



## Seasonal variation of gelatinous plankton consumption by fish in the South-western Atlantic Ocean: a question of strategy

Luciana Diaz Briz, Felisa Sánchez, Noemí Marí & Gabriel Genzano

To cite this article: Luciana Diaz Briz, Felisa Sánchez, Noemí Marí & Gabriel Genzano (2018): Seasonal variation of gelatinous plankton consumption by fish in the South-western Atlantic Ocean: a question of strategy, Marine Biology Research, DOI: [10.1080/17451000.2018.1508847](https://doi.org/10.1080/17451000.2018.1508847)

To link to this article: <https://doi.org/10.1080/17451000.2018.1508847>



Published online: 24 Aug 2018.



Submit your article to this journal [↗](#)



View Crossmark data [↗](#)

---



# Seasonal variation of gelatinous plankton consumption by fish in the South-western Atlantic Ocean: a question of strategy\*

Luciana Diaz Briz<sup>a,b</sup>, Felisa Sánchez<sup>c</sup>, Noemí Mari<sup>c</sup> and Gabriel Genzano<sup>a,b</sup>

<sup>a</sup>Estación Costera Nágera, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Buenos Aires, Argentina; <sup>b</sup>Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata (UNMDP), CONICET, Facultad de Cs. Exactas y Naturales, Buenos Aires, Argentina; <sup>c</sup>Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Buenos Aires, Argentina

## ABSTRACT

Gelatinous plankton is an important food resource for several species of fishes in the Southwestern Atlantic Ocean. Some fish depend heavily on these organisms and are specialized to feed on ctenophores, salps and medusae, while others only consume gelatinous plankton occasionally. We hypothesize that consumption of gelatinous plankton by fishes represents an alternative food resource when primary prey are not available during cold periods in the study area. To determine seasonal variations of gelatinous plankton consumption by fishes, data samples were grouped into cold and warm periods. A total of 64,567 stomachs belonging to 106 species of fish were analysed, of which 32,943 (51%) contained food items. Of those containing food items, 2719 (8.2%), from 38 fish species, contained gelatinous items. Fourteen species ingested gelatinous in warm period, nine in cold period, and 15 in both periods. The proportion of stomachs with gelatinous was significantly greater during the cold period. Ctenophores were the most predominant prey in both periods, followed by salps and medusae. Consumption of ctenophores, salps and medusae was unevenly distributed within the area during the different periods. Classification methods (group average sorting utilizing Bray–Curtis similarity measures based on  $\log(X + 1)$ ) identified eight areas of consumption. SIMPER (similarity percentages) analyses revealed that nine fish species contributed most to gelatinous plankton consumption. The seasonal and spatial variation of gelatinous consumption by fish would be related to the availability of food in each period. Strategies of gelatinous consumption, including survival, feeding opportunities and prey specialization, are discussed.

## ARTICLE HISTORY

Received 6 September 2017  
Accepted 28 July 2018

## KEYWORDS

Seasonality; fish predation; gelatinous plankton; strategy of consumption

## Introduction

It is well known that gelatinous organisms such as ctenophores, salps and medusae play an important role as prey for a wide variety of organisms, mostly fish (Arai 2005; Marques et al. 2016; Diaz Briz et al. 2017 and information therein). These soft-bodied organisms have the ability to form large aggregations (Graham et al. 2001), which may negatively impact tourism, health, aquaculture and fisheries (Ivanov et al. 2000; Mianzan et al. 2000, 2005; Doyle et al. 2008). According to Arai (1997), only fish present in sufficient numbers may have a significant impact on the populations of gelatinous zooplankton. Also, Harbison (1993) and Marques et al. (2016) suggest that certain medusophagous fish (e.g. Suborder Stromateoidei) potentially contribute to the direct control of these organisms in some ecosystems through top-down regulations of

gelatinous biomass. In this context, knowing which are the potential predator fish and when they consume this kind of gelatinous prey, provides valuable information about the dynamics of this highly productive and important ecosystem and facilitates the planning, assessment and management of fisheries (Mills 1995; Boero et al. 2008; Pauly et al. 2009; Condon et al. 2012; Mianzan et al. 2012; Diaz Briz et al. 2017). In recent studies, Diaz Briz et al. (2017) quantified the consumption of three gelatinous groups (ctenophores, salps and medusae) by almost 50 fish species and determined the different areas of plankton consumption in temperate waters of South-western Atlantic Ocean.

The information collected from the analysis of the stomach contents of fish would allow us to evaluate temporal and spatial changes in abundance and

**CONTACT** Luciana Diaz Briz ✉ diazbriz.luciana@gmail.com 📧 Estación Costera Nágera, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350 C.P. 7600, Mar del Plata, Buenos Aires, Argentina

\*This research was conducted at Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata (UNMDP), Buenos Aires, Argentina.

© 2018 Informa UK Limited, trading as Taylor & Francis Group

distributions of gelatinous organisms because changes in prey composition of opportunistic fish provide information about the population dynamics of gelatinous organisms (Link and Ford 2006). Belleggia et al. (2012) found that the trophic level of spiny dogfish (*Squalus acanthias* Linnaeus, 1758) decreased from 1990 to 2000 in the ecosystem of the Argentine sea (South Atlantic). These authors suggested that overfishing of their principal prey (Argentine hake and other demersal fish) led to an increase in consumption of *Illex argentinus* Castellanos, 1960 squid and ctenophores during that decade.

In spite of the importance of this kind of work, studies that analyse the seasonal variation of fish consumption on gelatinous zooplankton are very scarce. Mianzan et al. (1996) and Arkhipkin and Laptikhovskiy (2013) only quantified the seasonality of ctenophores consumption by some fishes in three areas of the south-western Atlantic Ocean (Río de la Plata, Peninsula Valdes and Falkland Islands).

The reasons why fish species incorporate gelatinous organisms as food are not clearly understood, but according to Mianzan et al. (2001), this behaviour may occur when the main prey are not available, which implies an adaptive food web. However, considering the large number of fish species that consume gelatinous items in the area (see Diaz Briz et al. 2017) it is possible that other strategies of consumption should also be considered. Some fish species depend heavily on gelatinous prey as a source of food, while others consume this type of prey only occasionally in accordance with availability of these gelatinous species in space and time (see Marques et al. 2016 and Diaz Briz et al. 2017 and all references cited therein). Therefore, to test the hypothesis that the consumption of gelatinous items by fish varies seasonally, stomach contents of several fish species were analysed from an extensive geographical area of the Southwestern Atlantic Ocean (33°–55° S), in the cold and warm period. Primary objectives of the study were to assess (1) seasonal trends in fish predator-gelatinous prey relationships, and (2) identify the areas where fishes consume gelatinous organisms during different seasons.

## Material and methods

### Study area and data collection

The study area comprised the Argentina Continental Shelf and southern of Uruguay (33°–55° S; Figure 1) which basically corresponds to the Subtropical (northern) and Subantarctic (southern) Biogeographical Region (Balech and Ehrlich 2008). This area is

characterized by the presence of two large water masses: a sub-Antarctic mass of cold temperate waters, the Falkland (Malvinas) Current and a sub-tropical mass of warm waters, the Brazil Current (see Guerrero and Piola 1997). The area presents different marine frontal zones, (see Acha et al. 2004; Sabatini et al. 2004; Mianzan and Acha 2008).

The data of the fish stomach contents were collected between 1986 and 2000 on the Argentinean Continental Shelf (33°–55° S; Table I) by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). This information comes from 33 research cruises performed by the Research Vessels 'Capitan Oca Balda' and 'Dr Eduardo Holmberg' of INIDEP. Overall, 1109 sample sites were analysed (Table I). 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 minutes in each sampling site, using a bottom trawl Engel type of 200 mm mesh in the wing and 103 mm in the cod end, 4 m vertical opening and 15 m horizontal aperture. The fish species were removed from the net and immediately sampled. The detail of non-gelatinous and gelatinous items was extracted from each specimen of examined fish species. The gelatinous items considered were ctenophores, salps and medusae.

### Data analysis

The data set of the three gelatinous (ctenophores, salps and medusae) and non-gelatinous prey-items were of presence/absence type. Stomachs with prey items were taken to be full, while those without were deemed to be empty.

The overall total number of empty and filled stomachs with contents, the total number of stomachs with non-gelatinous and gelatinous items, as well as the total number of stomachs with discriminated gelatinous items in ctenophores, salps and medusas were calculated as frequency of occurrence over the total analysed stomachs with contents (% F) per each fish species, respectively:

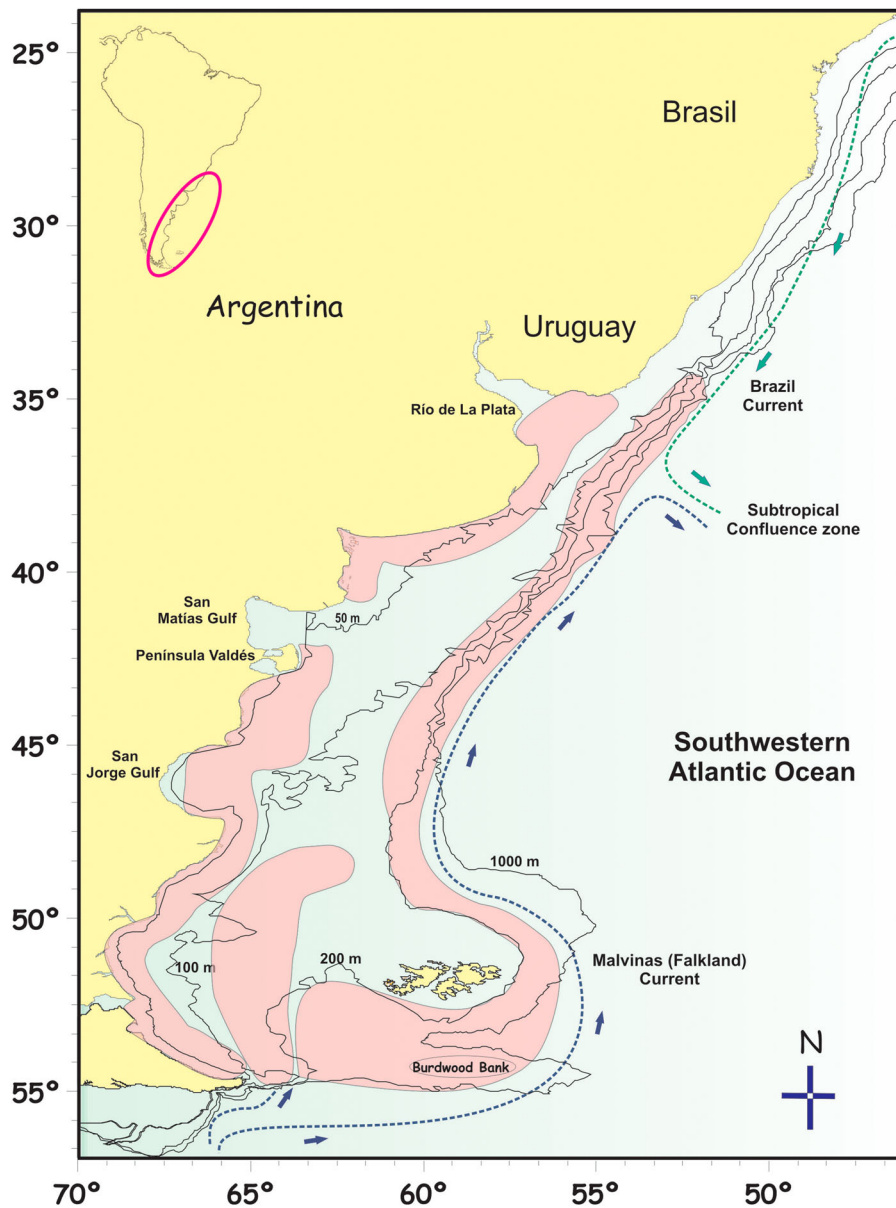
$$a- F_c(x_i) = N_{sc}(x_i) / N_{ts}(x_i) * 100$$

$$b- F_g(x_i) = N_{sg}(x_i) / N_{ts}(x_i) * 100$$

$$c- F_{ct/s/m}(x_i) = N_{s-ct/s/m}(x_i) / N_{ts}(x_i) * 100$$

$F_c$  = Frequency of stomachs with no gelatinous contents

$F_g$  = Frequency of stomachs with gelatinous contents



**Figure 1.** Study area: The colourful areas represent the Argentina and Uruguay frontal zones. Isobaths of 50, 100, 200 and 1000 m are remark.

$F_{ct,s,m}$  = Frequency of ctenophores, salps and medusae

$N_{sc}$  = Total number of stomachs with no gelatinous contents

$N_{sg}$  = Total number of stomachs with gelatinous organisms

$N_{s-ct/s/m}$  = Total number of stomachs with ctenophores, salps or medusae

$N_{ts}$  = Total number of analysed stomachs with contents

$(x_i)$  = a given fish species

To determine seasonal variations of gelatinous plankton consumption by fish, data samples were grouped in cold (samples from 15 April to 14

September) and warm periods (samples from 15 October until 14 March). The samples collected between 15 March and 14 April as well as between 15 September and 14 October ( $N = 75$  samples) were not considered in this analysis since these are considered transitional months (Table I).

The overall number of stomachs with gelatinous prey, as well as the overall number of each gelatinous item (ctenophores, salps and medusae) per fish species were calculated as frequency of occurrence (see above) in relation to the total number of stomachs with contents during each period. The overall number of stomachs with no gelatinous contents was calculated the same way. Differences between both

**Table I.** Detail of cruises for each analysed period. The total numbers of stomachs examined as well as the total number of samples analysed are given. Ni (%) = number of stomachs of fish (individuals) analysed.

| Period         | Name of cruises | Total number of stomachs (Ni) | Total number of samples | Total number of samples with gelatinous | Months            |
|----------------|-----------------|-------------------------------|-------------------------|---|-------------------|
| Warm           | OB - 06 - 1986  | 2153                          | 59                      | 19                                      | November          |
|                | OB - 08 - 1988  | 3005                          | 33                      | 28                                      | December          |
|                | OB - 07 - 1991  | 1879                          | 23                      | 16                                      | November          |
|                | EH - 01 - 1992  | 3264                          | 65                      | 29                                      | January/February  |
|                | EH - 08 - 1992  | 1908                          | 25                      | 9                                       | October           |
|                | EH - 01 - 1993  | 8485                          | 98                      | 27                                      | January /February |
|                | EH - 04 - 1993  | 1119                          | 35                      | 9                                       | February/March    |
|                | EH - 01 - 1994  | 2048                          | 33                      | 12                                      | January           |
|                | OB - 02 - 1994  | 3015                          | 49                      | 33                                      | February          |
|                | OB - 01 - 1995  | 1309                          | 29                      | 14                                      | January           |
|                | OB - 03 - 1995  | 2209                          | 44                      | 6                                       | February          |
|                | EH - 09 - 1995  | 241                           | 10                      | 2                                       | December          |
|                | OB - 08 - 1997  | 460                           | 23                      | 14                                      | December          |
|                | EH - 11 - 1998  | 3741                          | 46                      | 8                                       | December          |
|                | EH - 01 - 1999  | 482                           | 5                       | 1                                       | January           |
|                | Cold            | OB - 03 - 1986                | 2446                    | 43                                      | 16                |
| OB - 05 - 1986 |                 | 1385                          | 32                      | 1                                       | September         |
| OB - 02 - 1988 |                 | 423                           | 8                       | 4                                       | July              |
| OB - 06 - 1989 |                 | 2921                          | 17                      | 9                                       | March/April       |
| OB - 03 - 1987 |                 | 1093                          | 29                      | 11                                      | March/April       |
| OB - 02 - 1991 |                 | 5954                          | 63                      | 17                                      | May/June          |
| OB - 03 - 1991 |                 | 659                           | 6                       | 2                                       | June              |
| OB - 04 - 1991 |                 | 1267                          | 10                      | 1                                       | August            |
| OB - 07 - 1993 |                 | 1276                          | 24                      | 8                                       | June              |
| EH - 03 - 1994 |                 | 1506                          | 28                      | 7                                       | April/May         |
| OB - 04 - 1994 |                 | 5385                          | 75                      | 35                                      | March/April/May   |
| EH - 08 - 1994 |                 | 740                           | 25                      | 19                                      | July/ August      |
| EH - 11 - 1996 |                 | 842                           | 15                      | 5                                       | July              |
| OB - 04 - 1998 |                 | 1239                          | 12                      | 5                                       | May               |
| OB - 06 - 1998 |                 | 361                           | 35                      | 7                                       | July              |
| EH - 08 - 1998 |                 | 100                           | 17                      | 2                                       | July/ August      |
| EH - 07 - 1999 |                 | 1303                          | 63                      | 23                                      | September         |
| EH - 07 - 2000 | 349             | 30                            | 6                       | August                                  |                   |
| Totals         | 34 cruises      | 64,567                        | 1109                    | 405                                     |                   |

periods were evaluated by means of  $\chi^2$  test and residual analysis (Zar 1999).

To determine the main areas of gelatinous consumption by fishes during cold and warm periods, the 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 and period was calculated. For this analysis, a single species that consumed more than one gelatinous item was considered separately for each period and item consumed (e.g. *Squalus acanthias* with ctenophores (during the warm period); *S. acanthias* with salps (warm period); *S. acanthias* with medusae (warm period); *S. acanthias* with ctenophores (cold period); *S. acanthias* with salps (cold period) and *S. acanthias* with medusae (cold period) and so on). The square without species ( $n=25$  squares) as well as those fish species present in only one square were excluded from the analysis ( $n=41$ ). The final matrix consisted of 93 squares and 41 fish species. Classification methods (group average sorting of the Bray–Curtis similarity measures based on  $\log(X + 1)$  transformed data) were carried out using the PRIMER

6 software package (Clarke and Warwick 2001) to determine locations where consumption occurred. 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. A similarity profile analysis (SIMPROF) was used to test whether the groups obtained by the cluster analysis were significantly different. This method of data analysis employs null hypothesis testing to detect structure in ecological communities. A similarity profile is constructed from a set of species abundance, frequencies and composition data by first creating a similarity matrix using an ecologically appropriate resemblance measure (e.g. the Bray-Curtis metric). The value of SIMPROF is realized when it is used to objectively identify the members of 'real' groups present in the results returned from a classical hierarchical agglomerative clustering method (Clarke et al. 2008). A SIMPER analysis (similarity percentages) was used to determine the fish species that contributed most to (dis)similarities among and within groups in each period (Clarke and Warwick 2001).

## Results

Of a total 1109 sample sites analysed, 405 (36.5%) presented fish with any gelatinous items in their stomach contents (see Table I). A total of 64,567 stomachs belonging to 106 species of fish were quantified, of which 31,624 (49%) were empty and 32,943 (51%) had food items. Out of these stomachs with contents, 2719 (8.2%) belonging to 38 fish species contained gelatinous items of which 14 species eat in the warm

period, nine in the cold period and 15 in both periods (see Table II).

The proportion of fish stomachs with gelatinous and without gelatinous items varied significantly between the two periods. The proportion of stomachs with gelatinous items was greater during the cold period (11.8% in the cold period vs. 8.4% in the warm period), while the proportion of stomachs with no gelatinous items was lower in this period (87.9% in the cold period vs.

**Table II.** List of fish species that consume gelatinous organisms. In white species that consume during both periods, in red only those that consume in warm season and in blue only those consume in cold period. Ni (%) = number of stomachs with each gelatinous prey and its corresponding percentage value.

| Fish species                    | Warm                           |                    |                    |              |                | Cold          |                     |                    |              |                |
|---------------------------------|--------------------------------|--------------------|--------------------|--------------|----------------|---------------|---------------------|--------------------|--------------|----------------|
|                                 | Total number of stomachs with: |                    |                    |              |                |               |                     |                    |              |                |
|                                 | Contents                       | Gelatinous Ni (%)  | Ctenophores Ni (%) | Salps Ni (%) | Medusae Ni (%) | Contents      | Gelatinous Ni (%)   | Ctenophores Ni (%) | Salps Ni (%) | Medusae Ni (%) |
| <i>Bathyraja sp.</i>            | 144                            | 1 (0.69)           | 1 (100)            | 0            | 0              | 152           | 1 (0.65)            | 1 (100)            | 0            | 0              |
| <i>Conger orbignianus</i>       | 44                             | 3 (6.82)           | 2 (66.67)          | 1 (33.33)    | 0              | 165           | 31 (18.79)          | 13 (41.94)         | 17 (54.83)   | 1 (3.22)       |
| <i>Helicolenus lahillei</i>     | 31                             | 24 (77.4)          | 14 (58.33)         | 10 (41.67)   | 0              | 310           | 98 (31.61)          | 89 (90.82)         | 12 (12.24)   | 0              |
| <i>Macruronus magellanicus</i>  | 1,806                          | 46 (2.55)          | 20 (43.48)         | 26 (56.52)   | 0              | 1,139         | 113 (9.92)          | 48 (42.48)         | 65 (57.52)   | 0              |
| <i>Merluccius hubbsi</i>        | 7,050                          | 83 (1.18)          | 7 (8.43)           | 74 (89.16)   | 3 (3.61)       | 5,182         | 28 (0.54)           | 6 (21.43)          | 22 (78.57)   | 0              |
| <i>Micromesistius australis</i> | 218                            | 9 (4.13)           | 9 (100)            | 0            | 0              | 182           | 17 (9.34)           | 0                  | 17 (100)     | 0              |
| <i>Micropogonias furnieri</i>   | 400                            | 13 (3.25)          | 13 (100)           | 0            | 0              | 72            | 1 (1.38)            | 1 (100)            | 0            | 0              |
| <i>Nemadactylus bergi</i>       | 37                             | 2 (5.41)           | 2 (100)            | 0            | 0              | 397           | 8 (2.01)            | 6 (75)             | 0            | 2 (25)         |
| <i>Parona signata</i>           | 106                            | 21 (19.8)          | 0                  | 0            | 21 (100)       | 34            | 6 (17.65)           | 6 (100)            | 0            | 0              |
| <i>Patagonotothen ramsayi</i>   | 979                            | 126 (12.9)         | 86 (68.25)         | 39 (30.95)   | 2 (1.59)       | 358           | 61 (17.04)          | 5 (8.19)           | 40 (65.57)   | 18 (29.51)     |
| <i>Seriolella porosa</i>        | 184                            | 95 (51.6)          | 94 (98.95)         | 0            | 1 (1.05)       | 27            | 26 (96.3)           | 26 (100)           | 0            | 0              |
| <i>Squalus acanthias</i>        | 1,023                          | 304 (29.7)         | 264 (86.84)        | 11 (3.61)    | 30 (9.87)      | 2,286         | 966 (42.26)         | 810 (83.85)        | 61 (6.31)    | 122 (12.63)    |
| <i>Squalus sp.</i>              | 84                             | 3 (3.6)            | 3 (100)            | 0            | 0              | 70            | 3 (4.28)            | 2 (66.67)          | 1 (33.33)    | 0              |
| <i>Stromateus brasiliensis</i>  | 437                            | 430 (98.4)         | 417 (96.98)        | 11 (2.55)    | 2 (0.47)       | 64            | 64 (100)            | 37 (57.81)         | 0            | 27 (42.19)     |
| <i>Zearaja chilensis</i>        | 138                            | 2 (1.45)           | 1 (50)             | 1 (50)       | 0              | 631           | 5 (0.79)            | 4 (80)             | 0            | 1 (20)         |
| <i>Bathyraja albomaculata</i>   | 134                            | 2 (1.5)            | 1 (50)             | 1 (50)       | 0              | 141           | 0                   | 0                  | 0            | 0              |
| <i>Centrolophus niger</i>       | 2                              | 2 (100)            | 2 (100)            | 0            | 0              | 0             | 0                   | 0                  | 0            | 0              |
| <i>Dipturus trachyderma</i>     | 2                              | 1 (50)             | 0                  | 0            | 1 (100)        | 0             | 0                   | 0                  | 0            | 0              |
| <i>Icichthys australis</i>      | 1                              | 1 (100)            | 1 (100)            | 0            | 0              | 0             | 0                   | 0                  | 0            | 0              |
| <i>lluocoetes fimbriatus</i>    | 46                             | 1 (2.17)           | 0                  | 1 (100)      | 0              | 62            | 0                   | 0                  | 0            | 0              |
| <i>Macrourus carinatus</i>      | 39                             | 8 (20.5)           | 0                  | 8 (100)      | 0              | 6             | 0                   | 0                  | 0            | 0              |
| <i>Peprilus paru</i>            | 1                              | 1 (100)            | 1 (100)            | 0            | 0              | 0             | 0                   | 0                  | 0            | 0              |
| <i>Psammobatis sp.</i>          | 192                            | 1 (0.52)           | 0                  | 1 (100)      | 0              | 156           | 0                   | 0                  | 0            | 0              |
| <i>Salilota australis</i>       | 180                            | 2 (1.11)           | 2 (100)            | 0            | 0              | 71            | 0                   | 0                  | 0            | 0              |
| <i>Schedophilus sp.</i>         | 2                              | 2 (100)            | 2 (100)            | 0            | 0              | 0             | 0                   | 0                  | 0            | 0              |
| <i>Schroederichthys bivius</i>  | 353                            | 10 (2.83)          | 0                  | 9 (90)       | 1 (10)         | 176           | 0                   | 0                  | 0            | 0              |
| <i>Squalus mitsukuri i</i>      | 304                            | 38 (12.5)          | 38 (100)           | 0            | 0              | 0             | 0                   | 0                  | 0            | 0              |
| <i>Sympterygia bonapartii</i>   | 234                            | 2 (0.85)           | 0                  | 2 (100)      | 0              | 207           | 0                   | 0                  | 0            | 0              |
| <i>Trachurus lathami</i>        | 23                             | 1 (4.35)           | 0                  | 0            | 1 (100)        | 15            | 0                   | 0                  | 0            | 0              |
| <i>Bathyraja macloviana</i>     | 54                             | 0                  | 0                  | 0            | 0              | 75            | 1 (1.33)            | 1 (100)            | 0            | 0              |
| <i>Cottoperca gobio</i>         | 206                            | 0                  | 0                  | 0            | 0              | 21            | 1 (4.76)            | 0                  | 0            | 1 (100)        |
| <i>Dissostichus eleginoides</i> | 90                             | 0                  | 0                  | 0            | 0              | 118           | 8 (6.78)            | 0                  | 8 (100)      | 0              |
| <i>Macrourus holotrachys</i>    | 0                              | 0                  | 0                  | 0            | 0              | 49            | 40 (81.63)          | 0                  | 38 (95)      | 4 (10)         |
| <i>Mullus argentinae</i>        | 0                              | 0                  | 0                  | 0            | 0              | 59            | 3 (5.08)            | 3 (100)            | 0            | 0              |
| <i>Scomber japonicus</i>        | 45                             | 0                  | 0                  | 0            | 0              | 26            | 1 (3.84)            | 0                  | 1 (100)      | 0              |
| <i>Pagrus pagrus</i>            | 6                              | 0                  | 0                  | 0            | 0              | 38            | 1 (2.63)            | 0                  | 0            | 1 (100)        |
| <i>Squatina argentina</i>       | 127                            | 0                  | 0                  | 0            | 0              | 163           | 1 (0.61)            | 1 (100)            | 0            | 0              |
| <i>Trichiurus lepturus</i>      | 0                              | 0                  | 0                  | 0            | 0              | 149           | 1 (0.67)            | 1 (100)            | 0            | 0              |
| <b>Totals</b>                   | <b>14,722</b>                  | <b>1,234 (8.4)</b> | <b>980</b>         | <b>195</b>   | <b>62</b>      | <b>12,601</b> | <b>1,485 (11.8)</b> | <b>1,060</b>       | <b>282</b>   | <b>177</b>     |



**Table III.** Total number of stomachs with the three gelatinous items discriminated in ctenophores, salps, medusae and others content (non gelatinous) used for  $\chi^2$  analysis with its frequency (%) by corresponding period.

| Items                       | Warm (%)       | Cold (%)       | Totals         |
|-----------------------------|----------------|----------------|----------------|
| Ctenophores                 | 980 (6.66)     | 1,060 (8.41)   | 2,040 (7.47)   |
| Salps                       | 195 (1.32)     | 282 (2.24)     | 477 (1.74)     |
| Medusae                     | 62 (0.42)      | 177 (1.40)     | 239 (0.87)     |
| other items (no gelatinous) | 13,485 (91.60) | 11,082 (87.95) | 24,567 (89.91) |
| Totals                      | 14,722         | 12,601         | 27,323         |

91.6% in the warm period, see Table II) ( $\chi^2 = 87,351$ ;  $P < .001$ ).

The same analysis was performed to establish stomachs containing different proportions of ctenophores, salps and medusae. The three items were also consumed in greater quantities during the cold rather than the warm period (8.4% vs. 6.6% for ctenophores; 2.2% vs. 1.3% for salps and 1.4% vs. 0.4% for medusae, respectively) ( $\chi^2 = 145.6181$ , ( $P < .001$ ) (see Table III). In both periods, ctenophores were the most frequent prey in gut contents of the fish species analysed, followed by salps and medusae (see Table II)

### Seasonal and spatial variation of consumption

The consumption of ctenophores, salps and medusae was unevenly distributed within the study area in the different periods. According to the cluster analysis, a total of eight groups (consumption areas = G1- G8) were identified, which represented a 100% ( $N = 93$ ) of squares analysed (Figure 2). The SIMPER analysis (Parameters Resemblance: S17 Bray Curtis similarity and cut off for low contributions: 90.0%) indicated nine fish species contributed most to the consumption of each gelatinous item in each area and period. contributed to the consumption of each gelatinous item in each area and period.

In general terms, in the areas G1, G3 and G4 the consumption of gelatinous items by fish occurred only in the cold period (see Figures 2 and 3): Group 1 (24.39% internal similarity SIMPER analysis), grouped 11 squares located on the south slope in Patagonia (51°–55° S). Four fish species consumed gelatinous items in this area, but only *Patagonotothen ramsayi* (Regan, 1913) and *Macruronus magellanicus* Lönnberg, 1907 contributed significantly to the salps consumption with values of 59.05% and 15.65%, respectively.

Group 3 (66.44% internal similarity SIMPER analysis), concentrated four squares corresponding to the Buenos Aires Coast (38°S) and San Jorge Gulf (45°–46° S). Only two fish species were represented, *Stromateus brasiliensis* Fowler, 1906 and *Seriolaella porosa* Guichenot, 1848, with values of 46.23% and 45.37% for ctenophores, respectively.

Group 4 (66.37% internal similarity SIMPER analysis), grouped 20 squares located on the centre and southern part of the Argentina continental shelf (39°–53° S). In this area the fish species that most contributed was *Squalus acanthias* with value of 98.89% for the ctenophores item.

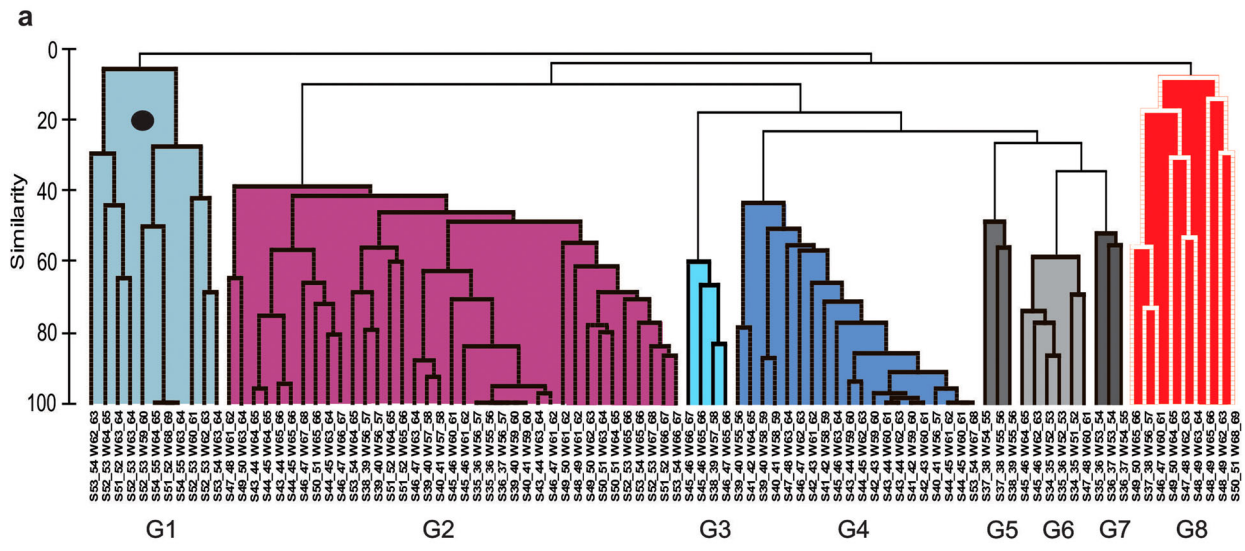
On the contrary, the consumption by fish in the areas G2 and G8 occurred in the warm period (see Figures 2 and 3):

Group 2 (50.11% internal similarity SIMPER analysis), consisted of 37 squares, located in the estuarine zone of Rio de la Plata (35°–36° S), in the tidal front zone of Peninsula Valdes (43°–44° S) and in the centre and southern continental shelf (38°–40° and 55°–53° S). In this area, two fish species dominated ctenophore consumption, *S. brasiliensis* with a value of 82.87% and *S. acanthias* with 8.81%.

Group 8 (18.70% internal similarity SIMPER analysis), consisted of nine squares, one located in the coast of Buenos Aires (37° S) and the remaining in the southern platform (46–50° S). Four species were represented in this area, with *P. ramsayi* and *Merluccius hubbsi* Marini, 1933 being the species that most contributed to gelatinous consumption with values of 38.37% for ctenophores and 35% for salps, respectively.

Finally, in the areas G5, G6 and G7 the consumption of gelatinous items by fish occurred in both periods (cold and warm) (see Figures 2 and 3).

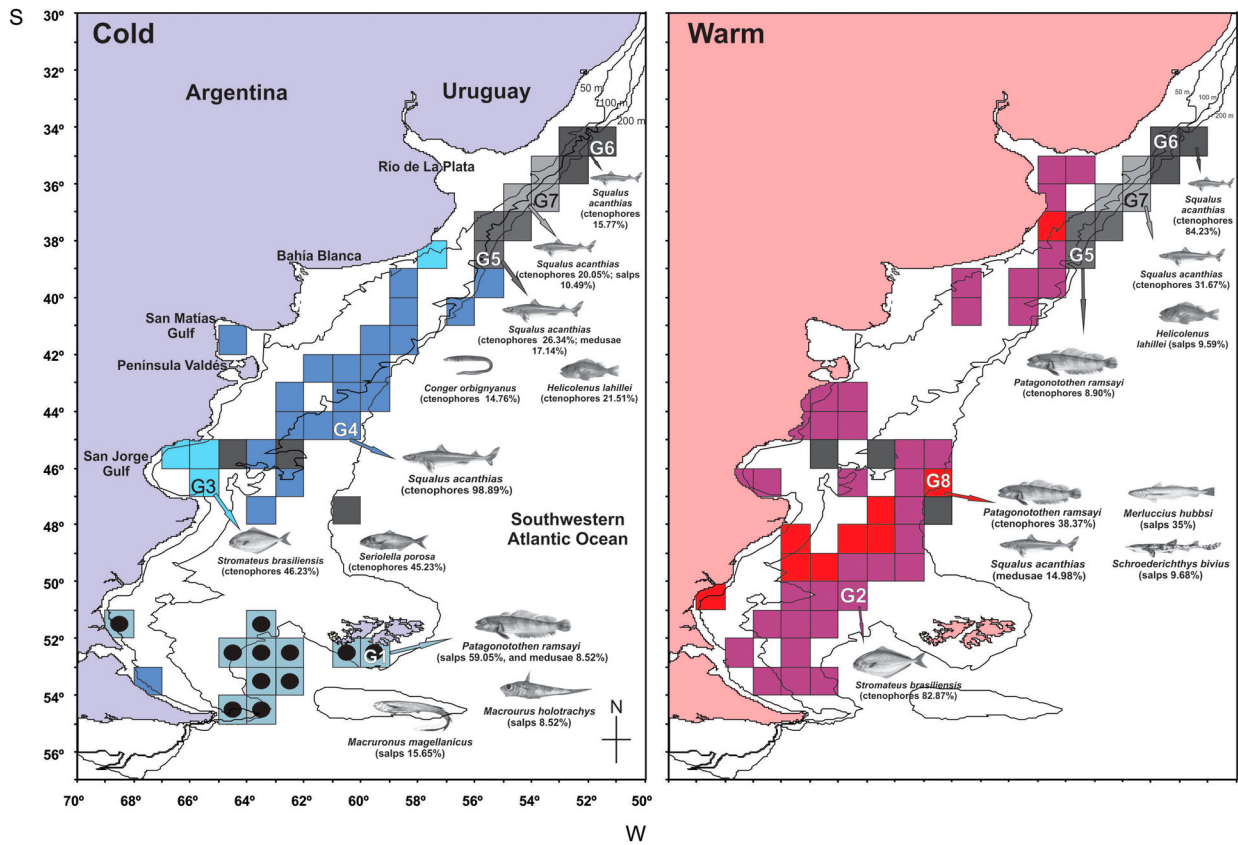
Group 5 (51.55% internal similarity SIMPER analysis), brought together a total of three squares located in the north of Argentina continental shelf and frontal slope zone (37°–38° S). In this area five species were



| Groups - (Average similarity %)              | Cold                       |           |           | Both periods |           |           |           | Warm      |       |       |
|--|----------------------------|-----------|-----------|--------------|-----------|-----------|-----------|-----------|-------|-------|
|  | 1 (24.39)                  | 3 (66.44) | 4 (66.37) | 5 (51.55)    | 6 (66.97) | 7 (53.34) | 2 (50.11) | 8 (18.70) |       |       |
| Species (gelatinous item)                    | Percentages contribution % |           |           |              |           |           |           |           |       |       |
|  |                            |           |           | C            | W         | C         | W         | C         | W     |       |
| <i>Cheilodactylus bergi</i> (ctenophores)    | -                          | -         | -         | -            | -         | -         | -         | 8.75      | -     | -     |
| <i>Conger orbignyanus</i> (ctenophores)      | -                          | -         | -         | 14.76        | -         | -         | -         | -         | -     | -     |
| <i>Helicolenus lahillei</i> (ctenophores)    | -                          | -         | -         | 21.51        | -         | -         | -         | -         | -     | -     |
| <i>Helicolenus lahillei</i> (salps)          | -                          | -         | -         | -            | -         | -         | -         | 7.04      | 9.59  | -     |
| <i>Macrourus holotrachys</i> (salps)         | 8.32                       | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Macruronus magellanicus</i> (salps)       | 15.65                      | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Merluccius hubbsi</i> (ctenophores)       | -                          | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Merluccius hubbsi</i> (salps)             | -                          | -         | -         | -            | -         | -         | -         | -         | -     | 35.00 |
| <i>Patagonotothen ramsayi</i> (ctenophores)  | -                          | -         | -         | -            | 8.90      | -         | -         | -         | -     | 38.37 |
| <i>Patagonotothen ramsayi</i> (salps)        | 59.05                      | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Patagonotothen ramsayi</i> (medusae)      | 8.52                       | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Schroederichthys bivius</i> (salps)       | -                          | -         | -         | -            | -         | -         | -         | -         | -     | 9.68  |
| <i>Seriotelella porosa</i> (ctenophores)     | -                          | 45.37     | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Squalus acanthias</i> (ctenophores)       | -                          | -         | 98.89     | 26.34        | 5.86      | 15.77     | 84.23     | 20.05     | 31.07 | 8.81  |
| <i>Squalus acanthias</i> (salps)             | -                          | -         | -         | -            | -         | -         | -         | 10.49     | -     | -     |
| <i>Squalus acanthias</i> (medusae)           | -                          | -         | -         | 17.14        | -         | -         | -         | -         | -     | 14.98 |
| <i>Stromateus brasiliensis</i> (ctenophores) | -                          | 46.23     | -         | -            | -         | -         | -         | -         | -     | 82.87 |
| <i>Stromateus brasiliensis</i> (salps)       | -                          | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Stromateus brasiliensis</i> (medusae)     | -                          | -         | -         | -            | -         | -         | -         | -         | -     | -     |
| <i>Squalus mitsukuri</i> (ctenophores)       | -                          | -         | -         | -            | -         | -         | -         | -         | 6.43  | -     |

**Figure 2.** (a) Dendrogram obtained from cluster analysis calculated in each period with the proportions of stomachs with ctenophores, salps and medusae per quadrant for each species of fish predator. Each colour represents each of the eight areas of consumption obtained with its corresponding latitude and longitude points; (b) Results of SIMPER analysis of eight groups, for each area, in each period, all the fish species that most contributed in the consumption of each gelatinous item and their corresponding values in % are given.





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

represented; however, *S. acanthias* and *Helicolenus lahillei* Norman, 1937 (with values of 26.34% and 21.51%) contributed more in the cold period while *P. ramsayi* (with a value of 8.90%) in the warm period, all of them preying over the ctenophores item.

Group 6 (66.97% internal similarity SIMPER analysis), concentrated a total of six squares, situated in the Uruguay continental shelf and north frontal slope zone (34°–35° S) and in the centre of Patagonia (45°–47° S). In this area, only *S. acanthias* contributed mainly in the consumption of ctenophores with values of 84.23% in the warm period and 15.77% in the cold period.

Group 7 (53.34% internal similarity SIMPER analysis), grouped a total of three squares in the north of Argentina continental shelf and frontal slope zone (36°–37° S). In this area, seven species were represented; however, only *S. acanthias* (with a value of 31.67% for the ctenophores item) and *H. lahillei* (with a value of 9.59% for the salps item) were the species that contributed more to the consumption in the warm period. In the cold period, *S. acanthias* contributed to the consumption of ctenophores and salps with a value of 20.05% and 10.49%, respectively.

## Discussion

Consumption of gelatinous prey by fishes was found to be slightly greater during the cold period than in the warm period in the South Atlantic Ocean, despite the fact that gelatinous organisms are more abundant in the warm season (Mianzan and Guerrero 2000). Primary production in the temperate Southwest Atlantic varies through the year. During winter, phytoplankton production is poor due to the low solar radiation. In spring, high concentrations of nutrients (such as nitrogen, phosphorus, silicon and certain other elements such as iron, copper and zinc) mix from bottom to the upper layers, and increased light levels promote the explosive growth of phytoplankton (see Mianzan and Acha 2008, and all references cited therein). Phytoplankton blooms rapidly deplete the nutrients, and an accompanying decline takes place in the ecosystem. Likewise, zooplankton populations, low in winter, expand rapidly and accelerate the reduction of phytoplankton concentrations at the end of spring and during summer. In temperate seas of the study area, phytoplankton attains a second peak in autumn after zooplankton numbers have declined and seasonal winds produce mixture. A new zooplankton peak is

then initiated while the light and temperature are still adequate (Mianzan and Acha 2008).

The gelatinous organisms also have seasonal rhythms and are more abundant during the warm period than during the cold period (Mianzan and Sabatini 1985; Mianzan et al. 1996; Mianzan and Guerrero 2000; Mianzan and Acha 2008). Both phytoplankton and herbivorous zooplankton (e.g. copepods) are the energy supply for gelatinous plankton. Therefore, the peak of ctenophores, salps and medusae follow the seasonal cycles of herbivorous zooplankton and phytoplankton (Boero et al. 2008).

Even though the population density of ctenophores, salps and medusae decreases during the cold period, these do not disappear completely from the environment because their pulses are often much longer than the other organisms that constitute the zooplankton (Boero et al. 2008). Conversely, the other organisms (no gelatinous) – such as copepods, hyperiid amphipods (e.g. *Themisto gaudichaudii* Guérin, 1825), euphausiids (e.g. *Euphausia lucens* Hansen, 1905), squids (e.g. *Illex*, *Doryteuthis gahi* d'Orbigny, 1835) and the anchovy (*Engraulis anchoita* Hubbs and Marini, 1935) – which support the most of fish stocks in the area (Perez Seijas et al. 1987; Brunetti and Ivanovic 1992; Sanchez and Prenski 1996; Garcia de la Rosa and Sánchez 1997; Brunetti et al. 1998; Brunetti 1999; Sabatini and Alvarez Colombo 2001; Marí and Sánchez 2002; Hansen 2004; Sanchez and Marí 2005; Padovani et al. 2012), decrease significantly in late fall and winter.

Our finding showed that the total proportion of stomachs with gelatinous organisms, as well as the proportion per discriminate gelatinous item was higher in the cold period than in the warm period. Conversely, the proportion of stomachs with no gelatinous prey was significantly lower during the cold period. Although the percent of stomachs (11.8%) with gelatinous prey was the highest during the cold period, we should not assume that it is a consequence of the greater abundance of gelatinous zooplankton during this period. Probably, it is due to the seasonal decline in the non-gelatinous preys that typically constitute the diets of these fish during warm periods. In this context, we assume that many fish use the gelatinous organisms as survival food when their favoured prey items are scarce (Kashkina 1986; Mianzan et al. 1996, 1997, 2001).

Eight areas of consumption (G1-G8) were determined in Argentina and Uruguay continental shelves. Almost all were coincident with some frontal zones of the Argentina Sea (see Mianzan and Acha 2008; Diaz Briz et al. 2017). These frontal areas play a key role in

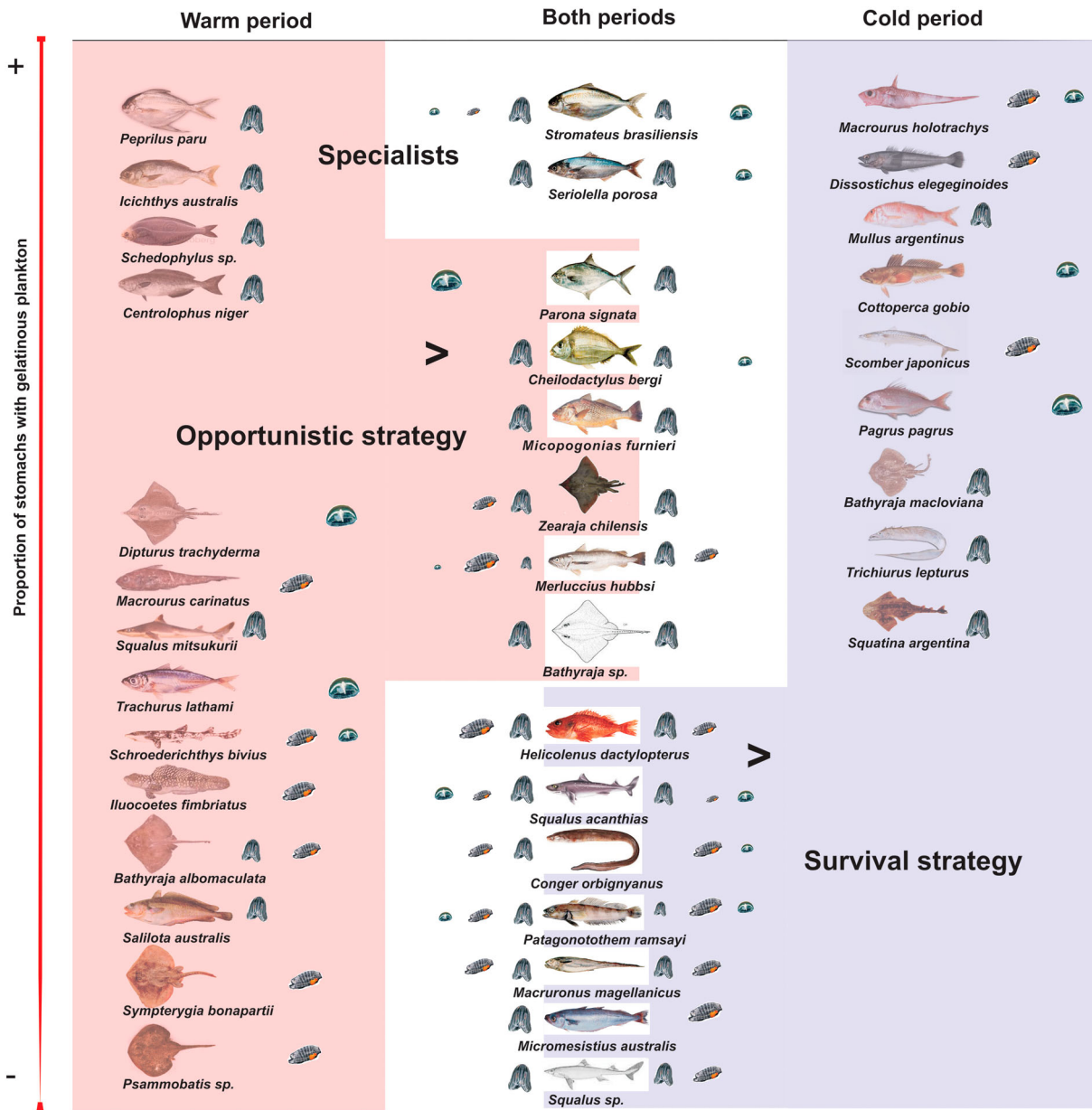
the trophic interactions between gelatinous organisms and fish. They provide the ideal environment favouring concentration of both prey and predators. Also, ctenophores, salps and medusae are very abundant and present all year long in these frontal zones (Mianzan and Guerrero 2000; Costello and Mianzan 2003; Mianzan and Acha 2008). In these areas, nine fish species (*S. acanthias*, *S. brasiliensis*, *S. porosa*, *H. lahillei*, *Macrourus holotrachys* Günther, 1878, *P. ramsayi*, *M. hubbsi*, *M. magellanicus* and *Schroederichthys bivius* (Müller and Henle 1838)) were the ones that contributed the most to the consumption of gelatinous plankton.

Of those species, some species consumed gelatinous zooplankton only during the cold or warm periods and other species consumed during both periods. This seasonal and spatial variation of gelatinous consumption by fish would be a consequence of prey availability during each period.

Several strategies were utilized by fish species preying on gelatinous organisms, including basic survival, opportunism, and food specialization (see Haedrich 1967; Fitch and Brownell 1971; Macpherson 1983; Kashkina 1986; Angelescu 1982a; Harbison 1993; Mianzan et al. 1996, 1997, 2001; Cardona et al. 2012; Marques et al. 2016; Diaz Briz et al. 2017 among other and Figure 4).

Those species that consume gelatinous organisms only during the cold period as well as those that consume these organisms throughout the year although mostly in the cold period when the energetically preferred food is absent they could consume them as a survival food strategy (see Angelescu 1982b; Kashkina 1986; Harbison 1993; Mianzan et al. 1996, 1997, 2001, Table III and Figures 3 and 4). In the first group stand out *Bathyraja macloviana* (Norman, 1937), *Cottoperca gobio* (Günther, 1861), *Dissostichus eleginoides* Smitt, 1898, *M. holotrachys*, *Mullus argentinae* Hubbs and Marini, 1933, *Scomber japonicas* Houttuyn, 1782, *Pagrus pagrus* (Linnaeus, 1758), *Squatina argentina* Marini, 1930 and *Trichiurus lepturus* Linnaeus, 1758. During the warm season these fish species prey on a wide range of non-gelatinous items but not over gelatinous (see Cousseau and Perrotta 2000).

The species of the second group such as *Conger orbignyana* Valenciennes, 1837, *H. lahillei*, *P. ramsayi*, *M. magellanicus*, *Micromesistius australis* Norman, 1937, *S. acanthias* and *Squalus* sp. increases the consumption of gelatinous during the cold period, but gelatinous plankton are part of the diet all year long. The best example of this strategy is represented by the diet of *S. acanthias*. Although this species consumes gelatinous organisms in both periods of the



**Figure 4.** Food strategy (Survival, Opportunistic and specialists) proposed in this study.

year, the consumption is most common during the cold period, since availability of their main prey – such as squid, Argentina hake and anchovy – decreases significantly during this period (García de la Rosa and Sánchez 1997; Cousseau and Perrotta 2000). Therefore, all of the survival strategist species, in the absence of their main food, would consume gelatinous organisms that remain available during unfavourable cold periods.

Contrary, the species that only consume during the warm period and those which consume throughout the year but they do primarily during the warm period could consume as opportunistic strategy (see Cardona et al. 2012; Marques et al. 2016; Diaz Briz et al. 2017,

Table III and Figures 3 and 4). The first group consists of: *Bathyraja albomaculata* (Norman, 1937), *Dipturus trachyderma* (Krefft and Stehmann, 1975), *Ilucoetes fimbriatus* Jenyns, 1842, *Macrourus carinatus* (Günther, 1878), *Psammobatis sp.*, *Salilota australis*, *S. bivius*, *Squalus mitsukurii* Jordan and Snyder, 1903, *Sympterygia bonapartii* Müller and Henle, 1841 and *Trachurus lathami*. Species in the second group were: *Bathyraja sp.*, *M. hubbsi*, *Micropogonias furnieri* (Desmarest, 1823), *Nemadactylus bergi* Norman, 1937, *Parona signata* (Jenyns, 1841) and *Zearaja chilensis* (Guichenot, 1848). During the warm period, all of these fish species take advantage of high ctenophores, salps and medusae densities in the area (see Mianzan and

Guerrero 2000; Alvarez Colombo et al. 2003; Costello and Mianzan 2003).

Finally, the species of fish such as *S. brasiliensis*, *S. porosa*, *Centrolophus niger* (Gmelin, 1789), *Icichthys australis* (Haedrich, 1966), *Peprilus paru* (Linnaeus, 1758) and *Schedophilus* sp., cannot be adequately described as *survival* or *opportunity* strategists because these fish, commonly known as *jellyfish eaters*, feed exclusively on gelatinous organisms regardless of the season or location. Therefore, they are *specialists* (see Haedrich 1967; Fitch and Brownell 1971; Macpherson 1983; Harbison 1993; Diaz Briz et al. 2017, Table III and Figures 3 and 4). For example, *S. brasiliensis*, consistently had high proportions of stomachs with gelatinous organisms in the warm period (97%) when this fish species reaches its maximum abundance on the continental shelf (spawning season), as well as in the cold period (100%) when their abundance decreases markedly in the area due to their migration to deeper waters of the continental shelf (Fitch and Brownell 1971)

The three gelatinous items considered in this study constitute an important part of the diet of many fish. Ctenophores are the most frequent prey. These results are consistent with those of several other studies reporting that these gelatinous organisms are the most frequently consumed item by these fish (Arai 1988; Mianzan et al. 1996; Arai et al. 2003; Diaz Briz et al. 2017). Salps are less common than ctenophores but they are an important item for several fish (Mianzan et al. 1996, 1997, 2001; Daponte et al. 2011; Diaz Briz et al. 2017). Finally, the medusae should be analysed individually. Our results indicate that they had the lowest number of predators and were the less frequently consumed gelatinous group. However, this fact may be due to an underestimation of these organisms during the sampling. Most of the works that reported consumption of medusae by fish cited mainly the scyphomedusae as prey-items (see Arai 1988, 2005; Ates 1988; Purcell and Arai 2001). These large medusae, with thick mesoglea, strong oral arms and rhopalium (balance organ situated in the margin of the bell), resist digestion and are relatively easy to identify in the gut contents of predators. Nevertheless, small-sized hydromedusae are easily digestible and difficult to detect in gut contents of fish. These medusae do not have large structures for macroscopic identification; therefore, they are less likely to be detected in fish gut contents. Arai (1988) suggested that a possible solution to this dilemma would be to make a squash or crushed preparation of the gelatinous mucus present in the fresh gut contents of a fish in

order to evaluate the presence of nematocysts (structures characteristic of medusae that resist digestion). Although this approach might permit identification of higher medusa taxonomic levels in fish guts, it is unlikely to identify individual medusa species due to the widespread occurrence of similar nematocysts between a numbers of hydromedusa species. However, by combining the type of nematocyst present in the stomachs of fish with the diversity, abundance and cnidae of hydromedusae in certain areas, we could infer which hydromedusae species could be consumed. Thus, Diaz Briz et al. 2015 detected nematocyst of hydromedusae in gut contents of *S. brasiliensis*, a fish known to consume ctenophores only.

Another important factor to be considered is hydromedusae seasonality. Unlike scyphomedusae that often survive for long periods in the water column (from months to over a year, see Mianzan and Cornelius 1999), hydromedusae typically have a short life and a marked seasonal regime characterized by high abundances during the warm period (Genzano, Mianzan, and Bouillon 2008). This group tends to disappear from the water column for long periods of time, being represented in their benthic or resistance forms (Genzano, Mianzan, Diaz-Briz, et al. 2008; Jaubet and Genzano 2011). Thus, predation on hydromedusae may be restricted to a short period of time during the year.

Future studies about life cycles, seasonality and distribution of hydromedusa populations as well as traditional analysis of fish stomach contents, stable isotopes and fat acids should be implemented to achieve a better understanding of the role that gelatinous organisms have in local pelagic food webs.

## 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 Laura Carlino for her help on the English of the early version. Also, Diego Giberto (INIDEP-CONICET) for providing a critical review on the early 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 [grant number PIP 2012-0152]; Universidad Nacional de Mar del Plata [grant number EXA 734/15, UNMdP]. LDB is supported by CONICET fellowship. This is INIDEP contribution No. 2133.



## References

- Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J. 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. *Journal of Marine Systems*. 44:83–105. doi:10.1016/j.jmarsys.2003.09.005
- Álvarez Colombo G, Mianzan HW, Madirolas A. 2003. Acoustic characterization of gelatinous plankton aggregations: four case studies from the Argentine continental shelf. *ICES Journal of Marine Science*. 60:650–657. doi:10.1016/S1054-3139(03)00051-1
- Angelescu V. 1982a. Ecología trófica de la merluza común del Mar Argentino (Merlucciidae, *Merluccius hubbsi*). In: Angelescu V, editor. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales. La estructura y las evaluaciones de los efectivos en su área de distribución. Series Contribución del Instituto Nacional de Investigación y Desarrollo Pesquero. Parte II. Mar del Plata: INIDEP; p. 561–205.
- Angelescu V. 1982b. Ecología trófica de la caballa Del Mar Argentino (Scombridae, *Scomber japonicus marplatensis*). *Revista de Investigación y Desarrollo Pesquero* (INIDEP). 1 (1):5–44.
- Arai MN. 1988. Interactions of fish and pelagic coelenterates. *Canadian Journal of Zoology*. 66:1913–1927. doi:10.1139/z88-280
- Arai MN. 1997. Coelenterates in pelagic foodwebs. *Proceedings of the International Conference on Coelenterate Biology*. 1995:1–9.
- Arai MN. 2005. Predation on pelagic coelenterates: a review. *Journal of the Marine Biological Association of the United Kingdom*. 85:523–536. doi:10.1017/S0025315405011458
- Arai MN, Welch DW, Dumsmuir AL, Jacobs MC, Ladouceur AR. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. *Canadian Journal of Fisheries and Aquatic Sciences*. 60:825–829. doi:10.1139/f03-071
- Arkhipkin AI, Laptikhovskiy VV. 2013. From gelatinous to muscle food chain: rock cod *Patagonotothen ramsayi* recycles coelenterate and tunicate resources on the Patagonian Shelf. *Journal of Fish Biology*. 83:1210–1220. doi:10.1111/jfb.12217
- Ates RML. 1988. Medusivorous fishes, a review. *Zoologische Mededelingen*. 62:29–42.
- Balech E, Ehrlich MD. 2008. Esquema biogeográfico del Mar Argentino. *Revista de Investigación y Desarrollo Pesquero*. 19:45–75.
- Belleggia M, Figueroa DE, Sánchez F, Bremec CS. 2012. Longterm changes in the spiny dogfish (*Squalus acanthias*) trophic role in the southwestern Atlantic. *Hydrobiologia*. 684:57–67. doi:10.1007/s10750-011-0967-y
- Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S. 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*. 356:299–310. doi:10.3354/meps07368
- Brunetti NE. 1999. Population structure and growth of *Illex argentinus*. Avances en métodos y tecnología aplicados a la investigación pesquera. Seminario final Proyecto INIDEP-JICA sobre Evaluación monitoreo de recursos pesqueros 1994–1999. Mar del Plata, INIDEP: 249 pages.
- Brunetti NE, Ivanovic ML. 1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the southwest Atlantic. *ICES Journal of Marine Science*. 49:175–183. doi:10.1093/icesjms/49.2.175
- Brunetti NE, Ivanovic M, Rossi G, Elena B, Pineda S. 1998. Fishery biology and life history of *Illex argentinus*. In: Okutani T, editor. Contributed paper to international symposium on large pelagic squid. Tokyo: Japan Marine Fishery Resources Research Center; p. 269.
- Cardona L, Álvarez de Quevedo I, Borrell A, Aguilar A. 2012. Massive consumption of gelatinous plankton by Mediterranean apex predators. *PLoS One* 7(3):e31329. 14 pages. doi:10.1371/journal.pone.0031329
- Clarke KR, Somerfield PJ, Gorley RN. 2008. Testing null hypotheses in exploratory community analyses: similarity profiles and biota-environmental linkage. *Journal of Experimental Marine Biology*. 366:56–69. doi:10.1016/j.jembe.2008.07.009
- Clarke KR, Warwick RM. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd ed. Plymouth: Plymouth Marine Laboratory. 90 pages.
- Condon RH, Graham WM, Duarte CM, Pitt KA, Lucas CH, Haddock SHD, Sutherland KR, Robinson KL, Dawson MN, Decker MB, et al. 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience*. 62:160–169. doi:10.1525/bio.2012.62.2.9
- Costello JH, Mianzan HW. 2003. Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? *Journal of Plankton Research*. 25:455–459. doi:10.1093/plankt/25.4.455
- Cousseau MB, Perrota RG. 2000. Peces marinos de Argentina: biología, distribución y pesca. Mar del Plata: INIDEP.
- Daponte MC, Calcagno JA, Acevedo-Luque MJJ, Martos P, Machinandriarena L, Esnal GB. 2011. Composition, density, and biomass of Salpidae and Chaetognatha in the southwestern Atlantic Ocean (34.5°S–39°S). *Bulletin of Marine Science*. 87:437–461. doi:10.5343/bms.2010.1014
- Diaz Briz LM, Martorelli SR, Genzano GN. 2015. The parasite *Monascus filiformis* (Trematoda, Digenea, Fellodistomidae) on *Stromateus brasiliensis* (Pisces, Perciformes, Stromateidae): possible routes of transmission involving jellyfish. *Journal of the Marine Biological Association of the United Kingdom*. 96:1483–1489. doi:10.1017/S0025315415001757
- Diaz Briz LM, Sánchez F, Marí N, Mianzan HW, Genzano GN. 2017. Gelatinous zooplankton (ctenophores, salps and medusae): an important food resource of fishes in temperate SW Atlantic Ocean. *Marine Biology Research*. 1–15.
- Doyle TK, De Haas H, Cotton D, Dorschel B, Cummins V, Houghton JDR, Davenport J, Hays GC. 2008. Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research*. 30:963–968. doi:10.1093/plankt/fbn052
- Fitch JE, Brownell RL. 1971. Food habits of the franciscana *Pontoporia blainvillei* (Cetacea: Platanistidae) from South America. *Bulletin of Marine science*. 21:626–635.
- García de la Rosa SB, Sánchez F. 1997. Alimentación de *Squalus acanthias* y predación sobre *Merluccius hubbsi* en el Mar Argentino entre 34° 47'–47°S. *Revista de Investigación y Desarrollo Pesquero*. 11:119–133.
- Genzano GN, Mianzan HW, Bouillon J. 2008. Hydromedusae (Cnidaria: Hydrozoa) from the temperate Southwestern Atlantic Ocean: a review. *Zootaxa*. 1750:1–18.
- Genzano GN, Mianzan HW, Diaz-Briz L, Rodríguez CS. 2008. On the occurrence of *Obelia* medusa blooms and empirical



- evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. Latin American Journal of Aquatic Research. 36:301–307. doi:10.3856/vol36-issue2-fulltext-11
- Graham WM, Pagés F, Hamner WM. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia. 451:199–212. doi:10.1023/A:1011876004427
- Guerrero RA, Piola AR. 1997. Masas de agua en la Plataforma Continental. In: Boschi E, editor. El Mar Argentino y sus Recursos Pesqueros. Volume 1. Antecedentes Históricos de las Explotaciones en el Mar y las Características Ambientales. Mar del Plata: Publicaciones Especiales INIDEP; p. 107–118.
- Haedrich RL. 1967. The stromateoid fishes: systematics and a classification. Bulletin of the Museum of Comparative Zoology. 135:31–139.
- Hansen JE. 2004. Anchoíta (*Engraulis anchoíta*). In: Sánchez RP, Bezzi SI, editor. El mar Argentino y sus recursos pesqueros. Tomo 4. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación. Mar del Plata: Publicaciones Especiales INIDEP; p. 10–115.
- Harbison GR. 1993. The potential of fishes for the control of gelatinous zooplankton. ICES CM. 1993/L:74.
- Ivanov V, Kamakin AM, Ushivtzev VB, Shiganova TA, Zhukova, O, Aladin N, Wilson SI, Harbison GR, Dumont HJ. 2000. Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). Biological Invasions. 2:255–258. doi:10.1023/A:1010098624728
- Jaubet ML, Genzano GN. 2011. Seasonality and reproductive periods of the hydroid *Clytia gracilis* in temperate littoral ecosystems. Is asexual reproduction the prime mechanism in maintaining populations? Marine Biology Research. 7:804–811. doi:10.1080/17451000.2011.578650
- Kashkina AA. 1986. Feeding of fishes on salps (Tunicata, Thaliacea). Journal of Ichthyology. 26:57–64.
- Link JS, Ford MD. 2006. Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Marine Ecology Progress Series. 320:153–59. doi:10.3354/meps320153
- Macpherson E. 1983. Ecología Trófica de Peces en las Costas de Namibia. 1. Hábitos Alimentarios. Barcelona: España. 30 pages.
- Marí NR, Sánchez F. 2002. Espectros tróficos específicos de varias especies de peces demersales de la región austral y sus variaciones anuales entre 1994 y 2000. INIDEP, Informe Técnico. 88:1–19.
- Marques R, Bouvier C, Darnaude AM, Molinero JC, Przybyla C, Soriano S, Tomasini JA, Bonnet D. 2016. Jellyfish as an alternative source of food for opportunistic fishes. Journal of Experimental Marine Biology and Ecology. 485:1–7. doi:10.1016/j.jembe.2016.08.008
- Mianzan HW, Acha M. 2008. Procesos ecológicos en el Mar Patagónico. In: Campagna C, editor. Estado de Conservación del Mar Patagónico y Áreas de Influencia. Puerto Madryn, Argentina: Fundación Patagonia Natural y otros, p. 21–62. Scientia Marina 64(S1):215–224.
- Mianzan HW, Cornelius PFS. 1999. Cubomedusae and Scyphomedusae. In: Boltovskoy D, editor. South Atlantic Zooplankton. Leiden: Backhuys; p. 513–559.
- Mianzan HW, Guerrero R. 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the South-western Atlantic Ocean. Scientia Marina. 64(S1):215–224. doi:10.3989/scimar.2000.64s1215
- Mianzan HW, Marí N, Prenski B, Sanchez F. 1996. Fish predation on neritic ctenophores from the Argentine continental shelf: a neglected food resource? Fisheries Research. 27:69–79. doi:10.1016/0165-7836(95)00459-9
- Mianzan HW, Pájaro M, Álvarez Colombo G, Madirolas A. 2001. Feeding on survival food: gelatinous plankton as a source of food for anchovies. Hydrobiologia. 451:45–53. doi:10.1023/A:1011836022232
- Mianzan HW, Pájaro M, Marchinandiarena L, Cremonte F. 1997. Salps: possible vectors of toxic dinoflagellates? Fisheries Research. 29:193–197. doi:10.1016/S0165-7836(96)00526-7
- Mianzan HW, Purcell JE, Frost JR. 2012. Preface: jellyfish blooms: interactions with humans and fisheries. Hydrobiologia. 690:1–2. doi:10.1007/s10750-012-1050-z
- Mianzan HW, Ramirez F, Costello J, Chiaverano L. 2005. Un mar de gelatina? Ciencia Hoy. 15:48–55.
- Mianzan HW, Sabatini M. 1985. Estudio preliminar sobre distribución y abundancia de *Mnemiopsis maccradyi* en el estuario de Bahía Blanca, Argentina (Ctenophora). Spheniscus. 1:53–68.
- Mianzan HW, Sorarrain D, Burnett J, Lutz L. 2000. Mucocutaneous junctional and flexural paresthesias caused by the holoplanktonic trachymedusae *Liriope tetraphylla*. Dermatology. 201:46–48. doi:10.1159/000018429
- Mills CE. 1995. Medusae, shiphonophores and ctenophores as planktivorous predators in changing global ecosystems. ICES Journal of Marine Science. 52:575–581. doi:10.1016/1054-3139(95)80072-7
- Padovani LN, Viñas MD, Sánchez F, Mianzan HW. 2012. Amphipods supported food web: *Themisto gaudichaudii*, a key food resource for fishes in southern Patagonian Shelf. Journal of Sea Research. 67:85–90. doi:10.1016/j.seares.2011.10.007
- Pauly D, Graham W, Libralato S, Morissette L, Palomares MLD. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia. 616:67–85. doi:10.1007/s10750-008-9583-x
- Pérez Seijas GM, Ramírez FC, Viñas MD. 1987. Variaciones de la abundancia numérica y biomasa del zooplancton de red en el Golfo San Jorge (año 1985). Revista de Investigación y Desarrollo Pesquero. 7:5–20.
- Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia. 451:27–44. doi:10.1023/A:1011883905394
- Sabatini ME, Álvarez Colombo GL. 2001. Seasonal pattern of zooplankton biomass in the Argentinian shelf off southern Patagonia (45°–55°S). Scientia Marina. 65:21–31. doi:10.3989/scimar.2001.65n121
- Sabatini M, Reta R, Matano R. 2004. Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer. Continental Shelf Research. 24:1359–1373. doi:10.1016/j.csr.2004.03.014
- Sánchez F, Marí NR. 2005. Interacciones tróficas entre especies de peces demersales en la región austral entre 45°S y 54°S. Revista de Investigación y Desarrollo Pesquero. 19:1–9.
- Sánchez F, Prenski LB. 1996. Ecología trófica de peces demersales en el Golfo San Jorge. Revista de Investigación y Desarrollo Pesquero. 10:57–71.
- Zar JH. 1999. Biostatistical Analysis. New Jersey: Prentice Hall. 663 pages.