

ORIGINAL ARTICLE

Biodiversity and distribution patterns of planktonic cnidarians in San Matías Gulf, Patagonia, Argentina

Elena Guerrero^{1,2}, Josep-María Gili¹, Carolina Rodríguez^{3,4}, Enilma M. Araujo^{3,5}, Antonio Canepa¹, Albert Calbet¹, Gabriel Genzano^{3,4}, Hermes W. Mianzan^{3,4,6} & Raúl A. González²

1 Institut de Ciències del Mar, CSIC, Barcelona, Spain

2 Instituto de Biología Marina y Pesquera Almirante Storni (IBMPAS), Universidad Nacional del Comahue, San Antonio Oeste, Argentina

3 Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – UNMdP, Mar del Plata, Argentina

4 Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

5 Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brasília, DF, Brazil

6 Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina

Keywords

Hydrography; Hydromedusae; *Pyrostephos vanhoeffeni*; Siphonophorae; Southwestern Atlantic Ocean.

Correspondence

Elena Guerrero, Institut de Ciències del Mar, CSIC, Pg. Marítim de la Barceloneta, 37-49, Barcelona 08003, Spain.

E-mail: eguerrero@icm.csic.es

Accepted: 2 October 2012

doi: 10.1111/maec.12027

Abstract

The special location (40–42°S in the Southwestern Atlantic Ocean) and the hydrodynamic regime (limited water exchange with open ocean) in San Matías Gulf (Argentina) seem to produce a particular fauna of planktonic cnidarians whose their abundances are mainly shaped by the Gulf circulation. Four oceanographic cruises, covering 93 stations in three different seasons during 2007 and 2008 were carried out to quantify species richness and abundance, as well as to analyse the distribution of these cnidarians. We identified 20 species of hydromedusae and one siphonophore, increasing the total number of hydromedusae for the area to 23. This value is similar to the one found in the abutting Argentine continental shelf (20), but with a different assemblage composition. Hydromedusae abundances found were low, except for a bloom of the *Leptomedusa Obelia* spp. during the cold season. The only siphonophore found in the area, *Pyrostephos vanhoeffeni*, has previously been thought to be endemic to Antarctic and sub-Antarctic waters, this being the first record for temperate waters of the Southwest Atlantic Ocean.

Introduction

Global patterns of biodiversity show that species richness generally increases towards lower latitudes (Gaston 2000), including marine planktonic cnidarians (Macpherson 2002). In the South Atlantic Ocean, species richness of Hydromedusae and Siphonophorae increases from the pole to c. 40°S, but further north shows little variation towards the equator (Macpherson 2002). Genzano *et al.* (2008a) observed a marked decrease in the number of hydromedusan species with increases in latitude in the continental shelf of Argentina and Uruguay (from 33° to 55°S). More locally, there is a positive relationship between cnidarian richness and coastal ecosystems, seasonality and inputs of allochthonous water masses. Gili & Hughes (1995) stated that the number of hydroids species

is higher in shallow coastal waters, probably due to their greater environmental heterogeneity, and the number decreases with depth. Seasonality produces a continuous change in the composition of hydroid and medusa populations, which proliferate or stay as resting stages according to the optimal season of each species (Boero 1984; Boero & Bouillon 1993). As regards inputs of allochthonous water masses, gelatinous zooplankton is particularly susceptible to mesoscale advective processes, which tend to increase their density and diversity (Gili *et al.* 1991; Pagès & Gili 1991).

San Matías Gulf is a coastal ecosystem with a marked seasonality and important intrusions of nutrient rich sub-Antarctic water coming from the adjoining continental shelf (Rivas & Beier 1990; Gagliardini & Rivas 2004; Tonini *et al.* 2006, 2007). However, before this report, only

nine species of planktonic cnidarians have been recorded in the area (Ramírez & Zamponi 1980; Ramírez 1996, 2007; Genzano *et al.* 2008a; C. Rodríguez unpubl. data). This is a low value compared to the at least 20 species cited for adjacent areas (Genzano *et al.* 2008a). Further away, given the three factors cited above, we hypothesize that the planktonic cnidarian richness in the Gulf should be even higher at this latitude (40°–42°) in the adjacent continental shelf. Likewise, we expect not just a positive influence of sub-Antarctic inputs into the Gulf on biodiversity and density, but that the oceanography of the area should shape the distribution of cnidarians as well.

To test this hypothesis we comprehensively sampled San Matías Gulf and adjacent waters in three different seasons over 1 year. We analysed planktonic cnidarians biodiversity as number of species, quantified their abundance, and measured and analysed physical parameters (temperature and salinity). Afterwards, we evaluated relationships between these biological and physical parameters and the hydrography of the area as well as the species composition.

Material and Methods

San Matías Gulf is located on the temperate Atlantic coast of South America, between 40°50′–42°15′S and 63°05′–65°10′W (Fig. 1). It is the second largest gulf in Argentina, covering an area of 19,700 km² (Canessa 1976 in Mazio & Vara 1983), and with maximum depths of over 200 m (Piola & Scasso 1988). Its mouth, which opens to the east onto the Argentine continental shelf, is

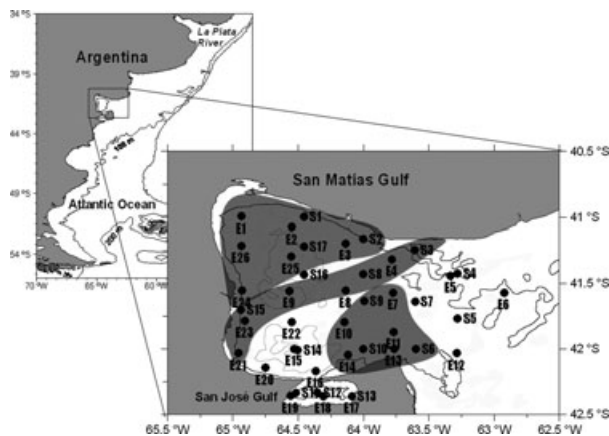


Fig. 1. The geographic location of San Matías Gulf on the Argentine coast and the positions of sampling stations in the study area: S = spring stations; E = stations for the rest of the year. Continuous lines refer to simplified bathymetry: black, 50 m depth; grey, 150 m depth. The shadowed areas correspond to the three sectors (NW, Central, SE) used in statistical analysis to compare the three *a priori* defined sectors.

approximately 100 km wide and has a sill at 70 m depth. Towards the east, the continental shelf is about 80 m deep.

A thermohaline frontal system, situated near 41°50′S, is formed during the austral spring and summer months. This frontal system divides the Gulf into a northwestern sector with warmer and saltier waters, and a southeastern sector with colder and less saline waters with ingress from the Patagonian Coastal Current coming from the south (Gagliardini & Rivas 2004).

The circulation within the Gulf has distinct seasonal variations. During the spring–summer period there is a large and well defined cyclonic gyre in its central area, which limits water exchange between the Gulf and the continental shelf. During the autumn–winter period the Gulf is divided into an anticyclonic gyre in the west coast of the Gulf, intensified by zonal offshore winds, and a poor-defined cyclonic gyre in the rest of the Gulf area. The latter facilitates water exchange between the Gulf and the continental shelf during the cold season. In addition, northerly winds favour upwelling events on the west coast of San Matías Gulf during the cold season (Williams 2004; Tonini *et al.* 2006; Tonini 2010).

We conducted four oceanographic cruises during June 2007, October 2007, February 2008 and June 2008. The four surveys matched three different seasons throughout the year: late austral autumn (both June dates), spring (October), and summer (February). Surveys were conducted under a long-term oceanographical and biological program to provide information for the management of fishery resources carried out by the IBMPAS and the Centro Nacional Patagónico.

The locations of the 26 sampling stations, which covered the whole San Matías–San José gulf area and the nearest external region of influence, were primarily chosen to assess possible relationships between hydrodynamic processes and the distribution of planktonic cnidarians. During the October survey, only 17 stations were sampled due to limited ship availability; those stations were chosen so that all areas were well represented.

At each station, water temperature and conductivity (c. 3 m depth) were measured with a YSI® 556 multi-parameter probe (precision ± 0.15 °C and ± 0.001 mS·cm⁻¹). Salinity was calculated from conductivity and temperature using the probe software ECOWATCH® (YSI Inc., Yellow Springs, OH, USA). Measurements were made at a sampling rate of one scan every 2 s for 1–2 min. Data were processed to achieve sample station averages and standard deviations. The zooplankton sampling methodology (vertical tows) was adopted due to restricted manoeuvrability of the ship. At every station, we sampled the whole water column (from bottom to surface) with a 200- μ m-mesh Hensen net of 39 cm mouth diameter, obtaining only

one sample that integrated the entire water column. Samples were fixed immediately with 4% formalin–seawater solution.

To quantify planktonic hydrozoan abundance and community composition, the volume of water filtered was calculated from the vertical distance (m) covered by the mouth area of the net, assuming 100% filtration efficiency. Hydromedusae and asexual and sexual stages of siphonophorae were separated from the sample, counted, and identified under a stereo-microscope using mainly the following taxonomic references: Kramp (1959), Bouillon (1999), and Totton (1965). Nectophores of the physonect siphonophore were counted and divided by 10 according to Pugh (1984) to approximate the actual number of colonies sampled. Counts of hydromedusae and siphonophores were standardized to number of individuals per 1000 m³ to obtain the abundances. Small juvenile preserved ctenophores were identified, following Mianzan (1999), as belonging to the order Cydippida because of the round body and presence of tentacle sheaths. However, these data are not presented here because they may underestimate true abundances due to the collection and preservation methods used in this study. The lobate ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 also was observed in each survey and manually removed from samples before preservation.

For statistical comparisons the four surveys were fitted into the three seasons by averaging physical and biological data of both Junes (2007 and 2008), thus we have named the three seasons as autumn (2007, 2008), spring and summer. Besides, three different sectors within the Gulf were identified *a priori* taking into account station locations and the main literature describing the oceanography of the area (Piola & Scasso 1988; Gagliardini & Rivas 2004; Tonini 2010). Of the 26 sampling stations, six were established as the most representative of the north-western (NW) sector, five of the south-eastern (SE) sector and five of the Central sector. In the case of the 17 stations carried out in the October 2007 survey, three stations were stated for each of these three sectors (see Fig. 1). Temperature and salinity data fulfilled normality and variance homogeneity requirements. They were compared among sectors and seasons using two-way analysis of variance (ANOVA) with a factorial design. This design allowed us to compare the effects of each factor and also their interaction over the temperature and salinity data. When interactions were significant Bonferroni pair-wise comparisons were conducted. To evaluate differences among sectors and seasons, abundance and richness data were evaluated using generalized linear mixed models (GLMM); the package ‘lme4’ (Bates *et al.* 2011) was used with a Poisson error family and a log link (Bolker *et al.* 2009; Zuur *et al.* 2009). Since determining abundance

involves counting (O’Hara & Kotze 2010), these models allow us to deal with other than normal or Gaussian data distributions. To eliminate the bias due to different sampling units (filtered volume of seawater by the net), we used the filtered volume as an offset inside the model (Penston *et al.* 2008; Zuur *et al.* 2009). Spatial autocorrelation of samples (near stations should be more similar than those far away) was eliminated, allowing stations to vary randomly, *i.e.* using a random intercept and slope for each station (Zuur *et al.* 2009; Bates *et al.* 2011). In addition, relationships between hydromedusae community indices (abundance and richness) and environmental variables (temperature and salinity) were evaluated using generalized additive mixed models (GAMM) applying the ‘gamm’ package (Wood 2006) in a similar way as in GLMM: (i) using Poisson family error distribution, with a log link, (ii) allowing the filtered volume to be an offset of the model, and (iii) eliminating the spatial autocorrelation of the sampling stations (Murase *et al.* 2009). For all models the amount of degrees of freedom for each term was restricted to four (equivalent to a polynomial regression term). In this case, when relationships with temperature were significant, two separate linear (GLMM) regressions were fitted to the data to evaluate the trends within the different ranges of the environmental variable.

Planktonic community structure were compared among season and areas, using the analysis of similarities (ANOSIM) under the ‘vegan’ package (Oksanen *et al.* 2012). Data were previously standardized to account for differences in variability due to high abundance species (Clarke 1993).

All analyses were done using the free-statistical software R, version 2.15.0 (R Development Core Team 2012).

Results

Hydrography

San Matías Gulf sea-surface temperature distributions in autumn were more homogeneous than those in summer and spring (Fig. 2, Table 1). For the three sectors, higher temperatures were recorded during summer, followed by autumn and last by spring (NW: $F_2 = 1537.0$, P -value < 0.01 ; Central: $F_2 = 1719.9$, P -value < 0.01 ; SE: $F_2 = 193.2$, P -value < 0.01). Only in the NW sector were autumn and spring temperatures not significantly different. For all seasons the SE sector was significantly colder than the NW one (autumn: $F_2 = 6.3$, P -value < 0.01 ; spring: $F_2 = 66.8$, P -value < 0.01 ; summer: $F_2 = 27.9$, P -value < 0.01) (Table 1). The sea-surface salinity distribution showed a consistent pattern for all sampling seasons (no significant differences among seasons), being constantly saltier in the NW sector and less saline in the SE one (autumn: $F_2 = 19.5$, P -value

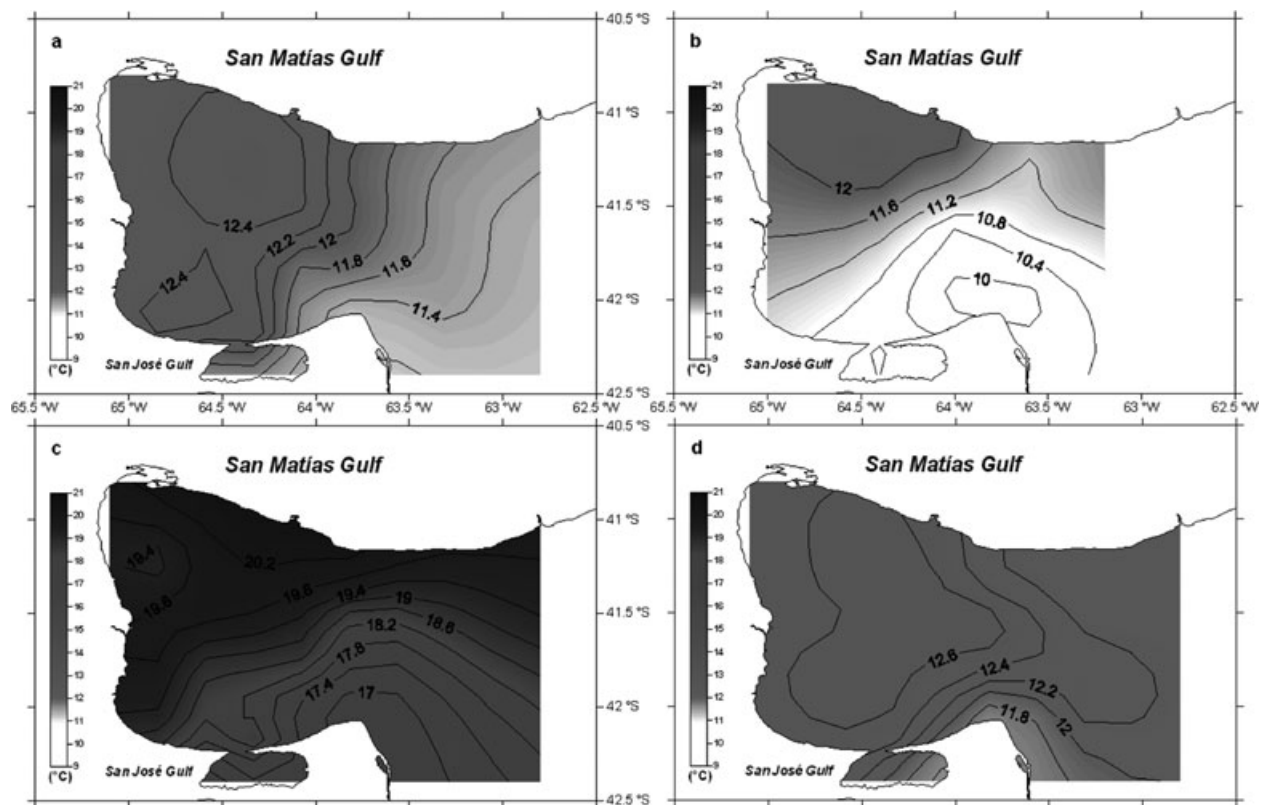


Fig. 2. Surface temperature distribution in San Matías Gulf throughout the annual cycle; (a) autumn 2007, (b) spring, (c) summer, (d) autumn 2008. Contiguous isothermal lines in (a) and (d) differ by 0.2 °C; in (b) and (c) they differ by 0.4 °C.

Table 1. Temperature and salinity data (mean \pm SD) for the three seasons and sectors analysed in San Matías Gulf.

	Autumn		Spring		Summer	
	T (°C)	S	T (°C)	S	T (°C)	S
NW	12.51 \pm 0.41	34.23 \pm 0.09	12.20 \pm 0.16	34.37 \pm 0.05	19.95 \pm 0.48	34.24 \pm 0.06
Central	12.37 \pm 0.26	34.20 \pm 0.06	11.37 \pm 0.22	34.34 \pm 0.03	19.82 \pm 0.23	34.21 \pm 0.13
SE	12.01 \pm 0.50	33.98 \pm 0.13	9.98 \pm 0.29	33.87 \pm 0.13	17.56 \pm 0.87	34.04 \pm 0.09

<0.01; spring: $F_2 = 35.1$, P -value <0.01; summer: $F_2 = 7.4$, P -value <0.01). No differences were found between NW and Central sectors.

Species richness composition

We identified 21 planktonic cnidarian species, 20 hydromedusae and one siphonophore (Table 2). Of the hydromedusa species, nine belonged to the Anthomedusae subclass and 11 to the Leptomedusae. The siphonophore belonged to the order Physonectae. It was found throughout all sampled seasons, although it never occurred in the San José Gulf. Species richness was significantly higher in spring (Z -value = 6.6, P -value <0.01) when 16 species

were found, contrasting with the four species found in autumn 2008. In total, 19 species were found in the San Matías Gulf area, and at least seven [*Bougainvillia muscus* (Allman, 1863); *Turritopsis nutricula* McCrady, 1857; *Proboscoidactyla mutabilis*; *Euphysa aurata* Forbes, 1848; *Cosmetirella davisi* (Browne, 1902); and *Clytia* and *Obelia* genera] in the San José Gulf. Only *B. muscus* appeared exclusively in the San José Gulf. No differences were found among sectors.

Abundance

Hydromedusae numerically dominated the catches, representing between 75.5% and 99.4% of the total abundance

Table 2. Planktonic cnidarian species collected in San Matías Gulf (2007–2008).

Species	June 2007					October 2007					February 2008					June 2008				
	MN	SD	n	D	F	MN	SD	n	D	F	MN	SD	n	D	F	MN	SD	n	D	F
Hydromedusae	4259	11,789	2990	99.40	88.0	1760	1503	1655	75.51	88.2	822	1224	634	98.72	92.3	130	231	91	83.33	48.0
Unidentifiable	–	–	59	1.96	–	–	–	107	4.86	–	–	–	264	41.03	–	–	–	24	21.74	–
<i>Bougainvillia muscus</i>	–	–	–	–	–	27	79	16	0.75	11.8	–	–	–	–	–	–	–	–	–	–
<i>Turritopsis nutricula</i>	18	49	18	0.60	16.0	–	–	–	–	–	7	33	4	0.64	3.8	15	52	8	7.25	8.0
<i>Hydractinia cf. areolata</i>	–	–	–	–	–	7	21	16	0.75	11.8	11	41	12	1.92	7.7	–	–	–	–	–
<i>Proboscoidactyla mutabilis</i>	155	175	177	5.88	60.0	514	616	541	24.67	70.6	54	92	70	10.90	34.6	63	175	40	36.23	24.0
<i>Halitiara formosa</i>	5	25	5	0.15	4.0	–	–	–	–	–	19	72	12	1.92	7.7	–	–	–	–	–
<i>Corymorpha januarii</i>	–	–	–	–	–	–	–	–	–	–	5	18	8	1.28	7.7	–	–	–	–	–
<i>Sarsia</i> sp.	–	–	–	–	–	28	80	25	1.12	11.8	38	68	29	4.49	26.9	–	–	–	–	–
<i>Euphysa aurata</i>	–	–	–	–	–	224	367	213	9.72	52.9	10	52	4	0.64	3.8	–	–	–	–	–
<i>Hybocodon chilensis</i>	20	74	14	0.45	8.0	35	69	41	1.87	23.5	–	–	–	–	–	–	–	–	–	–
<i>Aequorea coerulescens</i>	–	–	–	–	–	26	77	41	1.87	17.6	–	–	–	–	–	–	–	–	–	–
<i>Laodicea undulata</i>	4	19	5	0.15	4.0	98	229	74	3.36	35.3	166	555	119	18.59	19.2	–	–	–	–	–
<i>Eucheilota ventricularis</i> ^a	4	19	5	0.15	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cosmetrella davisi</i>	–	–	–	–	–	66	105	57	2.62	35.3	–	–	–	–	–	–	–	–	–	–
<i>Halopsis ocellata</i>	–	–	–	–	–	8	32	16	0.75	5.9	–	–	–	–	–	–	–	–	–	–
<i>Mitrocomella brownei</i>	13	45	14	0.45	8.0	7	30	8	0.37	5.9	71	206	58	8.97	23.1	–	–	–	–	–
<i>Mitrocomella frigida</i>	–	–	–	–	–	43	178	57	2.69	5.9	–	–	–	–	–	–	–	–	–	–
<i>Clytia</i> sp. (young specimens)	7	27	9	0.30	8.0	60	205	33	1.50	11.8	–	–	–	–	–	–	–	–	–	–
<i>Clytia gracilis</i> ^a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	11	4	3.62	4.0
<i>Clytia loma</i>	5	24	5	0.15	4.0	27	63	41	1.87	17.6	26	88	16	2.56	11.5	–	–	–	–	–
<i>Clytia simplex</i>	–	–	–	–	–	10	29	16	0.75	11.8	–	–	–	–	–	–	–	–	–	–
<i>Obelia</i> spp.	3973	11,772	2682	89.14	36.0	458	922	352	16.07	70.6	63	136	37	5.77	26.9	29	115	16	14.49	8.0
Siphonophorae	16	38	18	0.60	16.0	310	616	537	24.49	23.5	5	16	8	1.28	7.7	14	36	18	16.67	16.0
<i>Pyrosophos vanthoeffeni</i>	16	38	18	0.60	16.0	310	616	537	24.49	23.5	5	16	8	1.28	7.7	14	36	18	16.67	16.0
Total	4275	11,804	3008	100	88.0	2069	1595	2192	100	88.2	827	1222	642	100	92.3	143	237	109	100	52.0

MN = mean abundance (ind. 1000 m⁻³); SD = standard deviation; n = total abundance (ind. 1000 m⁻³); D = dominance (total abundance percentage of one species versus the entire species in total); F = frequency (percentage of samples in which the species occurs).

^aOnly a single specimen was found.

(spring and autumn 2007, respectively). Their abundance peaked in autumn 2007 ($4259 \pm 11,789$ ind. 1000 m^{-3}) and gradually decreased until autumn 2008 (130 ± 231 ind. 1000 m^{-3} ; Table 2, Fig. 3). This peak was mainly due to the Leptomedusa *Obelia* spp., which reached maximum abundances of $43,530$ ind. 1000 m^{-3} , mostly immature individuals recently liberated from the polyp stage.

The most frequently occurring species were *P. mutabilis* and *Obelia* spp., with frequencies of occurrence of 24–71% and 8–71%, respectively. These were the only species present in every survey; the other species occurred mainly in either one or two surveys (see Table 2). Only one specimen each was found of the species *Eucheilota ventricularis* McCrady, 1859 and *Clytia gracilis* (M. Sars, 1850).

Peak densities of the three most abundant species occurred for *Obelia* spp. in autumn 2007 ($3973 \pm 11,772$ ind. 1000 m^{-3}), *P. mutabilis* (Browne, 1902) in spring (514 ± 616 ind. 1000 m^{-3}) and *Laodicea undulata* (Forbes & Goodsir, 1851) in summer (166 ± 555 ind. 1000 m^{-3} ; see Table 2, Figs 4 and 5).

All colony components of the physonect siphonophore *Pyrostephos vanhoeffeni* Moser 1925 were found. Only 'adult-like' nectophores were used for calculating abundance values, which reached the highest mean abundance

(310 ± 616 colonies 1000 m^{-3}) and occurrence frequency (24%) in spring. Most of the gastrozooids caught during this season contained prey (e.g. fish eggs and larvae, copepods, and euphausiids) with one or two items per gastrozoid.

Spatio-temporal distributions and relationships with physical variables

As seen in Fig. 3, *Obelia* bloom abundances greatly influenced the total hydromedusa abundance; therefore, we decided to analyse the total hydromedusa abundance without taking into account *Obelia* spp. densities (Penton *et al.* 2008). The highest density of hydromedusae was found in spring (Z-value = 3.0, P-value <0.01), followed by summer and autumn (Z-value = -14.8, P-value <0.01). Only during summer were there significant differences among the three sectors, with the highest abundance in the SE (1204 ± 653 ind. 1000 m^{-3} ; Z-value = 9.6, P-value <0.01) and the lowest abundance in the NW (86 ± 41 ind. 1000 m^{-3} ; Z-value = 56.6, P-value <0.01). The percentage of explained hydromedusa abundance deviance was 63%.

Obelia spp. was more abundant in the Central sector in autumn (4234 ± 4194 ind. 1000 m^{-3}) and spring (1343 ± 1282 ind. 1000 m^{-3}) than in the other areas; although the differences were not significant. This image is mainly promoted by the bloom that occurred in the west coast stations (see Fig. 4). This species hardly occurred in the SE sector, ranging from 0 in autumn to 41 ± 41 ind. 1000 m^{-3} in spring (Z-value = -2.1, P-value <0.05). Likewise, *Obelia* spp. was less abundant during summer than during the rest of the year (Z-value = -96.3, P-value <0.01). The percentage of explained deviance for *Obelia* spp. abundance was 69%.

Pyrostephos vanhoeffeni appeared only in the NW sector during spring and in the Central and SE sectors during autumn. Maximum abundance occurred during spring (1366 ± 351 colonies 1000 m^{-3}) and the species barely was present in summer (9 ± 9 ind. 1000 m^{-3}) only present in two distant stations (Fig. 4).

Hydromedusa abundance (without *Obelia*) showed a negative trend (non-significant) with temperature and a slight positive trend (non-significant) with salinity. In the same way, richness was observed to be inversely correlated with temperature ($F_2 = 6.51$, P-value <0.01) but no appreciable relationship with salinity. As the temperature values measured were clearly differentiated into two ranges (from 9.82 to 12.74 °C for spring and autumn and from 16.49 to 20.30 °C for summer) they were analysed separately. With low explained deviance (12% and 2% for the colder and warmer temperature ranges, respectively) GLMMs showed that hydromedusa richness

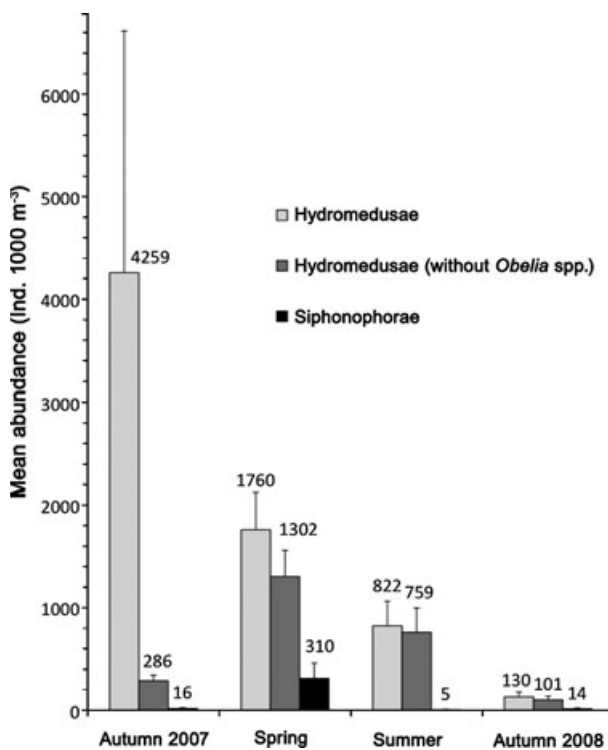


Fig. 3. Variation in the density (mean \pm SD) of planktonic cnidarians in the study area (2007–2008).

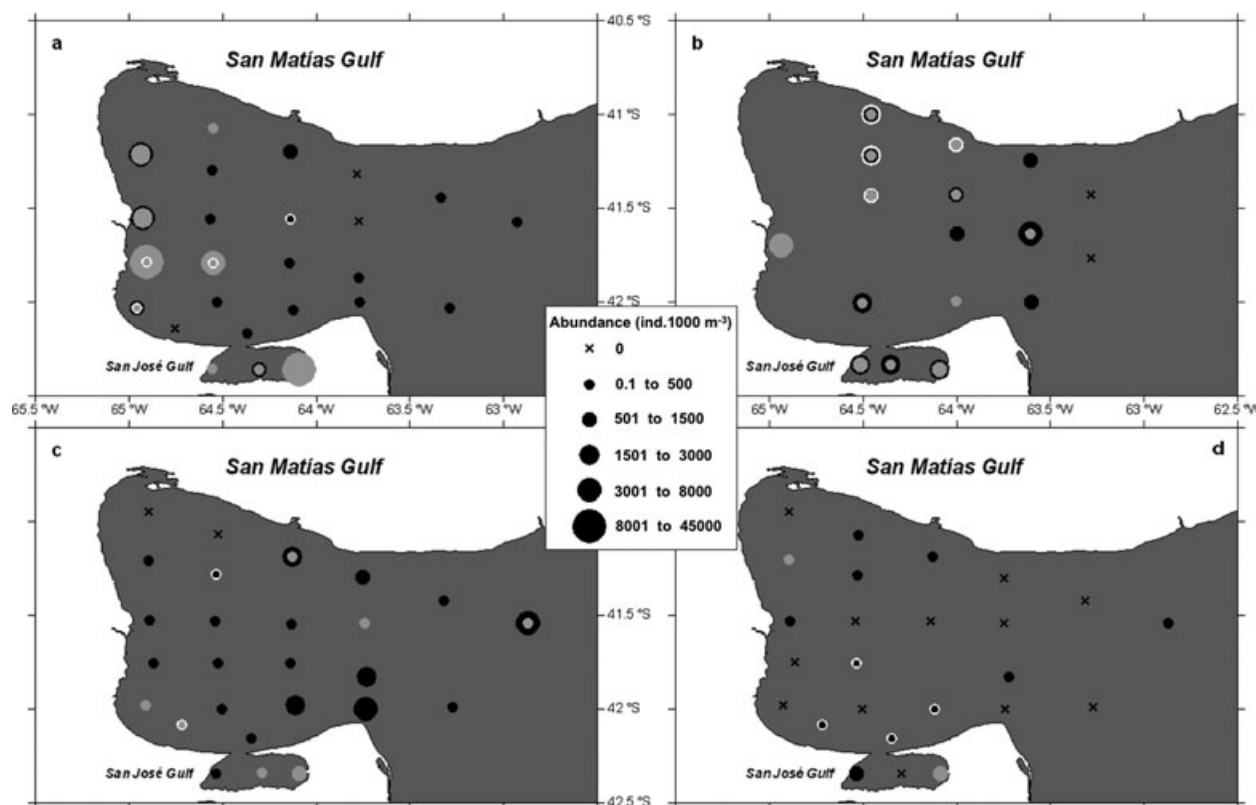


Fig. 4. Distributions of total hydromedusae (filled black circles), *Obelia* spp. (filled grey circles) and siphonophorae (open white circles) abundance (ind. 1000 m⁻³) in San Matías Gulf in (a) autumn 2007, (b) spring, (c) summer and (d) autumn 2008.

was always higher in colder waters: Richness = $8.3966 - 0.8514 \times \text{Temperature}$; Z-value = -5.1 , P-value <0.01 and Richness = $5.077 - 0.367 \times \text{Temperature}$; Z-value = -2.2 , P-value <0.05 , respectively. In both cases, these lowest temperatures corresponded to those registered in the SE area.

Analysis of similitude showed non-significant differences in the hydromedusae community composition among sectors and among seasons (Global R = 0.196; P-value >0.05 and 0.111; P-value >0.05 , respectively).

Discussion

Our hydrographical data agree with previous descriptions of San Matías Gulf hydrodynamics (Piola & Scasso 1988; Gagliardini & Rivas 2004; Tonini 2010). The Gulf can essentially be divided into a NW sector, with warmer and saltier water, and a colder and less saline SE sector, the differences being more evident in spring, when the thermal front starts to become conspicuous, and in summer, when the front is completely developed.

The present work increases the list of planktonic cnidarian species from the San Matías Gulf area by 20

hydromedusae and one siphonophore species. The total number of hydromedusan species reported for the area is therefore now 23, including the 20 from the present study plus two previous records: *Dipurena reesi* Vannucci, 1956 (Genzano *et al.* 2008a) and *Malagazzia carolinae* (Mayer, 1900) (Ramírez 2007) and *Olindias sambaquiensis* Müller, 1861, collected during other coastal surveys in the northern part of the (E. G. Gulf, pers. obs.). This hydromedusa richness for the area is similar to that of the neighbouring shelf (20 valid species; Table 3), but lower (45 valid species) than records on northern areas of Argentine–Uruguayan shelf (Genzano *et al.* 2008a). These data agree with the decrease in number of hydromedusan species with increased latitude previously observed in the temperate Southwestern Atlantic Ocean (Genzano *et al.* 2008a). In fact, San Matías Gulf and surrounding areas might be located where Macpherson (2002) observed a strong decrease in species richness for Hydromedusae and Siphonophorae in the Atlantic Ocean, around 40°S.

The aforementioned factors – coastal ecosystem (Gili & Hughes 1995), seasonality (Boero 1984; Boero & Bouillon 1993) and allochthonous water inputs (Gili *et al.* 1991; Pagès & Gili 1991) – do not appear to be promoting a

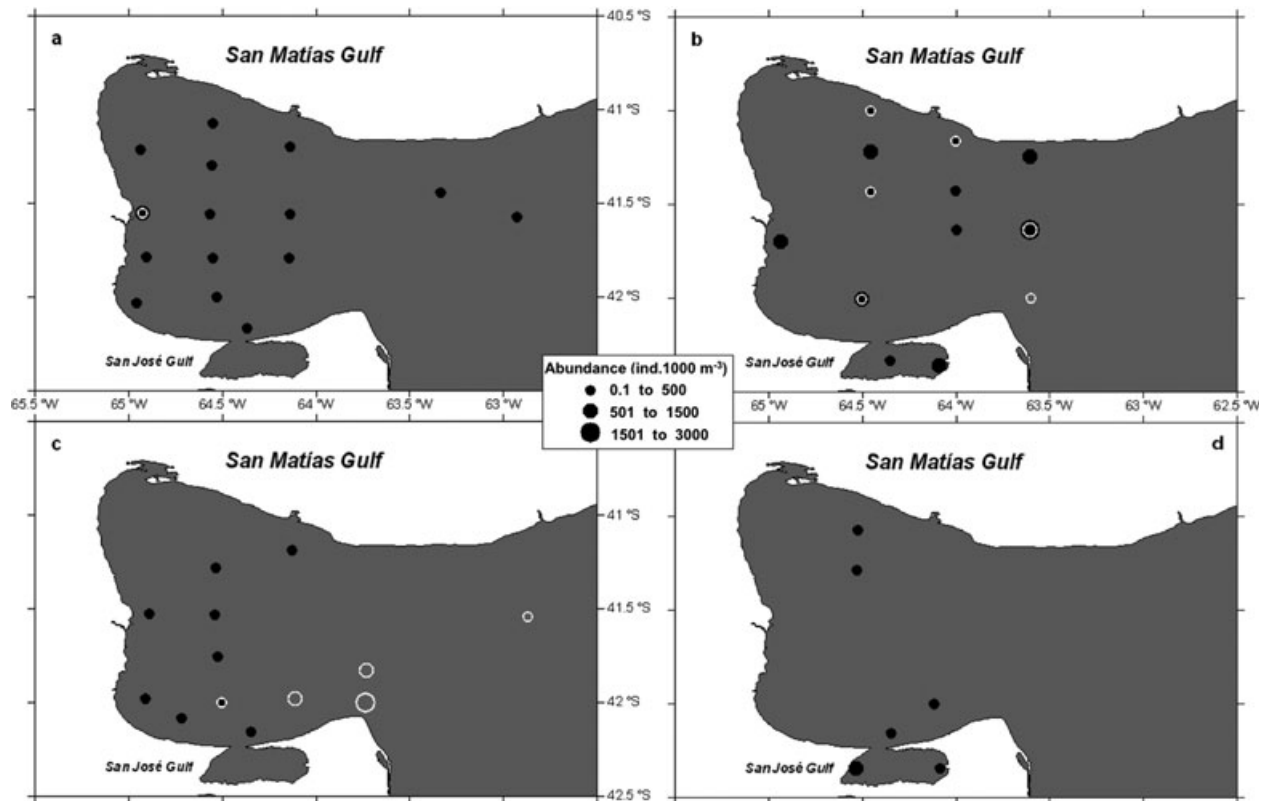


Fig. 5. Distributions of *Proboscoidactyla mutabilis* (filled black circles) and *Laodicea undulata* (open white circles) abundance in San Matías Gulf in (a) autumn 2007, (b) spring, (c) summer and (d) autumn 2008.

higher biodiversity in San Matías Gulf compared with the contiguous shelf. Nevertheless, the species composition inside the Gulf is rather different to the one found offshore in the continental shelf (Table 3). Both areas showed high similarity in Limnomedusae (100%) and Leptomedusae (80%), but low coincidence of Anthomedusae (25%) and none of Narco- and Trachymedusae (0%). In the Southwestern Atlantic Ocean, the two latter subclasses mostly have been found in oceanic and shelf break front environments (Genzano *et al.* 2008a) about 300 miles offshore from the Gulf mouth, which could explain the limited occurrence of oceanic cnidarians along the wide Patagonian continental shelf. It may also be possible that some medusae of these taxa entered the Gulf but failed to survive due to specific inner-Gulf environmental conditions. Carreto *et al.* (1974), Ramírez (1996) and Williams (2004) defined the seasonal cycle of primary and secondary productivity within the Gulf by short and limited pulses. In fact, Carreto *et al.* (1974) described the northern sector as an area where nutrient exhaustion prevents continuous primary production. On the other hand, there is an important population of filter-feeding bivalve molluscs, especially in the northern

part of the Gulf (Narvarte *et al.* 2007). These factors, among others, may be limiting food availability in the pelagic realm, meroplanktonic species being strongly favoured over holoplanktonic ones. We think the absence of calycophoran siphonophores in San Matías Gulf might result from factors similar to the ones for the holoplanktonic hydromedusan species.

Oceanographically, San Matías Gulf has been described as an ecosystem with limited communication with the open sea (Piola & Scasso 1988; Rivas & Beier 1990; Gagliardini & Rivas 2004). Latest studies in the area (Tonini *et al.* 2006, 2007; Tonini 2010) stated that the Gulf inner circulation limits water exchange, especially during the spring–summer period, whereas during the autumn–winter period only, the shallowest western coast keeps more isolated. This marked isolation would support the particular composition of planktonic cnidarians, as has been observed for other zooplankton groups (Ramírez 2007). This phenomenon has been also cited as responsible for the development of local sub-populations in several mollusc species (Narvarte *et al.* 2007) and for the Argentine hake (Sardella & Timi 2004; Machado Schiaffino *et al.* 2011), the latter being the major species of the

Table 3. List of hydromedusae species cited for the adjoining Argentine continental shelf between 40° and 44°S and their presence/absence in San Matías Gulf during the present study (2007–2008).

Argentine shelf (40°–44°S)	Sc	Author(s)	Present study
<i>Bougainvillia macloviana</i>	A	Zamponi (1983)	–
<i>Bougainvillia muscus</i>	A	Zamponi (1983)	Present
<i>Oceania armata</i> ^a	A	Ramírez & Zamponi (1980); Zamponi (1983)	–
<i>Amphinema dinema</i>	A	Zamponi (1983)	–
<i>Halitholus intermedius</i> ^a	A	Zamponi (1983)	–
<i>Proboscoidactyla mutabilis</i>	A	Genzano <i>et al.</i> (2008a)	Present
<i>Moerisia inkermanica</i> ^a	A	Zamponi (1983)	–
<i>Coryne eximia</i>	A	Genzano <i>et al.</i> (2008a)	–
<i>Aequorea coerulescens</i>	L	Genzano <i>et al.</i> (2008a)	Present
<i>Aequorea forskalea</i>	L	Genzano <i>et al.</i> (2008a)	–
<i>Eucheilota ventricularis</i>	L	Genzano <i>et al.</i> (2008a)	Present
<i>Laodicea undulata</i>	L	Genzano <i>et al.</i> (2008a)	Present
<i>Staurophora mertensii</i>	L	Zamponi (1983)	–
<i>Malagazzia carolinae</i>	L	Zamponi (1983)	–
<i>Cosmetirella davisii</i>	L	Ramírez & Zamponi (1980); Zamponi (1985)	Present
<i>Mitrocomella brownei</i>	L	Genzano <i>et al.</i> (2008a)	Present
<i>Mitrocomella frigida</i>	L	Ramírez & Zamponi (1980); Zamponi (1983); Genzano <i>et al.</i> (2008a)	Present
<i>Clytia simplex</i>	L	Ramírez & Zamponi (1980); Genzano <i>et al.</i> (2008a)	Present
<i>Obelia</i> sp.	L	Ramírez & Zamponi (1980); Zamponi (1983); Genzano <i>et al.</i> (2008a)	Present
<i>Obelia longissima</i>	L	Genzano <i>et al.</i> (2008a,b)	Genera present
<i>Olindias sambaquiensis</i>	Li	Mianzan (1989)	Present
<i>Solmundella bitentaculata</i>	N	Zamponi (1985)	–
<i>Halitrephes maasi</i>	T	Ramírez & Zamponi (1980); Zamponi (1983)	–
<i>Rhopalonema velatum</i>	T	Zamponi (1983)	–

Sc = Hydromedusae subclass; A = Anthomedusae; L = Leptomedusae; Li = Limnomedusae; N = Narcomedusae; T = Trachymedusae.

^aDoubtful species identification (Genzano *et al.* 2008a; C. Rodríguez, unpubl. data) not taken into account in the calculations.

main fishery in San Matías Gulf. The siphonophore *Pyrostephos vanhoeffeni*, the only holoplanktonic cnidarian found in San Matías Gulf, seems to be entering the Gulf with continental shelf water intrusions and staying inside for variable periods of time. During autumn, when the greater Gulf–shelf connexion takes place, the siphonophore, placed in the SE and Central sectors, could be entering the Gulf with the colder and nutrient richer sub-Antarctic water masses of the Patagonian Coastal Current (Gagliardini & Rivas 2004). During the spring season, then, the siphonophores may be confined in the NW area, trapped by the cyclonic gyre (Tonini *et al.* 2006, 2007; Tonini 2010). We do not have evidence of *P. vanhoeffeni* reproductive events inside the Gulf; however, maximum densities were found during spring, when it occupied the main spawning area for hake (Mercado *et al.* 1993; González *et al.* 2010), and, as seen in their gastrozoid content, the siphonophore should be favoured because of high prey availability. During summer, when surface temperatures reached over 20 °C, its abundance was scarce and scattered (Fig. 4c). *Pyrostephos vanhoeffeni* has been described as endemic to Antarctic and sub-Antarctic waters (Moser 1925; Totton 1965; Alvarino *et al.* 1990); we think this species may have a preference for

colder water, with summer temperatures probably causing high mortalities. Actually, *P. vanhoeffeni* is considered to be one of the few carnivorous gelatinous species well adapted to cold waters that has oleocysts with lipid reserves (Pagès & Schnack-Schiel 1996), which may allow their survival longer than other holoplanktonic hydromedusan and siphonophores in periods of low planktonic food availability in San Matías Gulf.

In general, hydromedusa abundance in San Matías Gulf was lower than that of other coastal ecosystems (Gili *et al.* 1988; Palma *et al.* 2007). The exception to that was the *Obelia* spp. bloom (Figs 3 and 4a) located mainly on the west coast of the Gulf during autumn 2007. Upwelling waters, together with the anticyclonic gyre described for this area during the cold season (Williams 2004; Tonini *et al.* 2006; Tonini 2010), might have influenced this event due to resuspension of organic matter and the isolation caused by the recirculation. Previous works (Boero *et al.* 2007) describe *Obelia* as a microphagous and filter-feeding medusa, at least at the onset of its medusan stage, and there is evidence of hydroid species of the same genus (*Obelia geniculata*; Orejas *et al.* 2000) achieving high ingestion rates (113% of the hydranth biomass per day) in upwelling areas.

Therefore, in conditions of high productivity in San Matías Gulf, *Obelia* spp. could produce an explosive increase of the hydroid and medusa population. In fact, strong interannual variability was detected for *Obelia longissima* medusae, which bloomed during October 2003 in the El Rincón area in the northern Argentine Sea, followed by massive hydroid shoreline accumulations (Genzano *et al.* 2008b). Following this line of reasoning, Gili *et al.* (1998) highlighted that some hydrozoan species take full advantage of episodes of temporary high prey availability to feed intensely and, furthermore, that hydro- and scyphomedusan jellyfish blooms might be due to efficient incorporation of planktonic matter by the benthic stages, reflecting their feeding success over the preceding months. This could also explain why this area presented the highest species richness of other meroplankton hydromedusae in that season. The absence of such a bloom the following year during the same period could indicate that the bloom requires rather unusual or very specific conditions to occur.

Reviews such as Haurly *et al.* (1978) and Denman & Powell (1984) attribute the control of spatial heterogeneity of zooplankton to hydrodynamic factors, and the regulation of temporal variability to biological factors. In the case of San Matías Gulf the highest abundances (without *Obelia*) and richness (see Results section) took place during spring, coinciding with high primary and secondary productivity values (Carreto *et al.* 1974; Ramírez 1996; Williams 2004). Furthermore, the negative relationship between hydromedusae abundance and richness with temperature in San Matías Gulf shows that hydromedusae are more abundant and rich related to the colder and nutrient rich sub-Antarctic water inputs occurring in the SE sector (Gagliardini & Rivas 2004; Tonini *et al.* 2007). Therefore, this input may be locally favouring the development of hydromedusa populations, both the medusa stage as well as the polyp, the last growing and increasing or triggering the liberation of medusae (Gili *et al.* 1988). Because no different hydromedusa species assemblages were detected among sectors, a poor or null contribution of allochthonous species within this water mass into the Gulf seems probable.

In conclusion, we may conclude that San Matías Gulf tends to have a particular composition of planktonic cnidarian species, favouring a meroplanktonic over a holoplanktonic life strategy, and the density and diversity distribution of these species is mainly shaped by hydrodynamic processes of the area.

This study contributes the following to the planktonic cnidarian biodiversity of the temperate Southwestern Atlantic Ocean:

- the first records of two hydromedusae: *Hybocodon chilensis* Hartlaub, 1905, a species previously recorded

in Chile and New Zealand (Galea 2006), and one species of the genus *Hydractinia* (*Hydractinia cf. areolata* Alder, 1862);

- the first record of the siphonophore *P. vanhoeffeni* in temperate Atlantic waters.

The latter record together with new records for the Argentine continental shelf (E. M. Araujo, unpubl. data) and the expansion of its geographical distribution into the Chilean coast from 41°30' to 56°S (Palma & Aravena 2001) suggest that *P. vanhoeffeni* species should not be considered Antarctic and sub-Antarctic endemic.

Acknowledgements

The authors would like to thank Prefectura Naval Argentina, especially the crew of the Coast Guard ships *Río Paraná* and *La Plata*. This work was funded by the projects PID 2003#371 and PICT-2006 Start up #1575 (Agencia Nacional de Promoción Científica y Tecnológica); EXA 465/11 (Universidad Nacional de Mar del Plata) and PIP – CONICET 112 201101 00152. E. Guerrero acknowledges financial support from AECI (Agencia Española de Cooperación Internacional-Ministerio Asuntos Exteriores). C. Rodríguez is supported by CONICET fellowship. E. M. Araujo acknowledges the fellowship support by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), Brazil. A. Canepa was funded by CONICYT (PFCHA/Doctorado al Extranjero 4ª Convocatoria, 72120016). The authors wish to thank three anonymous reviewers for their comments, which greatly improved the first manuscript. Special thanks go to Jennifer Purcell for revising the manuscript and for her valuable comments on it. This paper is dedicated to Francesc Pagès who introduced and taught the first author (E.G.) the art of planktonic cnidarians identification as well as he transmitted his enthusiasm for the gelatinous plankton ecology and systematics to many other researchers and friends. The publication of this paper is supported by CONISMA, the Italian National Interuniversity Consortium for Marine Sciences.

Conflicts of Interest

None of the authors have any potential conflict of interest.

References

- Alvarino A., Wojtan J.M., Martinez M.R. (1990) Antarctic siphonophores from plankton samples of the United States Research Program. Eltanin cruises for spring, summer, fall and winter (Cruises 3–5, 8–23, 25–28, 30, 35 and 38). *Biology of the Antarctic Seas* 14. *Antarctic Research Series*, **49**, 1–436.

- Bates D., Maechler M., Bolker B. (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4> [accessed on 12 July 2012].
- Boero F. (1984) The ecology of marine hydroids and effects of environmental factors: a review. *Marine Ecology*, **5**, 93–118.
- Boero F., Bouillon J. (1993) Zoogeography and life cycle patterns of Mediterranean Hydromedusae (Cnidaria). *Biological Journal of the Linnean Society*, **48**, 239–266.
- Boero F., Bucci C., Colucci A.M.R., Gravili C., Stabili L. (2007) *Obelia* (Cnidaria, Hydrozoa, Campanulariidae): a microphagous, filter-feeding medusa. *Marine Ecology*, **28**, 178–183.
- Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J. R., Stevens M.H.H., White J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* (Personal edition), **24**, 127–135.
- Bouillon J. (1999) Hydromedusae. In: Boltovskoy D. (Ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden: 385–465.
- Carreto J.I., Casal A.B., Hinojal A., Laborde M.A., Verona C.A. (1974) *Fitoplancton, pigmentos y condiciones ecológicas del Golfo San Matías. Informe n. 10*. Instituto de Biología Marina de Mar del Plata, Comisión de Investigación Científica, La Plata, Argentina: 76 pp.
- Clarke K.R. (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Denman K.L., Powell T.M. (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanography and Marine Biology*, **22**, 125–168.
- Gagliardini D.A., Rivas A.L. (2004) Environmental characteristics of San Matías Gulf obtained from LANDSAT-TM and ETM+ data. *Gayana*, **68**, 186–193.
- Galea H.R. (2006) Rediscovery and redescription of *Hybocodon chilensis* Hartlaub, 1905 (Cnidaria: Hydrozoa) from Comau Fiord, southern Chile. *Zootaxa*, **14**, 57–68.
- Gaston K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Genzano G.M., Mianzan H.W., Bouillon J. (2008a) Hydromedusae (Cnidaria: Hydrozoa) from the temperate southwestern Atlantic Ocean: a review. *Zootaxa*, **1750**, 1–18.
- Genzano G.M., Mianzan H.W., Díaz-Briz L., Rodríguez C. (2008b) 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.
- Gili J.M., Hughes R.G. (1995) The ecology of marine benthic hydroids. *Oceanography and Marine Biology*, **33**, 351–426.
- Gili J.M., Pagès F., Sabatés A., Ros J.D. (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. *Journal of Plankton Research*, **10**, 385–401.
- Gili J.M., Pagès F., Fusté X. (1991) Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician Coast (Northwestern Iberian Peninsula). *Scientia Marina*, **55**, 419–426.
- Gili J.M., Alvá V., Coma R., Orejas C., Pagès F., Ribes M., Zabala M., Arntz W., Bouillon J., Boero F., Hughes R.G. (1998) The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. *Zoologische Verhandelingen (Leiden)*, **323**, 99–105.
- González R., Ocampo-Reinaldo M., Schneider C., Romero M. A., Maggioni M., Williams G., Cabrera G., Narvarte M., Gagliardini A. (2010) Correlating SST satellite data to the spatial distribution of spawning aggregations of Argentine Hake (*Merluccius hubbsi*) in San Matías Gulf, Patagonia, Argentina. In: Barale V., Gower J., Alberotanza L. (Eds), *Proceedings of Oceans From Space Symposium 2010*, Venice (Italy). Joint Research Centre, European Commission. JRC Scientific and Technical Reports N°57986: 103–104. EUR 24324, ISBN 978-92-79-15577-2, ISSN 1018-5593. DOI: 10.2788/8394.
- Haury L., McGowan R., Wiebe P.H. (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele J.H. (Ed.), *Spatial Pattern in Plankton Communities*. Plenum, New York: 277–327.
- Kramp P.L. (1959) The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report*, **46**, 1–283.
- Machado Schiaffino G., Juanes F., García-Vázquez E. (2011) Identifying unique populations in long-dispersal marine species: Gulfs as priority conservation areas. *Biological Conservation*, **144**, 330–338.
- Macpherson E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **269**, 1715–1720.
- Mazio C.A., Vara C.D. (1983) Las mareas del Golfo San Matías. *Servicio de Hidrografía Naval. Informe Técnico 13/1983*, Buenos Aires: 69 pp.
- Mercado L., Pose M., Tesolin G., Villar C. (1993) Análisis de la distribución y abundancia del ictioplancton y zooplancton acompañante en el Golfo San Matías en noviembre de 1992. Seminario curso oceanografía biológica. Buenos Aires.
- Mianzan H.W. (1989) Distribución de *Olinidias sambaquiensis* Müller, 1861 (Hydrozoa; Limnomedusae) en el Atlántico Sudoccidental. *Iheringia, Série Zoológica*, **69**, 155–157.
- Mianzan H.W. (1999) Ctenophora. In: Boltovskoy D. (Ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden: 561–573.
- Moser F. (1925) Die Siphonophoren der Deutschen Südpolar-Expedition 1901–1903. *Deutschen Südpolar-Expedition*, **17**, 1–154.
- Murase H., Nagashima H., Yonezaki S., Matsukura R., Kitakado T. (2009) Application of a generalized additive model (gam) to reveal relationships between environmental

- factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan. *ICES Journal of Marine Science: Journal du Conseil*, **66**, 1417–1424.
- Narvarte M., González R., Filippo P. (2007) Artisanal mollusk fisheries in San Matías Gulf (Patagonia Argentina): an appraisal of the factors contributing to unsustainability. *Fisheries Research*, **87**, 68–76.
- O'Hara R.B., Kotze D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution*, **1**, 118–122.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P. R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. (2012) Vegan: Community Ecology Package. R package version 2.0-3. <http://CRAN.R-project.org/package=vegan> [accessed on 12 July 2012].
- Orejas C., Gili J.M., Alvà V., Arntz W. (2000) Predatory impact of an epiphytic hydrozoan in an upwelling area in the Bay of Coliumo (Dichato, Chile). *Journal of Sea Research*, **44**, 209–220.
- Pagès F., Gili J.M. (1991) Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Marine Ecology Progress Series*, **75**, 205–215.
- Pagès F., Schnack-Schiel S. (1996) Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). *Journal of Marine Systems*, **9**, 231–248.
- Palma S., Aravena G. (2001) Distribución de sifonóforos, quetognatos y eufáusidos en la región magallánica. *Ciencia y Tecnología del Mar*, **24**, 47–59.
- Palma S., Apablaza P., Soto D. (2007) Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). *Investigaciones Marinas, Valparaíso*, **35**, 71–82.
- Penston M.J., Millar C.P., Zuur A., Davies I.M. (2008) Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. *Journal of Fish Diseases*, **31**, 361–371.
- Piola A.R., Scasso L.M. (1988) Circulación en el Golfo San Matías. *Geoacta*, **15**, 33–51.
- Pugh P. (1984) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Progress in Oceanography*, **13**, 461–489.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>.
- Ramírez F.C. (1996) Composición, abundancia y variación estacional del zooplancton de red del Golfo San Matías. *Frente Marítimo*, **16**, 157–167.
- Ramírez F.C. (2007) Distribución y alimentación del zooplancton. In: Carreto J.I., Bremec C. (Eds), *El Mar Argentino y sus recursos pesqueros*, Vol. 5. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina: 45–69.
- Ramírez F.C., Zamponi M.O. (1980) Medusas de la plataforma bonaerense y sectores adyacentes. *Physis Secc A*, **39**, 33–48.
- Rivas A.L., Beier E.J. (1990) Temperature and salinity fields in the Northpatagonic Gulfs. *Oceanologica Acta*, **13**, 15–20.
- Sardella N., Timi J. (2004) Parasites of Argentine hake in the Argentine Sea: population and infracommunity structure as evidence for host stock discrimination. *Journal of Fish Biology*, **65**, 1472–1488.
- Tonini M. (2010) Modelado numérico del ecosistema de los Golfos Norpatagónicos. PhD thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Tonini M., Palma E., Rivas A. (2006) Modelo de alta resolución de los Golfos Patagónicos. In: Cardona A., Nigro N., Sonzogni V., Storti M. (Eds), *Mecánica Computacional*, Vol. 25. AMCA, Santa Fé: 1441–1460.
- Tonini M., Palma E., Rivas A. (2007) Simulación numérica de la circulación y frentes térmicos en los Golfos Norpatagónicos. In: Elaskar S.A., Pilotta E.A., Torres G.A. (Eds), *Mecánica Computacional*, Vol. 26. AMCA, Córdoba: 3757–3768.
- Totton A. (1965) *A Synopsis of the Siphonophora*. Trustees British Museum of Natural History, London: 230 pp.
- Williams G. (2004) Cuáles son las fuentes de nutrientes para mantener la productividad del Golfo San Matías? MSc thesis, Universidad Nacional de la Patagonia 'San Juan Bosco', Puerto Madryn, Argentina.
- Wood S.N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC, Boca Raton: 384 pp.
- Zamponi M.O. (1983) Ecología de las hidromedusas del Mar Epicontinental Argentino. *Neotrópica*, **29**, 65–81.
- Zamponi M.O. (1985) La alimentación de algunas especies de Hydromedusae. *Neotrópica*, **31**, 155–162.
- Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York: 574 pp.