



## BIOLOGICAL SCIENCES

# Spring and summer ichthyoplankton assemblages in a temperate Patagonian gulf: an overview of temporal and spatial patterns on their structure

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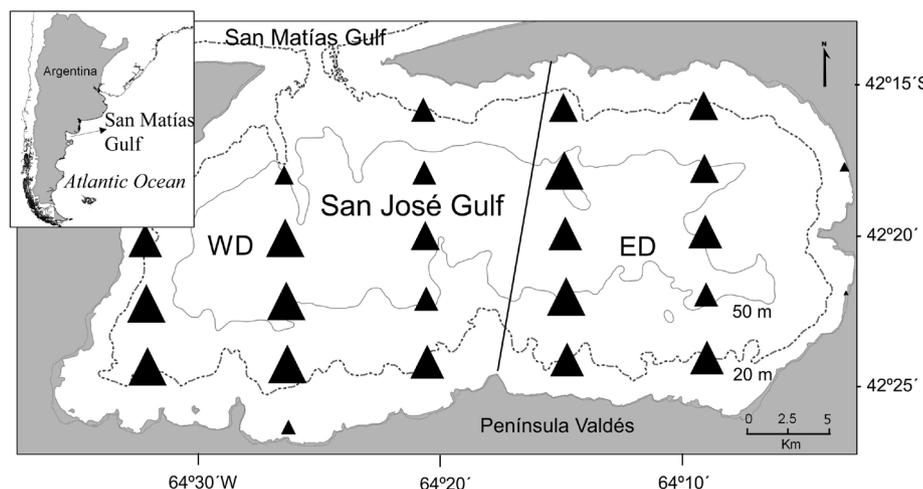
**Abstract:** Knowing about the spatio-temporal patterns in the structure of ichthyoplankton assemblages allows inferring about the spawning behaviour of adult fishes, understanding the recruitment dynamics, and predicting the potential effects of mid- and long-term changes. Here, we studied the ichthyoplankton assemblages from the San José Gulf (Northern Patagonia, Argentina) and investigated their changes in space and time. To do that, we took monthly samples during two consecutive years, in spring and summer. A total of 2088 larvae were caught; they comprised 36 taxa, from which 14 were identified to species, two to genus, one to family and one to order. There were large differences in the structure of the assemblages between years, coincidentally with marked changes in the surface water temperature. The structure of the ichthyoplankton assemblages also showed significant differences between the spring and summer: *Helcogrammoides cunninghami*, *Dules auriga* and larvae belonging to the family Engraulidae contributed most to these differences. The species diversity was higher in the colder year than in the warmer one. We discuss the potential role of environmental and oceanographic features on the interannual variability in the early stages of coastal fishes within a small gulf.

**Key words:** environmental variability, fish larvae, small gulfs, Southwest Atlantic Ocean, temperate waters.

## INTRODUCTION

The biology and early life-history of fishes, together with environmental and hydrographical factors, influence the occurrence, distribution, and abundance of fish larvae, and model the spatio-temporal patterns in the structure (*sensu* Begon 2006) of ichthyoplankton assemblages (e.g., Fig. 1 in Doyle et al. 1993). The study of these patterns can provide information both about the localization (in space and time) and about the spawning strategies of the adult fishes (Doyle et al. 1993, Paulic & Papst 2013). At the spatial scale, topographic features such

as bathymetry and bottom type, together with other mechanisms that affect the primary production (e.g., upwellings, marine fronts) as well as the behavior of the adults, determine the spawning areas, while physical processes influence the final distribution patterns of the early stages (Sabatés 1990, Sabatés & Olivar 1996, Alemany et al. 2006). At the temporal scale, the assemblages' composition may vary broadly (Guan et al. 2015). Larval fish assemblages in coastal waters undergo important changes in abundance and composition (Álvarez et al. 2012) due to the seasonality of reproductive timing for different species (e.g., Barletta-Bergan



**Figure 1.** Location of the oceanographic stations in the San José Gulf. WD and ED indicate the western and eastern domains, respectively (sensu Amoroso & Gagliardini 2010). The black line indicates the approximate location of the San José frontal system, which divides the gulf in two domains. The size of the triangles is proportional to the total number of tows made in each station (from 1 to 9) throughout the study.

et al. 2002, Ramos et al. 2006, Sabatés et al. 2007, Primo et al. 2010). In temperate regions, these seasonal changes are mainly related to water temperature, photoperiod, and food availability (McKaye 1984, Payne 1986). Less cyclical phenomena (e.g., thermal anomalies, and circulation and stratification patterns) modifying the oceanographic environment may also cause interannual variation in the spawning strategies, which may encompass timing, duration, and location of the spawning (Doyle et al. 1993). Hence, the structure of ichthyoplankton assemblages may change with a combination of multiple factors (Auth 2008, Brodeur et al. 2008), including, among others, temperature and salinity (Auth & Brodeur 2006, Parnel et al. 2008), overfishing and composition of the copepod community (Bui et al. 2010), spawning stock biomass and spawning location, and the occurrence of oceanographic currents that may advect eggs and larvae to different areas (Auth et al. 2011).

Some information on these sources of spatio-temporal variation exists for large semi-enclosed environments of the Northern Hemisphere, such as the Gulf of Alaska or the Strait of Georgia (Lanksbury et al. 2005, Guan et al. 2015). However, smaller gulfs, potentially

more dependent on environmental variability, have received less attention as is the case of the San José Gulf (SJG), Argentina, located in the Southern Hemisphere. The SJG (42°20'S, 64°19'W) is a shallow, semi-enclosed basin from Northern Patagonia, located in the transition region between two biogeographic provinces (Balech & Ehrlich 2008, Galván et al. 2009). The gulf is divided into two oceanographic domains (West and East domains) by a thermal front that forms in spring and summer (Amoroso & Gagliardini 2010). Waters in the western domain are homogeneous throughout the year, but stratification occurs in the eastern domain during spring and summer (Amoroso et al. 2011, Crespi-Abril et al. 2014). Recent work attributed changes in the mesozooplankton community to this particular oceanographic feature (Hernández Moresino et al. 2017). The area involving Península Valdés and the SJG has a long and complex history of protection, which dates back to 1967 (A. Cinti et al., unpublished data). It was declared as a Natural World Heritage Site by UNESCO in 1999, and now it is also included within the Valdés Biosphere Reserve<sup>1</sup>, mainly

<sup>1</sup><http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/latin-america-and-the-caribbean/argentina/valdes> (accessed 18.05.18).

due to its importance for the reproduction and conservation of charismatic marine birds and mammals. Other components of this ecosystem, however, have never been included in the conservation agendas. Paradoxically, despite the economic relevance of the marine resources from the Patagonian region, whose productivity sustains highly lucrative industrial fisheries (Góngora et al. 2012, Irusta et al. 2016), the ichthyoplankton assemblages of the Argentine Sea, particularly south of 41°S, have not been studied in detail (but see some preliminary information in Ciechomski et al. 1975, 1981, Ehrlich et al. 1999, Acha et al. 2012, and M. Sylvester et al., unpublished data). The lack of systematic monitoring of ichthyoplankton assemblages within the Northern Patagonian gulfs of Argentina and along the country's inner continental shelf has led to an information gap that also reaches the taxonomy. Only less than 20% of the early stages of the bony fishes inhabiting the Argentine Sea were described, and some descriptions of the early stages of even commercially important species were made only recently (e.g., Betti et al. 2009, Derisio et al. 2012, Villanueva Gomila et al. 2015).

The main goal in this study was to investigate the spatio-temporal patterns in the structure of larval fish assemblages within a small semi-enclosed basin, the SJG, strongly influenced by its surrounding waters, and to shed light about the potential effects of water temperature and oceanographic features on the ichthyoplankton composition. The main questions that we address in this work comprise: i) Do the ichthyoplankton assemblages of the SJG show any temporal differences at the seasonal and/or annual scales?; ii) Do the ichthyoplankton assemblages show clear spatial patterns within the SJG?; and iii) Which environmental factors may affect the structure of ichthyoplankton assemblages within the SJG?

## MATERIALS AND METHODS

### Study site

The northwestern margin of the SJG presents a narrow mouth (6.9 km width) that connects it with the much larger and deeper San Matías Gulf (SMG), through which up to 15% of the total water volume of the SJG flows in and out during each semidiurnal tidal cycle (Rivas 1990) (Fig. 1). The asymmetrical position of the gulf mouth combined with a strong year-round semilunar tidal circulation produces a homogeneous structure of the water column in the western area, while the eastern side is less affected allowing spring-summer stratification (Amoroso et al. 2011, Crespi-Abril et al. 2014). As a result, a frontal system forms during approximately half of the year, which divides the SJG into a western (WD) and an eastern (ED) hydrographic domain (Amoroso & Gagliardini 2010). The complexity of this system is further enhanced by the arrival of fertilized waters from the coastal, vertically-mixed side of the tidal front that develops off Península Valdés (Amoroso & Gagliardini 2010). In a recent article where the samples collected in the survey described below were used, the hydrodynamic differences between domains were associated with changes in the structure of the mesozooplankton community (Hernández Moresino et al. 2017). Furthermore, seasonal and interannual variations in the abundance and composition of the mesozooplankton were associated with differences in the chlorophyll-a concentration and water temperature in the SJG (Hernández Moresino et al. 2017).

### Sampling

A total of 155 ichthyoplankton samples were collected on a monthly basis in spring and summer during a 2-year survey that we conducted aboard outboard motorboats in the SJG, covering a regular grid of 25 stations

(of which 5 to 23 were surveyed each month) (Fig. 1), from October 2011 to March 2012 and from October 2012 to March 2013 (henceforth 'Year 1' and 'Year 2', respectively). No samples were available for January and November 2012. Ichthyoplankton tows were made with a Hensen net with a mouth diameter of 70 cm fitted with 300- $\mu\text{m}$  mesh. A General Oceanics R2020 flowmeter (Miami, United States) was mounted in the mouth of the net to estimate the volume of filtered water. Towing speed ranged between 77 and 154  $\text{cm}\cdot\text{s}^{-1}$ . Depending on bottom depth, the tows were oblique (mean bottom depth  $\pm$  SD: 33  $\pm$  9 m) or horizontal (mean bottom depth  $\pm$  SD: 14  $\pm$  5 m), to increase the volume of water sampled for 15 minutes. Horizontal tows were made close to the seafloor. Maximum depth during each ichthyoplankton tow was recorded by a depth sensor attached to the mouth of the net. Samples were fixed immediately after collection and preserved in 5% formalin. Larvae were quantified and identified in the laboratory to the lowest possible taxonomic level based on their morphology (Neira et al. 1998).

Moderate-Resolution Imaging Spectroradiometer (MODIS) Aqua Level-2 files were acquired for the study area from the NASA ocean color web site (<https://oceancolor.gsfc.nasa.gov>). We obtained the daytime sea surface temperature (SST) 11  $\mu\text{M}$  product that uses the 11 and 12  $\mu\text{M}$  bands. Values of satellite SST used were the averages of all unmasked pixels within a 3  $\times$  3-pixel box centered on the *in-situ* target. Temporal and spatial resolution was 24 h and 1.1 km, respectively. Due to the cloud cover usually present over the study area, the data acquired daily or even every week had many gaps. To solve this and also due to the strong spring winds that did not allow us to perform all tows on consecutive days within each month, we averaged the daily SST values obtained for each oceanographic station in the period elapsed between the first and the last

tow made in each month. The validity of the satellite data was corroborated throughout the study area (results not showed). To describe the mid-term SST regime in the SJG, we used a Hovmöller diagram (Hovmöller 1949). Thermal anomalies were estimated by subtracting the monthly 12-year SST average (the data used to calculate these mean values covered the period 2003-2014) to each monthly SST, for each gulf domain.

Finally, we modelled the daily SST during the spring and summer for each gulf domain and year, using the following sinusoidal model, modified from McCloskey (1986):

$$T_d = m + p \sin\left(\frac{2\pi d}{182} + h\right) \quad (1),$$

where  $T_d$  is the SST at day  $d$ ;  $d$  is an integer varying between 1 and 177, which represents each Julian day from 1 October to 26 March (when sampling ended on Year 2), covering the whole sampling period;  $m$  is the mean yearly SST;  $p$ , the amplitude for temperature variation; and  $h$ , a phase shift parameter indicating the beginning of the temperature cycle.

### Data analysis

Due to a large number of zeros observed in the abundance data, we were not able to use the raw data for the analyses. Instead, we used the weighted average density of larvae (individuals $\cdot\text{m}^{-3}$ ) of each taxon and the average SST by month and year (irrespective of the sampling stations), for each oceanographic domain (East and West). All the subsequent analyses were made from a Bray-Curtis similarity matrix (Bray & Curtis 1957), constructed from that data set (Warton et al. 2012). This matrix has 18 rows, which represents a combination of domain  $\times$  month  $\times$  year, and 16 columns, one per fish taxa. Larvae present in less than 2% of the

stations sampled (i.e., in three or less out of 155 stations), were removed from the analyses. We also did not include some unidentified taxa for which there were a limited number of individuals that covered a narrow size range, and hence did not allow assigning them univocally to a taxon (see Figure S1 - Supplementary Material).

As the distribution of the larval density values was not normal, we used a randomization test (Manly 1991) to contrast the overall median larval density between years. We chose the median instead of the mean to avoid the undue influence of a few extreme density values. We run the randomization test by constructing Monte Carlo distributions ( $n = 50000$ ) of the difference between median density values, under the null hypothesis of no differences between years, and ran a two-tailed test.

To explore the spatio-temporal variation of the ichthyoplankton assemblages in a single 2D plot, we ran a non-metric multidimensional scaling ordination (nMDS) (Clarke & Warwick 2001). In addition, to evaluate potential differences in the structure of the ichthyoplankton assemblages due to the effects of 'Gulf domain', 'Season', 'Year', 'SST' and 'Thermal anomaly', we ran a multivariate analysis

of variance with permutations (PERMANOVA: Anderson 2001) (Table I). This analysis assumes that the samples (i.e., rows of the original data matrix) are exchangeable under a true null hypothesis, which implies that the multivariate observations are independent and identically distributed (Anderson 2001). All the factors tested were considered fixed, and the number of permutations used for fitting the PERMANOVA models was 999. As the first model run pointed to seasonal and yearly effects on the community structure rather than spatial (i.e., 'Gulf domain') effects, we evaluated a model containing the interaction between both temporal factors, 'Season' and 'Year', as well as the other variables listed in Table I. In this model, data were randomized freely among the interaction cells. Before conducting the PERMANOVA analyses, we checked the assumption of similar multivariate dispersion of points among groups with the '*betadisper*' function included in the '*vegan*' package (Oksanen 2017) of the R software (R Development Core Team 2014).

To identify indicator species for each group of samples characterized by the relevant variables identified in the prior analyses (i.e., PERMANOVA and nMDS), we estimated the "Indicator species

**Table I. Explanatory variables tested in the PERMANOVA analysis. The numbers in parentheses indicate the number of levels in each factor. SJG: San José Gulf.**

Explanatory variable	Description
Domain	Factor (2). East and West.
Seasons	Factor (2). 'Spring': October to December, and 'Summer ': February to March.
Year	Factor (2). '1': October 2011 to March 2012, and '2': October 2012 to March 2013.
Surface water temperature (SST)	Numerical, measured in °C.
Thermal anomaly	Numerical. Difference between the mean monthly SST for the GSJ and the SST of the sampled stations.

values" index (IndVal, Dufrêne & Legendre 1997). IndVal is the product of two values: A (specificity) and B (fidelity). The specificity is based on the abundance of a particular species in a group relative to its abundance in all groups, and the fidelity is the percent frequency of one particular taxon in each group. Indicator values range from 0 (no indication) to 100 (perfect indication) (Dufrêne & Legendre 1997, Suntsov et al. 2012). A maximum ranking of 100 occurs when a single taxon is present in all samples of a group and only occurs in that group of samples (Dufrêne & Legendre 1997). The significance of the IndVal measure for each species was tested using the 'multipatt' function included in the 'indicspecies' package of the R software (De Cáceres et al. 2012).

The richness and diversity indexes traditionally used by ecologists have several limitations because they are highly sensitive to the number of individuals sampled, the number of samples, and the size of the surveyed area (Colwell et al. 2012, Chao et al. 2014). To overcome many of these shortcomings, we used rarefaction curves based on Hill numbers (Gotelli & Colwell 2011, Colwell et al. 2012, Chao et al. 2014). We compared the species richness and diversity indexes of the ichthyoplankton assemblages between groups of samples characterized by the relevant variables identified in the prior analyses. For these analyses, density data in the number of larvae·100 m<sup>-3</sup> were averaged for each species per season or year (see Results) and rounded to obtain integer values. We evaluated first- (q = 0 or species richness) and second-order (q = 1 or Shannon diversity index, which is the exponential of Shannon entropy) Hill numbers (Jost 2007). We extrapolated each curve to the double of the overall density (sample size) and estimated the 95% confidence bands through the bootstrap method (100 replicates) (Chao et al. 2014). The significance of the differences in richness and diversity between

the groups identified by PERMANOVA analysis was assessed through the overlapping of the confidence bands in the plots. We considered that richness or diversity differed when the corresponding confidence bands for each group did not overlap.

Multivariate statistical analyses, rarefaction curves, and the estimation of the 'Indicator species values' were performed with the packages 'iNEXT' (Hsieh et al. 2016), 'vegan' (Oksanen 2017), 'indicspecies' (De Cáceres 2013), and 'stats' of the R software (R Development Core Team 2014). Plots of density, nMDS, and rarefaction curves were built using the 'ggplot2' package for R (Wickham 2009). Parameters for the SST models were obtained with the 'nls2' R package (Grothendieck 2007). Aleatorization tests were run with an *ad-hoc* R code written by the authors.

## RESULTS

A total of 2088 larvae were caught during the ichthyoplankton surveys conducted in the SJG. These larvae comprised 36 taxa, from which 14 were identified to species, two to genus, one to family and one to order (Table II). A total of 332 larvae were unidentified, 189 of them were yolk-sac larvae, or their preservation state was too poor for identifying them properly. The remaining larvae (n = 143), ranging in numbers from 1 to 40 individuals, belonged to 18 different taxa not assigned to any particular species, genus, family, or order (See Figure S1).

SST differed between gulf domains; it was also higher in Year 1 compared to Year 2, particularly during summer (Fig. 2). Maximum modeled SST in SJG and the differences in mean SST between domains were both larger in Year 1 compared to Year 2 (Fig. 2 and see Figure S2). Maximum modelled SST for the ED and WD were

**Table II.** Larvae collected in the San José Gulf between October 2011 and March 2012 (Year 1), and between October 2012 and March 2013 (Year 2). %F: Frequency of occurrence (percentage of tows containing each species). \* Identified species removed from the analyses due their low %F value.

Order	Family	Species	%F		
			Year 1	Year 2	
Atheriniformes	Atherinopsidae	<i>Odontesthes</i> spp. Evermann and Kendall 1906	9.76	1.37	
Cupleiformes	Engraulidae	Engraulidae spp.	43.90	26.03	
Gadiformes	Merlucciidae	<i>Merluccius hubbsi</i> Marini 1933	10.97	2.74	
Ophidiiformes	Ophidiidae	<i>Raneya brasiliensis</i> (Kaup, 1856)	23.17	17.81	
Perciformes	Tripterygiidae	<i>Helcogrammoides cunninghami</i> Smitt 1989	51.22	20.55	
	Pinguipedidae	<i>Pseudoperca semifasciata</i> (Cuvier 1829)	28.05	15.07	
	Stromateidae	<i>Stromateus brasiliensis</i> Fowler 1906	15.85	5.48	
	Carangidae	<i>Trachurus lathami</i> Nichols 1920	8.54	1.37	
	Serranidae		<i>Dules auriga</i> Cuvier, 1829	21.95	8.22
			<i>Acanthistius patachonicus</i> (Jenyns 1840)	7.32	8.22
Percophidae		<i>Percophis brasiliensis</i> Quoy and Gaimard 1825*	1.22	0.00	
Pleuronectiformes	Paralichthyidae	<i>Paralichthys</i> spp.	8.54	5.48	
		<i>Xytreuys rasile</i> (Jordan 1891) *	3.66	0.00	
	Cynoglossidae	<i>Symphurus trewavasae</i> Chabanaud 1948	7.32	1.37	
	Unidentified	Pleuronectiformes spp.*	1.22	1.37	
Scorpaeniformes	Sebastidae	<i>Sebastes oculatus</i> Valenciennes 1833	40.24	16.44	
	Agonidae	<i>Agonopsis chiloensis</i> (Jenyns 1840)	8.54	4.11	
Syngnathiformes	Syngnathidae	<i>Syngnathus folletti</i> (Herald 1942)*	1.22	1.37	
Unidentified	Unidentified	NI-1	18.29	10.96	
		NI-2	7.32	5.48	

19.2°C and 17.8°C in the Year 1, and 17.6°C and 16.2°C in Year 2, respectively. The ED was always warmer than the WD. In spring, the difference between minimum modelled SST values for both domains were 1.1°C and 0.7°C for years 1 and 2, respectively. In summer, the difference between maximum modelled SST values were 1.4°C for both years. At a broader temporal scale, Year 1 was dominated by positive thermal anomalies,

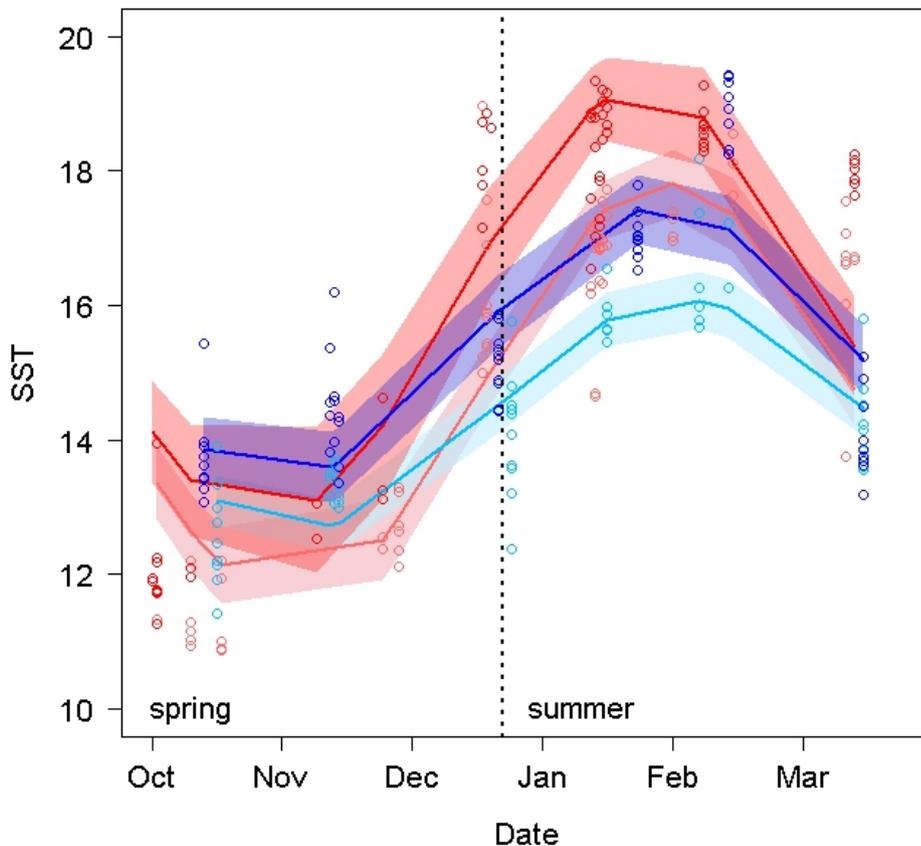
while during Year 2, negative thermal anomalies were more common (Fig. 3). Overall, the ED had more extreme thermal anomalies than the WD throughout the period 2003-2014 (ED range: -1.68°C to 3.43°C, and WD range: -1.38°C to 1.29°C).

The overall larval density differed largely between years: it was three times higher in the Year 1 than in the Year 2 (14.4 larvae·100 m<sup>-3</sup>

vs. 4.8 larvae·100 m<sup>-3</sup>, respectively;  $p < 0.001$ ) (Fig. 4). In Year 1, larval density was maximum in late spring (December) (Fig. 4a) while in Year 2, most larvae were caught in summer (February) (Fig. 4b). Five abundant species dominated the samples during the whole study period: *Helcogrammoides cunninghami*, *Raneya brasiliensis*, *Pseudopercis semifasciata*, *Sebastes oculatus*, and larvae belonging to the family Engraulidae (Table II and see Figure S3). Those species accounted for approximately 72% and 60% of all the larvae caught, in Years 1 and 2, respectively (see Figure S3). Each species occurred in the water column during particular periods. For example, larvae belonging to the family Engraulidae were sampled during all the months surveyed. Other species such as *Percophis brasiliensis* and *Xystreurys rasile* were collected only in one month (Fig. 4).

A total of 16 taxa were included in the multivariate statistical analyses (Table II). The analysis of similarity using nMDS suggested some differences among the ichthyoplankton assemblages: one defined by the season (spring vs. summer) and the other, less clear, defined by the year (Fig. 5). The PERMANOVA models showed that the factor 'Gulf domain' and the covariate 'Thermal anomaly' had no effect on the structure of the larval fish assemblages of the SJG (Supplementary Material - Tables SI and SII). In contrast, the PERMANOVA model that included the factors 'Season' and 'Year', the covariate 'SST', and the interaction 'Season × Year', revealed significant effects of the main effects and the covariate on the structure of the larval assemblages of the SJG, while the interaction was not significant (Table III).

Larvae belonging to the family Engraulidae were the most abundant species, and they were

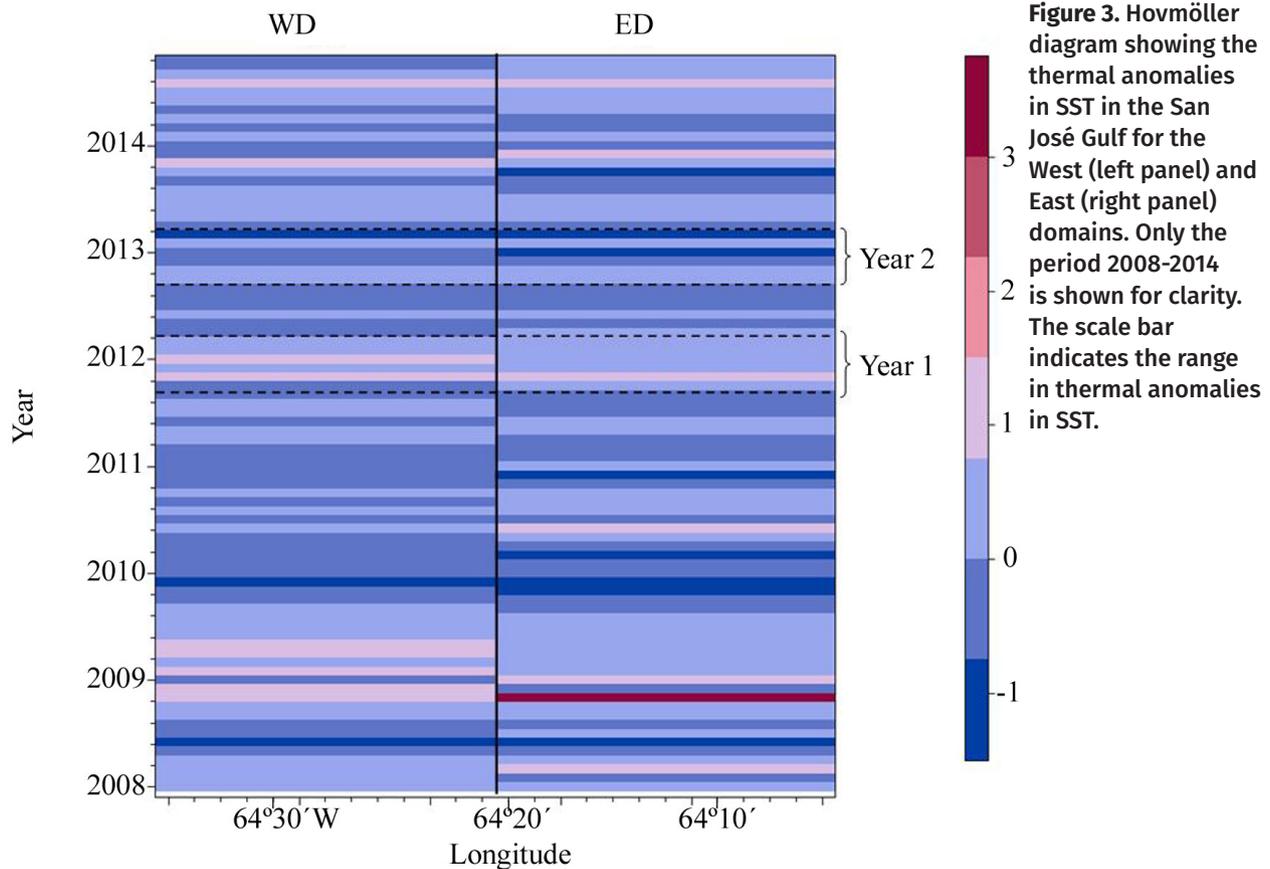


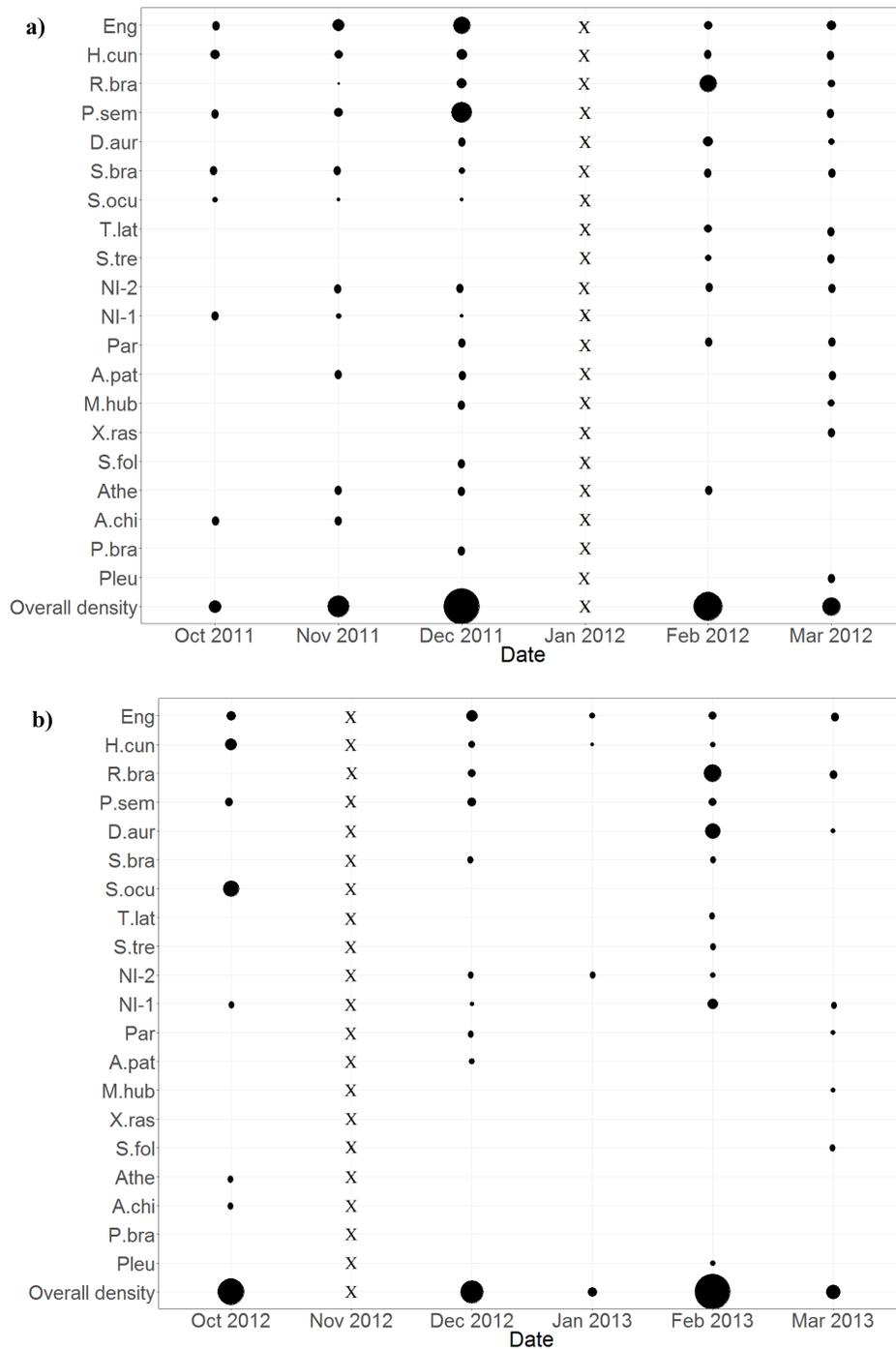
**Figure 2.** Sinusoidal satellite sea surface temperature (SST) models (solid lines) in the San José Gulf for Year 1: October 2011 to March 2012 (red: East domain and light-red: West domain), and Year 2: October 2012 to March 2013 (blue: East domain and light-blue: West domain). Shaded areas represent 95% confidence regions for each fitted curve. Raw data are showed as open circles. Note that the confidence regions overlap in spring, but they separate during summer. Thermal amplitude was greater during the first year sampled.

collected during the whole sampling period; hence, they were not a good indicator species. The species with the highest IndVal index for the spring were rocky reef fishes including: *H. cunninghami*, that appeared in all stations sampled during that season (i.e.,  $B = 1$ ) and was largely (but not completely) restricted to it (i.e.,  $A = 0.93$ ) ( $p < 0.01$ ); *S. oculatus* ( $A = 1$  and  $B = 0.80$ ;  $p < 0.01$ ), and *Agonopsis chiloensis* ( $A = 1$  and  $B = 0.50$ ;  $p < 0.05$ ), that appeared only in some spring stations. *Pseudopercis semifasciata* ( $A = 0.97$  and  $B = 0.80$ ;  $p < 0.05$ ) was also caught in some spring stations, but it was not restricted to that season. Finally, *Dules auriga* is a good indicator species for the samples collected in summer ( $A = 0.98$  and  $B = 0.88$ ;  $p < 0.01$ ).

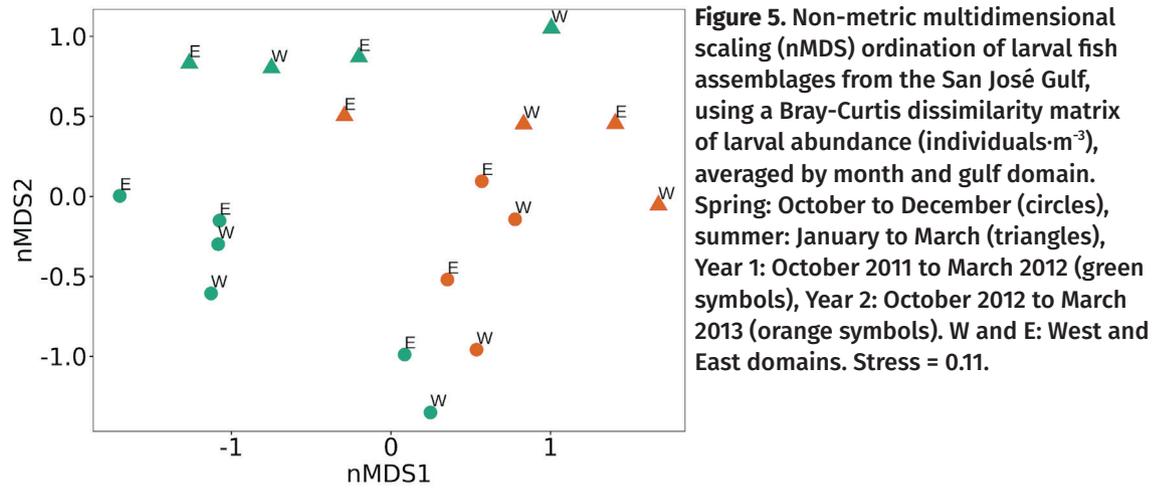
The species richness and diversity of the larvae assemblages were compared between

seasons and years, the temporal factors identified by the PERMANOVA analysis. The spring and summer had overlapping confidence intervals; hence, both indexes did not differ between seasons (Fig. 6a, b). Regarding the variable 'Year', the curves did not reach a plateau for Year 2 due to the low number of individuals collected. However, our results suggested a greater diversity in Year 2 (Fig. 6d). The species richness, however, was similar between years when only the species included in the analyses were considered (15 species in Year 1 and 13 species in Year 2) (Fig. 6c), as well as when all the taxa caught were taken into account (36 species in Year 1 and 28 species in Year 2).



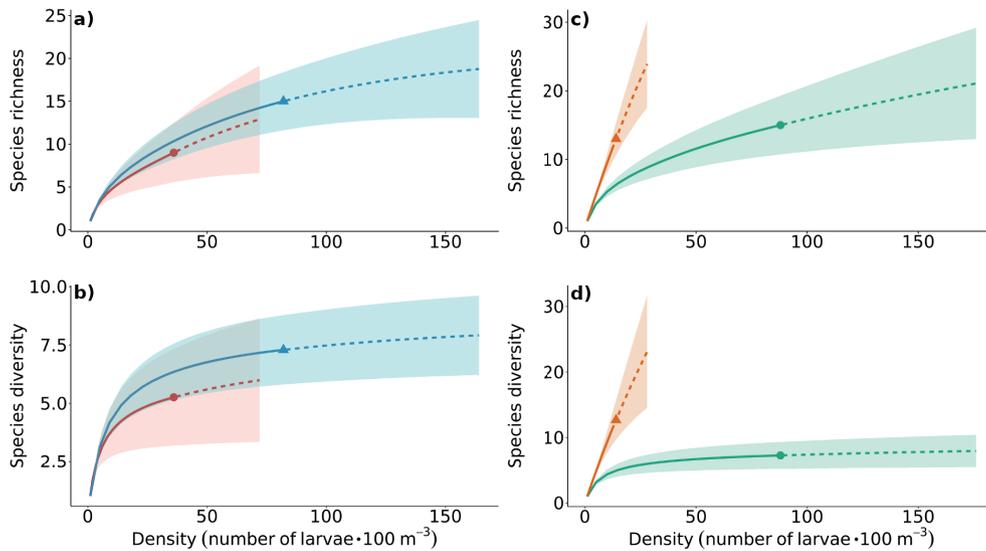


**Figure 4.** Bubble plots showing the mean monthly density of the larvae sampled within the San José Gulf during two consecutive years: a) Year 1: October 2011 to March 2012, and b) Year 2: October 2012 to March 2013. The diameter of the dots is proportional to larval density (number of larvae·100 m<sup>-3</sup>). The ranges for larval density were 0.01 larvae·100 m<sup>-3</sup> – 268.36 larvae·100 m<sup>-3</sup>, and 0.03 larvae·100 m<sup>-3</sup> – 21.91 larvae·100 m<sup>-3</sup> for Year 1 and 2, respectively. A.pat: *Acanthistius patachonicus*, A.chi: *Agonopsis chiloensis*, Athe: Atherinopsidae, D.aur: *Dules auriga*, Eng: Engraulidae, H.cun: *Helcogrammoides cunninghami*, M.hub: *Merluccius hubbsi*, Par: *Paralichthys* spp., P.bra: *Percophis brasiliensis*, Pleu: Pleuronectiformes, P.sem: *Pseudopercis semifasciata*, R.bra: *Raneya brasiliensis*, S.ocu: *Sebastes oculatus*, S.bra: *Stromateus brasiliensis*, S.tre: *Symphurus trewavasae*, S.fol: *Syngnathus folletti*, T.lat: *Trachurus lathami*, X.ras: *Xystreurus rasile*, NI: Unidentified species. X: Without data.



**Table III.** Results of the PERMANOVA model testing the effects of Season (S), Year (Y), their interaction (S×Y), and Sea Surface Temperature (SST) on the structure of the ichthyoplankton assemblages. \* Significant ( $p < 0.05$ ).

Model	Variables	Betadisper ( $p$ )	Pseudo- $F$	$p$
S + Y + S×Y + SST	Season	0.734	3.15	0.001*
	Year	0.231	3.09	0.002*
	Interaction term	-	1.46	0.119
	SST	-	2.30	0.008*



**Figure 6.** Sample size-based interpolation (solid lines) and extrapolation (dotted lines) sampling curves with 95% confidence bands (shaded areas) for the seasons (plots a and b) and years (plots c and d) separately, for species richness and Shannon diversity index. The solid symbols represent the index values associated to the overall density sampled at each season or year. Spring: October to December (circles and red lines), summer: January to March (triangles and light-blue lines). Year 1: October 2011 to March 2012 (circles and green lines) and Year 2: October 2012 to March 2013 (triangles and orange lines).

## DISCUSSION

This study revealed for the first time the temporal and spatial sources of variation in the structure of fish larval assemblages inhabiting the SJG, a small basin located in the Southwest Atlantic. The gap in the taxonomic knowledge that hampered the identification of about 15% of the larvae collected is often a pervasive problem in ichthyoplankton research due to the rapid morphological changes occurring during the early ontogeny (Hernandez et al. 2013). Here, we lacked complete developmental series for most species that would have allowed the comparison of larvae with juvenile fishes to identify them properly. The larval development of 27 bony fish species, of the *ca.* 50 species inhabiting the SJG, was described. However, in this study, we were able to identify most larvae at the species, genus, family, or order levels. Overall, our analyses included 86.4% of the larvae collected.

Our results showed that the structure of the larval assemblages in SJG varied at different temporal scales: both the nMDS and PERMANOVA revealed significant differences between seasons and years. The relationships between larval fish dynamics and environmental variability are complex, usually non-linear, and involve multiple environmental factors (Hsieh et al. 2005, Auth et al. 2011). While the multiple effects of water temperature (e.g., Auth 2008, Guan et al. 2017) on the biology of the species comprising the larval fish assemblages in Patagonian waters are mostly unknown, our study showed an association between the structure of the larval assemblages and SST. Indeed, Year 1 was warmer than Year 2, coincidentally with a greater density of fish larvae caught. The overall density of larvae was three times higher during Year 1 and, irrespective of the variety of reproductive strategies showed by different fishes; all the

species caught were more abundant during that period. Many studies associate changes in the structure of the ichthyoplankton assemblages with changes in water temperature (Genner et al. 2010, Kono et al. 2016) because it affects growth, egg maturation, spawning time (Bui et al. 2010), and spawning migrations (Genner et al. 2010).

Other factors associated with water temperature and temporal concurrency with the spawning of adults may exert their influence on the repetitive nature of larval groups (Hoffmeyer et al. 2009). For example, dominant currents and other oceanographic processes may cause the presence of certain species in a particular area due to their interaction with spawning areas, which persist from year to year (Gray & Miskiewicz 2000, Acha et al. 2012). The input of nutrients into SJG occurs mainly through shelf waters due to the absence of other important discharging sources (e.g., extreme rainfalls, river discharge, and human settlements) (Amoroso & Gagliardini 2010). Due to the morphology of the basin and its geographic characteristics, water temperature inside the SJG is strongly influenced by the heat exchange with the atmosphere (Rivas 1990). Thus, during a warm year (like, for example, Year 1), it is expected that SJG waters increase their temperature faster than the adjacent continental shelf. Coincidentally with this hypothesis, the ED presented more extreme positive thermal anomalies than the WD, whose temperature strongly depends on the exchange with shelf waters. The heat exchange between water masses through the narrow mouth of the SJG moderates the water temperature fluctuations within it. The mitigation of the rise in water temperature in warm years would demand the input of shelf water at a lower temperature than usual, or a greater volume of water exchanged (A. Rivas, personal communication). This process might have caused a greater input of nutrients, phyto, and

zooplankton, including fish larvae, from shelf waters into the SJG during the first year sampled. A greater volume of water exchanged could also have increased the availability of phyto and zooplankton, enhancing the survival of fish larvae. Although the environmental mechanisms that drive and sustain the chlorophyll-a cycle in this area have not been fully studied (Williams et al. 2018), the concentration of chlorophyll-a in the Argentine Continental Shelf was higher in Year 1 than in Year 2 (Andreo et al. 2016). Furthermore, the interannual variability in the ichthyoplankton structure was coincident with changes in the density and composition of other mesozooplanktonic groups in the SJG during the period studied (Hernández Moresino et al. 2017). Copepods, the main food source for fish larvae (e.g., Spinelli et al. 2012, Temperoni & Viñas 2013), were more abundant in SJG during the spring-summer of 2011-2012 than during the same seasons in 2012-2013, coincidentally with a higher concentration of chlorophyll-a (Hernández Moresino et al. 2017). This relationship between chlorophyll concentrations and zooplankton abundance has also been observed in the spawning area of other fishes of the Argentine Sea such as *Merluccius hubbsi* (Temperoni et al. 2014) and *Engraulis anchoita* (one of the species belonging to the family Engraulidae, Marrari et al. 2013).

Both the species richness and diversity play an important role in the processes related to ecosystem functioning and promote production and ecosystem stability (Bui et al. 2010). Our PERMANOVA results indicated a change in the composition of the larval assemblages between seasons, which adds to seasonal variations in the densities of particular dominant taxa (i.e., larvae belonging to the family Engraulidae, *H. cunninghami*, *P. semifasciata*, and *S. oculatus* were more abundant in spring) and to a greater number of species caught in summer than in

spring (15 vs. 9 species, respectively). These findings agree with the general tendencies observed through the rarefaction curves (i.e., they showed a greater species richness and diversity in summer). However, no significant differences were evident from this analysis in contrast to what had been expected for temperate waters (Berrios & Vargas 2000). The significant variation in the structure of the assemblages between years, identified by the PERMANOVA analysis, could be associated with the changes in diversity showed by the rarefaction curves. Species richness was similar between years; thus, the greater diversity found in Year 2 could be related to changes in the densities. In this context, the higher evenness in Year 2 (Fig. 4) could explain the greater diversity estimated for this year (Magurran 2004). Therefore, while the switches in the density of the dominant species contributed most to the seasonal changes in the assemblages, at the inter-annual scales the changes in the assemblages were the result of variations both in dominant and subdominant species. Nevertheless, conclusions should be taken with caution when analysing the comparisons of the rarefaction curves between years because the number of individuals collected in Year 2 was insufficient to obtain consistent estimates of richness and diversity (i.e., the rarefaction curves did not reach an asymptote).

All the indicator species (i.e., *H. cunninghami*, *P. semifasciata*, *S. oculatus*, *A. chiloensis*, and *D. auriga*), are rocky reef fishes and were also abundant in a preliminary ichthyoplankton study within the SJG (M. Sylvester et al., unpublished data). Together with the fact that most larvae caught were in a preflexion stage suggests that the SJG is an important area for the reproduction and breeding at least for these species.

The general knowledge about the composition of the ichthyoplankton

assemblages of the Argentine Sea is highly heterogeneous. More attention was put to study the ecology of the larval fish assemblages in certain areas, such as the coast of Buenos Aires Province (Hoffmeyer et al. 2009, Acha et al. 2012). The SJG and the Península Valdés region represent a transition zone between temperate waters (warm-temperate Argentine Province), with species ranging from Brazil to Northern Patagonia, and cold waters (cold temperate Magellanic Province), with species typical of higher latitudes occurring up to the mouth of Río de la Plata (Balech & Ehrlich 2008). This may be the reason why the larval fish assemblage from the SJG shares so many species with that from the coast of Buenos Aires Province (e.g., *E. anchoita*, *Stromateus brasiliensis*, *Acanthistius patachonicus*, *Odontesthes* spp., *Syngnathus folletti*, and *P. brasiliensis*), and with that found to the south of 46°S (e.g., *A. chiloensis*, *S. oculatus*, and *H. cunninghami*), where the hydrographic features of the Argentine Sea are different (Ciechomski et al. 1975, Ehrlich et al. 1999, Hoffmeyer et al. 2009, Acha et al. 2012). The scarce information available about the species composition of the ichthyoplankton assemblages from Northern Patagonia (41°S – 46°S) matches our results: *R. brasiliensis*, *H. cunninghami*, species belonging to the Engraulidae, *S. oculatus*, and *P. semifasciata* are the most common species reported at those latitudes (Ciechomski et al. 1981, Acha et al. 2018, L. Fernández Goya & P. Betti, unpublished data). Comparatively, the large number of taxa found in this study may be attributable to the high sampling effort made during two consecutive years on a monthly frequency. In a recent review describing the ichthyoplankton associated to frontal systems of the Southwest Atlantic, Acha et al. (2018) reported the occurrence of 19 species, one genus, two families and one order of fishes for a series of tidal fronts

located between the north of Península Valdés (42°S) and Isla de los Estados (55°S). Not only the number of taxa identified in this study ( $n = 18$ ) vs. in Acha et al. (2018) ( $n = 23$ ), but also the identity of the species found were similar, even when a punctual area was surveyed in our work compared to the large coastal extension encompassing 13 latitude degrees reviewed in that work.

Finally, it is well known that the spawning areas of some fish species present in the SJG are associated with frontal systems (e.g., *Engraulidae*, *M. hubbsi*, and *A. patachonicus*, among others; see Hansen et al. 2001, Álvarez-Colombo et al. 2011, Acha et al. 2018, M.I. Militelli et al., unpublished data). However, although a frontal system develops in the SJG during spring and summer, together with the occurrence of thermal stratification in the East domain (Amoroso & Gagliardini 2010), we did not find any spatial effects in the structure of the ichthyoplankton assemblages between domains. This lack of spatial effect could be due to the small dimension of the SJG and its shallow waters, which leads to reduced influence of stratification compared to tidal forcing (Tonini et al. 2013, Tonini & Palma 2017). In relation to this, our findings suggest that the structure of ichthyoplankton assemblages in small, shallow gulfs such as the SJG, might be stronger influenced by fluctuations in environmental and hydrographic variables such as winds (direction and intensity), atmospheric temperature, and water currents (Bailey et al. 1999, Lanksbury et al. 2005, Guan et al. 2015) than by local factors such as, for example, the thermal stratification observed in the ED mainly between January and March (Amoroso et al. 2011, Crespi-Abril et al. 2014). Improving our knowledge about the interactions between ichthyoplankton and oceanographic and environmental features is crucial to provide a better understanding of the

fluctuations of ichthyoplankton assemblages in small basis. This study represents a first step in that direction.

### Acknowledgments

We want to thank M López, P Fiorda, R Hernández-Moresino, L Getino, G Trobbiani, N Ortíz, D Remenar, I D'Ercole, M Camarero, and C Owen for their help during surveys. J Dignani designed and calibrated the depth recorder for the net. A Rivas and JP Pisoni made useful comments on an earlier version of this manuscript. Thanks also to the NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group (NASA OB.DAAC, Greenbelt, MD, USA) for the production and distribution of MODIS data. Fieldwork was conducted within a World Natural Heritage Site and was authorized by the Secretaría de Turismo y Áreas Protegidas del Chubut.

Funding: This work was supported by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2010–2461) (granted to L Venerus); Conservation, Research, and Education Opportunities International (granted to GL Villanueva-Gomila).

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## SUPPLEMENTARY MATERIAL

**Figures S1, S2 and S3.**  
**Tables SI and SII.**

### How to cite

VILLANUEVA-GOMILA GL, EHRLICH MD, MARTÍNEZ FJ, WILLIAMS GN & VENERUS LA. 2020. Spring and summer ichthyoplankton assemblages in a temperate Patagonian gulf: an overview of temporal and spatial patterns on their structure. *An Acad Bras Cienc* 92: e20181166. DOI 10.1590/0001-3765202020181166.

*Manuscript received on November 5, 2018;*  
*accepted for publication on July 22, 2019*

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### Author contributions

Villanueva-Gomila: field and laboratory work, data analysis, writing. Ehrlich: laboratory work, writing. Martínez and Venerus: statistical analysis, writing. Williams: spatial data analysis, writing.

