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## Jellyfish biodiversity and abundance patterns in northern Patagonia (Valdés Biosphere Reserve, UNESCO 2014)

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### Abstract

Understanding how key components of plankton food webs, such as jellyfish communities, are structured by local hydrography has important management implications for fisheries and higher trophic predators within the ecosystem. Here, we report for the first time on the jellyfish abundance, richness, and diversity distribution across the Nuevo Gulf (42° 42'S, 64° 30'W), a World Heritage Site in Argentine Patagonia and part of the Valdés Biosphere Reserve, during spring (2019 and 2020) and summer (2020 and 2021) at two depths. We found that the most abundant species was the hydromedusae *Eucheilota ventricularis*, followed by other Leptothecata species, representing more than 50 % of the total community's abundance. Abundance and diversity were significantly higher in spring than in summer, with seasonality playing a crucial role in modulating the jellyfish community dynamics and also being related to environmental variables and other mesozooplankton groups. Variability in the abundances across the Gulf and between depths was significantly and positively associated with chlorophyll *a* and ammonium, but negatively correlated with temperature, agreeing with previous results for the region. Jellyfish were more abundant near the mouth of the Gulf and during spring, possibly due to the connection and exchange of colder and nutrient-enriched water masses with those coming from the continental shelf. Significant correlations were found between jellyfish species and other mesozooplankton groups in spring. Our results highlight the importance of intensifying

37 sampling in the vertical and horizontal dimensions along an annual cycle to begin to  
38 elucidate and increase the current scarce knowledge about the jellyfish's distribution  
39 and abundance patterns in northern Patagonian gulfs.

40

41 **Keywords:** gelatinous zooplankton, seasonality, Patagonian Gulf

## 42 **1. Introduction**

43 The broader interest on jellyfish, the gelatinous zooplankton of the phyla Cnidaria  
44 and Ctenophora, has increased in recent years for ecological and socio-economic  
45 reasons (Richardson et al., 2009; Condon et al., 2012). These organisms play essential  
46 roles within the pelagic realm that are often enhanced when they massively reproduce  
47 or bloom (Boero et al., 2008). Jellyfish can shape food webs by preying on a broad  
48 spectrum of zooplankton species and fish and competing with other pelagic predators  
49 (Purcell and Arai, 2001; Pitt et al., 2008). They contribute substantially to  
50 biogeochemical fluxes driving secondary production and enhancing benthic processes  
51 (Sweetman and Chapman, 2011; Lebrato et al., 2012). As voracious predators,  
52 planktonic and benthic jellyfish stages play important roles in the benthopelagic  
53 coupling, influencing coastal ecosystems' production and biological structure (Pitt et al.,  
54 2008; Lucas et al., 2012). Several environmental factors, including food, light,  
55 temperature, and salinity, affect jellyfish occurrence and reproduction, acting differently  
56 on benthic and planktonic phases (Purcell, 2007; Möller and Riisgard, 2007; Boero et  
57 al., 2016; Goldstein and Steiner, 2020). In particular, the widely-distributed Hydrozoans,  
58 a relatively diverse group of jellyfish, is also valuable for defining biogeographic regions  
59 and reflecting short-term changes in the physical environment (Gibbons and Buecher,  
60 2001; Buecher et al., 2005; Gibbons et al., 2009; Gusmão et al., 2014; Ronowicz et al.,  
61 2019).

62 The temperate Southwestern Atlantic (SWA) is known worldwide for its high  
63 productivity and biodiversity due to the large number of marine fronts present in the  
64 region (Bisbal, 1995; Acha et al., 2004). Located in the SWA, the Valdés Biosphere  
65 Reserve (VBR; UNESCO, 2014) is characterized by a great diversity of fauna and is  
66 highlighted as one of the most relevant areas for the occurrence and development of  
67 gelatinous organisms on a broader scale (Diaz Briz et al., 2017; Schiariti et al., 2018,  
68 2021; Dutto et al., 2019). Nevertheless, this area remains poorly surveyed for plankton

69 in general (e.g., see Nocera et al., 2021) and gelatinous zooplankton in particular. Only  
70 one published study exists on Hydromedusae in the San José Gulf, northern VBR  
71 (Guerrero et al., 2013), and no specific studies on jellyfish exists in Nuevo Gulf (NG),  
72 southern VBR, whereas only sporadic records of gelatinous taxa are derived from  
73 zooplankton surveys (e.g., Esteves et al., 1997; Hoffmeyer et al., 2010; Menéndez et  
74 al., 2011; D'Agostino et al., 2018; Nocera et al., 2021).

75 The coastal marine environment of the VBR is exposed to anthropogenic  
76 activities with potential environmental risks (e.g., overexploitation, biological invasions,  
77 climate variability, etc.), whilst different spots used for recreation and marine wildlife  
78 sighting are valuable ecosystem services for the regional tourist industry. For instance,  
79 a recent study showed that several environmental variables in the VBR have undergone  
80 significant changes associated with climate change during the last two decades  
81 (Williams and Nocera, 2023). This may have consequences on the pelagic food web,  
82 particularly on zooplankton, as it has already been described for an area located further  
83 south in the SWA (Cepeda et al., 2022). Seasonal and reiterative jellyfish blooms can  
84 also have negative effects on fisheries and tourism-based local economies, as specific  
85 areas provide valuable ecosystem services for food security and the tourist industry in  
86 the region (e.g., marine wildlife sighting) (Lucas et al., 2014; Tomlinson et al., 2018;  
87 Ruíz-Frau, 2022). Therefore, studies on jellyfish assemblage and its spatiotemporal  
88 distribution within the VBR are of great interest to acquire a holistic understanding of  
89 the factors influencing the community structure and ecosystem functions. This will aid  
90 conservation and management plans, as well as inform sustainable exploitation within  
91 the SWA.

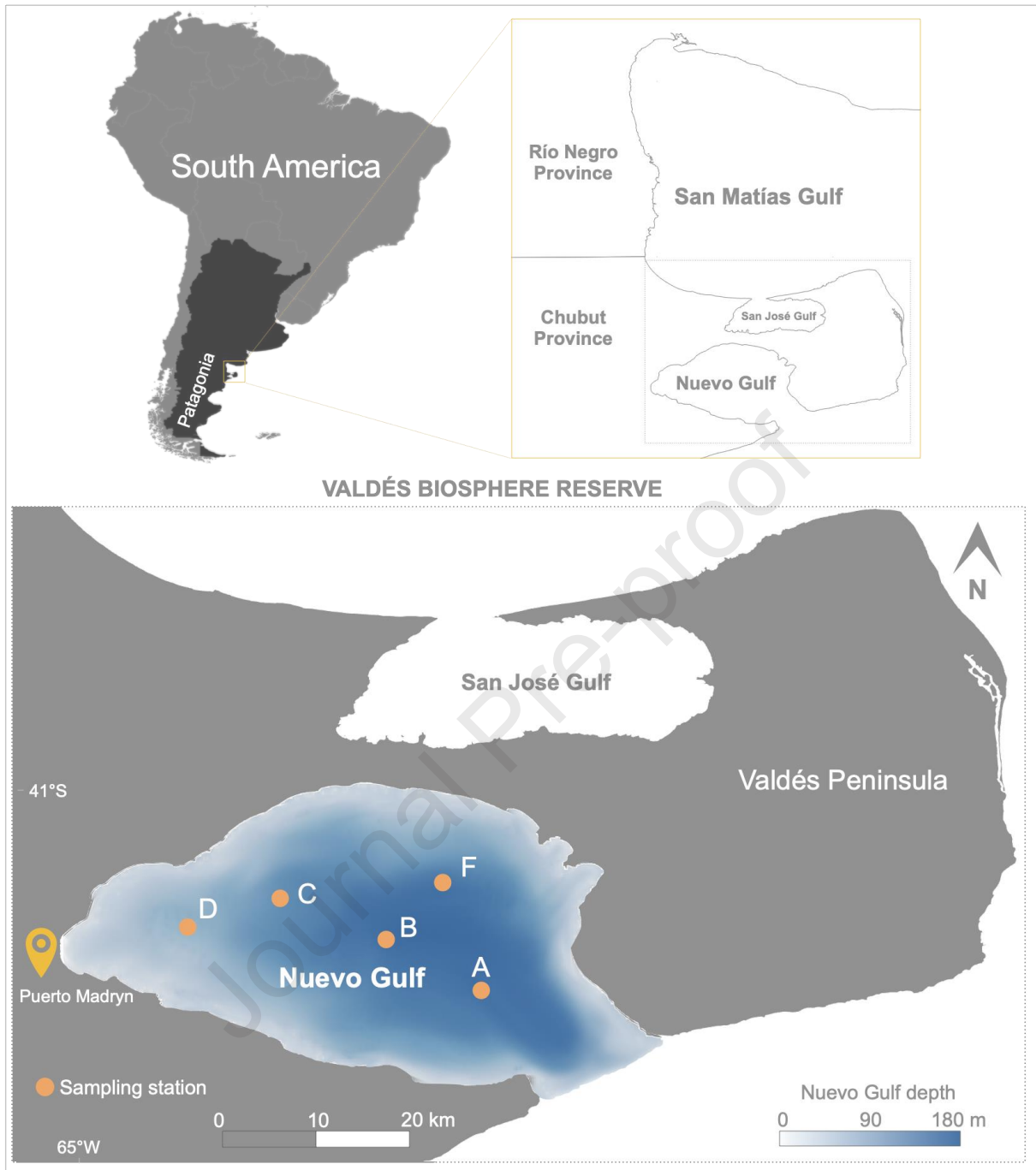
92 In this paper we aimed to: a) described the jellyfish community from the NG for  
93 the first time and b) explore the spatiotemporal variation in its abundance and diversity.  
94 To achieve this, we followed globally- (Lilley et al., 2011; Lucas et al., 2014) and  
95 regionally-recognized (Guerrero et al., 2013) abundance hypotheses established for this  
96 taxonomic group: (i) the jellyfish abundance is positively correlated with the sea surface  
97 temperature, and (ii) greater abundance is found in regions characterized by high  
98 primary production. We then explored relevant, considering the limitations of the data,  
99 environmental and biological factors affecting the seasonal dynamics in the jellyfish  
100 community, such as depth and mesozooplankton groups. This work increases our  
101 knowledge and understanding of the jellyfish community dynamics in the northern

102 Patagonian region. Finally, we propose some directions to be considered in future  
103 jellyfish research within this marine ecosystem.

## 104 **2. Methods**

### 105 **2.1 Study area**

106 The NG is a semi-enclosed basin located in the southern Valdés Peninsula within  
107 the Argentinean Patagonia (42°42'S, 64°30'W; Fig.1). It covers an area of 2,400 km<sup>2</sup>,  
108 with a maximum depth of 170 m at the center-north of the gulf and has a narrow mouth  
109 (16 km width, 44 m deep) connecting to the adjacent continental shelf waters (Fig. 1;  
110 Rivas and Beier, 1990; Rivas and Ripa, 1989). Precipitation is low (200 mm per year),  
111 with no permanent water courses present in the region that could discharge freshwater  
112 to the gulf. Temperature and salinity present homogeneous characteristics in its  
113 horizontal component, but vary gradually along the vertical axis (ca. 50 m), without  
114 showing a halocline and a thermocline presence in the water column during late  
115 summer (March; Solís, 1998). The annual thermal amplitude and salinity within the Gulf  
116 are greater than the surrounding waters, due to its bathymetry and topography, in  
117 addition to the relatively long water residence time (on average ~132 days; Tonini et al.,  
118 2022) which restricts the exchange with water masses from the continental shelf  
119 presenting colder and less salty waters coming from the Malvinas current (Rivas, 1990;  
120 Rivas and Beier, 1990).



121  
 122 Figure 1. Study area and sampling stations in the Nuevo Gulf ( $42^{\circ} 42' S$ ,  $64^{\circ} 30' W$ ;  
 123 NG) within the Valdés Biosphere Reserve (Patagonia, Argentina). Capital letters (A to  
 124 F) refer to station names, according to Nocera et al. (2021). The bathymetry is shown  
 125 only for the NG represented by shading on the blue scale.

## 126 **2.2 Sampling**

127 A detailed description of the fieldwork design can be found in Nocera et al.  
 128 (2021). In short, zooplankton horizontal hauls at 30 m (subsurface layer), and 70 m  
 129 (intermediate layer) were conducted (7 min at 2 knots) during daylight hours in three  
 130 consecutive years during austral spring (October 2019 and 2020) and summer (January

131 2020 and 2021). Plankton was collected using a 300  $\mu\text{m}$  mesh (40 cm diameter)  
132 plankton net equipped with a flowmeter (General Oceanics Inc., Miami, United States).  
133 Depending on weather conditions, surveys were carried out across three to five  
134 sampling stations at an average distance of 15 km from one another in NG (Fig. 1).  
135 Before each net deployment, temperature and salinity were recorded from discrete  
136 water samples obtained with a 5 L Niskin bottle at 1 m (subsurface layer) and 70 m  
137 (intermediate layer) with a multiparameter sonde (AQUACOMBO HM3070). Due to  
138 adverse meteorological conditions, station D was not sampled during spring 2019. The  
139 subsurface samples collected at station D and B in the summer of 2020 and 2021,  
140 respectively, were lost.

### 141 **2.3 Chlorophyll *a* and chemical analysis**

142 Chlorophyll *a* (as a proxy of phytoplankton biomass) was determined by filtering  
143 1000 mL of seawater through GF/F glass fiber filters (47 mm diameter, 0.7  $\mu\text{m}$  in  
144 nominal pore size) which were then stored at  $-80\text{ }^{\circ}\text{C}$  until analysis. Chlorophyll *a* was  
145 extracted in 10 mL, 90% acetone with a sonicator for 20 min and then placed in a  
146 refrigerator in the dark (24 h at  $4\text{ }^{\circ}\text{C}$ ). Extracts were then centrifuged at 3000 rpm for 10  
147 min. Chlorophyll *a* and phaeopigments were measured using a 10-AU fluorometer  
148 (Turner Designs), and concentrations were estimated according to Parsons et al.  
149 (1984). Phaeopigment values were obtained by acidifying the chlorophyll extract with  
150 two drops of HCl (5 %).

151 To determine nutrient availability, the remaining filtered seawater from the  
152 chlorophyll *a* filtration was collected, divided into two acid-cleaned plastic flasks (250  
153 mL each), and preserved at  $-20\text{ }^{\circ}\text{C}$  for further analysis. Nutrient determination was  
154 performed using a Skalar Autoanalyzer (Skalar Analytical 2005) at Centro Nacional  
155 Patagónico (CENPAT, Argentina). Only nitrate+nitrite, ammonium, and phosphate data  
156 were analyzed in this work (hereafter, “nutrients”).

### 157 **2.4 Zooplankton identification**

158 Samples were stored in 250- or 500-mL plastic flasks and preserved in 4%  
159 formaldehyde for their analysis in the laboratory. Mesozooplankton organisms were  
160 identified and enumerated under a binocular stereomicroscope (Leica SAPO) to obtain  
161 the abundance ( $\text{ind m}^{-3}$ ). A priori observations of the samples for a total or aliquots



162 counting were carried out. In case of abundant samples, the quantification was carried  
163 out by examining aliquots (5 mL) randomly extracted from homogenized samples (200  
164 mL) and replaced (Boltovskoy, 1981) until 10% volume of each sample was counted.  
165 The mesozooplankton community was divided into nine groups shown in Table 1.  
166 Jellyfish were identified at the lowest possible taxonomic level and counted under a  
167 binocular stereoscopic microscope (Nikon SMZ645) to obtain abundance ( $\text{ind } 10^3 \text{ m}^{-3}$ )  
168 based on total counting. Jellyfish identification was based on Bouillon (1999), Bouillon  
169 et al. (2004, 2006), and synonyms in Oliveira et al. (2016).

## 170 **2.5 Data analysis**

171 We calculated different diversity indexes to evaluate the jellyfish community,  
172 such as the richness index/number of species ( $S$ ), the Shannon-Wiener index ( $H'$ )  
173 (Shannon and Weaver, 1949), and Pielou's index evenness ( $J$ ) (Pielou, 1984), for the  
174 different stations, depths, seasons and years based on the sample composition and  
175 abundance. Data were analyzed using non-parametric tests because of the rejection of  
176 normality and homoscedasticity hypothesis. Comparisons among environmental  
177 variables, total jellyfish abundance, and diversity indexes were examined using the  
178 Mann-Whitney test for depth, seasons, and years, while the Kruskal-Wallis test was  
179 performed for sampling stations. R Statistical Software (R Core Team, 2018) was used  
180 for statistical analysis and plotting. The *vegan* package was used for biodiversity  
181 analysis. To test the presence of groups in the set of jellyfish samples (null hypotheses  
182 of "absence of structure"), the similarity profile routine (SIMPROF) was applied (Clarke  
183 et al., 2008), followed by hierarchical agglomerative clustering (CLUSTER) coupled with  
184 group-average linkage. This technique was based on triangular matrices using the  
185 Bray-Curtis similarity index on  $\log(x+1)$ -transformed abundance data to enhance the  
186 contribution of the less abundant taxa (Clarke and Warwick, 2001). Similarity  
187 percentage analysis (SIMPER) was then used to identify the species and/or taxa that  
188 contributed the most to each jellyfish group. It examines the contribution of each taxon  
189 to the similarity within each group already detected by SIMPROF and the dissimilarity  
190 between the groups. The relationship between jellyfish community composition and  
191 environmental variables were evaluated with Spearman correlation tests from the *stats*  
192 package and a Redundancy Analysis (RDA) also using R. In addition, the relationship  
193 between the jellyfish and other zooplankton groups were evaluated, considering  
194 published abundances in Nocera et al. (2021) and unpublished data by the same



195 authors (Table 1). In both cases, abundances were previously transformed using the  
 196 Hellinger transformation (Legendre and Gallagher, 2001). Differences in RDA analyses  
 197 were considered significant at a  $p$ -value  $< 0.05$ . All jellyfish and mesozooplankton  
 198 abundances and the values of the environmental parameters are presented as the  
 199 mean  $\pm$  standard deviation.

200 Table 1. List of genera and/or species of each mesozooplankton group from this study  
 201 and Nocera et al. (2021) for October 2019 and 2020, and January 2020 and 2021 in  
 202 Nuevo Gulf.

Group	Acronym	Genus, species, and/or development stage
Apendicularians	AP	<i>Oikopleura</i> spp.
Diplostraca	DIP	<i>Evadne nordmanni</i> , <i>Podon</i> spp.
Large copepods	LCO	<i>Calanoides carinatus</i> , <i>Calanus australis</i>
Small copepods	SCO	<i>Paracalanus parvus</i> , <i>Ctenocalanus vanus</i> , <i>Oithona</i> spp., <i>Acartia</i> spp., <i>Drepanopus forcipatus</i>
Euphausiids	EU	<i>Euphausia</i> spp. larvae
Bryozoa	BRY	Cypris larvae
Decapoda	DEC	Larvae of <i>Munida</i> spp., <i>Pachycheles chubutensis</i> , <i>Cyrtograpsus</i> spp., and unidentified Decapoda eggs and larvae
Chaetognatha	CHA	<i>Parasagitta</i> spp.
Ichthyoplankton	ICH	<i>Engraulis anchoita</i> (eggs), eggs and larvae of unidentified fishes

### 203 3. Results

#### 204 3.1 Environmental variables

205 Chlorophyll *a* mean values, without considering the different layers, varied by an  
 206 order of magnitude among years ( $1.83 \pm 0.88$  and  $0.68 \pm 0.57$  mg m<sup>-3</sup> in 2019 and 2020,  
 207 respectively) and were significantly higher ( $p < 0.05$ ) in spring than in summer ( $0.37 \pm$

208 0.54 and  $0.14 \pm 0.11 \text{ mg m}^{-3}$  in 2020 and 2021, respectively) (Fig. 2a). Average  
 209 phaeopigment values showed patterns similar to those of chlorophyll *a*, being higher in  
 210 spring ( $2.58 \pm 1.24$  and  $0.1 \pm 0.1 \text{ mg m}^{-3}$  in 2019 and 2020, respectively) than in summer  
 211 ( $0.52 \pm 0.81$  and  $0.01 \pm 0.02 \text{ mg m}^{-3}$  in 2020 and 2021, respectively) (Fig. 2b) but no  
 212 significant differences were found between seasons ( $p = 0.06$ ).

213 The average seawater temperature was significantly lower for spring ( $10.93 \pm$   
 214  $0.42$  and  $10.51 \pm 0.44 \text{ }^\circ\text{C}$  in 2019 and 2020, respectively,  $p < 0.05$ ), being the surface  
 215 layer warmer than the intermediate one (Fig. 2c). During summer, the highest  
 216 temperature was recorded at  $18.2 \text{ }^\circ\text{C}$  for station F (January 2021 at surface layer), while  
 217 mean values were higher than those recorded during spring ( $14.65 \pm 2.08$  and  $15.85 \pm$   
 218  $1.97 \text{ }^\circ\text{C}$  in 2020 and 2021, respectively,  $p < 0.05$ ) (Fig. 2c).

219 Nitrates plus nitrites did not show significant differences between seasons (Table  
 220 2) but presented higher values in the first two surveys ( $3.42 \pm 4.31$  and  $3.93 \pm 2.98 \text{ } \mu\text{M}$   
 221 in spring 2019 and summer 2020, respectively) compared to the last two ( $1.72 \pm 0.96$   
 222 and  $1.94 \pm 1.85 \text{ } \mu\text{M}$  in spring 2020 and summer 2021, respectively), always being higher  
 223 (but not significant  $p = 0.69$ ) in the intermediate layer irrespective of season or year  
 224 (Fig. 2d). Regarding ammonium, both springs presented significantly higher values  
 225 ( $0.83 \pm 0.93$  and  $0.65 \pm 0.22 \text{ } \mu\text{M}$  in 2019 and 2020, respectively, Table 2) compared to  
 226 summer, with similar average values in both years ( $0.14 \pm 0.05$  and  $0.13 \pm 0.08 \text{ } \mu\text{M}$  in  
 227 2020 and 2021, respectively; Fig. 2e). Lower phosphate concentrations were found in  
 228 the first two samples ( $1.11 \pm 0.19$  and  $1.2 \pm 0.24 \text{ } \mu\text{M}$  in spring 2019 and summer 2020,  
 229 respectively) than in the last two samples ( $2.53 \pm 0.59$  and  $2.08 \pm 0.27 \text{ } \mu\text{M}$  in spring  
 230 2020 and summer 2021, respectively; Fig. 2f), without significant differences between  
 231 seasons (Table 2).

232 Salinity was constant during all surveys and between seasons (Table 2), showing  
 233 an average value of  $33.98 \pm 0.04 \text{ PSU}$  (not shown in Fig. 2).

234 Table 2. Summary of the  $p$ -values obtained in the contrasts analysis for the  
 235 environmental variables when they were compared between years (2019, 2020 vs.  
 236 2021) and seasons (spring vs. summer).

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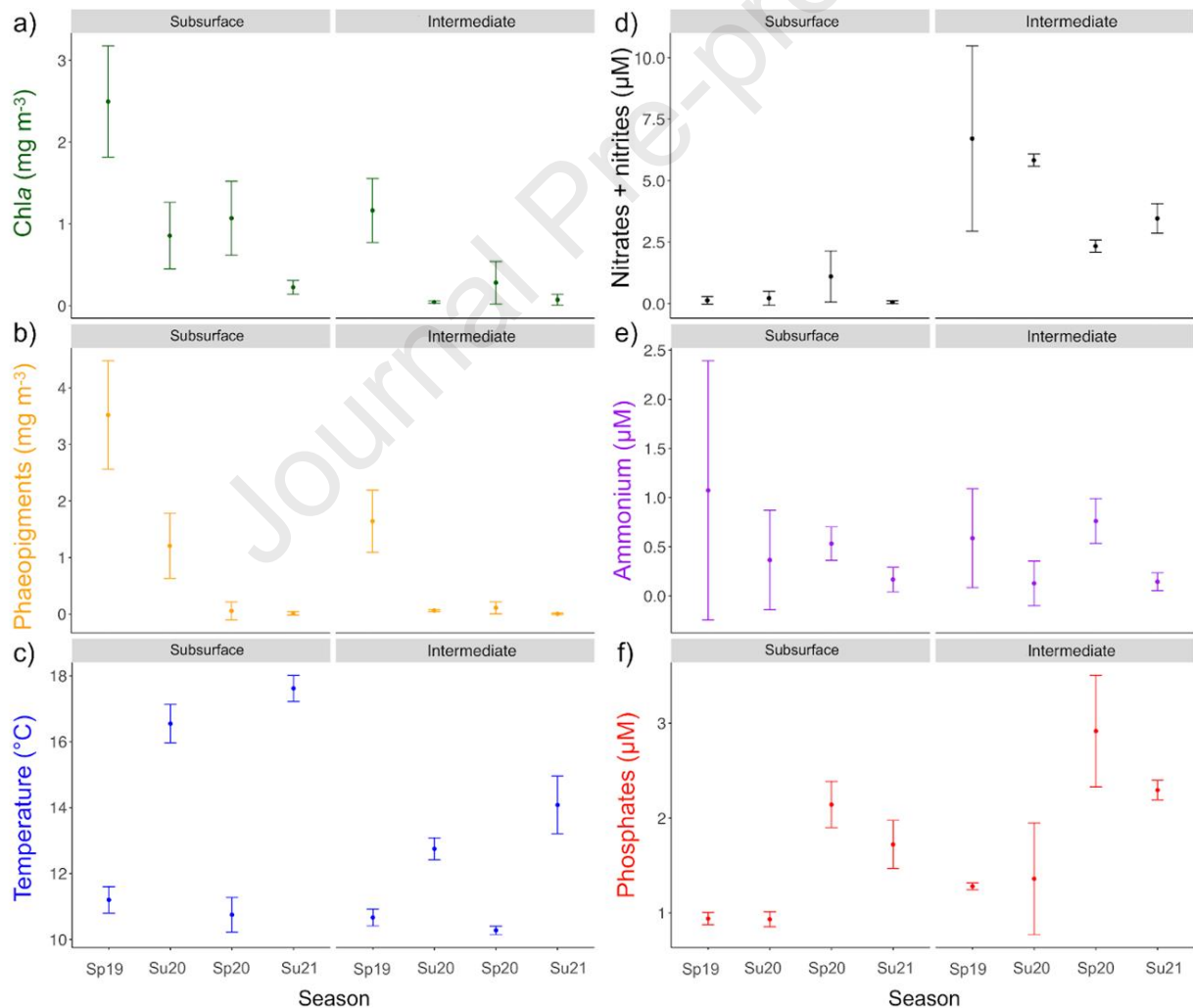
Years

Seasons

---

<b>Chlorophyll a</b>	*	*
<b>Phaeopigments</b>	*	0.06
<b>Temperature</b>	*	*
<b>Nitrates + nitrites</b>	0.73	0.85
<b>Ammonium</b>	*	*
<b>Phosphates</b>	*	0.76
<b>Salinity</b>	0.14	0.28

237 \*  $p < 0.05$

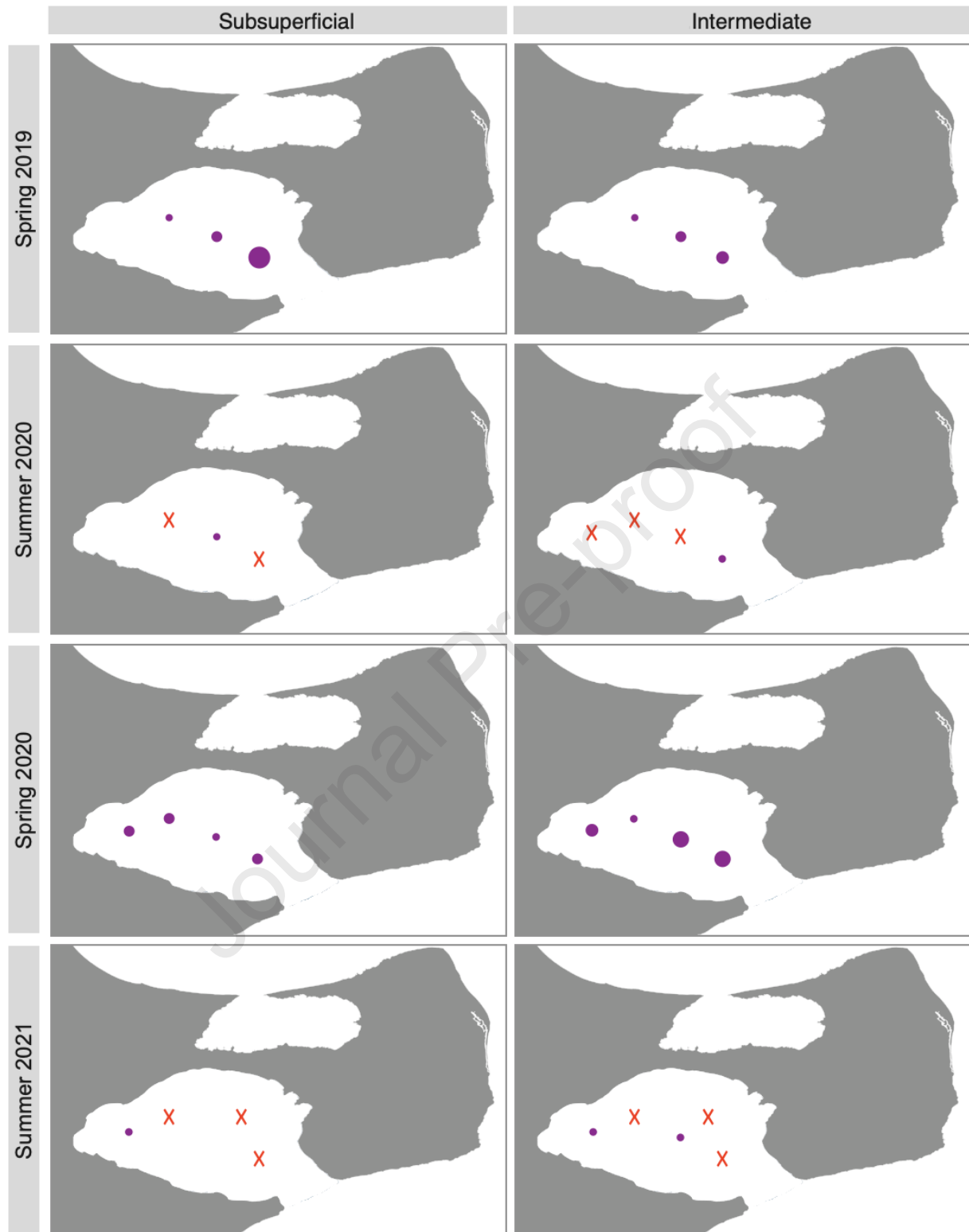


238  
 239 Figure 2. Seasonal and interannual average values ( $\pm$  SD) of a) chlorophyll a (mg m<sup>-3</sup>),  
 240 b) phaeopigments (mg m<sup>-3</sup>), c) temperature (°C), d) nitrates plus nitrites (μM), e)  
 241 ammonium (μM) and f) phosphates (μM) for the subsurface (1 m) and intermediate (70  
 242 m) layers in the Nuevo Gulf. Sp: spring. Su: summer.

### 243 **3.2 Jellyfish composition, abundance and diversity**

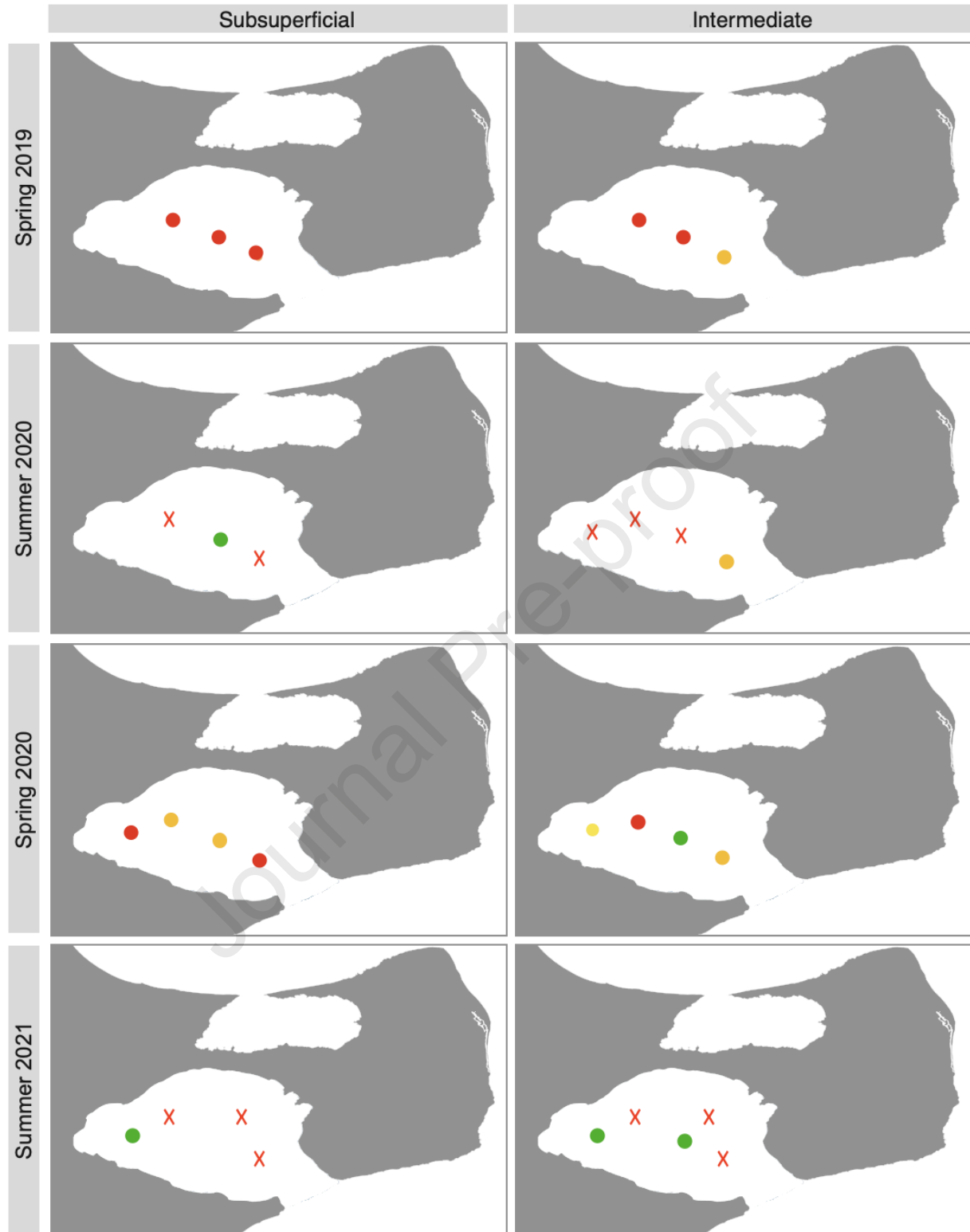
244 From the 30 samples analyzed for the study period, 19 presented at least one  
245 medusa. No ctenophores were found in the samples. Sixteen Hydromedusae species  
246 and small juveniles of one Scyphomedusae were identified from a total of 883  
247 individuals (Table 3). Total jellyfish abundance ranged between 35.1 and 6210 ind  $10^3$   
248  $m^{-3}$ , with significantly higher average values in spring ( $1918.15 \pm 1524.85$  ind  $10^3$   $m^{-3}$ ,  
249  $p < 0.05$ ) than in summer ( $38.89 \pm 86.46$  ind  $10^3$   $m^{-3}$ ) ( $W = 210$ ,  $p < 0.001$ ; Fig. 3). No  
250 significant differences were found in total jellyfish abundance among sampling stations  
251 or between depths ( $X^2 = 4.46$  and  $W = 111$  and,  $p = 0.72$  and  $0.77$  for stations and  
252 depths, respectively). The highest abundance for spring 2019 was found in the upper  
253 layer and near the NG mouth (6210 ind  $10^3$   $m^{-3}$  for station A), while for spring 2020,  
254 abundances showed larger values in the intermediate layer, but again near the mouth  
255 and the center of the gulf (3324.2 and 3292.2 ind  $10^3$   $m^{-3}$ , for stations A and B,  
256 respectively). On two occasions, jellyfish species were represented by a single genus,  
257 *Obelia* spp. (station D in January 2021 at both layers), or a single species, *Euphysa*  
258 *aurata* (station B in January 2020 for the intermediate layer). None of the species or  
259 genera were present at all sampling stations during the study period. The highest  
260 contribution to the jellyfish community was given by *Eucheilota ventricularis* (41.06%),  
261 followed by unidentified Leptothecata jellyfish (15.88%), *Clytia simplex* (14.16%),  
262 *Mitrocomella frigida* (6.33%), and *Cosmetirella davisii* (5.04%). All the remaining taxa  
263 represented less than 4% of the total gelatinous zooplankton community (Table 3).

264 The highest richness values were found in all cases in the subsurface layer and  
265 during spring ( $S = 12$  at station A;  $S = 11$  at station D, and  $S = 10$  at station B). The  
266 highest diversity was also detected in the subsurface layer during spring, with maximum  
267 values at the nearest station to the coastline, station D ( $H' = 2.03$ ), followed by stations  
268 B ( $H' = 1.98$ ) and C ( $H' = 1.92$ ) (Fig. 4). Maximum equitability was found in station C,  
269 both in the subsurface ( $J' = 0.92$ ) and intermediate ( $J' = 0.90$ ) layers, followed by station  
270 B in the subsurface layer ( $J' = 0.86$ ). Significant differences in equitability were observed  
271 only between seasons being higher in spring ( $W = 209.5$ ,  $208$ , and  $145$  in  $S$ ,  $H'$ , and  $J'$ ,  
272 respectively,  $p < 0.001$ ).



Abundances (ind  $10^3 \text{ m}^{-3}$ ):  $\bullet < 1 \times 10^3$   $\bullet 1-2 \times 10^3$   $\bullet 2-3 \times 10^3$   $\bullet 3-4 \times 10^3$   $\bullet \geq 4 \times 10^3$  X no Jelly

273  
 274 Figure 3. Spatial and temporal distribution of jellyfish abundances (ind  $10^3 \text{ m}^{-3}$ ) in the  
 275 subsurface (30 m) and intermediate layers (70 m) within Nuevo Gulf during spring 2019,  
 276 summer 2020, spring 2020, and summer 2021.



277

278

279

280

Figure 4. Spatial and temporal distribution of the Shannon-Wiener index ( $H'$ ) for jellyfish in the subsurface (30 m) and intermediate layers (70 m) within Nuevo Gulf during spring 2019, summer 2020, spring 2020, and summer 2021.

281 Table 3. List of jellyfish taxa found in Nuevo Gulf during all surveys (spring 2019,  
 282 summer 2020, spring 2020, and summer 2021). R%: relative abundance of jellyfish  
 283 (genus or species) over total gelatinous zooplankton expressed as a percentage.

Genus or species	Abundance (ind 10 <sup>3</sup> m <sup>-3</sup> )		
	Mean	Maximum	R%
<i>Aequorea coerulea</i>	5.64	73.44	0.62
<i>Amphinema rugosum</i>	5.42	48.51	0.59
<i>Bougainvillia muscus</i>	3.92	38.65	0.43
<i>Clytia hemisphaerica</i>	34.12	533.64	3.73
<i>Clytia gracilis</i>	1.62	48.51	0.18
<i>Clytia lomae</i>	10.07	85.08	1.10
<i>Clytia simplex</i>	129.54	1082.3	14.16
<i>Cosmetirella davisii</i>	46.16	388.11	5.05
<i>Eucheilota ventricularis</i>	375.68	3216.8	41.08
<i>Euphysa aurata</i>	2.46	38.65	0.27
<i>Hybocodon chilensis</i>	1.89	56.72	0.21
<i>Laodicea undulata</i>	12.66	66.65	1.38
<i>Leuckartiara octona</i>	2.83	84.93	0.31
<i>Mitrocomella brownei</i>	23.08	125.63	2.52
<i>Mitrocomella frigida</i>	57.97	485.08	6.34
<i>Mitrocomella polydiademata</i>	25.78	291.08	2.82
<i>Obelia</i> spp.	17.27	95.03	1.89
<i>Chrysaora plocamia</i>	11.22	115.96	1.23
Leptothecata	145.21	1164.3	15.88
Hydroidolina	2.06	36.72	0.23

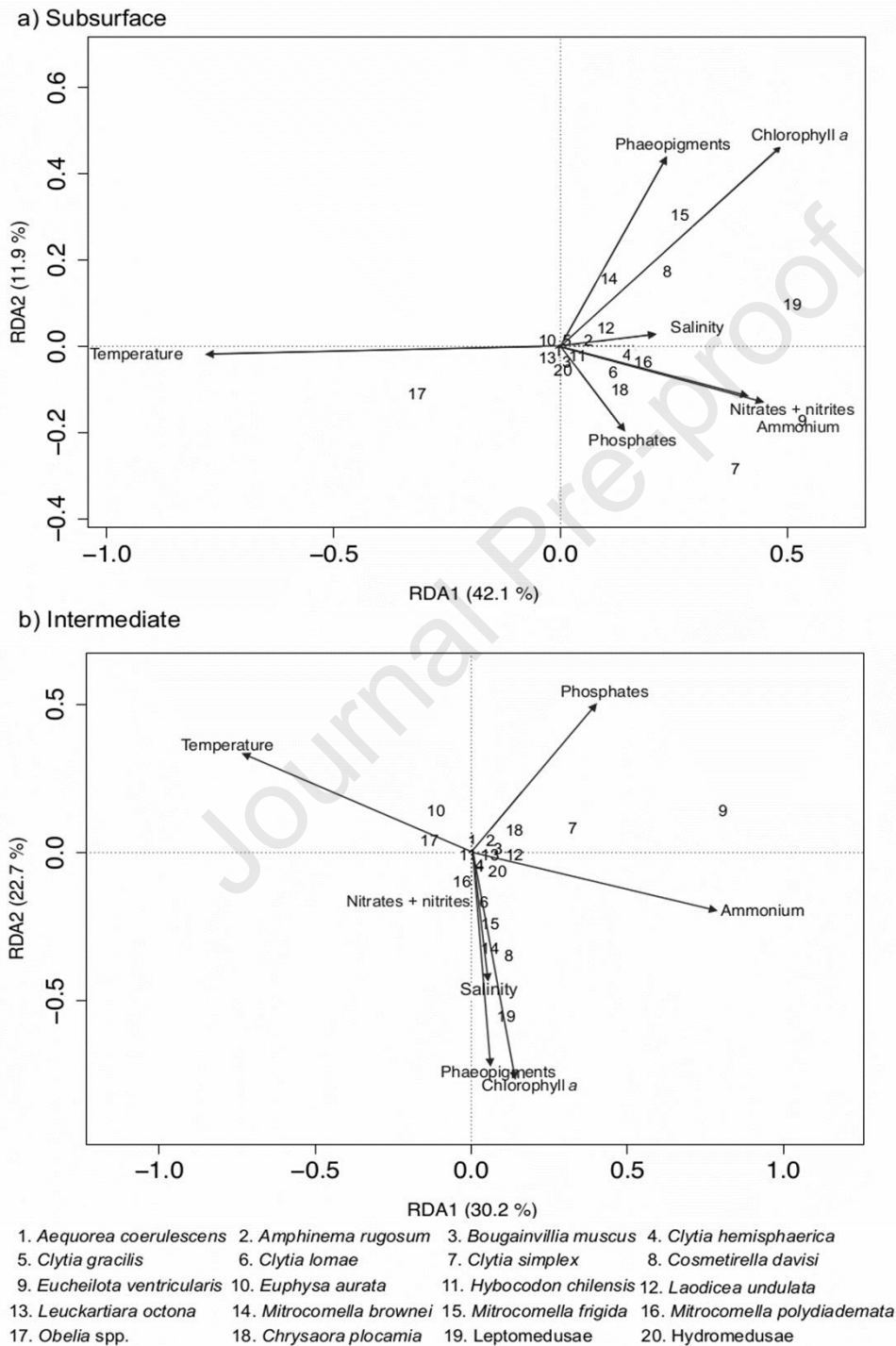
### 284 3.3 Jellyfish assemblage

285 Two jellyfish species clusters (G1 and G2) were detected (SIMPROF:  $P_i = 9.36$ ,  
 286  $p = 0.001$ ) (Fig. 5). The G1 (average similarity of 94.85%) consisted of three sampling  
 287 points (stations D subsurface and intermediate, and B subsurface) during summer 2020  
 288 and 2021, and was entirely formed by the contribution of *Obelia* spp. (100%). The G2





309 significant (Fig. 6a). On the contrary, the RDA ordination diagram for the intermediate  
 310 layer showed that chlorophyll *a*, temperature, and ammonium significantly explained  
 311 (52.9%,  $p < 0.05$  after 999 permutations) the jellyfish genera and species variability in  
 312 relation to their abundance and composition (Fig. 6b).



313

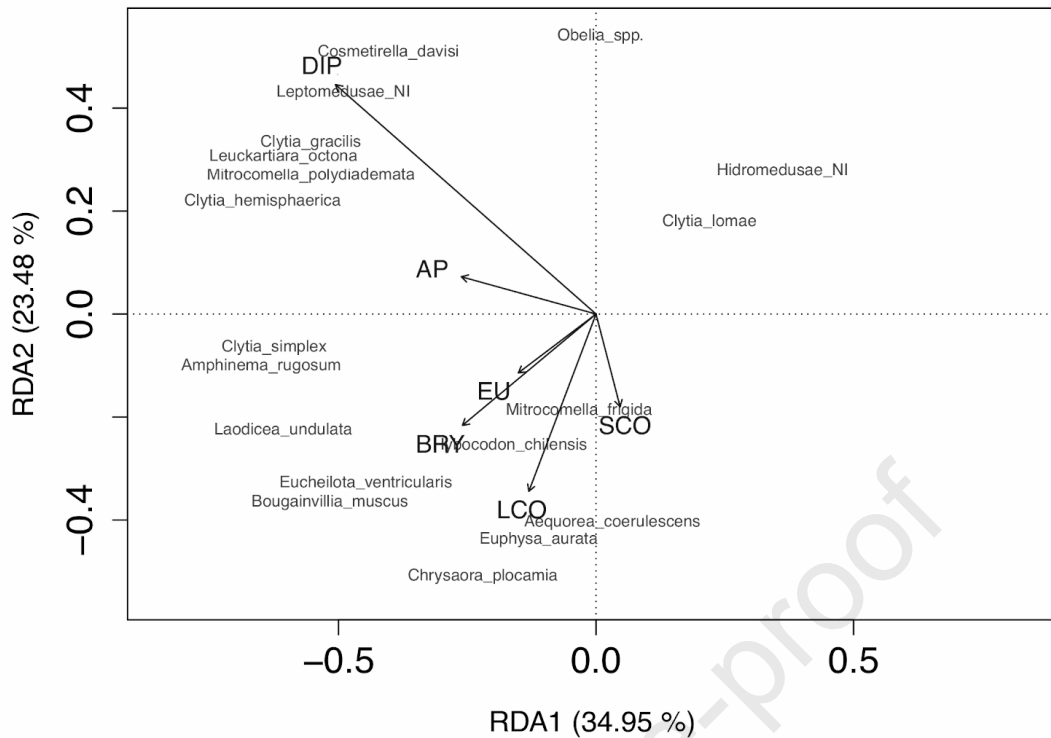
314 Figure 6. RDA ordination of jellyfish species and genera abundance and environmental  
 315 predictors (chlorophyll *a*, phaeopigments, temperature, salinity, ammonium, nitrates  
 316 plus nitrites and phosphates) at the 30-m subsurface layer (a) and 70-m intermediate

317 layer (b) during spring (2019 and 2020) and summer (2020 and 2021), and across  
318 sampling stations (A, B, C, and D) in Nuevo Gulf.

### 319 **3.5 Relationship with other mesozooplankton groups**

320 Total jellyfish abundance negatively correlated, but not significantly, with all  
321 groups when considering both seasons together (spring and summer). The strong  
322 negative correlation between total jellyfish abundance and temperature and the  
323 opposite association between the potential prey (non-gelatinous mesozooplankton  
324 groups) and temperature may mask some associations between jelly species and their  
325 potential prey. For this reason, data were explored considering seasons separately.  
326 Significant and positive correlations were found when the abundance of jellyfish species  
327 was analyzed taking into account the mesozooplankton groups in spring; *C.*  
328 *hemisphaerica* with LCO ( $\rho = 0.56$ ,  $p < 0.05$ ), *Obelia* spp. with DIP ( $\rho = 0.55$ ,  $p <$   
329  $0.05$ ), *L. undulata* with BRY ( $\rho = 0.65$ ,  $p < 0.05$ ) and DEC ( $\rho = 0.55$ ,  $p < 0.05$ ), and  
330 *C. davisii* with DEC ( $\rho = 0.58$ ,  $p < 0.05$ ), EU ( $\rho = 0.82$ ,  $p < 0.001$ ), AP ( $\rho = 0.65$ ,  $p$   
331  $< 0.05$ ) and DIP ( $\rho = 0.79$ ,  $p < 0.001$ ). No significant correlations were found among  
332 single jellyfish taxa, which occurred several times in summer (*Obelia* spp.), or  
333 mesozooplanktonic groups.

334 In the RDA analysis, taking into account only spring after the results mentioned  
335 above, the first two axes explained together 58.43% of the total variability in the jellyfish  
336 abundance related to other mesozooplankton groups (Fig. 7). The RDA1 (34.95%)  
337 explained the variability in jellyfish abundance mainly by the separation of SCO from  
338 LCO, EU and BRY. On the other hand, the RDA2 (23.48%) was positively associated  
339 with DIP and AP compared to the rest of the mesozooplankton groups. The exclusion  
340 criterion was used to leave out the groups that did not contribute to the explanation of  
341 the jellyfish abundance, which eliminated the taxonomic groups CHA, DEC and ICH.



342

343 Figure 7. RDA ordination of jellyfish mean abundance and mesozooplankton groups  
 344 during spring (2019 and 2020) in Nuevo Gulf. AP: appendicularians, BRY: bryozoans,  
 345 DIP: diplostracans, EU: euphausiids, LCO: large copepods, SCO: small copepods.

#### 346 4. Discussion

347 This work presents the first spatiotemporal analysis of the abundance distribution  
 348 and species assemblage of gelatinous zooplankton organisms in NG, an understudied  
 349 coastal ecosystem within the VBR (northern Patagonia, SWA). Even though the original  
 350 sampling strategy was not designed to study jellyfish, the high abundance of these  
 351 organisms provided a unique opportunity to expand knowledge on gelatinous  
 352 zooplankton in the region. The jellyfish community in NG was mainly represented by  
 353 hydrozoan species previously recorded in the surroundings of the gulf (Guerrero et al.,  
 354 2013; Dutto et al., 2019), although never cited for NG itself (see Esteves et al., 1997;  
 355 Menéndez et al., 2011; D'Agostino et al., 2018). In this sense, our study increases the  
 356 list of planktonic Hydromedusae for the NG by at least 18 species, some of which are  
 357 cryptic (e.g., *Obelia* spp.; Govindarajan et al., 2006). Furthermore, several individuals  
 358 could not be identified due to external damage or poor preservation. The only recorded  
 359 scyphozoan jellyfish species was *C. plocamia* (only juveniles), which is relatively  
 360 common in northern Patagonian coasts between 42° and 47°S (Schariti et al., 2018).  
 361 Although we expected ctenophore species such as *Pleurobrachia pileus* and

362 *Mnemiopsis leidyi* to be seasonally abundant in the area (Schiariti et al., 2021 and  
363 references therein), they were not recorded during the study period.

364 Hydrozoan and meroplanktonic jellyfish species prevailed in NG, and the  
365 community was dominated by Leptothecata followed by Anthoathecata, both orders  
366 typically represented in coastal waters (Gibbons and Richardson, 2009; Gibbons et al.,  
367 2009). The richness values recorded in NG were similar to those recorded at a larger  
368 basin, the San Matías Gulf, located north of the VBR (Fig. 1; Guerrero et al., 2013).  
369 Therefore, NG represents an interesting area for studying hydrozoan species diversity  
370 and composition. Recorded abundances were higher close to the gulf mouth in spring,  
371 probably explained by high local productivity in the ecosystem due to the intrusion of  
372 colder and nutrient-enriched continental shelf waters into the gulf persists until late  
373 spring, when the exchange of water masses decreases from 20% in early spring to 5%  
374 in late spring (Tonini et al., 2022). In addition, the species assemblage showed that the  
375 “spring group” was defined by leptomedusae species, mostly *E. ventricularis*. This  
376 species is frequent and seasonally abundant in temperate waters of the SWA,  
377 particularly in productive zones (Dutto et al., 2019; Puente Tapia and Genzano, 2019;  
378 Teixeira-Amaral et al., 2021), where it plays an important ecological role as a secondary  
379 host of endoparasites of fish (Diaz Briz et al., 2012). On the other hand, *Obelia* spp.  
380 were the only hydromedusae to occur several times during summer, outside the period  
381 of maximum productivity for the area (D'Agostino et al., 2018; Nocera et al., 2021),  
382 representing the “summer group”. *Obelia* is a common and abundant component of  
383 coastal habitats worldwide (Bouillon, 1995; Palma et al., 2007; Miglietta et al., 2008;  
384 Primo et al., 2012; Yahia et al., 2003). However, its ecological role has been poorly  
385 studied (Boero et al., 2007; Sutherland et al., 2016). Unlike many hydromedusae  
386 species, *Obelia* medusae can effectively capture and consume bacterioplankton and  
387 microplanktonic prey (Boero et al., 2007; Sutherland et al., 2016). During summer,  
388 *Obelia* may take advantage of other available prey different from the non-gelatinous  
389 zooplankton, surviving and growing under a microphagous diet in NG. Therefore, *Obelia*  
390 blooms could have a relevant role in modulating the microplankton and bacterioplankton  
391 communities (Boero et al., 2007).

392 Results indicated that temperature might modulate the jellyfish community in NG.  
393 Temperature is one of the main factors driving jellyfish reproduction, growth, and

394 feeding (Lucas et al., 2012; Möller and Riisgard, 2007; Boero et al., 2016). In some  
395 scyphozoan and hydrozoan jellyfish, the maximum specific growth and clearance rates  
396 increase exponentially within a temperature range but decline at higher temperatures  
397 (Matsakis, 1993; Möller and Riisgard, 2007). Sexual and asexual reproduction (e.g.,  
398 budding, strobilation) are also conditioned by temperature (Purcell, 2007; Lucas et al.,  
399 2012; Patry et al., 2014). In this sense, high abundances were observed during spring  
400 in northern VBR in the past (Guerrero et al., 2013), coinciding with our results in NG,  
401 where abundance was negatively correlated with temperature. This suggests that  
402 jellyfish populations may benefit from intermediate temperatures but be limited by  
403 higher ones. Temperature may also indirectly affect the medusa phase through food  
404 availability since the highest primary and secondary productivity in NG occurs in spring  
405 (D'Agostino et al., 2018; Nocera et al., 2021). The decrease in the planktonic medusa  
406 phase observed in summer may be due to a combination of high-temperature conditions  
407 limiting the gelatinous zooplankton abundance, the reduction or absence of asexual  
408 reproduction, and a bottom-up control mechanism where jellyfish depend on the  
409 occurrence of prey organisms (Pitt et al., 2007).

410 Positive correlations were found between jellyfish abundances with chlorophyll *a*  
411 and ammonium. Phytoplankton blooms during spring are often triggered by favorable  
412 environmental conditions after winter conditions, such as warmer temperatures,  
413 increased light levels, and high nutrient availability (e.g., Rasconi et al., 2015). Such  
414 conditions often lead to the proliferation of zooplankton and gelatinous taxa as their prey  
415 becomes more conspicuous. In turn, ammonia excretion by zooplankton and, to a lesser  
416 extent, by jellyfish has a potential contribution to phytoplankton requirements to growth,  
417 representing in some cases up to 43% of the total nitrogen demand (Alcaraz et al.,  
418 1994; Pitt et al., 2009). Bacterioplankton (not considered in this study) competition for  
419 nutrient supply, in addition to the possible decoupling between rate processes and  
420 phyto- and zooplankton abundances, may explain the apparent excess of regenerated  
421 ammonia (Alcaraz et al., 1994).

422 In spring, some jellyfish taxa were associated with specific zooplankton groups,  
423 such as large copepods, diplostracans, euphausiids, and bryozoans, reinforcing the  
424 higher jellyfish abundance in spring compared to summer. This may be associated with  
425 colder and more nutrient-rich waters remaining from the winter vertical mixing process



426 and the absence of a water column stratified structure (Guerrero et al., 2013; Tonini et  
427 al., 2022). The weak link between gelatinous predators and their potential prey, when  
428 both seasons were considered, may be partially explained by the relatively low  
429 abundance of jellyfish compared to the remaining zooplankton organisms. At this point,  
430 it is important to note that the mesh size used in this work may underestimate the  
431 abundance of small species, as well as larval stages of zooplankton (Antacli et al.,  
432 2010), preventing the observation of relationships between the groups. It might also be  
433 masked by the strong but opposed associations between both the jellyfish abundance  
434 and the remaining zooplankton groups' abundance with temperature. It is widely known  
435 that hydrozoan jellyfish can prey heavily on different size classes of mesozooplankton  
436 and fish eggs and larvae (Purcell and Arai, 2001; Stibor and Tokle, 2003), hence  
437 modulating ecosystem dynamics. Additionally, jellyfish are sensitive to prey availability,  
438 which controls the interannual variability of the gelatinous zooplankton population  
439 (Chiaverano et al., 2013).

#### 440 **4.1 Some additional considerations**

441 A baseline question derived from our study is, to what degree are seasonal  
442 differences in jellyfish abundance driven by physical factors (e.g., currents or nutrients)  
443 vs. biological factors (e.g., food quality/quantity)? Further studies focusing on more  
444 sampling sites, especially on the northern and southern coasts of the gulf, and a broader  
445 temporal scale, are needed to more comprehensively answer this question. Including  
446 other seasons, such as autumn, and/or intensifying sampling during spring, may be  
447 beneficial to understand the seasonal dynamics of jellyfish in the area. Other potentially  
448 important environmental variables not included in this study should be considered as  
449 they can modulate the abundances and distribution patterns (vertically and/or  
450 horizontally) of jellyfish. For example, dissolved and particulate organic matter is  
451 sometimes used as secondary food source when phytoplankton abundance is low, or  
452 dissolved oxygen and apparent oxygen utilization is relevant as jellyfish have shown to  
453 tolerate low oxygen concentrations to avoid predation (Lucas et al., 2014; Morais et al.,  
454 2017).

455 Recent literature including reviews and some new findings focusing on  
456 gelatinous zooplankton along the Argentinean platform, left out some important areas  
457 of the Patagonian region, particularly its gulfs (Díaz Briz et al., 2017; Schiariti et al.,



458 2018, 2021; Dutto et al., 2019). In addition, most of these works focused on jellyfish  
459 assemblages rather than exploring hydrography as the cause for their distribution and  
460 diversity, and considering only temperature and salinity to explain multispecies  
461 (Guerrero et al., 2013) and *Cunina octonaria* patterns (Puentes-Tapia et al., 2020). We  
462 found that chlorophyll *a* and ammonium may also be important factors in the jellyfish  
463 dynamics determined at the community level, although more studies should be carried  
464 out on this regard.

465 Experiments focused on studying the relationship between feeding and medusa  
466 development, as well as determining the optimal thermal range for reproduction and the  
467 specific temperature that triggers medusa production, are needed to confirm some of  
468 the observed results. In addition, trophic experimental studies, such as gut content and  
469 trophic biomarkers analysis from field-collected *Obelia*, may help to confirm the  
470 presence of only this genus during summer. The simultaneous study of jellyfish'  
471 potential prey and predators could further shed light on their role in the NG food web.  
472 These represent some ideas to start bridging the current gap in gelatinous zooplankton  
473 knowledge in the region.

## 474 **5. Conclusions**

475 The present study reveals for the first time the temporal and spatial variation of  
476 jellyfish abundance and diversity in Nuevo Gulf on the southern coast of Valdés  
477 Biosphere Reserve. We have explored the connection between taxa within the  
478 gelatinous zooplankton group itself, and described their association with environmental  
479 features in an area with no previous detailed characterizations of this community. The  
480 dynamics of the jellyfish community appear to be driven mostly by temperature,  
481 chlorophyll *a* and ammonium, all higher during spring compared to summer, reflecting  
482 the seasonality described for the NG. In addition, the highest abundance found close to  
483 the mouth of the gulf may be related to the advection of colder and nutrient-rich waters,  
484 although no clear patterns were found with depth or across sampling stations. Further  
485 research on jellyfish from the Patagonian coast must be carried out due to the biological,  
486 ecosystemic and socio-economic importance of these organisms in this marine  
487 ecosystem.

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**Highlights:**

- Jellyfish abundance and diversity from Nuevo Gulf (Argentina) obtained for the first time
- Abundance was higher during spring, associated to chlorophyll *a* and ammonium, but negatively related to temperature
- Seasonality is an important factor in modulating the jellyfish community dynamic

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**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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