



## Research papers

# The seasonal dynamics of plankton communities relative to the foraging of the southern right whale (*Eubalaena australis*) in northern Patagonian gulfs, Península Valdés, Argentina

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## ABSTRACT

This is the first exploratory study that addresses simultaneously the phytoplankton and mesozooplankton seasonal dynamics associated with some environmental factors in the northern Patagonian gulfs: Golfo Nuevo (GN) and Golfo San José (GSJ), Argentina, during an annual cycle (December 2014–2015 and January 2015–2016, respectively). It also reports data on mesozooplankton composition and abundance in a sample collected while southern right whales (*Eubalaena australis*) were feeding at the sea surface in Bahía Pirámide (GN). The phytoplankton community was represented by 69 taxa in GN and by 83 taxa in GSJ. In GN, phytoplankton was mainly dominated by diatoms and dinoflagellates whereas in GSJ diatoms dominated the phytoplankton community throughout the year. In GN, the highest phytoplankton biomass and density values were registered during austral spring, 2015 which coincided with a *Pseudo-nitzschia australis* bloom. In contrast, the lowest biomass values, which were associated with elevated abundances of dinoflagellates, were observed in late spring 2014. In GSJ, the highest biomass values showed two equal peaks in austral autumn and spring 2015. The latter was associated with the maximum cell density recorded in this gulf during a *Chaetoceros debilis* bloom. In contrast, the lowest biomass values were recorded in winter 2015. Mesozooplankton was represented by 63 taxa in GN and by 61 taxa in GSJ. In GN, this community was mainly represented by cladocerans and copepods, whereas it was dominated by copepods in GSJ. The lowest mesozooplankton abundances were recorded in austral winter in both gulfs. In GN, the highest abundances were recorded in austral summer and spring 2015, whereas in GSJ, the maximum mesozooplankton abundances were observed during austral summer and autumn 2015. The major prey items for *E. australis* were the copepods *Calanoides carinatus*, *Ctenocalanus vanus*, *Calanus australis*, and *Paracalanus parvus*, zoeae of the squat lobster *Munida gregaria*, calyptopis and furcilia of *Euphausia lucens*, and fish eggs and larvae. In both gulfs, the warm seasons were mainly characterized by higher relative abundances of diatoms, while the cold seasons were mostly associated with higher abundances of dinoflagellates and Dictyochophyceae. Salinity and phaeopigments were related with copepod and appendicularian abundances, whereas surface sea water temperature seemed to modulate the seasonal distribution pattern of cladocerans and decapods.

## 1. Introduction

Phytoplankton and mesozooplankton dynamics results from the interaction of multiple physical, chemical, and biological factors (Parsons et al., 1984; Mullin, 1993; Boltovskoy, 1999; Folt and Burns,

1999; Almandoz et al., 2011). The water circulation patterns as well as biotic processes, such as competition, predation, and resource availability affect both abundance and spatial distribution of planktonic organisms (Carreto, 1989; Miquel, 1991; Ichii et al., 1998; Atkinson et al., 1999; Ward et al., 2005).

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Phytoplankton is responsible for more than 45% of the net primary production of the planet (Falkowski et al., 2004). In the sea, it is the productive base of food webs, therefore most marine animals depend on these microalgae either directly or indirectly for their survival (Carreto, 1989). In terms of abundance, the most important phytoplankton groups are diatoms, dinoflagellates, and coccolithophores (Barton et al., 2013; Segura et al., 2013).

Zooplankton occupies a key position in the pelagic food webs as a result of its role in the transfer of matter and energy through predator-prey relationships from primary producers to higher trophic levels (Kjørboe, 1993; Lenz, 2000). In many marine ecosystems within mesozooplankton communities (0.2–20 mm in size according to Sieburth et al., 1978) copepods are the most abundant group (Raymont, 1983; Kjørboe, 1998; Mauchline, 1998; Bradford-Grieve et al., 1999; Lenz, 2000). From a trophic point of view, copepods feed on phytoplankton, small heterotrophic organisms, and detritus (van Duren and Videler, 1996) and they are also an important food source for numerous fish larvae and adults, other larger zooplankton organisms, and some marine mammals, such as right whales (Mauchline, 1998; Lenz, 2000; Hoffmeyer et al., 2010; Leandro et al., 2010; Baumgartner et al., 2013, 2017; D'Agostino et al., 2016).

Golfo Nuevo (GN), Golfo San José (GSJ), and Golfo San Matías (GSM) in Argentina surround Península Valdés Protected Area (Fig. 1), a natural reserve designated as a World Heritage Site and Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO) because of its importance for marine conservation. GSJ, which is located in the northern margin of Península Valdés (Fig. 1), is the shallowest (mean depth 30 m, maximum 80 m) and smallest gulf (817 km<sup>2</sup>) of the northern Patagonian gulfs and it is connected by a narrow mouth to the larger and deeper GSM (18,000 km<sup>2</sup>). The tidal regime of GSJ is semidiurnal; mean amplitude varies between 7.01 and 4.57 m (Amoroso and Gagliardini, 2010). Salinity and temperature are vertically homogeneous throughout most of the year, with a weak stratification during summer (Rivas, 1990). The vertical structure of this gulf is similar to that of GN (Rivas, 1990). The high nutrient concentration and productivity that characterize GSJ and that are comparable to those of upwelling areas has been attributed

to the penetration of nutrient-rich waters from the adjacent shelf and from GSM (Charpy et al., 1980; Esteves et al., 1986). These highly productive waters provide trophic nourishment to an artisanal fishery based on the capture of the scallop *Aequipecten tehuelchus* (Orensanz et al., 2007; Amoroso et al., 2011). GN is located on the southern sector of Península Valdés (Fig. 1) and is connected to the Atlantic Ocean by a mouth of 16 km. The area of this gulf is 2500 km<sup>2</sup>, its mean depth is 44 m, with a maximum of 184 m (Mouzo et al., 1978). The tidal regime is semidiurnal with average amplitude of 1.9 m (Rivas and Ripa, 1989). In GN precipitations are scarce (annual average 200 in GN and 180 mm in GSJ, respectively), and there are no permanent water courses in the entire region. Both GN and GSJ are the most important calving grounds in Argentina for the southern right whale (*Eubalaena australis*) population of the south-western Atlantic Ocean. The first whales arrive annually in May and the calving season extends to December with a peak of whale abundance from August through September (Crespo et al., 2014). Although this area is not a typical feeding ground and is mainly for calving and reproduction, adults and juveniles of *E. australis* were documented feeding on zooplankton, mainly calanoid copepods, either by skimming at the sea surface or by diving to greater depths mainly during spring, when denser zooplankton patches follow the phytoplankton blooms (Sironi, 2004; Menéndez et al., 2007; Hoffmeyer et al., 2010; D'Agostino et al., 2016). In mid-December almost all individuals of *E. australis* leave Península Valdés to spend summer in their feeding grounds located at mid and high latitudes of the South Atlantic and Subantarctic regions (Payne, 1986; Rowntree et al., 2008; Valenzuela et al., 2009). In addition, a recent study (Zerbini et al., 2018) documented that when some whales leave these gulfs after the calving season they go to Península Valdés' front which is located east of Península Valdés where they stay for a while, probably for feeding.

Although phyto- and zooplankton dynamics has been extensively investigated in the Argentine Sea (e.g. Sabatini and Martos, 2002; Viñas et al., 2002; Marrari et al., 2004; Almandoz et al., 2011; Sabatini et al., 2012, 2016), in GN and GSJ, in particular, research on plankton has either been rather scarce as well as geographically or temporally partial (see Esteves et al., 1996; Santinelli, 2008; Hoffmeyer et al., 2010; Menéndez et al., 2011; Cadaillón, 2012; Hernández Moresino et al., 2014;

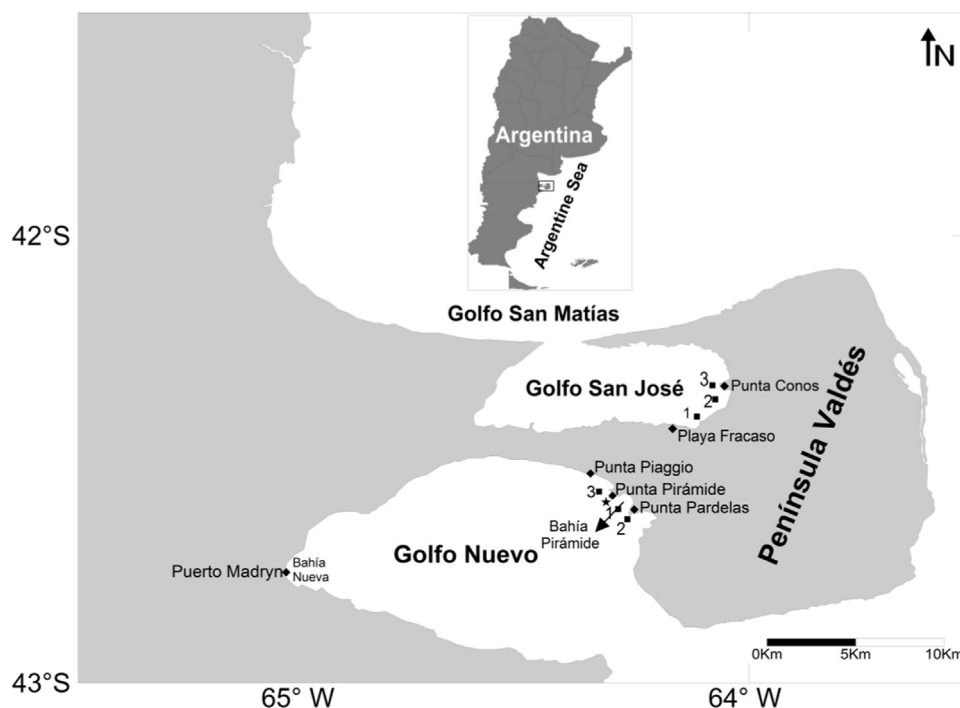


Fig. 1. Study area showing sampling site locations in Golfo Nuevo and Golfo San José and the sample collection site during a feeding event (★) of southern right whales (*Eubalaena australis*) in Bahía Pirámide, Golfo Nuevo.

Hernández-Moresino et al., 2017) or has been focused on a particular group within plankton (Sastre et al., 2007; Crespi-Abril et al., 2014; Dellatorre et al., 2014; D'Agostino et al., 2015). In addition, no systematic sampling research programs have been performed to date.

Previous research on the annual phytoplankton cycle in GN reveals that it is generally dominated by diatoms (Gayoso, 2001; Sastre et al., 2001; Santinelli, 2008; Cadaillón, 2012). Studies conducted in GSJ report partial knowledge on the phytoplankton community (see Andrinolo et al., 1999; Cadaillón, 2012) and are mainly focused on the composition and abundance of toxic species (Santinelli et al., 2002). Still, no investigations on the entire phytoplanktonic community through the annual cycle have been performed to date. Previous studies of samples collected during a short lapse in GSJ report a great diversity of diatoms, the genera *Chaetoceros* and *Pseudo-nitzschia* being the most abundant components, whereas dinoflagellates were observed to be numerically important in spring and summer (Andrinolo et al., 1999; Cadaillón, 2012).

On the other hand, it has been found that the copepods *Ctenocalanus vanus* and *Calanus australis* were the most abundant species in the deeper (around 40 m depth) stations of Bahía Nueva (GN, Fig. 1) during winter and spring (Hoffmeyer unpublished results). In line with this, Menéndez et al. (2011) observed a similar distribution pattern of *C. australis* in GN during winter. These authors also observed that *C. vanus* was the most abundant species followed by *Paracalanus parvus* in winter. Wilson et al. (2015) reported seasonal variability in mesozooplankton abundance with peaks in spring and autumn (Bahía Nueva, GN, December 1997 to September 1998) that had been previously observed by Esteves et al. (1996). As to GSJ, only two studies have been performed to date on the composition of the entire zooplankton community during the warm season (Hernández Moresino et al., 2014; Hernández-Moresino et al., 2017). Hernández Moresino et al. (2014); Hernández-Moresino et al. (2017) reported that calanoid copepods were the most abundant group followed by cladocerans, larvae and adults of malacostracans, fish eggs, appendicularians-chaetognaths, and fish larvae.

To our knowledge, ours is the first exploratory study carried out with the aims of analyzing phyto- and mesozooplankton seasonal dynamics as available food for whales along the year, and exploring the role of some environmental drivers on plankton communities.

## 2. Materials and methods

### 2.1. Sampling activities

Plankton and seawater samples were collected on an approximately monthly basis at three stations in GN and GSJ (Fig. 1). These stations were selected from coastal waters of GN and GSJ where southern right whales had been observed opportunistically foraging during their stay in Península Valdés calving ground (Sironi, 2004; Hoffmeyer et al., 2010; D'Agostino et al., 2016) (Fig. 1). Sampling was carried out in GN from December 2, 2014 to December 21, 2015, and in GSJ from January 23, 2015 to January 13, 2016.

At each sampling site, surface seawater temperature was measured in situ with a portable thermometer. Seawater was subsequently sampled at a 3 m and 10 m depth using a 2.5 l Van Dorn bottle from a boat. One liter of water from each depth was mixed and 500 ml were taken for the analysis of chlorophyll *a* and phaeopigments, and a 250 ml aliquot was fixed with Lugol's solution at a final concentration of 0.4 ml 100 ml<sup>-1</sup> (Ferrario et al., 1995) for quantitative phytoplankton analyses. Phytoplankton net tows were carried out to collect higher density samples for qualitative taxonomic studies. Samples were collected using oblique net tows from a 20 m depth to the surface from a motor boat using a 20 µm mesh net while traveling over a 7 min period at a speed of 2 knots. They were put in 250 ml plastic bottles and fixed with 4% formaldehyde. For the mesozooplankton quantitative taxonomic analyses, samples were collected using a 335 µm mesh net (i.e., it was used

to mimic the capture of mesozooplankton organisms by the northern right whales' baleen, according to Mayo et al., 2001) equipped with a flow meter (General Oceanics Model 2030R) on the net mouth. Net tows were performed obliquely from 30 m to surface for a 7 min period from the motor boat at a speed of 2 knots. Samples were put in 250 ml plastic flasks and fixed with 4% formaldehyde. In GN, sampling was not possible at site 3 (Fig. 1) during September (September 4, 2015) because of the harsh weather conditions. Nonetheless, when weather conditions became favorable, individuals of *E. australis* were observed feeding by skimming at the sea surface. An additional sample was therefore collected at this site (Fig. 1).

### 2.2. Laboratory analyses

For chlorophyll *a* determination, the seawater samples were filtered through GF/F filters (25 mm and 0.7 µm in pore size) which were stored frozen at -20 °C. Chlorophyll *a* was extracted during 24 h at 4 °C with 5 ml 90% acetone in darkness. Extracts were centrifuged at 1680 × g for 5 min. Chlorophyll *a* and phaeopigments were subsequently quantified using a spectrofluorometer (Shimadzu RF-5301PC) at λEx/λEm: 430/671 nm and concentrations were estimated according to Holm-Hansen et al. (1965) equations. Chlorophyll *a* is a photosynthetic pigment common to all autotrophic phytoplankton organisms. Concentration data from HPLC analysis were therefore used to estimate phytoplankton biomass (Almandoz et al., 2011; Gonçalves-Araujo et al., 2016). Chlorophyll *a* values were corrected for phaeopigments by acidification with HCl (0.1 N). Phaeopigments (mainly phaeofitin) were used as principal indicators of Chlorophyll *a* degradation as a result of herbivorous zooplankton grazing (Lorenzen, 1967; Helling and Baars, 1985; Head and Harris, 1992).

Net tow samples for phytoplankton identification were examined with a phase contrast microscope (Olympus CX31), whereas the species in bottle samples were enumerated with an inverted microscope (Leica DML) following Utermöhl (1958)'s methodology. For diatom frustule identification, cleaning was performed according to the method of Hasle and Fryxell (1970). Naphrax mounted slides (Ferrario et al., 1995) were observed with an optical microscope equipped with phase contrast and selected samples were observed by SEM (Jeol JSM-6360 LV) for species identification. Phytoplankton abundances were expressed as cells per liter (cells l<sup>-1</sup>). Quantitative phytoplankton data were not available in GSJ for the early summer of 2016 because of sample deterioration.

Mesozooplankton samples were examined under a stereo microscope Nikon SMZ645 for species identification and enumeration. Taxa were identified to the lowest possible taxonomic level using appropriate literature (Boltovskoy, 1981a, 1999; Kirkwood, 1982; Cervellini, 1988; Bradford-Grieve et al., 1999; Harris et al., 2000; Young, 2002). Based on the abundance of the organisms observed *a priori* in the samples collected, total or aliquot counts were applied. In the latter case, samples were divided in aliquots (1/10 sample volume) after homogenization (Boltovskoy, 1981b) and all individuals present were identified and counted. Mesozooplankton abundances were expressed as the number of individuals per cubic meter (ind m<sup>-3</sup>).

### 2.3. Data analysis

Both Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were used for the multivariate analysis of data. PCA was used to identify the seasonal patterns of phyto- and mesozooplankton abundance. The relationship between plankton composition and environmental variables (temperature, chlorophyll *a*, phaeopigments, and salinity) was assessed using RDA. The statistical significance of the model described by RDA was tested by the Monte Carlo permutation test (n = 5000). Calculations were made using the statistical software R Core Team (2016). Plankton abundance data were transformed (Hellinger transform, Legendre and Gallagher, 2001) before PCA and

**Table 1**

Seasonal average  $\pm$  standard deviation of temperature, chlorophyll *a*, phaeopigments, and plankton abundance registered in Golfo Nuevo and Golfo San José during the annual cycle studied (December 2014–December 2015 in GN and January 2015–January 2016 in GSJ). ND: no data.

Period	Temperature (°C)	Chlorophyll <i>a</i> ( $\mu\text{g l}^{-1}$ )	Phaeopigments ( $\mu\text{g l}^{-1}$ )	Phytoplankton abundance ( $\times 10^4$ cells $\text{l}^{-1}$ )	Mesozooplankton abundance (ind $\text{m}^{-3}$ )
<b>Golfo Nuevo</b>					
Spring 2014 (Dec)	16.67 $\pm$ 0.58	0.48 $\pm$ 0.22	0.57 $\pm$ 0.13	8.62 $\pm$ 1.62	1119
Summer 2015 (Jan-Mar)	18.50 $\pm$ 0.43	0.60 $\pm$ 0.16	0.34 $\pm$ 0.14	4.39 $\pm$ 6.17	1666 $\pm$ 1528
Autumn 2015 (Apr-Jun)	15.42 $\pm$ 1.77	0.81 $\pm$ 0.38	0.41 $\pm$ 0.13	3.91 $\pm$ 0.8	1220 $\pm$ 1177
Winter 2015 (Jul-Sep)	11.17 $\pm$ 0.29	0.81 $\pm$ 0.30	0.40 $\pm$ 0.12	2.48 $\pm$ 3.31	368 $\pm$ 321
Spring 2015 (Oct-Dec)	14.44 $\pm$ 2.74	2.27 $\pm$ 2.24	0.75 $\pm$ 0.31	35.9 $\pm$ 60.5	4630 $\pm$ 7069
<b>Golfo San José</b>					
Summer 2015 (Jan-Mar)	18.92 $\pm$ 1.02	1.03 $\pm$ 0.52	0.31 $\pm$ 0.10	19.97 $\pm$ 17.10	1466 $\pm$ 926
Autumn 2015 (Apr-May)	15.75 $\pm$ 1.37	2.01 $\pm$ 0.59	1.15 $\pm$ 0.57	15.10 $\pm$ 2.11	895 $\pm$ 283
Winter 2015 (Jul-Aug)	11.33 $\pm$ 0.52	0.88 $\pm$ 0.35	0.59 $\pm$ 0.16	1.63 $\pm$ 1.43	304 $\pm$ 105
Spring 2015 (Sep-Nov)	13.33 $\pm$ 2.40	2.01 $\pm$ 1.07	1.12 $\pm$ 0.49	80.30 $\pm$ 65.60	336 $\pm$ 448
Summer 2016 (Jan)	16.33 $\pm$ 1.15	1.20 $\pm$ 0.03	0.64 $\pm$ 0.06	ND	191

RDA analysis, whereas environmental variables were standardized for RDA analysis. Taking into account that salinity in these gulfs is considered rather constant (Rivas and Ripa, 1989; Rivas, 1990; Rivas and Beier, 1990; Pisoni, 2012) and because salinity in the field could not be measured in this study, for the latter statistical test analyses mean salinity data for GN and GSJ were taken from Rivas and Beier (1990) (i.e., two cruises carried out between 14 April and 20 April 1986 and 29 September and 4 October 1986). In addition, abundance values of plankton groups were considered in both gulfs from summer until spring 2015 because a higher number of samples had been collected during these climatic seasons. A 0.05 significance level was applied to all the statistical analyses.

### 3. Results

#### 3.1. Seasonal temperature and salinity

The mean value of seawater surface temperature registered in both gulfs was significantly lower in austral winter than in summer (Student's *t*-test;  $p < 0.05$ ) (Table 1). The mean salinity data taken from Rivas and Beier (1990) for both gulfs showed a decrease from April to September (from 33.92 to 33.87, respectively) in GSJ but increased from April to September (from 33.92 to 34.04, respectively) in GN. These researchers reported that the geometry of the mouth of these gulfs restricts communication with the open sea and, consequently, the water of GN and GSJ is more efficiently influenced by atmospheric forcing than by the platform waters. They also documented that throughout the year these gulfs gain heat and salt across the air-sea interface.

#### 3.2. Phytoplankton

##### 3.2.1. Taxonomic composition

In GN, a total of 69 taxa were identified, of which 42 belonged to Bacillariophyceae (diatoms), 23 to Dinophyceae (dinoflagellates), 2 to Dictyochophyceae (silicoflagellates), 1 to Euglenophyceae, and 1 to Cryptophyceae (cryptophytes) (Table 2). In GSJ, a total of 83 taxa were identified, of which 52 belonged to Bacillariophyceae, 28 to Dinophyceae, 2 to Dictyochophyceae, and 1 to Euglenophyceae (Table 2). Several unidentified nanoflagellates were also recorded in both gulfs (Table 2).

##### 3.2.2. Biomass and seasonal abundance

In GN, phytoplankton biomass mean values were observed to be lowest during late spring 2014 and were associated with high abundances of an unidentified dinoflagellate (Table 1 and Fig. 2a). In contrast, they were found to be highest during spring 2015 (max. =

5.13  $\mu\text{g l}^{-1}$ ; October, Fig. 2a), which coincided with a bloom of *Pseudonitzschia australis* (Table 1 and Fig. 2a and b). In GSJ, phytoplankton biomass mean values were found to be lowest in winter 2015 with a minimum record in July (Fig. 2d). In contrast, they were found to be highest with two peaks of equal concentration, one which occurred in autumn 2015 (max. = 2.21  $\mu\text{g l}^{-1}$ ) which coincided with the high abundance values of *Eucampia zodiacus* observed in April, and the other one which occurred in spring 2015 (max. = 2.74  $\mu\text{g l}^{-1}$ ) and was associated with a bloom of *Chaetoceros debilis* in October (Table 1 and Fig. 2d).

In general, phaeopigment values in GN and GSJ showed a pattern similar to that of chlorophyll *a* levels (Table 1 and Fig. 2a and d). In GN, the highest mean values of phaeopigment concentration occurred during the spring bloom of *P. australis* (October) (Table 1 and Fig. 2a and b). In GSJ, the highest mean values of these pigments were detected during autumn and spring (max. = 1.56 and 1.47  $\mu\text{g l}^{-1}$  in April and October, respectively), which coincides with the highest mean phytoplankton biomass values recorded (Table 1 and Fig. 2d and e).

In GN and GSJ, cell abundances were lowest in winter, with a minimum in July 2015 (Table 1 and Fig. 2b and e). In contrast, cell abundances in GN were highest during the two sampled springs, maximum densities being recorded in December 2014 and October 2015 (Table 1 and Fig. 2b). In GSJ, it was observed that cell abundances were highest during summer 2015 with maximum values in March and spring 2015 with a peak in November (Table 1 and Fig. 2b).

In terms of relative abundance, phytoplankton in GN was dominated by dinoflagellates during late spring 2014 (Dec-14), reaching a 71% of total phytoplankton abundance and was mainly represented by an unidentified dinoflagellate (Fig. 2b and c). In early summer 2015 (Jan-15), the phytoplankton community was dominated by diatoms which reached 82% of total phytoplankton abundance and which were followed by dinoflagellates (14%) (Fig. 2c). In this period the most abundant species were *Chaetoceros* sp. (Fig. 2b) and unidentified dinoflagellates. By mid-summer (Feb-15), the low densities observed were dominated by dinoflagellates which reached a relative abundance of 91% of which the most abundant species was *Prorocentrum micans* (Fig. 2d and c). Towards late summer (Mar-15), phytoplankton was only represented by dinoflagellates and diatoms with a relative abundance of 58% and 42%, respectively (Fig. 2c). The most abundant taxa were *Prorocentrum micans* (Fig. 2b) and *Chaetoceros* sp., respectively. During autumn (Apr-15 and Jun-15), diatoms dominated the community, which reached 71% and 75% and were followed by dinoflagellates (Fig. 2c). Among diatoms, the most abundant species identified were *Rhizosolenia setigera* (April) and *Chaetoceros debilis* (June) (Fig. 2b) and dinoflagellates were mainly represented by *Tripos muelleri* (April) and *Amphidinium* sp. (June). By early winter (Jul-15), the phytoplankton community was observed to be dominated by dinoflagellates (50%),

**Table 2**

Phytoplankton taxa identified in Golfo Nuevo (GN) and Golfo San José (GSJ) during the sampling period. The name of the gulf between parentheses indicates that a specific taxon was identified only in that gulf.

Class BACILLARIOPHYCEAE	Class BACILLARIOPHYCEAE
<i>Amphora</i> sp. (GSJ)	<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve (GSJ)
<i>Asterionellopsis glacialis</i> (Castracane) Round	<i>Thalassiosira gravida</i> Cleve (GSJ)
<i>Bacillaria paxillifera</i> (Müller) Marsson (GSJ)	<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky
<i>Bacteriastrium furcatum</i> Shadbolt	<i>Thalassiosira</i> spp.
<i>Ceratoneis closterium</i> Ehrenberg	<i>Toxarium undulatum</i> Bailey
<i>Cerataulina pelagica</i> (Cleve) Hendey (GSJ)	<i>Trieres mobiliensis</i> (Bailey) Ashworth and Theriot
<i>Chaetoceros concavicornis</i> Mangin (GN)	<i>Trigonium alternans</i> (Bailey) Mann (GSJ)
<i>Chaetoceros convolutus</i>	<i>Tryblionella compressa</i> (Bailey) Poulin (GSJ)
<i>Chaetoceros curvisetus</i> Cleve (GSJ)	<b>Class DINOPHYCEAE</b>
<i>Chaetoceros debilis</i> Cleve	<i>Alexandrium tamarense</i> (Lebour) Balech
<i>Chaetoceros decipiens</i> Cleve	<i>Amphidinium</i> sp.
<i>Chaetoceros didymus</i> Ehrenberg (GN)	<i>Ceratium massiliense</i> (Gourret) Karsten
<i>Chaetoceros lorenzianus</i> Grunow	<i>Ceratium symmetricum</i> (Pavillard) (GSJ)
<i>Chaetoceros socialis</i> H.S.Lauder	<i>Ceratium gibberum</i> Gourret (GSJ)
<i>Chaetoceros</i> spp.	<i>Ceratium</i> spp.
<i>Cocconeis scutellum</i> Ehrenberg (GN)	<i>Dinophysis acuminata</i> Claparède and Lachmann
<i>Corethron pennatum</i> (Grunow) Ostefeld	<i>Dinophysis acuta</i> Ehrenberg (GSJ)
<i>Coscinodiscus</i> spp.	<i>Dinophysis caudata</i> Saville-Kent (GN)
<i>Ditylum brightwellii</i> (West) Grunow	<i>Dinophysis tripos</i> Gourret
<i>Eucampia zodiacus</i> Ehrenberg	<i>Diplopsalis lenticula</i> Bergh
<i>Eucampia</i> sp.	<i>Gonyaulax ceratocoroides</i> Kofoid
<i>Grammatophora marina</i> (Lyngbye) Kützing (GN)	<i>Gymnodinium</i> sp.
<i>Guinardia striata</i> (Stolterfoth) Hasle (GSJ)	<i>Gyrodinium</i> sp. (GSJ)
<i>Gyrosigma acuminatum</i> (Kützing) Rabenhorst	<i>Lepidodinium chlorophorum</i> (Elbrächter and Schnepf) Gert Hansen, Botes and de Salas
<i>Gyrosigma fasciola</i> (Ehrenberg) Griffith and Henfrey	<i>Noctiluca scintillans</i> (Macartney) Kofoid and Swezy (GSJ)
<i>Leptocylindrus danicus</i> Cleve	<i>Prorocentrum lima</i> (Ehrenberg) Stein (GN)
<i>Leptocylindrus minimus</i> Gran	<i>Prorocentrum micans</i> Ehrenberg
<i>Licmophora abbreviata</i> Agardh	<i>Protoperidinium divergens</i> (Ehrenberg) Balech
<i>Licmophora flabellata</i> (Greville) Agardh	<i>Protoperidinium oceanicum</i> (VanHöffen) Balech
<i>Lithodesmium undulatum</i> Ehrenberg	<i>Protoperidinium ovatum</i> Pouchet (GSJ)
<i>Meuniera membranacea</i> (Cleve) Silva (GSJ)	<i>Protoperidinium pallidum</i> (Ostenfeld) Balech (GSJ)
<i>Navicula</i> spp.	<i>Protoperidinium pentagonum</i> (Gran) Balech (GSJ)
<i>Nitzschia longissima</i> (Brébisson) Ralfs	<i>Protoperidinium latissimum</i> (Kofoid) Balech (GN)
<i>Odontella aurita</i> (Lyngbye) Agardh (GSJ)	<i>Protoperidinium steinii</i> (Jørgensen) Balech (GN)
<i>Odontella sinensis</i> (Greville) Grunow (GSJ)	<i>Protoperidinium</i> spp.
<i>Paralia sulcata</i> (Ehrenberg) Cleve	<i>Pyrocystis</i> sp. (GN)
<i>Pleurosigma strigosum</i> Smith	<i>Scrippsiella trochoidea</i> (Stein) Loeblich III
<i>Pseudo-nitzschia australis</i> Frenguelli	<i>Torodinium</i> sp. (GSJ)
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup and Hasle	<i>Tripos furca</i> (Ehrenberg) F. Gómez (GSJ)
<i>Pseudo-nitzschia delicatissima</i> Cleve P.T. (GSJ)	<i>Tripos fusus</i> (Ehrenberg) F. Gómez
<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle	<i>Tripos lineatus</i> (Ehrenberg) Gómez
<i>Pseudo-nitzschia pungens</i> (Grunow ex Cleve) Hasle	<i>Tripos muelleri</i> Bory
<i>Rhabdonema adriaticum</i> Kützing (GSJ)	<b>Class DICTYOCOPHYCEAE</b>
<i>Rhizosolenia acuminata</i> (Peragallo) Peragallo (GSJ)	<i>Dictyocha fibula</i> Ehrenberg
<i>Rhizosolenia setigera</i> Brightwell	<i>Dictyocha speculum</i> Ehrenberg
<i>Rhizosolenia striata</i> Greville (GSJ)	<b>Class EUGLENOPHYCEAE</b>
<i>Roperia tessellata</i> (Roper) Grunow ex Pelletan (GSJ)	<i>Eutreptia</i> sp.
<i>Skeletonema costatum</i> (Greville) Cleve (GN)	<b>Class CRYPTOPHYCEAE</b>
<i>Stephanopyxis turris</i> (Greville) Ralfs	<i>Rhodomonas</i> spp. (GN)
<i>Striatella unipunctata</i> (Lyngbye) Agardh (GN)	Nanoflagellates
<i>Synedra</i> sp. (GN)	

diatoms (33%), and silicoflagellates (17%) (Fig. 2c), all being represented respectively by several species of these groups which reached low cell densities (e.g. *Tripos muelleri*, *Prorocentrum micans*, *Thalassiosira* spp., *Dictyocha speculum*) (Fig. 2b). In late winter (Sep-15), diatoms were the most abundant group, representing 87% of total phytoplankton organisms followed by dinoflagellates (10%) (Fig. 2c). *Chaetoceros socialis* was the most important species (Fig. 2b), whereas dinoflagellates were represented by *Tripos muelleri*. In spring (Oct-15, Nov-15 and Dec-15), the phytoplankton community was found to be dominated by diatoms which reached 100%, 95%, and 86%, respectively (Fig. 2c). During this season, an intense bloom of *P. australis* was observed in October reaching a peak of  $8.21 \times 10^5$  cells  $l^{-1}$ , whereas in November and December, the phytoplankton community was observed to be dominated by unidentified centric diatoms (Fig. 2b).

In GSJ, no seasonal differences were observed in the composition of the phytoplankton community. Throughout our study, diatoms

dominated phytoplankton in this gulf (summer = 93.82%, autumn = 83.42%, winter = 87.84%, spring = 99.38%) and they were followed by dinoflagellates (Fig. 2e and f). During October and November (spring), two blooms were registered in which diatoms represented 100% of total phytoplankton abundance (Fig. 2f). The first one was dominated by *Chaetoceros debilis* (Fig. 2e) and *Chaetoceros socialis*. The second one, whose cell densities were lower than those of the first bloom, was mainly represented by *C. socialis* (Fig. 2e).

### 3.3. Mesozooplankton

#### 3.3.1. Taxonomic composition

In GN, the mesozooplankton community was represented by 63 taxa (Table 3). The most diverse groups were copepods and decapods (larvae) which were represented by more than 10 species each (Table 3). Within mesozooplankton in GSJ, 61 taxa were identified

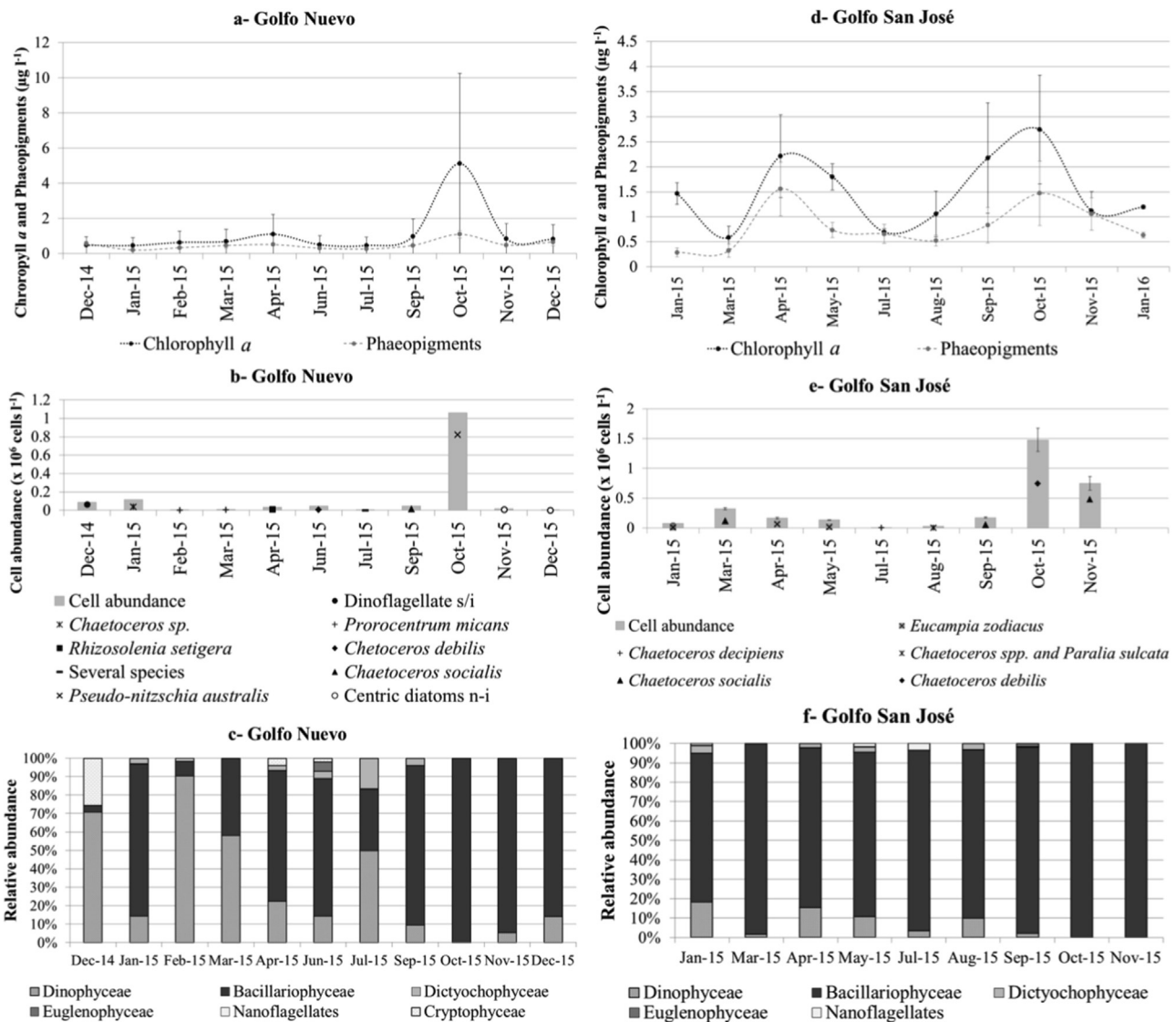


Fig. 2. Seasonal variability in Golfo Nuevo and Golfo San José of (a and d) mean (SD) phytoplankton biomass (Chlorophyll a) and phaeopigments, (b and e) mean (SD) phytoplankton abundance. Symbols indicate the most abundant species at each sampling date throughout the study period and (c and f) the relative abundance of the phytoplankton groups identified. n-i: unidentified.

(Table 3). The most diverse groups in this gulf were decapods which were represented by 14 species and were followed by copepods belonging to about 9 species (Table 3).

### 3.3.2. Seasonal abundance

In GN and GSJ, the values corresponding to total mesozooplankton abundance were found to be lowest in winter with minimum abundance values in July 2015 (Fig. 3a and c). Mesozooplankton was dominated by *Ctenocalanus vanus* in GN and by the large copepodites fam. Calanidae in GSJ (Table 1 and Fig. 3a and c). In GN, abundance values were recorded to be highest in summer and spring 2015, reaching maximum values during March and October, respectively (Table 1 and Fig. 3a). In both cases, it was dominated by the cladoceran *Evadne nordmanni* (Fig. 3a). In GSJ, mesozooplankton abundance values were observed to be highest during summer and autumn 2015 (Table 1). During summer, the maximum value was recorded in January when the mesozooplankton community was dominated by zoeae of *Cyrtograpsus angulatus* and during autumn in April, when the community was dominated by *E. nordmanni* (Fig. 3c).

In terms of relative abundance, in GN it was observed that in late spring 2014 mesozooplankton was dominated by copepods, which

reached 96% of the total abundance of the organisms identified (Fig. 3b). The most abundant species were *Paracalanus parvus* (Fig. 3a) followed by *Calanus australis*. During summer 2015, cladocerans and decapods were the most abundant groups, with a maximum peak in March dominated by *E. nordmanni* (Fig. 3a and b) and eggs of decapods. Likewise, in January bryozoa cyphonautes also dominated the mesozooplankton community (Fig. 3a). In autumn, mesozooplankton was dominated by cladocerans reaching 73% (Apr-15) and 67% (Jun-15) of the total of the mesozooplankton organisms recorded (Fig. 3b). The most abundant taxa were *Podon* spp. (April) and *E. nordmanni* (June) (Fig. 3a). Copepods were the second most abundant group during this period, representing about 14% and 29% (April and June, respectively) of total mesozooplankton abundance (Fig. 3b), *C. australis* and *C. vanus* being respectively the most abundant species. In winter, the mesozooplankton community was dominated by copepods and cladocerans, reaching 96% and 67% in July and September, respectively, of total mesozooplanktonic organisms (Fig. 3b). The dominant species were the calanoid copepod *C. vanus* in July and the cladoceran *E. nordmanni* in September (Fig. 3a). At the beginning of spring 2015 (Oct-15), cladocerans were the most abundant group showing a relative abundance of 88% (Fig. 3b). *Evadne nordmanni* was the most important species of this

**Table 3**

Mesozooplankton taxa identified during the sampling period in Golfo Nuevo (GN) and Golfo San José (GSJ). The name of the gulf between parentheses indicates that a specific taxon was identified only in that gulf. The names of particular development stages are between parentheses. n-i: unidentified.

COPEPODA	EUPHAUSIACEA
Calanoida (Nauplius)	Eggs (GN)
Pontellidae (Nauplius)	Nauplius (GN)
<i>Acartia tonsa</i> Dana	Calyptopis
<i>Calanoides carinatus</i> (Krøyer)	Furcilia (GN)
<i>Calanus australis</i> Brodsky	<i>Euphausia lucens</i> (Calyptopis) Hansen
Calanidae (Copepodites 1–3)	<i>Euphausia lucens</i> (Furcilia) Hansen
<i>Ctenocalanus vanus</i> Giesbrecht	<i>Euphausia lucens</i> (Juveniles) Hansen (GN)
	<i>Euphausia lucens</i> (Adults) Hansen (GN)
<i>Euterpina acutifrons</i> (Dana)	<b>CLADOCERA</b>
<i>Labidocera fluviatilis</i> Dahl	<i>Bosmina</i> sp. (GSJ)
<i>Monstrilla</i> sp.	<i>Evadne nordmanni</i> Lovén
<i>Oithona</i> spp.	<i>Pleopis polyphaemoides</i> (Leuckart)
<i>Oithona nana</i> Giesbrecht	<i>Podon</i> spp.
<i>Oithona</i> sp. (GN)	<b>MOLLUSCA</b>
<i>Paracalanus parvus</i> (Claus)	Bivalvia (Veliger) Linnaeus
<i>Pontella patagoniensis</i> (Lubbock)	Gastropoda (Veliger) Cuvier
<i>Tisbe</i> spp.	<b>POLYCHAETA</b>
<b>CIRRIPEDIA</b>	Polychaeta Larvae n-i
Cypris	Spionidae (Nectochaeta) Grube
Nauplius	<b>CHAETOGNATHA</b>
<b>AMPHIPODA</b>	<i>Parasagitta friderici</i> (Ritter-Záhony)
<i>Themisto gaudichaudii</i> Guérin (GN)	<b>ECHINODERMATA</b>
<b>DECAPODA</b>	Bipinnaria larvae
Eggs	Echinopluteus larvae
Nauplius	Ophiopluteus larvae
Megalopa (GSJ)	<b>BRYOZOA</b>
Protozoa	Ciphonautes
<i>Austinixa patagoniensis</i> (Zoea) (Rathbun)	<b>CNIDARIA</b>
<i>Callinassa</i> spp. (Zoea)	
<i>Cyrtograpsus altimanus</i> (Zoea) Rathbun	Ceriantharia (Cerinula)
<i>Cyrtograpsus angulatus</i> (Zoea) Dana (GSJ)	<i>Obelia</i> sp.
<i>Danielethus patagonicus</i> (Zoea) (Milne-Edwards)	<i>Turritopsis nutricula</i> McCrady (GSJ)
<i>Halicarcinus planatus</i> (Zoea) (Fabricius)	Hydrozoa
<i>Libidoclaea granaria</i> (Zoea) Milne Edwards and Lucas	<b>ASCIDIACEA</b>
<i>Libinia spinosa</i> (Zoea) Guérin	Tadpole
<i>Munida gregaria</i> (Zoea) (Fabricius)	<b>APPENDICULARIA</b>
<i>Neohelice granulata</i> (Dana) (GSJ)	<i>Oikopleura</i> sp.
<i>Ovalipes trimaculatus</i> (Zoea) (De Haan)	<i>Fritillaria</i> sp.
<i>Pachycheles chubutensis</i> (Zoea) Boschi	<b>ICHTHYOPLANKTON</b>
<i>Peisous petrunkevitchi</i> (Zoea) Burkenroad (GSJ)	Eggs n-i
<i>Pleoticus muelleri</i> (Zoea) (Spence Bate) (GSJ)	
<i>Stomatopoda</i> larvae (GN)	Larvae
<i>Tumidothera maculatus</i> (Zoea) (Say)	<i>Engraulis anchoita</i> (eggs) Hubbs Marini

group (Fig. 3a). In mid-spring (Nov-15), copepods dominated the mesozooplankton community, reaching 96% of the total organisms identified (Fig. 3b), *C. carinatus* being the most abundant species (Fig. 3a). In contrast, a low abundance of mesozooplankton was observed towards late spring (Dec-15) (Fig. 3a) and was represented by ichthyoplankton organisms (40%), copepods (20%), bryozoa ciphonautes (19%), and cerianthids (17%) (Fig. 3b).

In GSJ, copepods were the most abundant group during summer 2015, representing respectively 47% (Jan-15) and 52% (Mar-15) of total mesozooplankton during this season, and were followed by cladocerans and decapods (Fig. 3d). The most abundant species were the calanoid copepods *Acartia tonsa*, *C. australis*, *C. vanus*, and *P. parvus* (in decreasing order of abundances). In addition, *E. nordmanni* was dominant among cladocerans, whereas the larvae zoea of *C. angulatus* was dominant among decapods (Fig. 3c). Other important taxa in terms of

relative contribution during this period were ichthyoplankton which was mainly represented by *Engraulis anchoita* eggs and chaetognaths which were represented by *Parasagitta friderici* (Fig. 3d). In autumn 2015, the mesozooplankton community was mainly dominated by cladocerans and copepods, which reached, respectively, 70% (Apr-15) and 94% (May-15) of total mesozooplankton abundance (Fig. 3d). Among cladocerans, *E. nordmanni* was the most abundant species, and among copepods, *C. carinatus* was dominant in this group (Fig. 3c). In winter 2015, copepods dominated the mesozooplankton community, large copepodites calanidae reaching the highest abundance values (Fig. 3c and d). Another taxon – within this group – that reached high abundances was *C. vanus*, with a maximum in August. Cladocerans and appendicularians were mainly represented by *E. nordmanni* and *Oikopleura* sp., respectively, which were also numerically important during August (Fig. 3d). During spring 2015, copepods were the dominant group of the mesozooplankton community, reaching a relative abundance of 78% (Sep-15), 76% (Oct-15) and 41% (Nov-15) (Fig. 3d). Likewise, during September and October appendicularians were the second most important group (Fig. 3d). The most abundant species in September were the calanoid copepod *C. vanus* (Fig. 3c) and, among appendicularians, the genus *Oikopleura* sp.. In October, the copepod *P. parvus* (Fig. 3c), followed by *C. vanus* and *C. carinatus* and the *Fritillaria* sp. appendicularian, were the dominant taxa. By late spring (Nov-15), *A. tonsa*, *E. nordmanni*, and *Oikopleura* sp. were the most abundant taxa. In early summer 2016, copepods, cladocerans, and ichthyoplankton were the most abundant groups reaching relative abundances of 36%, 30%, and 21%, respectively (Fig. 3d). The most important taxa were *A. tonsa* (Fig. 3c), *Podon* spp., and fish eggs.

#### 3.4. Relationships between plankton composition, abundance and environmental conditions

##### 3.4.1. Phytoplankton

In the PCA analysis, PC1 and PC2 explained 95.75% of the total variability in the abundances of phytoplankton classes among the climatic seasons of 2015 (Fig. 4). PC1 explained 78.34% of the total variability and mainly separated the cold seasons (autumn and winter) from the warm ones (spring and summer) (Fig. 4). Spring in both gulfs and summer in GSJ were characterized by high abundances of diatoms (Bacillariophyceae) (Fig. 4). The cold seasons in both gulfs and summer in GN were characterized – to a greater extent – by dinoflagellates (Dinophyceae) which were followed by the class Dictyochophyceae (Fig. 4). PC 2 explained 17.41% of the total variability observed, and separated spring in both gulfs and autumn in GN, which were associated with Euglenophyceae and Cryptophyceae from summer and winter in the two gulfs and autumn in GSJ, which were – in turn – mainly associated to nanoflagellates (Fig. 4). The results derived from RDA analysis for phytoplankton abundance data and environmental variables were not statistically significant and they were therefore not included.

##### 3.4.2. Mesozooplankton

In the PCA analysis, PC1 and PC2 explained together 84.58% of the variability in the abundances of the mesozooplankton groups among the climatic seasons of 2015. RDA presented a similar ordination to the PCA analysis, therefore only the RDA ordination diagram is shown (Fig. 5). RDA revealed that the environmental variables considered (i.e. temperature, salinity, chlorophyll *a*, and phaeopigments) explained a significant fraction of the variability in the abundances and composition of mesozooplankton (F-ratio = 4.74,  $p = 0.039$ ). The first and second RDA axes explained together 85.60% of the total variability observed (Fig. 5). The first axis mostly explained variability (77.38%) and mainly separated GN from GSJ (Fig. 5). The positive values of this axis were associated to the climatic seasons in GSJ, which were characterized by high abundances of copepods (Fig. 5). In the negative sector of axis 1, the seasons of GN were located and they were

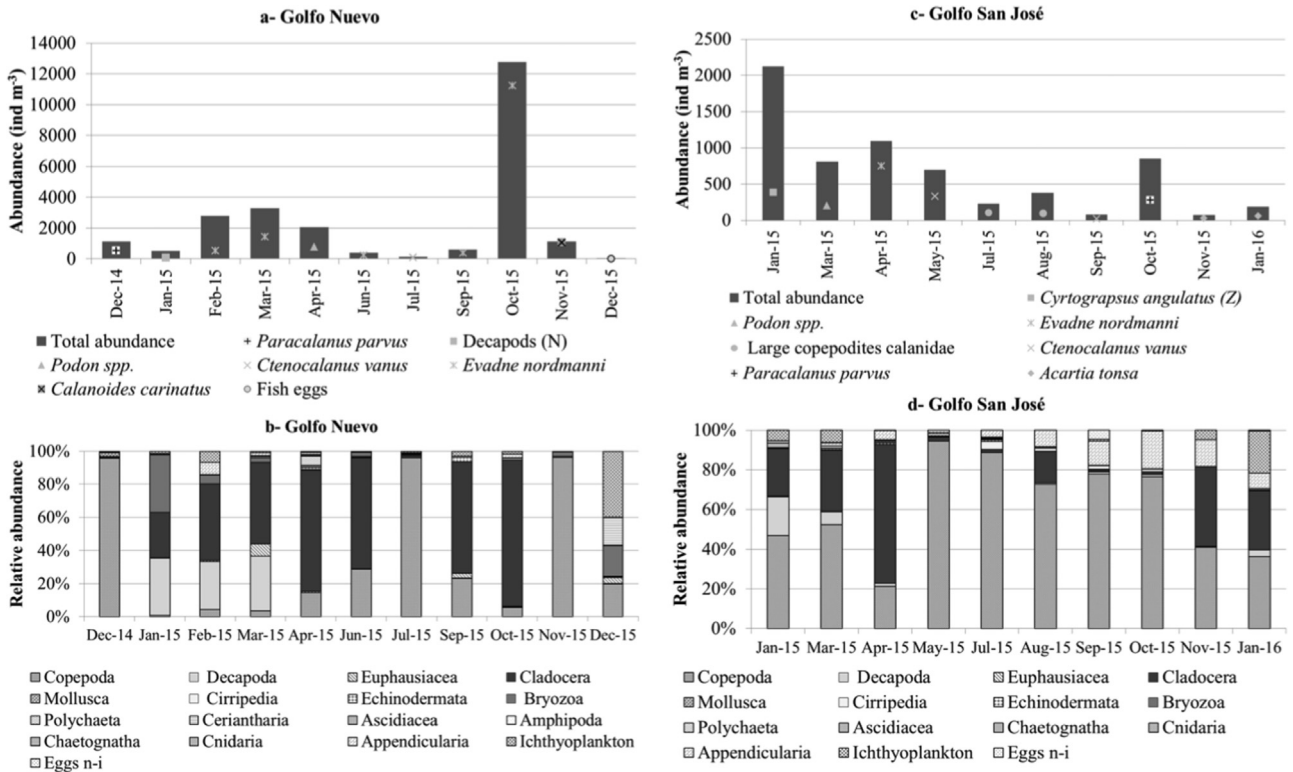


Fig. 3. Mean seasonal variability in Golfo Nuevo and Golfo San José of (a and c) mesozooplankton abundance. Symbols indicate the most abundant species during the sampling period and (b and d) the relative abundance of the mesozooplankton groups identified. n-i: unidentified. N: Nauplius. Z: Zoeta.

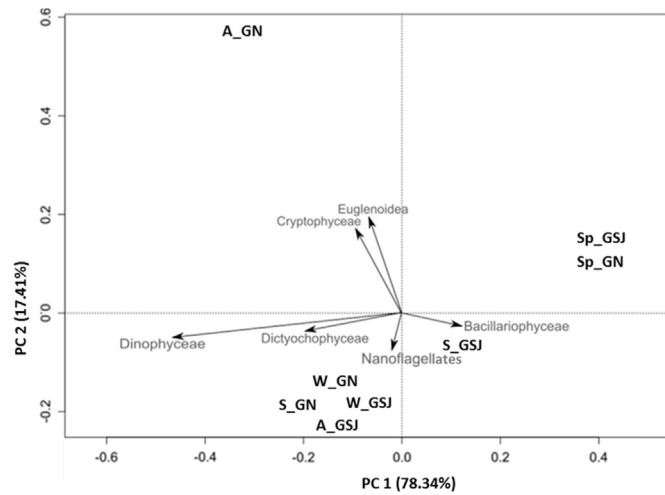


Fig. 4. PCA ordination of phytoplankton groups during the climatic seasons of 2015 in Golfo Nuevo (GN) and Golfo San José (GSJ). W: winter; A: autumn, Sp: spring, S: summer.

associated to cladocerans (Fig. 5). Axis 2 explained 8.20% of variability and its positive sector was associated with autumn and winter in both gulfs, as well as with spring in GN, and was characterized by high abundances of cladocerans, appendicularians, and copepods (Fig. 5). On the other hand, the negative sector of this axis, separated summer in both gulfs and spring in GSJ (Fig. 5). These climatic seasons were characterized by high abundances of decapods and – to a lesser extent – ichthyoplankton (Fig. 5). The groups that best characterized GSJ were mainly associated with salinity and phaeopigments whereas those taxa associated with GN seasons showed a positive relationship with temperature (Fig. 5).

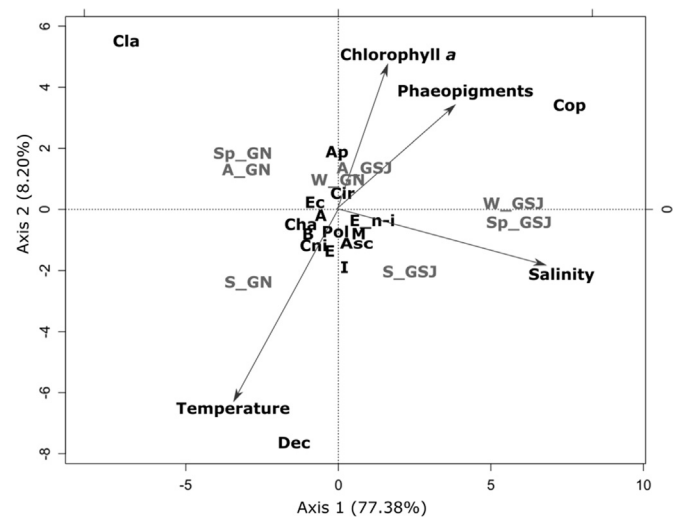


Fig. 5. RDA ordination of mesozooplankton abundance and environmental variables during seasons of 2015 in Golfo Nuevo (GN) and Golfo San José (GSJ). W: winter; A: autumn, Sp: spring, S: summer. A: Amphipoda, Ap: Appendicularia, Asc: Ascidiacea, B: Bryozoa, Cop: Copepoda, Cha: Chaetognatha, Cir: Cirripedia, Cla: Cladocera, Cni: Cnidaria, Dec: Decapoda, Ec: Echinodermata, E: Euphausiacea, E\_ni: Unidentified eggs, I: Ichthyoplankton, M: Mollusca, Pol: Polychaeta.

3.5. Composition and abundance of mesozooplankton during an *Eubalaena australis* feeding event in Golfo Nuevo

The mesozooplankton abundance in the sample collected on September 4, 2015 at the site where ~ 17–20 southern right whale individuals were feeding was higher than that in the samples collected at the sampling sites 1 and 2 (Table 4). During the feeding event, mesozooplankton was mainly dominated by cladocerans and copepods



**Table 4**

Total abundance of mesozooplankton groups recorded in Golfo Nuevo on 4-Sep-2015 during the feeding event of *Eubalaena australis* at the feeding site and at the sampling sites (Fig. 1). Only the abundances of the Southern right whale's prey items found during the feeding event are compared.

Group	Total abundance (ind m <sup>-3</sup> )		
	Feeding site	Sampling site	
		1	2
Cladocera	4808.90	248.31	151.92
Copepoda	2293.60	75.17	61.75
Decapoda	492.04	1.41	0.17
Euphausiacea	370.25	11.82	4.85
Ichthyoplankton	60.51	12.67	5.35
Chaetognatha	20.86	0	0.17
Bryozoa	16.99	0	0.33
Appendicularia	7.98	4.22	0
Cirripedia	1.29	0.56	0.17
Ceriantharia	0.26	0	0
Cnidaria	0.26	0	0
Polychaeta	0.26	0	0
<b>Total</b>	<b>8073.19</b>	<b>354.17</b>	<b>224.71</b>

(Table 4). Among cladocerans, only *E. nordmanni* was recorded, which reached a remarkable abundance value (Table 4). Copepods were represented mainly by *C. carinatus*, which reached 1252.63 ind m<sup>-3</sup>. Likewise, *C. vanus* and *C. australis* were also important components of this group, reaching an abundance level of 507.74 ind m<sup>-3</sup> and 328.80 ind m<sup>-3</sup>, respectively. Decapods were another group that contributed – in a smaller proportion – to the mesozooplankton community (Table 4). The zoeas larvae of *Munida gregaria* dominated this group, reaching 464.23 ind m<sup>-3</sup>. Euphausiids were also observed during this feeding event (Table 4). This group was exclusively represented – in decreasing order of abundance – by calyptopis and furcilia larvae, juveniles, and adults of *Euphausia lucens*.

#### 4. Discussion and conclusions

During the annual cycle analyzed in the study area within GN, the phytoplankton community was dominated mainly by diatoms and dinoflagellates. The predominance of diatoms observed throughout the annual cycle in GN was also reported in previous research (Gayoso, 2001; Sastre et al., 2001; Santinelli, 2008). In addition, Gayoso (2001) documented two recurrent peaks of phytoplankton abundance through the annual cycle in this gulf, one occurring during autumn and another during spring. Although, in agreement with Gayoso's study, phytoplankton abundance was found to be highest during spring in our study, another peak of phytoplankton abundance was also observed in summer rather than in autumn. The increase in cell abundance recorded in late spring 2014 was associated with the highest abundance values of dinoflagellates observed. Similarly, this group was an important component during summer. These findings agree with Gayoso (2001)'s observations according to which dinoflagellates were abundant during spring and summer in GN. On the other hand, the high cell densities and highest biomass values observed in this gulf during spring 2015 were both associated to an intense bloom of *P. australis* recorded in October. It should be noted that the cell densities of *P. australis* recorded in this study in GN ( $8.21 \times 10^5$  cells l<sup>-1</sup>) have been the highest recorded in the Argentine Sea to date (Negri and Inza, 1998; Sastre et al., 2001; Negri et al., 2004; Almandoz et al., 2007, 2017), whereas the highest cell abundances registered during summer were detected in January when the phytoplankton community was dominated by *Chaetoceros* sp.

In GSJ, only a few studies have addressed the entire phytoplankton community (see Andrinolo et al., 1999; Cadaillón, 2012) and no comprehensive study has been carried out to date on phytoplankton

composition and abundance throughout the annual cycle in this gulf. Most of the studies conducted in GSJ have been focused on the dynamics of toxic species in order to warn about the presence of toxic species as a result mainly of the economic activities that are carried out in this gulf, such as fishing on natural shellfish banks.

In the present study, phytoplankton abundance in GSJ showed two peaks, as observed in GN. One occurred in summer and the other in spring. However, in this gulf diatoms dominated the phytoplankton community throughout the year, reaching 100% of the total phytoplankton organisms found by late spring (October and November). Among diatoms, the most abundant genus in GSJ was *Chaetoceros*, with a peak of abundance in October. The dominance of *Chaetoceros* spp. in this gulf was also recorded by Andrinolo et al. (1999) who documented that this genus was a common and abundant component in GSJ between November and May. The second important group in this gulf was represented by dinoflagellates which were nonetheless recorded at low cell densities. This group reached maximum abundances during early summer (January) and during the cold seasons (autumn and winter).

Potentially toxic species were also identified in the present study, namely *A. tamarensis*, *D. acuminata*, *D. acuta*, *D. tripos*, *D. caudata*, *P. micans*, *P. lima*, *P. fraudulenta*, *P. calliantha*, *P. australis*, *P. pungens*, and *P. pseudodelicatissima*. These species have been reported to be frequent in the phytoplankton community in GN and GSJ (Andrinolo et al., 1999; Gayoso, 2001; Sastre et al., 2001, 2007; Santinelli et al., 2002; Santinelli, 2008; Cadaillón, 2012; D'Agostino et al., 2015; Gracia Villalobos et al., 2015). The presence of potentially toxic species has been worthy of note particularly in GSJ as a result of the small-scale fishery activities that are focused on *Tehuelche scallop* in this gulf (Orensanz et al., 2007). A Harmful Algal Bloom and Shellfish Toxicity Monitoring Program has therefore been implemented and is, in fact, being carried out in the coastal waters of Península Valdés since 2000. In line with this, shellfisheries in GN and GSJ are closed every year when the levels of paralytic shellfish toxins (PSTs), produced by the dinoflagellate *A. tamarensis* (Carreto et al., 1986; Esteves et al., 1992), are above the regulatory limit of 80 µg STX eq/100 g of mussel tissue (Wilson et al., 2015). However, they have not been closed in cases of amnesic shellfish poisoning (ASP) produced by species of the diatom genus *Pseudo-nitzschia* (the regulatory limit for Domoic Acid (DA) is 20 µg/g). Nonetheless, although no cases of ASP events have been documented to date either in wildlife or in humans in Península Valdés, previous research from our laboratory (D'Agostino et al., 2017) showed the presence of DA in phytoplankton and mesozooplankton samples as well as in whales' fecal samples collected at similar sites and on similar dates to those of the present study. In line with this, Wilson et al. (2015) detected levels of DA in blood samples from an adult female southern right whale and a male calf that died in GN and GSJ, respectively. These findings demonstrate that *E. australis* is exposed to DA while it remains in its calving ground in Península Valdés. This could, in turn, become a risk for other species that feed on zooplankton.

In general, in both gulfs, phytoplankton in the warm seasons was mainly characterized by a relatively high abundance of diatoms (mainly during spring), while in the cold seasons it was mostly characterized by high abundance of dinoflagellates and the class Dictyochophyceae. However, dinoflagellates had been previously reported to be most abundant during summer and spring in both GN and GSJ (Gayoso, 2001; Santinelli, 2008; Cadaillón, 2012). Euglenophyceae and Cryptophyceae were associated with spring in both gulfs and with autumn in GN. This agrees with findings from previous studies carried out in GN (Gayoso and Fulco, 2006; Cadaillón, 2012). As to nanoflagellates, they were mainly observed in both gulfs in summer and winter and in GSJ in autumn. In agreement with our results, previous research has also documented higher densities of nanoflagellates in GN during summer and winter (Esteves et al., 1997; Santinelli, 2008) and in GSJ in late summer (Andrinolo et al., 1999).

There is a limited knowledge on the entire mesozooplankton community both in GN and GSJ. No studies have been conducted to date on

the mesozooplankton taxonomic composition and abundance in GSJ throughout the annual cycle and only one study has been performed which describes the entire community in Bahía Nueva (GN) throughout the year (see Wilson et al., 2015; Hoffmeyer, unpubl. research). Ours is therefore the first study on mesozooplankton and phytoplankton seasonal dynamics over a complete year in the areas where whales usually feed during their reproductive stay in GN and GSJ (Sironi, 2004; Hoffmeyer et al., 2010; D'Agostino et al., 2016). However, the analysis of mesozooplankton in our study from samples obtained from a 335 µm mesh net may lead to an underestimation of the smaller organisms of the mesozooplankton fraction under study (Di Mauro et al., 2009).

Mesozooplankton in the selected coastal zone of GN showed two peaks of abundance during the annual cycle studied, the first one occurring during spring 2015 following the annual phytoplankton maximum, and the other occurring during late summer. In Wilson et al. (2015) and Hoffmeyer (unpubl. research) a similar seasonal pattern was reported for Bahía Nueva (GN), consisting in a mesozooplankton high abundance peak during spring and another abundance peak in autumn. These findings also agree with Hoffmeyer et al. (2010)'s results for Bahía Pirámide (GN, Fig. 1) according to which both the mesozooplankton abundance and biomass values were found to be higher in austral spring (October) than in winter (Hoffmeyer, unpubl. data). In line with this, in Hoffmeyer et al. (2010)'s study it was observed that the highest mesozooplankton abundance found in October was coincident with the foraging of southern right whales.

The mesozooplankton community in GN was dominated mainly by cladocerans and copepods, a scenario that has also been observed in previous research conducted in the Argentine Sea (Sabatini and Martos, 2002; Marrari et al., 2004) and in further previous studies carried out in this gulf (Hoffmeyer et al., 2010; Hoffmeyer unpubl. res.). Among cladocerans, *E. nordmanni* was the numerically most important species present throughout the year except in December (late spring 2014). Dominance of *E. nordmanni* over other species of cladocerans was also documented in various shelf zones of the Argentine Sea (Viñas et al., 2007). The dominance of copepods within the mesozooplankton community was also recorded by different authors in the Argentine Sea (Sabatini and Álvarez Colombo, 2001; Sabatini et al., 2001, 2012) as well as in GN (Esteves et al., 1996; Hoffmeyer et al., 2010; Menéndez et al., 2011). In agreement with previous studies carried out in GN (Esteves et al., 1996; Hoffmeyer et al., 2010; Menéndez et al., 2011), in the present study it was observed that calanoid copepods dominated this group. The copepod *C. carinatus* was the most abundant species (1216.11 ind m<sup>-3</sup>) throughout the annual cycle followed by *C. vanus* (868.65 ind m<sup>-3</sup>), *P. parvus* (798.54 ind m<sup>-3</sup>), and *C. australis* (484.16 ind m<sup>-3</sup>). Other studies have reported that *C. carinatus* is a dominant species in shelf waters south of Península Valdés, between 42° and 45°S in spring and summer (Ramírez and Sabatini, 2000; Sabatini et al., 2000). This agrees with results from our study which show that the abundance levels of this species were highest in spring and mid-summer. Decapods were another important group within the mesozooplankton community in GN. This group was present throughout the annual cycle and their densities peaked during summer.

Mesozooplankton in GSJ showed two peaks of abundance. One occurred during summer 2015 which coincided with the phytoplankton peak recorded in this season, and the other one occurred during autumn. The mesozooplankton community in this gulf was mainly dominated by copepods throughout the annual cycle although cladocerans were also an important group during all the climatic seasons. This finding coincides with results from a previous semi-automatic image analysis of mesozooplankton in GSJ during spring and summer (Hernández Moresino et al., 2014; Hernández-Moresino et al., 2017). The researchers who conducted this analysis observed, in agreement with our results, that the dominance of small and large copepods of the order Calanoida was followed by cladocerans. A thorough taxonomic analysis carried out in our present study revealed that throughout the year *C. vanus* and *P. parvus* were the most abundant species among the

order Calanoida (total abundance = 856.77 ind m<sup>-3</sup> and 849.73 ind m<sup>-3</sup>, respectively) which was followed by *C. carinatus* which, in turn, was numerically more important than *C. australis* (total abundance = 541.89 ind m<sup>-3</sup> and 272.23 ind m<sup>-3</sup>, respectively). The dominance of *C. carinatus* can be attributed to the high primary productivity that characterizes the water mass of GSJ. It has been reported that the high levels of nutrients and primary productivity observed in this gulf, as a result of the entrance of nutrient-rich water masses from adjacent areas, are similar to those reported for upwelling areas (Charpy et al., 1980; Esteves et al., 1986). *Calanoides carinatus* is a dominant species in many coastal areas characterized by upwelling (Verheye, 1991; Lopes et al., 1999; Ceballos et al., 2004). In line with this, in the Argentine Sea this species is also related to local upwelling events (Ramírez and Sabatini, 2000).

Among cladocerans, *E. nordmanni* was the numerically most important species throughout the year except during late summer (March) and early summer 2016 (January) when *Podon* spp. were the most abundant taxa. In line with this, Hernández Moresino et al. (2014) documented an apparent replacement of the cladocerans species indicating that *E. nordmanni* dominates during spring and that towards summer this species is replaced by *Podon* spp. Although this succession was not observed in the present study on account of the fact that *E. nordmanni* was found all throughout the year, *Podon* spp. were more abundant during summer than in any of the other climatic seasons.

Appendicularians were another important group of the mesozooplankton community in GSJ. This group, which was present all throughout the annual cycle, dominated the mesozooplankton community during early spring (September and October) together with copepods. Although this agrees with findings reported by Sabatini and Martos (2002) who documented that this group also showed high abundance values during spring in Península Valdés shelf frontal system, it contrasts with Hernández Moresino et al. (2014)'s observations in this gulf. The latter authors reported that appendicularians showed low abundance values in GSJ during spring and that chaetognaths were more abundant than appendicularians during summer, as observed in our study during summer 2015. Ichthyoplankton (eggs and fish larvae) was present throughout the annual cycle and, in agreement with Hernández Moresino et al. (2014), this group was most abundant during summer. In addition, this group was dominated by eggs of *E. anchoita* during the same season.

Salinity and phaeopigments were the principal variables that showed an association with copepod and appendicularian abundance. This finding regarding salinity is consistent with results reported in other studies (e.g. Sabatini et al., 2012; Marrari et al., 2004) which documented the importance of this variable in the spatial and temporal distribution of certain copepod species. The association between higher salinity values and appendicularian abundance was also recorded in several sectors of the Argentine Sea (Viñas et al., 2002). Phaeopigments are a product of chlorophyll *a* degradation mainly as a result of grazing upon phytoplankton by herbivorous zooplankton (Lorenzen, 1967; Helling and Baars, 1985; Head and Harris, 1992) and natural degradation, as photoinhibition. Therefore, this association (grazing vs phaeopigments) is expected to occur in parallel with copepod abundance peaks because the most abundant copepod species registered in our study -*C. vanus*, *P. parvus*, *C. australis* and *C. carinatus*- have been defined as preferably herbivorous (Santos and Ramírez, 1991; Huggett, 2001; Viñas et al., 2002; D'Agostino, 2013; Antacli et al., 2014). In our study it was also found that temperature was the main factor affecting cladoceran and decapod abundances both in GN and GSJ. This agrees with previous studies carried out in the Argentine Sea (Viñas et al., 2007) and in GN (Hoffmeyer et al., 2010) and in GSJ (Hernández Moresino et al., 2014) which reported the highest abundances of cladocerans in spring and summer.

The decreased availability of food for adult female whales in their typical feeding grounds has been recently postulated to explain the high mortality levels of calves recorded in Península Valdés (Rowntree et al., 2013). Reduction in the availability of food (mainly Krill) could lead to

a poor nutrition of adult females which, in turn, could give rise to reproductive failures and deaths of calves as it was postulated for the northern right whales (*E. glacialis*) (Caswell et al., 1999; Kenney et al., 2001). Our findings could therefore demonstrate that in the selected zone from GN and GSJ the highest abundances of calanoid copepods (potential prey of southern right whales) occur during the whale season (from winter to late spring).

In agreement with previous research carried out in Península Valdés' coast (Menéndez et al., 2007; Hoffmeyer et al., 2010; D'Agostino et al., 2016; Hoffmeyer, unpubl. res.), our study shows that southern right whales feed mainly on copepods. Although during the whales' feeding event recorded in the present study the cladoceran *E. nordmanni* reached a remarkable abundance, no record of right whales feeding mainly on this group is known to date. This group dominated the mesozooplankton dense patch in which the whales were feeding, and because right whales are not able to select their prey (Mayo et al., 2001), it is more likely that cladocerans could have been retained together with the food available for *E. australis* individuals in the area. During the feeding event documented in our study, the dominant species within copepods was the large calanoid *C. carinatus*. Previous studies have reported that southern right whales feed on *C. carinatus* in both GN and GSJ. Evidences of this have been the presence of mandibular gnathobases similar to those of *C. carinatus* species in fecal samples from *E. australis* individuals (Menéndez et al., 2007; D'Agostino et al., 2016) and the presence of *C. carinatus* in dense zooplankton patches on which whales feed themselves in the area (Hoffmeyer et al., 2010). It has been reported that *C. carinatus* has the largest lipid reserves in comparison with any other calanoid copepod (Borchers and Hutchings, 1986; Armstrong et al., 1991; Ceballos et al., 2004), which leads to conclude that this species represents an important source of energy for the southern right whales when it dominates the zooplankton patches in Península Valdés. In line with this, and in agreement with Hoffmeyer et al. (2010), other copepods numerically important during the recorded feeding event were, in decreasing order of abundance, *C. vanus*, *C. australis*, and *P. parvus*. Another taxon that showed an abundance peak during the feeding event was *Munida gregaria* (Zoea larvae). In agreement with our results, several researchers have observed southern right whales feeding on dense patches of *M. gregaria* in GN (Matthews, 1932; Bastida and Rodríguez, 2009; Werner et al., 2011). Furthermore, in agreement with Hoffmeyer et al. (2010)'s observations, calyptopis and furcilia larvae of *E. lucens* were recorded in the present study as another numerically important component within mesozooplankton when the whales were feeding in GN. Ichthyoplankton (eggs and fish larvae) was also found to be a major prey item for these whales.

The scarce and geographically partial previous investigations on plankton carried out in GN and GSJ until now justify the need to perform further integrated studies to increase the temporal data resolution and to better understand plankton dynamics in the study area. Nevertheless, although further thorough research on plankton composition and structure in GN and GSJ is still pending, our study provides, for the first time, a simultaneous description of phyto- and mesozooplankton communities throughout an annual cycle in an area which is small within these gulfs but important for whales' foraging. In agreement with Hoffmeyer et al. (2010), the present study confirms that during the southern right whales' stay in their calving and reproductive ground in Península Valdés, dense patches of mesozooplankton composed of high-calorie prey items are exploited by them. Therefore, even though opportunistic, whales' foraging in Península Valdés could be considered an extra source of energy that helps both juvenile and adult whales, mainly lactating females, to improve their physical condition before migrating to their feeding areas.

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