of these species, classifying the diets can sometimes be difficult. Even so, in this study, the possibility for developing this bias was minimized by arranging for all skate species to be captured in similar spatial and temporal ranges.

The stomach contents analysis of *B. albomaculata* was largely annelid dominated (64%), followed by crustaceans (31%), and also polychaetes and isopods to a lesser degree. These results indicate that this

species feeds on small prey. Ruocco *et al.* (2009), documented ontogenetic shifts in smaller skates (< 40cm) that consumed amphipods, while larger individuals consumed polychaetes. Given that the average sample size was between 64 and 75 cm, *B. albomaculata* can thus be classified as a polychaete specialist.

B. macloviana specialized predominantly on annelids and crustaceans (78% and 22%, respectively), preying mostly on *A. alta* and isopods. Both *B. albomaculata* and *B. macloviana* had similar diets (Figure 3). They have previously been reported feeding on low mobility polychaetes (Mabragaña *et al.*, 2005).

B. brachyurops can be considered as a fish specialist with benthic-demersal feeding habits, with a tendency towards hake and southern cod. While crustaceans and annelids were common, their relative importance was low. Other authors have also classified *B. brachyurops*, along with *D. chilensis* and *Bathyraja griseocauda*, within the group of skates that display piscivorous feeding habits (Jones, 2007; Belleggia *et al.*, 2008). Both studies found ontogenetic shifts in these species, because they switch from crustaceans to demersal-pelagic and demersal-benthic fish as they grow.

Remarkably, *B. brachyurops* also showed scavenger habits, which was evidenced by the presence of *M. hubbsi* heads found in the stomach contents. Interestingly enough, the *M. hubbsi* heads, which come from the processing on board, have also been frequently found in the diet of different skate species from the year 2000 onwards (Buren, 2004; Herrera *et al.*, 2012). This was to be expected, because approximately 40% of the fish waste (approximately 26,000 tons) generated by the *M. hubbsi* filleting process is discarded (Dato, 2006; Cretton *et al.*, 2016). Consequently, these skate species adopt opportunist feeding habits, and this is also characteristic of degraded benthic communities. Changes in the feeding habits, including items discarded by the fishery, had been previously documented for ecosystems that have been subjected to overfishing (Dolgov, 2005). The inclusion of the hake heads and their high frequency could be indicators of similar exploitation conditions in the central Patagonian region of the Argentine Sea.

B. magellanica consumed a great diversity of prey, ranging from small fish to polychaetes. However,

in spite of this, its diet can be classified as crustacean dominated, and they feed mainly on the crab *Danielethus patagonicus* (Milne-Edwards 1879), as previously reported by Sánchez and Mabragaña (2002). *B. multispinnis* was also a crustacean feeder with benthic feeding habits that mainly concentrates on large crab species, *Peltarion spinusulum* (White 1843) and *L. spinosa* specifically. This was also reported by Belleggia *et al.* (2014) who also reports the importance of *B. multispinnis*' crushing dentition as a morphological adaption to a carcinophagous diet (Bizikov *et al.*, 2004).

Trophic overlapping among species

There was no general or specific trophic overlapping present across any of the five analysed species. This indicates that none of these species can be used reliably as a “diet standard” for these skates. Barbini (2011) reported a similar result when studying the trophic ecology of seven species of skate in the north of an Argentina-Uruguay ecosystem. In spite of the morphological similarities, and a benthic habitat preference, a partitioning of the trophic resources within and among species does exist. The author attributed this partitioning to body size and to seasonal variations and habitat location changes (Barbini, 2011). Flores-Ortega *et al.* (2011) studied the habitat use of three skate species of the family Rajidae in Mexico. The skates showed a similar pattern and no difference was found in the use of habitat related to the size, sex or season. They concluded that competition, and predation had little influence on the structure of the populations (Flores-Ortega *et al.*, 2011).

The cluster analysis indicated that the skate species are grouped in three classes. The first is the piscivorous group comprised of *B. brachyurops*. Its dominant diet does not overlap with the diet of the rest of species studied. However, this species may have a similar trophic niche to that of species of different genera such as *D. chilensis*, which also feeds on *P. ramsayi* and *M. hubbsi*, including fishing discards (Lucifora *et al.*, 2000; Buren, 2004).

The second is the annelid group made up by *B. macloviana* and *B. albomaculata*. Ruocco *et al.* (2012)

reported that this pair show interspecific competition, with *B. albomaculata* as the dominant competitor. The effect that fisheries have on *B. albomaculata* (larger sizes and late maturity), and *B. macloviana* (smaller size and early maturity) is an increase in their population numbers. Our overlapping analysis results indicate, contrary to Ruocco *et al.* (2012), that even though the feeding habits are similar, competition for trophic resources does not occur.

Lastly, the third trophic group that was clustered included *B. magellanica* and *B. multispinnis*. Although, this group of skates were classified as crustacean feeders, they preyed on different sized crustaceans, and it is evident that a trophic niche partitioning exists based on both the prey species and sizes selected. This is supported by the results, which indicate that there is no complete overlap occurring. This fact was also reported by Platell *et al.* (1998), who described a similar situation for four species of Batoidea in Australian.

Our results support the hypothesis that skates species in Patagonia, which play a crucial role in the trophic structuring of their ecosystems (Sommerville *et al.*, 2011), have undergone a process of niche partitioning in which species that are morphologically similar share space, and avoid competition by using different resources. The partition of resources is a successful feeding strategy to avoid competition between species, as well as between individuals within the same population (Flores-Ortega *et al.*, 2011). Changes in the trophic niche could be a consequence of the overfishing scenario that these skate species are being subjected to. Such an impacted scenario also may be evidenced by changes in reproductive parameters and decreasing trend in biomass south of 45° S for these skate species (García de la Rosa *et al.*, 2000; Marí & Cussi, 2005; Ruocco *et al.*, 2007; Scenna, 2011). Because fisheries and the marine species share the same resources, it could be vital for future studies to consider the fishery as a possible competitor within the scope of trophic interactions in a marine community.

This information on the trophic interactions between species available, and being able to correlate

this with the fishery data, could possibly facilitate a more holistic approach in investigations pertaining to marine ecosystems (Crespi-Abril *et al.*, 2013). This approach will allow for better decision making when implementing strategies to promote the conservation and management of these ecosystems.

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SUPPORTING INFORMATION

TABLE S1 Diet composition of *Bathyraja albomaculata*; *Bathyraja brachyurops*; *Bathyraja macloviana*; *Bathyraja magellanica* and *Bathyraja multispinnis* in function of percent of the percent of relative importance index

TABLE S2. Prey specific overlap (I_{so}) and U statistic ($\alpha=0.05$) estimation for each pair of predator species, considering prey species

TABLE S3. Prey specific overlap (I_{so}) and U statistic ($\alpha=0.05$) estimation for each pair of predator species considering zoological group species

CONTRIBUTIONS

L. T.: Data generation and analysis, figures, tables and manuscript preparation, writing, and editing.

F. C.: Ideas, dissections, stomach contents analysis, data generation and data analysis.

M. A. G.: Ideas, collection and maintenance of samples, dissections, stomach contents analysis and data generation.

E. A. C.: Ideas, funding, sample collection and manuscript writing and editing.

M. A. C. Ideas, funding, sample collection, data analysis and manuscript writing and editing.

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Figure Captions

FIGURE 1 Study Area showing position of commercial fishing trips where specimens of *Bathyraja albomaculata* (●), *Bathyraja brachyurops* (▲), *Bathyraja macloviana* (■), *Bathyraja magellanica* (✦) and *Bathyraja multispinnis* (◆) were captured.

FIGURE 2 Mean cumulative prey curves (solid lines) and 95% CIs (shaded area), according to the number of non-empty stomachs sampled for a) *Bathyraja albomaculata*; b) *Bathyraja brachyurops*; c) *Bathyraja macloviana*; d) *Bathyraja magellanica*; and e) *Bathyraja multispinnis*

FIGURE 3 Hierarchical cluster analysis of prey similarity between skate species. (UPGMA method using Euclidean distance- Cophenetic correlation factor: 0.938) The Euclidean distances were estimated for the species of prey that presented a %I_{PSRI} > 1%. The skate species were clustered in three trophic groups **A**: *Bathyraja brachyurops*; **B**: *Bathyraja magellanica* and *Bathyraja multispinnis*; **C**: *Bathyraja albomaculata* and *Bathyraja macloviana*

TABLE 1 Skate species sample in the northern and central Patagonia.

Predator species	n		$L_T \pm S.E$ (cm)	$D_w \pm S.E$ (cm)	$M \pm S.E$ (kg)	Capture period
	M	F				
<i>Bathyraja albomaculata</i>	1	14	69.83 ± 3.02	49.23 ± 2.07	2.81 ± 0.40	November 2000-September 2005
<i>Bathyraja brachyurops</i>	62	53	68.64 ± 9.36	49.30 ± 7.04	2.62 ± 1.01	March 2001–September 2005
<i>Bathyraja macloviana</i>	9	7	58.80 ± 2.47	38.86 ± 1.70	1.44 ± 0.19	July 2003–July 2007
<i>Bathyraja magellanica</i>	7	21	58.06 ± 8.55	39.02 ± 5.50	1.52 ± 0.64	March 2002–June 2005
<i>Bathyraja multispinnis</i>	2	8	85.54 ± 15.74	62.85 ± 11.22	4.58 ± 3.09	July 2003 –September 2005

n: number of sampled stomach contents; M: males; F: females; L_T : total length; D_w : disc width; M : mass; Mean ± Standard error (S.E)

TABLE 2 Diet composition of *Bathyraja albomaculata*; *Bathyraja brachyurops*; *Bathyraja macloviana*; *Bathyraja magellanica*; and *Bathyraja multispinnis*.

Prey species	E	<i>B. albomaculata</i> (n=14)				<i>B. brachyurops</i> (n=111)				<i>B. macloviana</i> (n=16)				<i>B. magellanica</i> (n=27)				<i>B. multispinnis</i> (n=10)			
		%		%		%		%		%		%		%		%		%			
		F_O	N_P	P	PSRI	F_O	N_P	P	PSRI	F_O	N_P	P	PSRI	F_O	N_P	P	PSRI	F_O	N_P	P	PSRI
Fish		7.	6.5	12	4.5	69	57.	10	55.					33	20	84.	17.	10	19.	7.	1.3
	G	14	3	1.1	8	7	09	5	82					.3	.3	73	51		23	66	4

<i>Engraulis anchoita</i>	P				0.90	27.48	5.19	0.15						3.70	20.30	16.24	3.38	10	19.23	7.66	1.34	
<i>Genypterus blacodes</i>	D B				0.90	27.48	23.90	0.23														
<i>Merluccius hubbsi</i>	D B				22.52	41.76	20.77	28.04						3.70	20.30	45.50	1.22					
<i>Mixine</i> sp.	B				0.90	27.48	13.63	0.19														
<i>Patagonotothen ramsayi</i>	D B				39.64	73.06	59.41	26.26						7.41	20.30	16.35	1.36					
<i>Patagonotothen</i> sp.	D B	7.14	6.53	12.11	4.56																	
<i>Paralichthys isosceles</i>	B													3.70	20.30	68.55	1.65					
<i>Percophis brasiliensis</i>	D B				0.90	27.48	13.99	0.75														
<i>Raneya brasiliensis</i>	D B													14.81	20.30	11.33	9.90					
Unidentified elasmobranch	D B				0.90	27.48	17.49	0.20														
Crustaceans		78.57	31.15	47.69	30.97	47.55	10.42	9.23	27.08	87.00	39.01	11.89	22.31	96.00	84.03	42.04	60.84	10.00	96.15	84.04	90.29	
Amphipode Gammaridae	B	14.29	13.05	0.64	0.98																	
Unidentified Amphipode	N A	35.71	13.70	0.96	2.62					18.75	11.85	0.25	1.13									
Unidentified Euphausiidae	P				0.90	27.48	0.18	0.12		6.25	7.11	0.75	0.25									
<i>Danielethus patagonicus</i>	B													48.15	81.20	23.64	25.2					
<i>Eurypodius latreillei</i>	B													22.22	27.07	14.09	4.57	20	28.85	39.06	6.79	

Isopode sp.	B	50	33. 57	16. 81	12. 59	10 .8 1	59. 53	1.2 7	3.2 9	87 .5	35 .5 6	10. 72	20. 24								
<i>Libinia spinosa</i>	B	7. 14	9.7 9	39 4.3 5	14. 43	15 .3 2	10 5.0 5	14. 08	9.1 2					18 .5 2	97 .4 4	29. 63	11. 77	60	41. 67	50 .9 9	27. 80
<i>Munida espinosa</i>	B													3. 70	40 .6 0	21. 83	1.1 6				
<i>Munida gregaria</i>	B					3. 60	27. 48	0.7 6	0.5 1												
<i>Munida subrugosa</i>	B					7. 21	41. 21	4.4 2	1.6 4					7. 41	20 .3 0	13. 91	1.2 7				
<i>Pagurus gaudichaudi</i>	B													3. 70	20 .3 0	61. 78	1.5 2	20	10 5.7 7	11 3	21. 88
<i>Peltarion spinosulum</i>	B	7. 14	3.2 6	0.6 3	0.1 4	9. 91	27. 48	7.9 6	1.7 6					11 .1 1	81 .2 0	79. 41	8.9 2	70	63. 19	33 .4 4	33. 82
<i>Pleoticus muelleri</i>	D B													11 .1 1	20 .3 0	56. 26	4.2 5				
<i>Pterygosquilla armata armata</i>	B					13 .5 1	49. 46	5.3 9	3.7 1					3. 70	40 .6 0	31. 29	1.3 3				
<i>Serolis schythei</i>	B					9. 01	15 1.1 1	2.7 8	6.9 3					7. 41	20 .3 0	1.6 2	0.8 1				
<i>Stomatopoda sp.</i>	B									6. 25	7. 11	14. 95	0.6 9								
Annelids		85 .7 1	87. 57	62. 85	64. 46	14 .4 1	27. 48	17. 28	3.2 3	10 0	65 .7 8	89. 60	77. 69	37 .0 4	30 .4 5	68. 40	18. 31				
<i>Aphroditella alta</i>	B	35 .7 1	20. 23	11 2.4 8	23. 70	13 .5 1	27. 48	18. 41	3.1 0	68 .7 5	34 .2 6	12 2.3 3	53. 83	33 .3 3	29 .3 2	70. 64	16. 66				
<i>Aphrodite longirostris</i>	B													3. 70	20 .3 0	37. 40	1.0 7				
<i>Eunereis patagónica</i>	P	14 .2 9	22. 84	3.8 4	1.9 1																
<i>Glycera americana</i>	B	7. 14	9.7 9	14. 54	0.8 7									3. 70	20 .3 0	10. 85	0.5 8				
<i>Lumbrineridae</i>	B	35 .7 1	15. 66	2.6 3	3.2 7					18 .7 5	7. 11	0.7 5	0.7 4								

eunicidae

Unidentified Nereidae	P								6.25	71.11	7.48	2.46	
Unidentified errant polychaeta	B	64.29	65.27	10.97	24.51				75	21.93	2.31	9.09	
Unidentified tube polychaeta	B	42.86	38.07	9.60	10.22	0.90	27.48	0.28	0.13	43.75	45.71	7.21	11.58

Molluscs						10.81	25.19	41.74	3.62					3.70	20.30	16.05	3.35	10	19.23	14.8	8.37	
<i>Eledone massyae</i>	B													3.70	20.30	16.05	3.35					
Gastropoda						1.80	27.48	16.11	0.39													
<i>Illex argentinus</i>	B					4.50	27.48	87.60	2.59										10	19.23	14.8	8.37
<i>Octopus tehuelchus</i>	B					0.90	27.48	22.43	0.22													
<i>Semirossia tenera</i>	B					2.70	27.48	2.76	0.41													
Others						12.61	31.40	13.12	10.26													
<i>M. hubbsi</i> discard	A					12.61	31.40	13.12	10.26													

n: sample size; % F_O : percent frequency of occurrence; % N_p : percent prey-specific number; % W_p percent prey-specific wet weight; and % I_{PSRI} : percent prey-specific index of relative importance. EG: ecological group; B: benthic; DB: demersal benthic; DP: demersal pelagic; P: pelagic; NA: not assigned.





