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To cite this article: Luciana Diaz Briz, Felisa Sánchez, Noemí Marí, Hermes Mianzan & Gabriel Genzano (2017): Gelatinous zooplankton (ctenophores, salps and medusae): an important food resource of fishes in the temperate SW Atlantic Ocean, Marine Biology Research, DOI: [10.1080/17451000.2016.1274403](https://doi.org/10.1080/17451000.2016.1274403)

To link to this article: <http://dx.doi.org/10.1080/17451000.2016.1274403>



Published online: 03 May 2017.



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Gelatinous zooplankton (ctenophores, salps and medusae): an important food resource of fishes in the temperate SW Atlantic Ocean

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ABSTRACT

This study quantifies the occurrence of gelatinous zooplankton in the stomach contents of fishes from the southwest Atlantic Ocean (33°–55°S). More than 69,000 fish stomachs belonging to 107 species were examined. A total of 39 fishes were documented as consumers of gelatinous zooplankton, 23 of which were newly discovered. Three gelatinous organism consumption categories are recognized: (1) very frequent consumers (10 species, six of which were exclusive); frequent consumers (five species); and occasional consumers (26 species). Three types of gelatinous prey (ctenophores, salps and medusae) were found in the stomach contents of fishes. Ctenophores were consumed at high levels across almost the entire continental shelves of Argentina and Uruguay. Salps were frequent prey on the slope and southern shelf. In contrast, medusae were consumed in coastal areas, slopes and the southern shelf. Classification methods (group average sorting of the Bray–Curtis similarity measures based on log ($X + 1$)-transformed percentage data) determined six areas where fishes preyed on gelatinous organisms. SIMPER (similarity percentages) analysis determined which fishes contributed more to the consumption of gelatinous organisms. Results revealed that two fish species (*Stromateus brasiliensis* and *Squalus acanthias*) had high gelatinous zooplankton predation rates throughout the entire study area, while another six species (*Patagonotothen ramsayi*, *Helicolenus dactylopterus lahillei*, *Macrourus holotrachys*, *Merluccius hubbsi*, *Schroederichthys bivius*, and *Macruronus magellanicus*), while widely distributed, seemed to have specific areas where consumption occurred. This study not only provides new knowledge about the importance of gelatinous zooplankton in the diet of numerous fishes, but might also be valuable for planning and managing local fisheries.

ARTICLE HISTORY

Received 11 August 2016
Accepted 15 December 2016

RESPONSIBLE EDITOR

Haakon Hop

KEYWORDS

Fish; predation; gelatinous plankton; consumption areas; South Atlantic Ocean

Introduction

Gelatinous zooplankton includes representatives of several phyla of marine invertebrates that are characterized by their transparency and fragility, as well as by the high percentage of water in their tissues (>90%). Among them, ctenophores (Ctenophora), salps (Chordata) and jellyfishes (Cnidaria) stand out due to their abundance and richness of species (Raskoff et al. 2003; Haddock 2004).

Ctenophores and medusae are known to be active predators of microzooplankton and copepods, as well as of fish eggs, larvae and adults (Alvarino 1980, 1985; Purcell 1985, 1991, 1992; Larson 1987; Purcell & Arai 2001). Conversely, salps can consume bacteria, flagellates, small diatoms and zooplankton, but feed primarily on phytoplankton (see Boero et al. 2008; Sutherland et al. 2010; Daponte et al. 2011; Von

Harbou et al. 2011). Consequently, all these organisms compete directly or indirectly with fishes and other organisms for food (Cushing 1975; Atkinson et al. 2004; Morales-Ramírez & Nowaczyk 2006; Boero et al. 2008). In relation to their potential role as prey, it is well known that fishes, turtles, birds and marine mammals utilize ctenophores, medusae and even salps as a food resource (Harrison 1984; Arai 1988, 2005; Arai et al. 2003; Ates 1988, 1991; Mianzan et al. 1996, 1997, 2001; Hsieh et al. 2001; James & Herman 2001; Purcell & Arai 2001; Hume et al. 2004; Houghton et al. 2006; Link & Ford 2006; Pope et al. 2010; Cardona et al. 2012). Purcell & Arai (2001) pointed out that gelatinous zooplankton are not only important predators (consuming larvae and fish eggs) and competitors (eating the same prey as some fishes) in marine food webs, but they are also important prey items for

many fish species, a topic more difficult to study. In the absence of measured digestion rates, it is not possible to calculate feeding rates or to assess the dietary importance of gelatinous organisms to fishes. Recent studies with newer sampling methods, such as stable isotope and fatty acids analyses, among others, indicate that the biomass of gelatinous organisms has been underestimated as food (Cardona et al. 2012; Gonzalez Carman et al. 2013). Hence, additional quantitative work is needed on interactions of gelatinous organisms with both fish and other marine groups to evaluate their trophic position and importance in pelagic ecosystems. The fragility, rapid digestion and absence of preservable hard parts in gelatinous organisms makes their identification in the stomach contents of predators problematic. This led Arai (1988) to suggest the immediate analysis of fresh stomach contents on board as a good alternative.

This methodology allows the recognition of a few structures more resistant to digestion (such as comb plates or ctenes of ctenophores, muscle bands of salps, rhopalia and/or bell fragments of some jellyfishes) and to quantify predators. Although the analysis of stomach contents is a standard practice in trophic ecology (Hyslop 1980), it is not always feasible on board ship. Consequently, few databases include sufficient samples of stomachs of multiple fish species to reliably quantify the consumption of gelatinous zooplankton. In addition, most records of the consumption of gelatinous organisms by fishes and other vertebrates are based on reports from localized areas or from scattered literature reviews that refer to this type of interaction (Duhamel & Hureau 1985; Arai 1988, 1997, 2005; Ates 1988, 1991; Mianzan et al. 1997, 2001; Purcell 1997; Purcell & Arai 2001; Purcell & Sturdevant 2001; Arai et al. 2003; Hume et al. 2004). The work of Mianzan et al. (1996) is unique in quantifying the consumption of ctenophores by several fish species.

Few studies have been undertaken on the consumption of gelatinous zooplankton in Argentina or elsewhere. As noted above, Mianzan et al. (1996) quantified the consumption of ctenophores by fishes in two regions: on the north Buenos Aires coast (34°–38°S) and the Península Valdés/San Jorge Gulf (42°–46°S). In the latter area, Mianzan et al. (1997) reported the high mortality of many chub mackerels (*Scomber japonicus* Houttuyn, 1782) because of the massive ingestion of salps which had accumulated toxins of the dinoflagellate *Alexandrium tamarense* (Lebour, 1925) Balech, 1995. Mianzan et al. (2001) suggested that gelatinous zooplankton could be a survival food resource of the Argentine anchovy *Engraulis anchoita* Hubbs & Marini, 1935, and González Carman et al.

(2013) reported the consumption of gelatinous plankton by the green sea turtle *Chelonia mydas* (Linnaeus, 1758) on the Buenos Aires coast. Other records of this type of predator–prey interaction in the area were found only in occasional reports of gelatinous organisms in fish stomach contents resulting from analysis of the trophic spectrum of certain species of commercial importance (Angelescu 1982; Wöhler & Sanchez 1994; Sanchez & Prenskey 1996; Garcia de la Rosa & Sánchez 1997; Montoya et al. 1997; Sanchez & Garcia de la Rosa 1999; Laptikhovsky 2001; Koen Alonso et al. 2002; Garcia de la Rosa et al. 2004; Belleggia et al. 2012).

It is well-known that gelatinous zooplanktonic organisms have the ability to form large aggregations (Graham et al. 2001), which may impact negatively on tourism, health, aquaculture and fisheries (Ivanov et al. 2000; Mianzan et al. 2000, 2005; Doyle et al. 2008). Various anthropogenic factors such as overfishing, eutrophication and global climate changes have been considered as possible causes for the increases in populations of gelatinous organisms (Arai 2001; Mills 2001; Condon et al. 2012, among others). In this context, exploring the trophic ecology of gelatinous plankton is important because knowing potential predators and the frequency with which these gelatinous organisms are consumed may allow the planning, management and study of fisheries in particular areas (Pauly et al. 2009).

The hypothesis that gelatinous organisms are an important food resource for many fish species allowed us to create for the first time a large database covering a vast region of the southwestern Atlantic Ocean (33°–55°S) and to quantitatively analyse the role of ctenophores, salps and medusae in the diet of fishes from the continental shelf of Argentina and Uruguay. The main objectives of this study were to: (1) identify the fish species which consume gelatinous prey; (2) quantify the frequency of consumption of the different jellies; and (3) establish in which areas these trophic relationships take place.

Material and methods

Study area and data collection

The study area comprised the continental shelves of Argentina and Uruguay (33°–55°S; Figure 1). This area corresponds to the Subantarctic Biogeographical Region (Balech & Erlich 2008), characterized by the presence of two large water masses: a sub-Antarctic mass of cold temperate waters, the Malvinas (Falkland) Current and a subtropical mass of warm temperate waters, the Brazil Current. A recent review can be

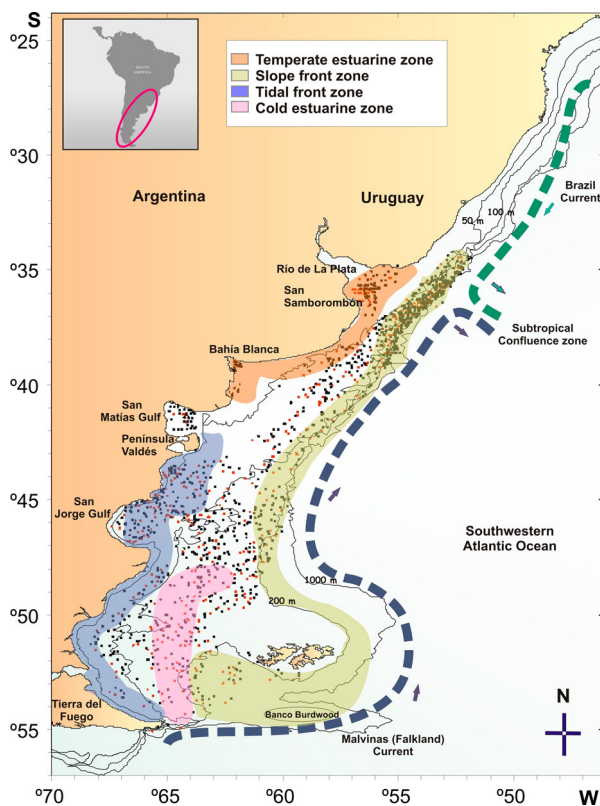


Figure 1. Study area: continental shelves of Argentina and Uruguay. The dotted and slim lines represent the 50, 100 and 200 m isobaths and marine currents of the region. The coloured areas indicate the different frontal zones of the region. Black dots correspond to the total net trawls sampled while red dots represent those with gelatinous zooplankton in fish stomachs.

found in Guerrero and Piola (1997). The region is relatively narrow at its northern end but widens progressively to the south, reaching a maximum width of 850 km near Burdwood Bank (off southern Patagonia). From Río de la Plata to Tierra del Fuego, there are several major coastal embayments (San Borombón, Bahía Blanca, and San Matías and San Jorge Gulfs), and the headland of Península Valdés. The area presents different marine frontal zones, such as the temperate estuarine area (35°–40°S) that includes the estuaries of the Río de la Plata and Bahía Blanca, the slope front area (33°–55°S) that covers the entire length of the slope (north, centre and south), the tidal fronts area (43°–54°S), which includes the tidal fronts of Península Valdés, San Jorge Gulf and the Strait of Magallanes in Patagonia, and the cold estuarine area located in the central region of the southern Argentina continental shelf (64°W between 49° and 57°S) (see Acha et al. 2004; Sabatini et al. 2004; Mianzan & Acha 2008; Figure 1).

This study makes use of data on fish stomach contents collected between 1986 and 2000 on the

Argentinean continental shelf (33°–55°S; Figure 1) compiled by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). The available information comes from 34 research cruises performed by the Research Vessels ‘Capitan Oca Balda’ and ‘Dr. Eduardo Holmberg’ of INIDEP during the warm period (October–April). The sampling procedure was designed to acquire data on abundance, age structure and life history of fish species of commercial value from the Argentinean continental shelf. Fishing was conducted throughout the day, at 3–4 knots for 30 min at each sampling site, using a bottom trawl (Engels-type, 200 mm mesh in the wing and 103 mm in the cod ends, 4 m vertical opening and 15 m horizontal aperture). The fish species were removed from the net and immediately sampled. Non-gelatinous and gelatinous items extracted from each specimen of examined fish were recorded. Gelatinous items considered were ctenophores, salps and medusae.

Data analysis

The data set comprised presence/absence records of the three gelatinous groups (ctenophores, salps and medusae) as well as those of non-gelatinous prey. Therefore, the overall total number of empty and filled stomachs with non-gelatinous and gelatinous contents, as well as the total number of stomachs per fish species with non-gelatinous and gelatinous items, was calculated as frequency of occurrence on the total (%F).

All fish species that consumed gelatinous organisms were grouped into three categories based on the frequency of stomachs containing these jelly organisms: very frequent consumers, with frequency values >30%; frequent consumers, between 10% and 30%; and occasional consumers, with values <10% (based on and modified from Mianzan et al. 1996).

To identify the geographic locations of where the consumption of gelatinous animals occurred, the study area was divided into 119 one-degree grid squares. For each square the frequency of stomachs with ctenophores, salps and medusae for each fish species was calculated. Squares that had no species of fish consuming gelatinous zooplankton ($n=21$ squares) and fish species present in just one square were excluded from the analysis ($n=29$, e.g. *Mullus argentinae* Hubbs & Marini, 1933). Species that consumed more than one gelatinous type of organism were considered separately in this analysis (e.g. *Squalus acanthias* Linnaeus, 1758 (with ctenophores), *S. acanthias* (with salps) and *S. acanthias* (with

Table 1. Taxonomic list of 107 species of analysed fish species following the classification of Cousseau & Perrotta (2000). Species with * correspond to the new records of fishes that consumed gelatinous organisms, and species with ** those previously reported from the area by Mianzan et al. (1996). Species highlighted in bold indicate those that were found to consume gelatinous organisms in this study.

Fish species analysed	Common name	No. of analysed specimens
Phylum Chordata		
Subphylum Vertebrata		
Superclass Gnathostomata		
Class Elasmobranchii		
<i>Amblyraja doellojuradoi</i> (Pozzi, 1935)	Southern thorny skate	12
<i>Atlantoraja castelnaui</i> (Miranda Ribeiro, 1907)	Spotback skate	108
<i>Atlantoraja cyclophora</i> (Regan, 1903)	Eyespot skate	49
<i>Atlantoraja platana</i> (Günther, 1880)	La Plata skate	7
<i>Bathyraja albomaculata</i> (Norman, 1937)*	White-dotted skate	332
<i>Bathyraja brachyurops</i> (Fowler, 1910)	Broadnose skate	75
<i>Bathyraja griseocauda</i> (Norman, 1937)	Graytail skate	11
<i>Bathyraja macloviana</i> (Norman, 1937)**	Patagonian skate	168
<i>Bathyraja magellanica</i> (Philippi, 1902)	Magellan skate	38
<i>Bathyraja multispinis</i> (Norman, 1937)	Multispine skate	2
<i>Bathyraja</i> sp.*	–	435
<i>Dasyatis pastinaca</i> (Linnaeus, 1758)	Common stingray	4
<i>Dipturus trachyderma</i> (Krefft & Stehmann, 1975)*	Ray	2
<i>Discopyge tschudii</i> Heckel, 1846	Apron ray	252
<i>Galeorhinus galeus</i> (Linnaeus, 1758)	Tope shark	163
<i>Mustelus schmitti</i> Springer, 1939	Narrownose smooth-hound	517
<i>Mustelus</i> sp.	–	478
<i>Myliobatis goodei</i> Garman, 1885	Southern eagle ray	261
<i>Myliobatis</i> sp.	–	3
<i>Narcine brasiliensis</i> (Olfers, 1831)	Brazilian electric ray	10
<i>Notorynchus cepedianus</i> (Péron, 1807)	Broadnose sevengill shark	3
<i>Raja</i> sp.	–	95
<i>Psammobatis bergi</i> Marini, 1932	Blotched sand skate	107
<i>Psammobatis</i> sp.*	–	406
<i>Rioraja agassizii</i> (Müller & Henle, 1841)	Rio skate	16
<i>Rhinobatos horkelii</i> Müller & Henle, 1841	Brazilian guitarfish	42
<i>Squalus acanthias</i> Linnaeus, 1758**	Picked dogfish	5789
<i>Schroederichthys bivius</i> (Müller & Henle, 1838)*	Narrowmouthed catshark	678
<i>Squalus mitsukurii</i> Jordan & Snyder, 1903*	Shortspine spurdo	431
<i>Squalus</i> sp.*	–	157
<i>Squatina argentina</i> (Marini, 1930)**	Argentine angel shark	1498
<i>Sympterygia acuta</i> Garman, 1877	Bignose fanskate	35
<i>Sympterygia bonapartii</i> Müller & Henle, 1841*	Smallnose fanskate	516
<i>Sympterygia</i> sp.	–	63
<i>Zearaja chilensis</i> (Guichenot, 1848)*	Yellownose skate	952
Class Holocephali		
<i>Callorhynchus callorhynchus</i> (Linnaeus, 1758)	Plownose chimaera	152
Class Actinopterygii		
<i>Acanthistius brasiliensis</i> (Cuvier, 1828)	Argentine seabass	406
<i>Austrolycus laticinctus</i> (Berg, 1895)	–	2
<i>Balistes capriscus</i> Gmelin, 1789	Grey triggerfish	8
<i>Bassango albescens</i> (Barnard, 1923)	Hairy conger	11
<i>Bothidae</i> sp.	–	4
<i>Bovichtus argentinus</i> MacDonagh, 1931	–	1
<i>Brevoortia aurea</i> (Spix & Agassiz, 1829)	Brazilian menhaden	12
<i>Centrolophus niger</i> (Gmelin, 1789)*	Rudderfish	2
<i>Chaetodon</i> sp.	Butterflyfish	2
<i>Coelorinchus fasciatus</i> (Günther, 1878)	Banded whiptail	264
<i>Conger orbignianus</i> Valenciennes, 1837**	Argentine conger	376
<i>Congiopodus peruvianus</i> (Cuvier, 1829)	Horsefish	551
<i>Cottoperca gobio</i> (Günther, 1861)*	Channel bull blenny	363
<i>Cynoscion guatucupa</i> (Cuvier, 1830)	Stripped weakfish	369
<i>Dissostichus elegendoides</i> Smitt, 1898*	Patagonian toothfish	364
<i>Eleginops maclovinus</i> (Cuvier, 1830)	Patagonian blennie	1
<i>Engraulis anchoita</i> Hubbs & Marini, 1935	Argentine anchovy	12
<i>Genidens barbatus</i> (Lacepède, 1803)	White sea catfish	49
<i>Genypterus blacodes</i> (Forster, 1801)	Pink cusk-eel	3519
<i>Helicolenus lahillei</i> Norman, 1937*	Blackbelly rosefish	795
<i>Icichthys australis</i> (Haedrich, 1966)*	Southern driftfish	1
<i>Iluocoetes fimbriatus</i> Jenyns, 1842*	Vinda	227
<i>Lophius gastrophysus</i> Miranda Ribeiro, 1915	Blackfin goosefish	5
<i>Lopholatilus villarii</i> Miranda Ribeiro, 1915	Tile fish	42
<i>Macrondon ancydon</i> (Bloch & Schneider, 1801)	King weakfish	632
<i>Macrourus carinatus</i> (Günther, 1878)*	Ridge scaled rattail	53

(Continued)

Table I. Continued.

Fish species analysed	Common name	No. of analysed specimens
<i>Macrourus holotrachys</i> Günther, 1878**	Bigeye grenadier	122
<i>Macruronus magellanicus</i> Lönnberg, 1907**	Patagonian grenadier	6534
<i>Menticirrhus americanus</i> (Linnaeus, 1758)	Southern kingcroaker	39
<i>Merluccius australis</i> (Hutton, 1872)	Southern hake	144
<i>Merluccius hubbsi</i> Marini, 1933*	Argentine hake	28,214
<i>Micromesistius australis</i> Norman, 1937*	Southern blue whiting	1152
<i>Micropogonias furnieri</i> (Desmarest, 1823)**	Whitemouth croaker	1454
<i>Mugil platanus</i> Günther, 1880	Lebranche mullet	3
<i>Mullus argentinae</i> Hubbs & Marini, 1933**	Argentine goatfish	94
<i>Nemadactylus bergi</i> (Norman, 1937)**	Castaneta	751
<i>Notophycis marginata</i> (Günther, 1878)	Dwarf codling	25
<i>Odontesthes smitti</i> (Lahille, 1929)	Silverside	36
<i>Pagrus pagrus</i> (Linnaeus, 1758)*	Red porgy	172
<i>Paralichthys isosceles</i> Jordan, 1891	Lenguado	168
<i>Paralichthys patagonicus</i> Jordan, 1889	Patagonian flounder	283
<i>Paralichthys</i> sp.	–	320
<i>Paralonchurus brasiliensis</i> (Steindachner, 1875)	Banded croaker	90
<i>Parona signata</i> (Jenyns, 1841)**	Parona leatherjacket	300
<i>Patagonotothen ramsayi</i> (Regan, 1913)**	Longtail southern cod	2072
<i>Peprilus paru</i> (Linnaeus, 1758)*	American harvestfish	3
<i>Percophis brasiliensis</i> Quoy & Gaimard, 1825	Brazilian flathead	417
<i>Physiculus</i> sp.	–	2
<i>Pinguipes brasilianus</i> Cuvier, 1829	Brazilian sandperch	98
<i>Polyprion americanus</i> (Bloch & Schneider, 1801)	Wreckfish	11
<i>Pomatomus saltatrix</i> (Linnaeus, 1766)	Bluefish	82
<i>Porichthys porosissimus</i> (Cuvier, 1829)	Toadfish	18
<i>Prionotus nudigula</i> Ginsburg, 1950	Red searobin	195
<i>Prionotus punctatus</i> (Bloch, 1793)	Bluewing searobin	276
<i>Pseudopercis semifasciata</i> (Cuvier, 1829)	Argentinian sandperch	166
<i>Psychrolutes marmoratus</i> (Gill, 1889)	Fathead	2
<i>Salilota australis</i> (Günther, 1878)**	Tadpole codling	1829
<i>Sarda sarda</i> (Bloch, 1793)	Atlantic bonito	4
<i>Schedophilus</i> sp.*	Butterfish	2
<i>Scomber japonicus</i> Houttuyn, 1782*	Chub mackerel	110
<i>Sebastes oculatus</i> Valenciennes, 1833*	Patagonian redfish	402
<i>Seriolaella porosa</i> Guichenot, 1848**	South Atlantic bream	316
<i>Stromateus brasiliensis</i> Fowler, 1906**	Southwest Atlantic butterfish	984
<i>Thunnus</i> sp.	–	16
<i>Thyrstites atun</i> (Euphrasen, 1791)	Snoek	2
<i>Trachurus lathami</i> Nichols, 1920*	Rough scad	105
<i>Trichiurus lepturus</i> Linnaeus, 1758**	Largehead hairtail	357
<i>Umbrina canosai</i> Berg, 1895	Argentine croaker	91
<i>Urophycis brasiliensis</i> (Kaup, 1858)	Brazilian codling	126
<i>Xystreurus rasile</i> (Jordan, 1891)	Flounder	277
<i>Zenopsis conchifer</i> (Lowe, 1852)	Silvery John Dory	273
107 species		69,075

medusae)). The final matrix consisted of 98 squares and 33 species of fishes.

Classification methods (group average sorting of the Bray–Curtis similarity measures based on $\log(X + 1)$ -transformed prevalence data) were carried out using the PRIMER 6 software package (Clarke & Warwick 2001). This logarithmic transformation was used to balance the contribution of rare and common species in the analysis, and thus any dominant effect of extreme or anomalous samples was removed (Clarke & Warwick 2001). A SIMPROF analysis was used to test whether groups obtained by cluster analysis were significantly different. A SIMPER (similarity percentages) analysis was used to identify fish species that contributed most to dis/similarities among and within groups. This analysis calculates the ‘average similarity’ (contribution of the i th species to the

overall dissimilarity between the groups considered) and the ‘internal similarity’ (contribution each species makes to the average similarity within each group considered) (see Clarke & Warwick 2001 for details).

Results

Of 1184 net trawls analysed, 436 (36.8%) included fishes with gelatinous organisms in their stomach contents (Figure 1). A total of 69,075 stomachs belonging to 107 species of fish were examined, of which 33,855 (49.0%) were empty and 35,220 (50.9%) had several kinds of food items. Of those with full stomachs, 2914 (8.3%) had jelly items and corresponded to 39 species of fishes (36.4% of the total species). Twenty-three fish species were reported for the first time as jelly consumers in the study area

Table II. List and categories of consumption of the 39 fish species that consumed gelatinous organisms. Categories: Very frequent (> 30%), frequent (between 10% and 30%) and occasional (< 10% of the stomachs with gelatinous organisms as prey items). Ni (%) = number of stomachs with each gelatinous prey and its corresponding percentage value.

Fish species that consume jelly	Total number of examined stomachs	Total number of stomachs with gelatinous Ni (%)	Categories of consumption	Total number of stomachs with		
				Ctenophores Ni (%)	Salps Ni (%)	Medusae Ni (%)
<i>Squalus acanthias</i>	3511	1329 (37.8)	Very frequent	1133 (85.3)	72 (5.4)	152 (11.4)
<i>Stromateus brasiliensis</i>	558	551 (98.7)	Very frequent	510 (92.6)	13 (2.4)	29 (5.3)
<i>Helicolenus lahillei</i>	438	184 (42.0)	Very frequent	165 (89.7)	22 (11.9)	0
<i>Seriolaella porosa</i>	218	124 (56.9)	Very frequent	123 (99.2)	0	1 (0.8)
<i>Macrourus holotrachys</i>	49	40 (81.6)	Very frequent	0	38 (95)	4 (10)
<i>Dipturus trachyderma</i>	2	1 (50)	Very frequent	0	0	1 (100)
<i>Centrolophus niger</i>	2	2 (100)	Very frequent	2 (100)	0	0
<i>Schedophilus</i> sp.	2	2 (100)	Very frequent	2 (100)	0	0
<i>Icichthys australis</i>	1	1 (100)	Very frequent	1 (100)	0	0
<i>Peprilus paru</i>	1	1 (100)	Very frequent	1 (100)	0	0
<i>Patagonotothen ramsayi</i>	1402	189 (13.5)	Frequent	92 (48.7)	79 (41.8)	21 (11.1)
<i>Squalus mitsukurii</i>	304	38 (12.5)	Frequent	38 (100)	0	0
<i>Conger orbignianus</i>	223	34 (15.2)	Frequent	15 (44.1)	18 (52.9)	1 (2.9)
<i>Parona signata</i>	140	27 (19.3)	Frequent	6 (22.2)	0	21 (77.8)
<i>Macrourus carinatus</i>	45	8 (17.8)	Frequent	0	8 (100)	0
<i>Merluccius hubbsi</i>	12,979	116 (0.9)	Occasional	18 (15.5)	96 (82.7)	3 (2.3)
<i>Macruronus magellanicus</i>	3374	164 (4.9)	Occasional	68 (41.5)	95 (57.9)	1 (0.6)
<i>Zearaja chilensis</i>	792	7 (0.9)	Occasional	5 (71.4)	1 (14.3)	1 (14.3)
<i>Schroederichthys bivius</i>	560	10 (1.8)	Occasional	0	9 (90)	1 (10)
<i>Micropogonias furnieri</i>	482	14 (2.9)	Occasional	14 (100)	0	0
<i>Sympterygia bonapartii</i>	458	2 (0.4)	Occasional	0	2 (100)	0
<i>Notodactylus bergi</i>	452	11 (2.4)	Occasional	9 (81.8)	0	2 (18.2)
<i>Micromesistius australis</i>	400	26 (6.5)	Occasional	9 (34.6)	17 (65.4)	0
<i>Bathyraja</i> sp.	376	2 (0.5)	Occasional	2 (100)	0	0
<i>Squatina argentina</i>	310	1 (0.3)	Occasional	1 (100)	0	0
<i>Psammobatis</i> sp.	352	1 (0.3)	Occasional	0	1 (100)	0
<i>Bathyraja albomaculata</i>	275	2 (0.7)	Occasional	1 (50)	1 (50)	0
<i>Salilota australis</i>	267	2 (0.7)	Occasional	2 (100)	0	0
<i>Cottoperca gobio</i>	251	1 (0.4)	Occasional	0	0	1 (100)
<i>Trichiurus lepturus</i>	212	1 (0.5)	Occasional	1 (100)	0	0
<i>Dissostichus eleginoides</i>	209	8 (3.8)	Occasional	0	8 (100)	0
<i>Squalus</i> sp.	154	6 (3.9)	Occasional	5 (83.3)	1 (16.7)	0
<i>Bathyraja macloviana</i>	129	1 (0.8)	Occasional	1 (100)	0	0
<i>llucoetes fimbriatus</i>	109	1 (0.9)	Occasional	0	1 (100)	0
<i>Pagrus pagrus</i>	75	1 (1.3)	Occasional	0	0	1 (100)
<i>Scomber japonicus</i>	71	1 (1.4)	Occasional	0	1 (100)	0
<i>Mullus argentinus</i>	59	3 (5.1)	Occasional	3 (100)	0	0
<i>Trachurus lathami</i>	41	1 (2.4)	Occasional	0	0	1 (100)
<i>Sebastes oculatus</i>	13	1 (7.7)	Occasional	1 (100)	0	0
Totals	29,296	2914		2228 (76.46)	483 (16.58)	241 (8.27)

(see Table I). Of the 39 species of fishes that consumed gelatinous organisms, 10 species (25.6%) were categorized as very frequent consumers (six of which had gelatinous organisms as a unique prey item), five species (12.8%) were frequent consumers, while 24 species (61.5%) were only occasional consumers (see Table II).

Species with the highest frequency of gelatinous zooplankton items in their stomachs were the picked dogfish *Squalus acanthias* (45.6%), Southwest Atlantic butterfish *Stromateus brasiliensis* Fowler, 1906 (18.9%), longtail southern cod *Patagonotothen ramsayi* (Regan, 1913) (6.5%), blackbelly rosefish *Helicolenus lahillei* Norman, 1937 (6.3%), Patagonian grenadier *Macruronus magellanicus* Lönnberg, 1907 (5.6%) and South Atlantic bream *Seriolaella porosa* Guichenot, 1848 (4.3%). The remaining species had frequency values of less than 1.3%.

Three kinds of gelatinous organisms were identified in the stomachs: ctenophores, salps and medusae. Ctenophores were most frequent, occurring in 2228 stomachs (76.5% of stomachs with jelly animals) of 27 species of fishes (69.2%). In contrast, salps and medusae were present in 483 (16.6%) and 241 (8.3%) stomachs of 19 and 16 fish species (48.7% and 41.0%, respectively) (see Table II; Figure 2a).

Most of the fish species consumed one or two gelatinous items. Only seven species, *S. acanthias*, *S. brasiliensis*, *P. ramsayi*, *Conger orbignianus* Valenciennes, 1837, *Merluccius hubbsi* Marini, 1933, *M. magellanicus* and *Zearaja chilensis* (Guichenot, 1848), consumed all three gelatinous items mentioned above (see Table II). Thirty-five specimens belonging to five species had two gelatinous items in their stomachs at the same time: *S. acanthias* with ctenophores and medusae ($n = 14$), medusae and salps ($n = 10$) and

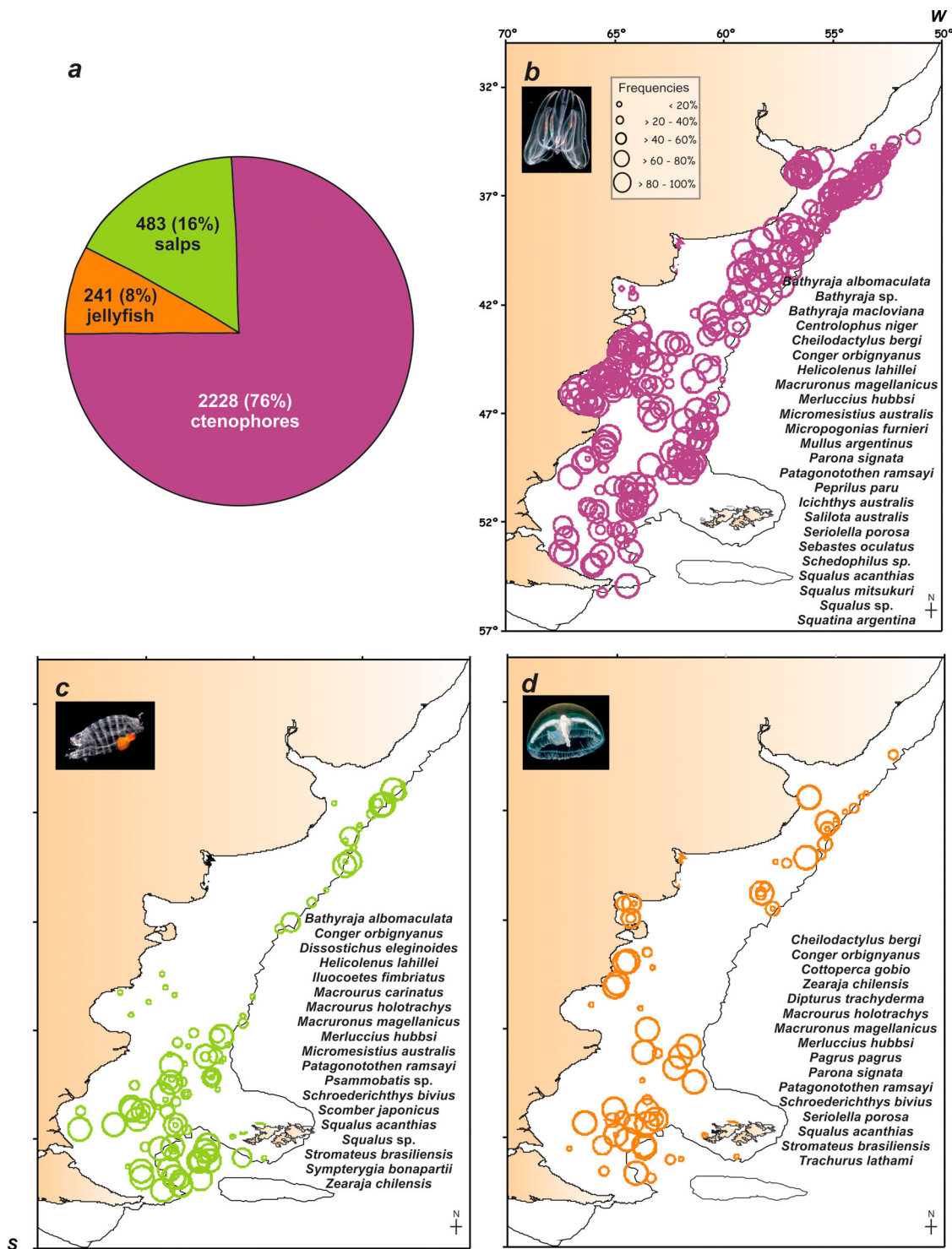


Figure 2. (a) Number of stomachs with each gelatinous item and its equivalent in % (related to the total number of stomachs with gelatinous plankton = 2914); (b–d) Spatial distribution of the stomachs of fishes with: (b) ctenophores, (c) salps and (d) medusae.

ctenophores and salps ($n = 4$); *P. ramsayi* with ctenophores and salps ($n = 1$) and medusae and salps ($n = 2$); *Macrourus holotrachys* Günther, 1878 with medusae and salps ($n = 2$); *H. lahillei* with ctenophores and salps ($n = 1$); and *M. hubbsi* with medusae and salps ($n = 1$).

The consumption of gelatinous zooplankton occurred throughout the entire study area (Figure 1). However, when each kind of gelatinous organism was analysed separately, geographical differences were observed (Figure 2b–d). The consumption of ctenophores seemed to be uniform in almost all

areas, with high and similar values of frequency (Figure 2b). Fish species with the highest consumption rates (frequency) were *S. acanthias*, *S. brasiliensis*, *H. lahillei*, *S. porosa*, *C. orbignyanus*, *P. ramsayi* and *M. magellanicus* (Table II). In contrast, stomachs containing salps were located mainly along the entire slope area and in the southern Argentinian continental shelf, where frequency values of this group were higher (Figure 2c). The main predators that consumed salps were *M. holotrachys*, *P. ramsayi*, *C. orbignyanus*, *M. magellanicus* and *M. hubbsi* (see Table II). Stomachs with medusae occurred more frequently along the coastal areas of Río de La Plata, San Matías Gulf, Península Valdés, and north of the slope, as well as in the southern continental shelf area of Argentina (Figure 2d). Fewer fish species (with fewer stomachs) consumed medusae in relation to the other two gelatinous animal groups: *S. acanthias*, *P. ramsayi* and *Parona signata* (Jenyns, 1841) were among the most important (Table II).

The frequencies of occurrence of gelatinous zooplankton in fish stomachs varied considerably among the different groups defined by the cluster analysis. A total of six groups or consumption areas (G1–G6) were identified, representing 100% ($n = 98$) of squares analysed. The SIMPER analysis indicated which fish species contributed the most to the consumption of gelatinous zooplankton in each of these areas (Figure 3).

Group 1 (19.2% internal similarity SIMPER analysis) clustered eight squares on the southern continental shelf of Argentina (47°–53°S). In this area, the species of fishes that contributed most were *M. hubbsi* (52.7%), *Schroederichthys bivius* (Müller & Henle, 1838) (12.1%), *M. magellanicus* (11.5%) and *S. acanthias* (4.8%) for salps, and *S. brasiliensis* (10.7%) for medusae (see Figure 4).

Group 2 (27.4% internal similarity SIMPER analysis) consisted of 10 dispersed squares, one located on the coast of Buenos Aires (37°S), two in the southern platform (49°–51°S) and seven on the south front of the slope (46°–56°S). In this group, the species most represented were *P. ramsayi*, with contribution values of 73.1% and 15.0% for ctenophores and salps, respectively, and *M. holotrachys*, with values of 9.0% for salps (Figure 4).

Group 3 (53.6% internal similarity SIMPER analysis) comprised 53 quadrants corresponding to the Río de la Plata (35°–36°S), centre of the slope (41°–45°S), Península Valdés, San Jorge Gulf and several areas on north, central and southern regions of the continental shelf (38°–53°S). Seventeen fish species were represented, of which *S. brasiliensis* and *S. acanthias*

contributed most, with values of 74.0% and 18.4%, respectively, for ctenophores (Figure 4).

Group 4 (48.9% internal similarity SIMPER analysis) combined seven quadrants on the northern front slope (35°–39°S). Eleven species of fishes consumed gelatinous organisms in this area, but only *H. lahillei* and *S. acanthias* contributed significantly to ctenophores, with values of 42.0% and 37.8%, respectively (Figure 4).

Group 5 (77.9% internal similarity SIMPER analysis) pooled a total of 16 quadrants, two located on the Uruguayan platform (34°S), two on the southern end of Argentina platform (53° and 55°S) and 12 in the middle of the continental shelf and slope zone of Argentina (40°–45°S). In this group, only *S. acanthias* contributed significantly to the consumption of ctenophores, with a value of 100% (Figure 4).

Group 6 (55.9% internal similarity SIMPER analysis) combined a total of four quadrants, two situated in the south of the continental shelf (47° and 52°S), coinciding in part with the cold estuarine zone of Patagonia, one on the front slope north (39°S), and another in San Matías Gulf (40°S). In this group, only *S. acanthias* contributed much to the consumption of medusae, with a value of 52.8% (see Figure 4).

Thus, eight species of fishes were the largest contributors in the consumption of gelatinous plankton in the six areas described above (Figure 4).

Discussion

A total of 107 fish species were analysed in this study, 39 of which had gelatinous organisms (ctenophores, salps and medusae) in their stomachs. Of these, 23 were reported for the first time as jellyfish eaters. Although Mianzan et al. (1996) had earlier reported on the consumption of gelatinous animals by fishes, our findings double the number of fish consumers previously known from the area, providing evidence that such interactions are more common than previously realized. The number of fishes that consume gelatinous organisms could be higher ($n = 44$) if five other fish species, reported for the area but not found in this study, are considered: *Mustelus schmitti* Springer, 1939, *Urophycis brasiliensis* (Kaup, 1858), *Pseudocyttus* sp., *Macrodon ancylodon* (Bloch & Schneider, 1801) and *Engraulis anchoita* (see Mianzan et al. 1996, 1997, 2001).

The fact that a large number of fish species commonly consumed gelatinous zooplankton does not mean that they are exclusive consumers of these organisms. Nevertheless, there are a few fish species

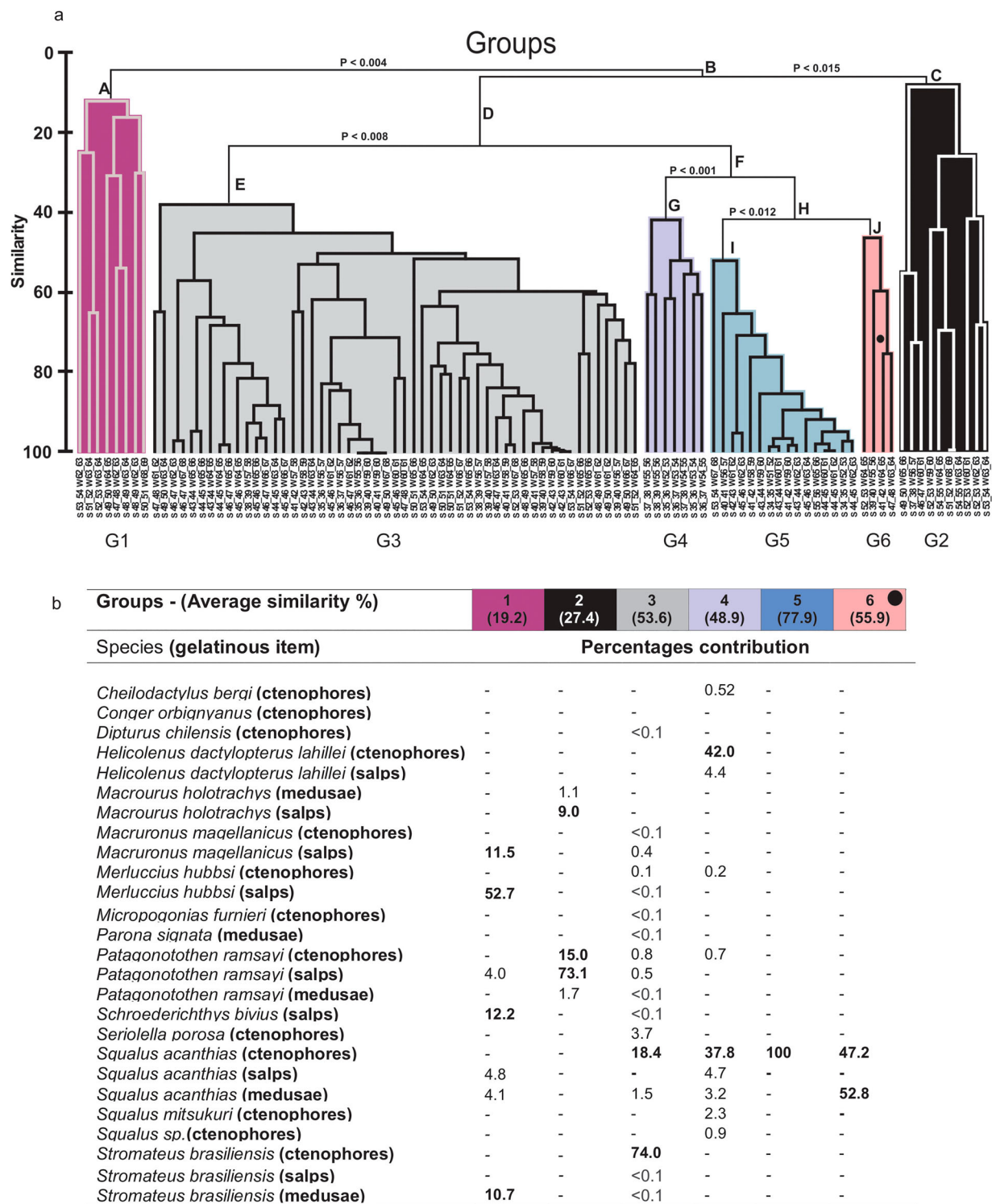


Figure 3. (a) Dendrogram obtained from cluster analysis calculated with the proportions of stomachs with ctenophores, salps and medusae per quadrant for each species of fish predator. Each colour represents one of the six areas of consumption identified in the analysis. Capital letters correspond to the most important nodes of the cluster obtained in a SIMPROOF analysis. (b) Results of SIMPER analysis for each group: all the fish species that contributed to the consumption of each gelatinous item, as well as their corresponding values in %, are given.

that do consume gelatinous zooplankton as their main source of nutrition (Harbison 1993; Arai et al. 2003). Among gelatinous zooplanktivorous fish, the

Carangidae, Stromateidae, Salmonidae, Nototheniidae and Molidae stand out. Some representatives of these families consume gelatinous organisms almost

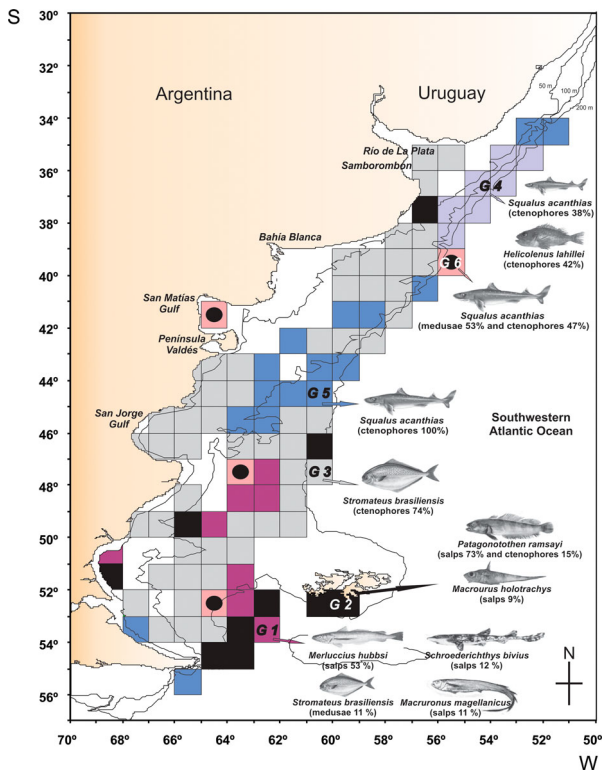


Figure 4. Map of the six groups of quadrants (areas of consumption) obtained from the cluster analysis (Figure 3). The species of fish that contributed most for each gelatinous prey per area with their values of contribution in % is indicated.

exclusively (see Harbison 1993; Arai et al. 2003; Arai 2005; Pope et al. 2010).

According to the categorizations adopted in this work, 10 fish species were considered very frequent consumers, five were considered frequent and 24 were considered occasional consumers. Among the very frequent consumers, only six species are exclusive consumers of gelatinous plankton and all of them belong to the suborder Stromateoidei: *S. brasiliensis* (Stromateidae), *S. porosa* (Centrolophidae), *Ichthyos australis* (Haedrich, 1966) (Centrolophidae), *Centrolophus niger* (Gmelin, 1789) (Centrolophidae), *Schedophilus* sp. (Centrolophidae) and *Peprilus paru* (Linnaeus, 1758) (Stromateidae). Their gelatinivory is evidenced by the high proportion of stomachs with gelatinous organisms observed as a single item (*S. porosa*, 57%, *S. brasiliensis*, 98% and the others 100%). Among previous records found for the area, only *S. porosa* and *S. brasiliensis* have been reported as exclusive consumers of gelatinous animals by Mianzan et al. (1996), with similar proportional values. The presence of gelatinous organisms as the main prey in the stomachs of these six fish species reflects the typical specific feeding behaviour of the fish families Centrolophidae and

Stromateidae. As already mentioned, both families belong to the suborder Stromateoidei, a group commonly known as medusophages (see Haedrich 1967; Macpherson 1983) due to the presence of a series of anatomical adaptations in their digestive tract that facilitate the predation of these jelly organisms. Their specialized pharyngeal pouches coated with buds and conical denticles (which serve to crush their prey and prevent regurgitation), their large stomachs (to store large amounts of gelatinous material) and their long digestive tracts are some of the adaptations thought relevant to consumption of gelatinous organisms (Harbison 1993). Such adaptations are reminiscent of those present in herbivorous fish; indeed, gelatinivory may have evolved from herbivory, or vice versa (Harbison 1993). The remaining species of this category (*H. dactylopterus lahillei*, *Dipturus trachyderma* (Kreffft & Stehmann, 1975), *M. holotrachys* and *Squalus acanthias*) are not considered exclusive consumers of jellies because their diets also include a wide variety of other prey items (Mianzan et al. 1996; Cousseau & Perrotta 2000). Particular attention should be directed to the cartilaginous fish *S. acanthias* (picked dogfish). This fish is a large, demersal–pelagic species, an active swimmer and a dynamic generalist–opportunistic predator; however, it is a regular consumer of gelatinous organisms, which covers their basal metabolic requirements (Cousseau & Perrotta 2000; Belleggia et al. 2012). Among their main prey items in the western South Atlantic are Argentine hake *M. hubbsi*, Argentine anchovy *Engraulis anchoita*, squid *Illex argentinus* (Castellanos, 1960) and the ctenophores *Pleurobrachia pileus* (O.F. Müller, 1776) and *Mnemiopsis leidyi* A. Agassiz, 1865 (see Mianzan et al. 1996; Garcia de la Rosa & Sánchez 1997; Cousseau & Perrotta 2000), as well as medusae and salps (this study).

Regarding the frequent consumers, fishes such as *P. ramsayi*, *Squalus mitsukurii* Jordan & Snyder, 1903, *C. orbignyanus*, *P. signata* and *Macrourus carinatus* (Günther, 1878) are active predators, mostly fish-eaters, except *P. ramsayi* which is a benthic species that feeds mainly on seaweed, sea squirts, small crustaceans and polychaetes (Sanchez & Prenski 1996; Cousseau & Perrotta 2000). For these species, gelatinous consumption occurs continuously, although it undergoes seasonal variations (Mianzan et al. 1996; Sanchez & Prenski 1996; this study).

Finally, the occasional fish consumers present a wide trophic spectrum and a wide range of eating habits (pelagic, bathy–pelagic, demersal–pelagic, demersal–benthic and benthic), as well as a diversity of prey

items such as Argentine hake (*M. hubbsi*), Argentine anchovy (*E. anchoita*) and several myctophids, squids, small crustaceans (hyperiid amphipods and euphausiids), crabs, polychaetes and occasionally gelatinous organisms such as ctenophores, salps and medusae (this study) (see Cousseau & Perrotta 2000; Gilberto 2008; Wöhler & Sánchez 1994; Sánchez & Prenski 1996; Sánchez & Garcia de la Rosa 1999).

The fact that ctenophores, salps and medusae have the ability to form natural aggregations with large biomass and high densities (Mianzan & Acha 2008) make them a potential food source for many fishes (Mianzan et al. 1996). In the study area, ctenophores are the most abundant and frequent macrozooplankton organisms (Mianzan et al. 1996). Large biomasses of *M. leidyi*, *Beroë ovata* Bruguière, 1789 and *P. pileus* have been reported in the region, with values greater than 50% over other planktonic organisms (Mianzan & Sabatini 1985; Mianzan 1986; Mianzan & Guerrero 2000). Ctenophores are widely distributed in several coastal areas (estuarine zones and bays), on the continental shelves of Argentina and Uruguay, and in deep waters of the Patagonian region (Mianzan & Guerrero 2000; Costello & Mianzan 2003; Mianzan et al. 2010). Conversely, salps are abundant in the oceanic domain and rare in coastal waters. An exception is *Soestia zonaria* (Pallas, 1774), a common species found with high levels of biomass on the outer edge of the saline front of the Río de la Plata (see Mianzan & Guerrero 2000; Alvarez Colombo et al. 2003), the Subtropical Convergence zone, Buenos Aires coastal areas and in deep waters on the continental shelves of Argentina and Uruguay (Mianzan et al. 2001; Daponte et al. 2011, 2013). In the case of medusae, hydromedusae are particularly abundant in semi-enclosed areas of the continental shelf of Argentina, such as the estuarine zone of Río de la Plata, the gulfs of San Matías and San Jorge and some coastal areas in the south (Genzano et al. 2008a; Guerrero et al. 2013). Scyphomedusae can reach large sizes and are common in estuarine, coastal and open water environments (Mianzan & Cornelius 1999).

In this study, all three taxa of gelatinous organisms were found in the fish stomachs. The most common of these were ctenophores, while salps and medusae were less frequent. These results were consistent with those already reported by Mianzan et al. (1996) for the Argentine shelf. The spatial distribution of stomachs with each item (ctenophores, salps and medusae) coincided with the distribution of these organisms in the study area. The consumption of ctenophores occurred over the entire area, of salps more frequently in the north and centre of the slope zone and in the

deep waters of the continental shelf, and of medusae most often in Samborombón Bay, San Matías Gulf, tidal fronts of Península Valdés and in deep waters of platform (Mianzan & Guerrero 2000). The three gelatinous items considered represent an important and even exclusive part of the diet of many analysed fish species, in spite of their low caloric content (Doyle et al. 2007). When ctenophores and medusae reach high densities, a significant decrease commonly occurs in other components of the zooplankton (mainly copepods); hence, jellies become the only food resource available (Alvariño 1980; Mianzan & Sabatini 1985; Mianzan et al. 1996). In the same way, under favourable conditions, salps can form dense swarms which cause intense grazing pressure on phytoplankton, depleting food for the remaining zooplankton (Boero et al. 2008, 2013; Daponte et al. 2013). Consequently, salps also turn into an important food source (Mianzan et al. 1996, 1997, 2001; Pájaro 2002). Daponte et al. (2011) reported that after a rapid increase in the abundance of *S. zonaria* and *Ihlea magalhanica* (Apstein, 1894) in the South Atlantic, there was a peak of 60 times higher availability of carbon for other trophic levels, including fishes and birds.

Considering the high densities reached by medusae and ctenophores, several species of fishes may consume enough of these organisms to meet their basal metabolic requirements or even surpass it, a fact confirmed by several laboratory experiments (see Arai 1988; Riascos et al. 2012). Purcell & Arai (2001) mentioned that North Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758) preferentially consume medusae rather than copepods and other zooplanktonic organisms.

The low nutritional value of ctenophores and medusae (with low carbon and high percentages of water present in their tissues) may be compensated for by the large size that these jelly organisms present. Specifically, a high gelatinous intake may still exceed the calories and supply the basic energy requirements for many fishes (Larson 1986; Arai 1988). Also, the large size reached by ctenophores and medusae (mainly scyphomedusae) would make them more visible and thus more vulnerable to predation. Moreover, their low mobility not only facilitates their consumption, but also implies little required energy expenditure by predators in order to catch such gelatinous prey (Arai 1988).

Cluster and SIMPER analyses showed six consumption areas (G1–G6) on the continental shelves of Argentina and Uruguay, where eight species of fishes (*S. acanthias*, *S. brasiliensis*, *H. lahillei*, *M. holotrachys*, *P. ramsayi*, *M. hubbsi*, *M. magellanicus* and *S. bivius*)

contributed significantly to the consumption of gelatinous zooplankton. *Stromateus brasiliensis* (in G3) and *S. acanthias* (in G3–G6) mostly consumed ctenophores in nearly all areas of the Argentine continental shelf, coinciding with the distribution of comb jellies in the area. *Stromateus brasiliensis* and *S. acanthias* are both very common and widely distributed in the area. In contrast, the other six species, despite their extensive distributions, seem to have specific areas where they consume gelatinous zooplankton. Specifically, while the distributions of *P. ramsayi* and *M. holotrachys* cover sub-Antarctic waters from 37°S on the continental slope, platform and south of the continental shelf area (Cousseau & Perrotta 2000), these two species consume ctenophores and salps mainly in the southern region of the slope front and continental shelf (G2). *Helicolenus lahillei* is distributed from southern Brazil to 41°S in the middle shelf of Argentina, but the species consumes only ctenophores on the northern front slope (35°–38°S G4). Finally, *M. hubbsi* and *S. bivius* (which are widely distributed throughout the continental shelves of Argentina and Uruguay) and *M. magellanicus* (which occurs from 38° to 54°S in the intermediate platform related to the Malvinas Current and the gulfs of San Matías and San Jorge) both consumed salps only in cold estuarine zone and south front slope (G1). The affinity observed between these groups (G1, G2, G4 and G5) is likely attributable to some shared geographical, physical and chemical characteristics. For example, these areas mostly correspond with the frontal zones (see Acha et al. 2004; Figure 1). A front consists of the intersection of two water masses having different physical–chemical properties, and is often accompanied by high biological activity. Usually in these areas, vertical and horizontal mixing increases primary production (phytoplankton), and secondary production (zooplankton) benefits. High availability of food attracts nektonic organisms (fishes, turtles and marine mammals), allowing the energy produced in these areas to be transferred to higher trophic levels (Acha et al. 2004). This fact highlights the importance of frontal areas in the consumption of gelatinous organisms by fishes. In these areas, large aggregations of gelatinous zooplankters are commonly observed which, under certain circumstances, dominate the rest of the zooplankton (Mianzan & Sabatini 1985; Mianzan 1986, 1989; Pagès 1997; Mianzan et al. 2000; Mianzan & Guerrero 2000; Álvarez Colombo et al. 2003; Costello & Mianzan 2003; Mianzan & Acha 2008; Genzano et al. 2008b). Thus, we can assume that frontal areas play a key role in trophic interactions between jelly organisms and fishes (see Mianzan & Guerrero 2000; Mianzan & Acha 2008).

Conclusions

It is often stated that overfishing removes a vast number of top predators, leaving a greater amount of food available to lower trophic levels and culminating with changes in the species composition of marine ecosystems. For example, reports frequently suggest that the depletion of top predators or higher trophic levels by fishing down marine chains can lead to an increase of organisms in lower trophic levels, such as invertebrates or planktivorous fishes. In extreme cases, it may lead to an increase in gelatinous zooplankton (Pauly et al. 2009; Utne-Palm et al. 2010). Thus, information gathered from analyses of the gut contents of fishes allows us to evaluate changes in abundance and distribution of gelatinous organisms, because changes that occur in prey composition of opportunistic fishes can provide information about the population dynamics of gelatinous organisms (Link & Ford 2006). In another example, Belleggia et al. (2012) found that the trophic level of *Squalus acanthias* had decreased from one decade to another in the Argentine Sea. These authors suggested that overfishing of their principal prey (Argentine hake and other demersal fish) led to an increase in consumption of *Illex* squid and ctenophores.

Meanwhile, only fishes present in sufficient numbers may have a significant impact on the populations of gelatinous zooplankton (Arai 1997). According to Harbison (1993), certain medusophagous fish (Suborder Stromateoidei) potentially exercise direct control over these organisms in some ecosystems. In this context, stomach content analyses provide not only valuable information about the dynamics of this highly productive and important ecosystem, but facilitate the planning, assessment and management of fisheries.

Our findings also improve knowledge about those fish species involved in the local trophic web and provide a basis for the application of future research techniques. For example, stable isotopes of carbon (C) and nitrogen (N) could be used to establish the trophic level of a particular organism, integrating the assimilated energy that flows through different trophic levels, and utilization of tissues as the object of analysis (Post 2002).

Acknowledgements

We are especially grateful to Dr Dale Calder of the Royal Ontario Museum for revising the grammar and style of this manuscript and to our friend Steven Ryan Gray for his help on the English of the early version. We also thank Dr Claudia Bremec for her comments, which greatly improved this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas under grant number PIP 2012-0152 and Universidad Nacional de Mar del Plata under grant number EXA 734/15, UNMdP. LDB is supported by a Consejo Nacional de Investigaciones Científicas y Técnicas fellowship. This is INIDEP contribution No. 2045.

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