




MARINE IMPACTS IN THE ANTHROPOCENE

Linking long-term changes of zooplankton community to environmental variability at the EPEA station (Southwestern Atlantic Ocean)

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ABSTRACT. A significant sea surface temperature increase has been reported for the Southwestern Atlantic Ocean between 20° S-50° S over the last decades. Zooplankton organisms are highly sensitive to temperature rise. They play a very important role in marine ecosystems by providing the main pathway of energy transfer from primary producers to consumers. Seasonal and interannual (2000-2017) variability of metazooplankton in relation to environmental changes, particularly temperature, were analyzed at the EPEA station (38° 28' S-57° 41' W). Copepods, appendicularians, cladocerans, chaetognaths, and lamellibranch larvae were identified and quantified. Temperature exhibited a positive interannual trend during the series, whereas the Simpson parameter showed a decreasing tendency and salinity remained almost constant. Adults, copepodites, and *nauplii* of small copepods belonging to Oithonidae (mostly *Oithona nana*) and Paracalanidae-Clausocalanidae families dominated the metazooplankton community during the study period. Three groups of taxa with different seasonal patterns of variability were clearly identified. Members of Oithonidae exhibited positive interannual trends, whereas lamellibranch larvae and Calanidae showed negative interannual trends. A direct influence of temperature anomaly on these changes is suggested as well as possible indirect effects of this anomaly upon zooplankton through different phytoplankton fractions. Under the current scenario of climate change, the maintenance of this time-series becomes crucial in order to evaluate the eventual transfer of the environmental variability to the local food webs through planktonic organisms.



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Key words: Microzooplankton, mesozooplankton, time-series, EPEA station, Buenos Aires shelf, Southwestern Atlantic.

Relación entre los cambios a largo plazo de la comunidad de zooplancton y la variabilidad ambiental en la estación EPEA (Océano Atlántico Sudoccidental)

RESUMEN. En las últimas décadas se ha registrado un aumento significativo de la temperatura superficial del mar en el Océano Atlántico Sudoccidental, entre 20° S-50° S. Los organismos del zooplancton son muy sensibles al aumento de la temperatura. Ellos cumplen un rol muy importante en los ecosistemas marinos dado que constituyen la principal vía de transferencia de energía desde los productores primarios a los consumidores. En este trabajo se analizó la variabilidad estacional e interanual (2000-2017) del metazooplancton en la estación EPEA (38° 28' S-57° 41' W), en relación con los cambios ambientales, en particular de la temperatura. Copépodos, apendicularias, cladóceros, quetognatos y larvas de lamelibranquios fueron identificados y cuantificados. La temperatura exhibió una tendencia interanual positiva de las anomalías durante la serie mientras que el parámetro de

Simpson mostró una tendencia decreciente y la salinidad prácticamente se mantuvo invariable. Adultos, copepoditos, y *nauplii* de los copépodos pequeños pertenecientes a las familias Oithonidae (en su mayoría *Oithona nana*) y Paracalanidae-Clausocalanidae dominaron la comunidad del metazooplancton durante el período de estudio. Se identificaron claramente tres grupos de taxa con diferentes patrones estacionales de variabilidad. Miembros de la Familia Oithonidae exhibieron tendencias interanuales positivas mientras que las larvas de lamelibranquios y la Familia Calanidae mostraron tendencias interanuales decrecientes. Se sugiere un efecto directo de las anomalías de la temperatura sobre estas variaciones así como posibles efectos indirectos de este parámetro sobre el zooplancton, a través de su influencia sobre diferentes fracciones del fitoplancton. En el actual escenario de cambio climático, el mantenimiento de esta serie temporal es de gran importancia para evaluar la transferencia eventual de la variabilidad ambiental a la trama trófica local a través del plancton.

Palabras clave: Microzooplancton, mesozooplancton, serie temporal, estación EPEA, plataforma bonaerense, Atlántico Sudoccidental.

INTRODUCTION

Since the beginning of the twentieth century, our planet has been experiencing a gradual increase of the mean global temperature, with an intensification of the warming rate over the last decades (IPCC 2019).

An analysis of time series of satellite sea surface temperatures (SST) carried out in the South Atlantic Ocean during the last 30 years prior to 2012 indicated a SST increase in almost 86% on this region (Muller-Karger et al. 2017). However, whereas in the north Argentine continental shelf, areas of significant increase of surface temperature were observed between 20° S-50° S, others with a cooling trend were registered in latitudes of 49° S-52° S in the south Patagonian shelf (Risaro 2020).

Water temperature and salinity are excellent indicators of the physical environment in which plankton are living, affecting them both directly (i.e., through physiology and growth rates) and indirectly (i.e., through water column stratification and related nutrient availability) (O'Brien et al. 2013).

Marine zooplankton communities are highly diverse and thus perform a variety of ecosystem functions (Richardson 2008 and references within). The most important role of these organisms is to act as major grazers in food-webs by providing the principal pathway for energy from primary producers to consumers at higher trophic levels.

Zooplankton can be, moreover, recognized as beacon of climate change for several reasons (Richardson 2008). Because of their physiology and short live cycles, zooplanktonic species are highly sensitive to temperature rise (Mauchline 1998; Edwards and Richardson 2004; Beaugrand and Kirby 2018). Therefore, present climate changes may strongly affect their population dynamics and phenology (Hays et al. 2005; Rice and Stewart 2016). As these organisms are generally not commercially exploited, their long-term trends of variability are mostly due to environmental changes (Richardson 2008).

Sustained ocean time-series, particularly ship-based repeated measurements, represent one of the most valuable tools to characterize and quantify ocean ecosystem cycles and fluxes, from the plankton up to higher trophic levels, and their association to changing climate (Edwards et al. 2010; Valdés and Lomas 2017). Time-series observations over multiple decades are necessary to differentiate between natural and anthropogenic variability (O'Brien et al. 2017 and references within).

In the northern coastal waters of Argentina (38° 28' S-57° 41' W) (Figure 1), a biogeochemical time-series was established at the EPEA station (Estación Permanente de Estudios Ambientales/Permanent Station of Environmental Studies), as part of the DIPLAMCC (Dinámica del Plancton Marino y Cambio Climático/Dynamics of Marine Plankton and Climate Change) Project of INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero). Several chemical, physical,

photo-biological, and planktonic variables are monitored there on a monthly basis since 2000. In this coastal station, phytoplankton community reaches its maximum biomass in winter, mainly represented by 20-200 μm diatoms of the micro-phytoplankton fraction (Negri and Silva 2011). Ultraphytoplankton fraction $< 5 \mu\text{m}$ makes its major contribution to total biomass in summer, thus configuring an oligotrophic-like ecosystem (Silva et al. 2009; Negri and Silva 2011; Viñas et al. 2013). The first approach to analyze phytoplankton dynamics at the EPEA station in an interannual scale (2000-2009) indicated an increasing trend in chlorophyll concentrations during the last years of the study period, mainly due to the contribution of the smallest phytoplankton size fraction, i.e. the picophytoeukariotic organisms (Silva 2011). The proliferation of these organisms due to climatic variations has been reported on a large scale (Li and Harrison 2008; Moran et al. 2010) highlighting the increasing importance of small phytoplankton in a future global warming scenario (Sarmiento et al. 2004; Behrenfeld et al. 2006).

Considering the zooplankton community, Di-
visalvi (2006), Temperoni et al. (2011), Cepeda (2013) and Viñas et al. (2013) analyzed the annual cycle of abundance, size structure, and biomass of its main components at the EPEA station, whereas Daponte et al. (2004) and Capitano et al. (2008) focused particularly on chaetognaths and appendicularians, respectively. Small-sized copepods ($< 1 \text{ mm}$ total length) dominated by *Oithona nana* and members of Paracalanidae constitute the bulk of the metazooplankton (81%) throughout the year in the EPEA station with maximum values in summer in terms of abundance and biomass (Viñas et al. 2013). It is known that the reproductive cycle of small copepods in temperate seas (Pittois et al. 2009) is positively controlled by temperature (Viñas 1990; Uye and Shibuno 1992; Temperoni et al. 2011).

The present work shows an analysis of the interannual patterns of variability of main components of metazooplankton and their relationship with physical cues carried out for the first time at the EPEA station between March 2000 and November 2017 (18 years). The concurrent analy-

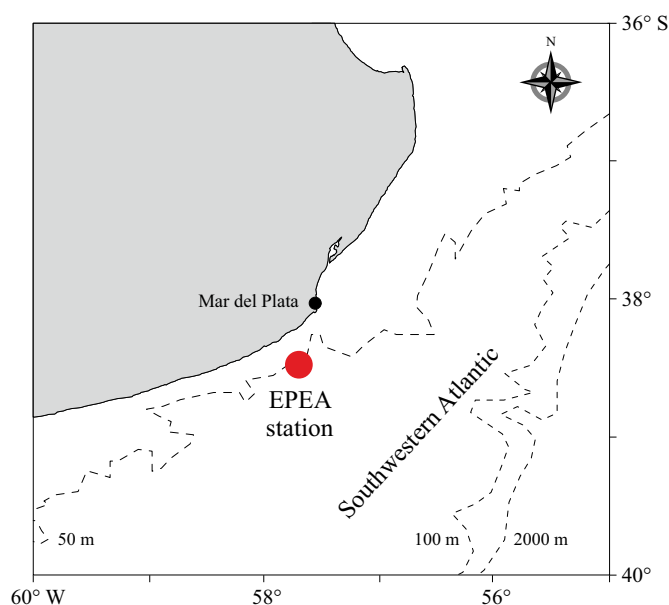


Figure 1. Location of the EPEA station ($38^{\circ} 28' \text{ S } -57^{\circ} 41' \text{ W}$).

sis of seasonal patterns of zooplankton abundance in relationship to the environmental factors will contribute to the interpretation of changes observed in the long-term scale. We hypothesized that during the studied period, under a scenario of Climate Change with increasing of both sea surface temperature and smallest phytoplankton size fraction concentration, a rise in the abundance of small copepod species is to be expected.

MATERIALS AND METHODS

Hydrography

During each cruise to the EPEA station, conductivity and temperature profiles were obtained with a Seabird CTD (SBE19) 01 CTD. Data were processed, quality checked, and stored in the Regional Oceanographic Database (BaRDO) at the Physical Oceanography Laboratory of INIDEP.

Zooplankton sampling and laboratory analysis

A total of 93 zooplankton samples were obtained with a small Bongo net (67 and 220 μm meshes) equipped with flowmeters in each mouth for calculation of the filtered water volume. The net was obliquely trawled through the water column from 5 m of the bottom (48 m depth) to the surface. Tows were short (towing time: 2 min; towing rate: 20 m min^{-1}) with the ship moving at 2 knots speed. After obtained, samples were immediately preserved in 4% formaldehyde solution. For the present study, only samples from the finest mesh net were analyzed considering the strong dominance of microzooplankton and mesozooplankton smaller than 1 mm total length previously reported at this station (Viñas et al. 2013) and the adequacy of this mesh size to retain them (Di Mauro et al. 2009).

Zooplankton components were identified under stereoscopic microscopy and grouped into the following categories:

- Oithonidae (OIT): includes adult and copepodite stages of *O. nana* and *O. aff. helgolandica*.
- Oithonidae (OITN): includes *nauplii* of *O. nana* and *O. aff. helgolandica*.
- Paracalanidae-Clausocalanidae (PACL): includes adult and copepodite stages of *Paracalanus parvus*, *Parvocalanus scotti* and *Ctenocalanus* spp.
- Paracalanidae-Clausocalanidae (PACLN): includes *nauplii* of *Paracalanus parvus*, *Parvocalanus scotti* and *Ctenocalanus* spp.
- Calanidae (CAL): includes only adult and copepodite stages of *Calanoides carinatus*.
- *Evdne nordmanni* (ENO).
- *Penilia avirostris* (PAV).
- Appendicularians (APP).
- Chaetognaths (CHA).
- Lamellibranchs larvae (LLA).

The number of individuals per cubic meter (ind. m^{-3}) for each category was estimated from the counts of individuals in different aliquots of the original sample and the filtered volume by the net. The aliquot size of each taxon was established according to its original concentration in the sample.

Data analysis

Considering that the zooplankton sampling was performed obliquely through a portion of the water column, mean temperature (MT) and mean salinity (MS) were measured taking into account the maximum depth attained by the net. To determine the location of the transition between stratified waters and mixed waters, the stability Simpson parameter (ϕ) was estimated (Simpson 1981). This is a measure of the mechanical work required to vertically mix the water column. Small values of ϕ indicate

poorly stratified waters while high values are associated with stratified ones. In this work, the value of 40 J m^{-3} was used as the limit between homogeneous ($\varphi < 40$) and stratified ($\varphi > 40$) waters, as established by Sabatini and Martos (2002).

Analyses of both seasonal and interannual variability were performed on the zooplankton data and then related with changes in physical data (MT, MS, and φ).

As with other time-series worldwide, sampling at the EPEA station exhibited irregularity in time-frequency. This fact was recurrent in the time-series and calculation of an annual average of zooplankton abundance can be greatly influenced by time of sampling. This problem is further compounded by missing months within sampling years. Mackas et al. (2001) proposed a solution to this difficulty in which the annual anomaly is calculated as an average of individual monthly anomalies. This method, adopted by the Working Group on Zooplankton Ecology (WGZE) of ICES, reduces many of the issues of low frequency and/or irregular sampling and also removes seasonal signal from the year-to-year analysis (O'Brien et al. 2008). In order to estimate interannual and seasonal anomalies of physical and biological variables in the EPEA time-series, the method of Mackas et al. (2001) was used.

For seasonal analysis, the year was divided into four periods of three months each, starting in January for summer. Kruskal-Wallis non-parametric test was employed to compare abundances by seasons in view of the non-normality of the data. Before data analysis, the outliers of each

taxonomic category were estimated considering the mean ± 1.96 SD of its abundance and eliminating all minor or major values from the database. This procedure was applied for each season considered separately. After that, $\log(x + 1)$ transformation was applied to the remaining data.

A Principal Component Analysis (PCA) was employed to identify patterns in the data set corresponding to the original variables (zooplankton categories). Correlations among the biological variables and between these and the physical ones were used to interpret the grouping patterns produced by PCA. Analyses were performed employing Statistica v7 software (StatSoft Inc. 2007).

RESULTS

Hydrography

Temperature varied seasonally, with minima in winter (10.93 ± 0.85 °C, July-September), and maxima in summer (19.20 ± 0.88 °C, January-March) (Table 1). Salinity did not exhibit a clear seasonal variation and values fluctuated between 33.74 ± 0.14 in spring (October-December) and 33.94 ± 0.15 in autumn (April-June). Vertical stratification, quantified by φ , was more accentuated in summer (50.42 ± 44.23) and spring (23.50 ± 23.52) than in autumn (4.26 ± 11.72) and winter (2.63 ± 2.61). Mixing of water column, typical of the winter months, was reflected in the lowest value of φ recorded during this season.

Table 1. Mean seasonal values \pm SD of MT, MS and φ at the EPEA station during the period 2000-2017.

Season	MT	MS	φ
Summer (J-F-M)	19.20 ± 0.88	33.76 ± 0.24	50.42 ± 44.23
Autumn (A-M-J)	15.71 ± 2.12	33.94 ± 0.15	4.26 ± 11.72
Winter (J-A-S)	10.93 ± 0.85	33.89 ± 0.13	2.63 ± 2.61
Spring (O-N-D)	13.71 ± 2.26	33.74 ± 0.14	23.50 ± 23.52

Interannual anomalies were analyzed in physical parameters during the study period. Whereas temperature displayed an increasing trend, Simpson parameter showed a decreasing tendency, and salinity did not show any important variation (Figure 2).

Zooplankton

Composition and seasonal abundance

Microzooplankton was dominated by *nauplii* of copepods and lamellibranch larvae (Table 2). Within the mesozooplankton, adults and copepodites of small copepods (< 1 mm), represented

mostly by Oithonidae and members of Paracalanidae-Clausocalanidae, dominated throughout the year, alternating their preeminence among seasons (Table 2; Figure 3). Thus, the dominance of Oithonidae was higher in spring and winter. On the contrary, Paracalanidae-Clausocalanidae predominated upon Oithonidae in summer and autumn. Appendicularians were also abundant all year round followed by cladocerans. Calanidae and chaetognaths were the less abundant taxa.

Adult and copepodite stages of Oithonidae attained their highest abundance in spring with a mean of 11,293 ind. m⁻³, followed by a mean of 7,159 ind. m⁻³ in summer (Table 2). Minimum

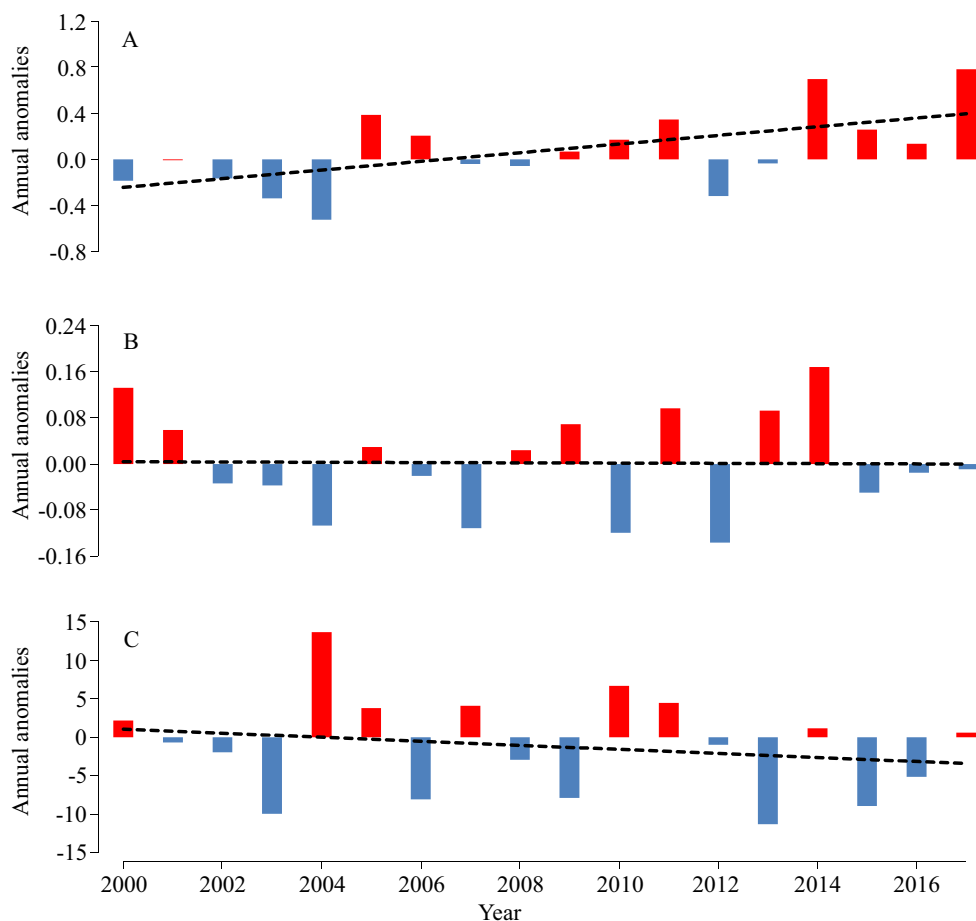


Figure 2. Annual anomalies of mean temperature (A), mean salinity (B) and ϕ (C) at the EPEA station during the period 2000-2017. Dashed line: ns. trend.

Table 2. Seasonal abundance of main components of micro and mesozooplankton (mean \pm SD) at the EPEA station during the period 2000-2017. A: adults, C: copepodites. Within parentheses: number of seasonal observations.

	Summer	Autumn	Winter	Spring
Microzooplankton				
<i>Nauplii</i> of Oithonidae	3,546.09 \pm 4,108.83 (18)	958.54 \pm 921.65 (15)	6,498.75 \pm 5,913.18 (16)	15,932.14 \pm 13,939.34
(16)				
(OITN)				
<i>Nauplii</i> of Paracalanidae-	6,315.29 \pm 5,967.95 (20)	2,640.30 \pm 1,849.01 (15)	2,563.48 \pm 1,921.88 (19)	2,895.74 \pm 1,984.82 (18)
Clausocalanidae (PACLN)				
Micro-mesozooplankton				
Lamellibranch larvae	1,021.46 \pm 1,096.61 (21)	261.26 \pm 289.13 (18)	1,175.85 \pm 1601.68 (21)	604.25 \pm 734.60 (20)
(LLA)				
Mesozooplankton				
Oithonidae (A + C) (OIT)	7,159.12 \pm 10,289.04 (21)	1,218.72 \pm 967.50 (18)	5,039.15 \pm 4,494.19 (21)	11,792.59 \pm 9,200.15 (21)
Paracalanidae-	7,295.85 \pm 5,730.31 (21)	2,540.22 \pm 1,225.83 (17)	1,867.29 \pm 1,311.71 (15)	2,956.31 \pm 2,771.98 (21)
Clausocalanidae (A + C)				
(PACL)				
Calanidae (A+C) (CAL)	26.46 \pm 81.86 (22)	36.57 \pm 90.51 (19)	115.34 \pm 123.02 (22)	69.84 \pm 177.27 (22)
<i>Evadne nordmanni</i> (ENO)	108.32 \pm 143.15 (21)	1.41 \pm 5.98 (18)	10.90 \pm 27.85 (21)	281.46 \pm 430.75 (21)
<i>Penilia avirostris</i> (PAV)	735.33 \pm 988.47 (20)	66.74 \pm 125.93 (18)	0 \pm 0 (21)	0 \pm 0 (20)
Appendicularians (APP)	2,515.97 \pm 2,279.54 (21)	526.89 \pm 622.60 (18)	1,740.70 \pm 1,846.93 (21)	2,485.34 \pm 2,608.36 (21)

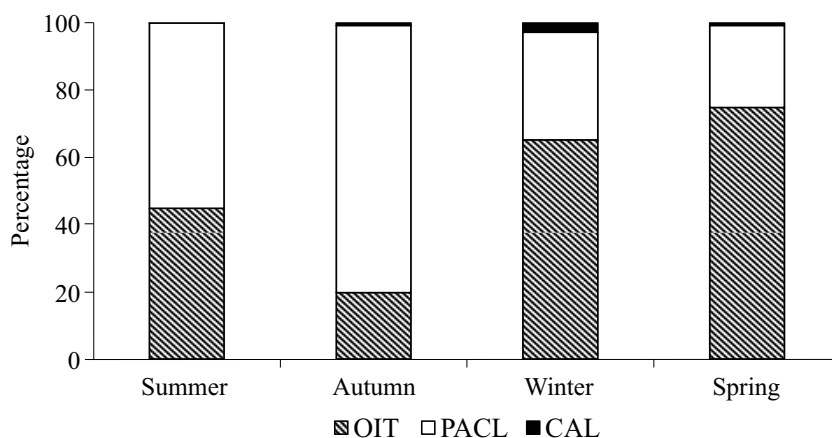


Figure 3. Mean seasonal percentages of contribution of OIT, PACL and CAL to copepods abundance at the EPEA station during the period 2000-2017.

occurred in autumn (1,219 ind. m^{-3}) which differed significantly from others seasons (Kruskal Wallis test, $H_{(3, N=81)} = 26.08$; $p = 0.000$). Similarly, *nauplii* of Oithonidae exhibited a clear increase of abundances from winter onwards with the highest densities occurring in spring (15,932 ind. m^{-3}), a gradual decrease in summer (3,546 ind. m^{-3}) and minimum (958 ind. m^{-3}) in autumn (Table 2). Highly significant differences ($H_{(3, N=65)} = 29.69$; $p = .0000$) among seasonal abundances were recorded for these *nauplii*. Autumn was significantly different from winter and spring, while the latter differed from summer ($p < 0.01$).

The highest abundance (7,296 ind. m^{-3}) of adults and copepodites of Paracalanidae-Clausocalanidae was registered in summer (7,296 ind. m^{-3}) and the lowest in winter (1,867 ind. m^{-3}), exhibiting significant differences among seasons ($H_{(3, N=80)} = 18.68$; $p = .0003$). Summer significantly differed from winter and spring ($p < 0.05$) (Table 2, Figure 5 A). Although *nauplii* of Paracalanidae-Clausocalanidae showed also the highest values in summer (6,315 ind. m^{-3}), non-significant differences were observed among seasons ($H_{(3, N=72)} = 4.230$; $p = 0.24$).

Among the Calanidae (> 2 mm), *Calanoides carinatus* was the only identified species. It was very scarce all around the year exhibiting the

highest abundance in winter (115 ind. m^{-3}) and the lowest one in summer (82 ind. m^{-3}) (Table 2). Significant dissimilarities among seasons were documented for this species ($H_{(3, N=85)} = 20.23$; $p = .0002$), with winter differing from summer and spring ($p < 0.05$).

The abundance of lamellibranch larvae showed the highest seasonal value in winter (1,176 ind. m^{-3}), another minor peak in summer (1,021 ind. m^{-3}), and the lowest value in autumn (261 ind. m^{-3}) (Table 2). This group showed significant seasonal differences ($H_{(3, N=80)} = 8.95$; $p = .0299$) in general, but no significant differences were detected between pairs of seasons.

Among cladocerans, *E. nordmanni* presented the peak of abundance in spring with 281 ind. m^{-3} and the minimum in autumn (1.4 ind. m^{-3}) with significant seasonal differences ($H_{(3, N=81)} = 27.89$; $p = 0.0000$). Autumn was dissimilar from summer ($p < 0.05$) and spring ($p < 0.001$) and the latter differed from winter ($p < 0.005$) (Table 2; Figure 7 A). *P. avirostris* was absent in winter and spring and was more abundant in summer (735 ind. m^{-3}) (Table 2). Significant differences among seasons were detected ($H_{(3, N=79)} = 47.77$; $p = .0000$), with summer differing from autumn ($p < 0.05$).

Appendicularians presented higher abundances in summer and spring (2,516 and 2,485 ind. m^{-3} ,

respectively) and the lowest value in autumn (527 ind. m^{-3}) (Table 2). Significant differences were recorded among seasons ($H_{(3, N=81)} = 14.02$; $p = .0029$), with autumn differing from summer and spring ($p < 0.05$).

Chaetognaths exhibited their highest abundance in summer (75 ind. m^{-3}) and the lowest one in spring (19 ind. m^{-3}) (Table 2). Significant differences among seasons were observed ($H_{(3, N=80)} = 10.79$; $p = 0.0129$) but only winter and spring distinguished significantly ($p < 0.05$) between them.

Grouping of taxa and their correlation with physical variables

Factors 1, 2, and 3 of the PCA explained 56.67% of the variance (Figure 4). In the space configured by factors 1 and 2, a group of six taxa (OIT, PACL, OITN, PACLN, ENO, and APP) evidenced negative correlations with factor 1 (Table 3; Figure 4) and clearly separated from CAL and PAV. These six taxa occurred all year

round with higher abundances during spring and summer. In several cases, significant positive correlations among them and physical variables, especially MT and ϕ , were observed (Table 4).

On the contrary, CAL was strongly associated with negative values of factor 2 (Table 3; Figure 4). CAL occurred throughout the year with the highest abundance in winter, showing a negative correlation with PAV and a positive one with CHA. As regards physical variables, CAL was negatively correlated with MT and ϕ (Table 4).

PAV was strongly and positively related to factor 2 (Table 3). This species was partially present throughout the year, with maximum abundance in summer and showing a positive correlation with PACL and a negative one with OITN and CAL (Table 4).

CHA was positively associated to factor 3 (Figure 4). This taxon presented the lowest abundances in spring, a negative correlation with both OIT and ϕ ($p < 0.05$), and a strong positive correlation with CAL ($p < 0.001$) (Table 4).

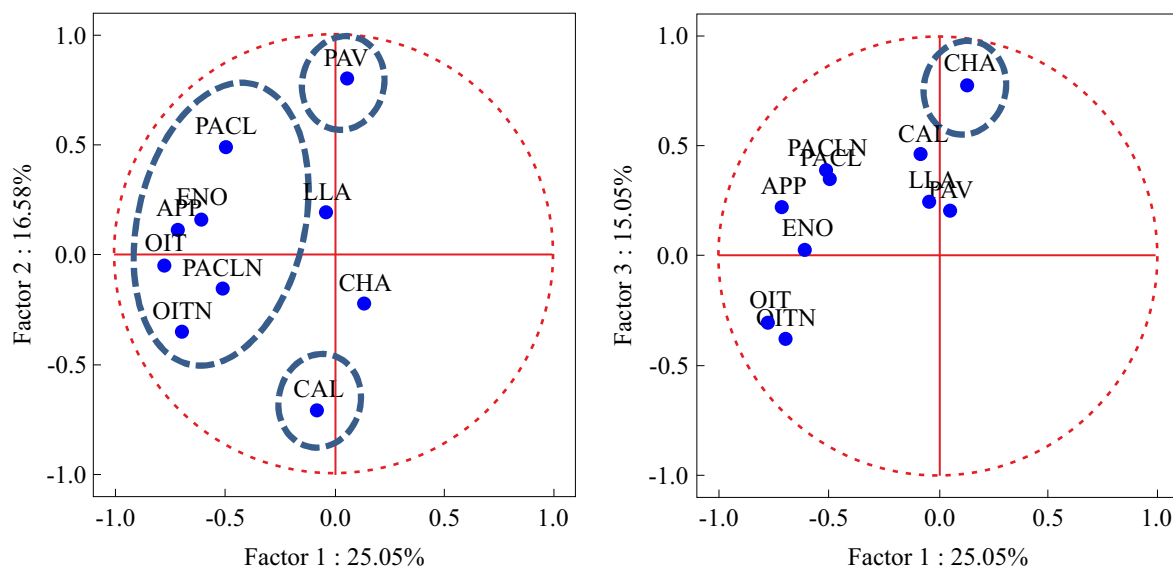


Figure 4. Principal Component Analysis (PCA) results. Projection of variables on the factor planes 1 x 2 (on the left) and 1 x 3 (on the right). Oithonidae (OIT), Paracalanidae-Clausocalanidae (PACL), *Evdne nordmanni* (ENO), *Penilia avirostris* (PAV), *nauplii* of Oithonidae (OITN), *nauplii* of Paracalanidae-Clausocalanidae (PACLN), Appendicularians (APP), Calanidae (CAL), Chaetognaths (CHA), Lamellibranch larvae (LLA). Blue dashed ellipses indicate grouping of taxa (see text).

Table 3. Principal Component Analysis (PCA) results. Factor coordinates of the variables. Variables that contributed the most to each factor are indicated in bold.

Variable	Factor 1	Factor 2	Factor 3
OIT	-0.78	-0.05	-0.30
OITN	-0.70	-0.35	-0.38
PACL	-0.50	0.49	0.35
PACLN	-0.51	-0.15	0.40
ENO	-0.61	0.16	0.03
APP	-0.71	0.12	0.23
PAV	0.05	0.80	0.21
CHA	0.13	-0.22	0.78
CAL	-0.08	-0.71	0.47
LLA	-0.04	0.19	0.25

Long-term interannual variability

Among all the zooplankton categories analyzed, OIT and OITN showed increasing patterns of variation, but trends were not statistically significant (Figure 5 A and 5 B). By contrast, CAL, LLA and CHA exhibited decreasing anomalies (Figures 6 A, 6 B and 9 B).

Other taxa such as PACL, PACLN, ENO, PAV and APP displayed neutral trends (Figures 7 A, 7 B, 8 A, 8 B and 9 A). No significant relationships among anomalies of biological and physical variables were observed.

Long-term seasonal variability

Non-significant annual trends were observed in the analyzed taxa of this time series. However, at a seasonal scale, some significant tendencies were registered. CAL and LLA exhibited decreasing trends in winter ($p = 0.05$ and $p = 0.03$, respectively). Also, a negative tendency was observed for chaetognaths in summer ($p = 0.03$) and a positive one for appendicularians in spring ($p = 0.02$). These anomalies had no significant correlation with those of the physical parameters.

DISCUSSION

Hydrography

In terms of the seasonal cycle, temperature at the EPEA station behaves like a region influenced by the deep water of Península Valdés (Luz Clara et al. 2019). Minimum temperatures occurred in July-September (with a peak in August) and maximum values corresponded to January-March (peaking in February), in response to the annual radiative cycle effect, as observed in other studies in the South Atlantic Ocean (e.g. Podestá et al. 1991; Lentini et al. 2000; Martínez-Avellaneda 2005; Luz Clara et al. 2019).

Zooplankton

Composition and seasonal abundance

PCA analysis grouped zooplankton taxa with similar environmental affinity. The resulting pattern was comparable in composition with that found by Viñas et al. (2013) in their annual 2000-2001 study of zooplankton at the EPEA station. One group, including species with more affinity

Table 4. Significant linear correlations among biological variables ($\log x + 1$) and between these ones and physical variables.

Biological variable 1	Biological variable 2	r	p	N
OIT	OITN	0.665	0.000	80
OIT	PACL	0.362	0.001	80
OIT	PACLN	0.232	0.038	80
OIT	APP	0.321	0.004	80
OIT	ENO	0.222	0.048	80
OIT	CHA	-0.265	0.017	80
PACL	PACLN	0.297	0.007	80
PACL	APP	0.346	0.002	80
PACL	PAV	0.348	0.002	80
CAL	PAV	-0.328	0.003	80
CAL	CHA	0.382	0.000	80
APP	ENO	0.518	0.000	80
APP	OITN	0.310	0.005	80
APP	PACLN	0.251	0.025	80
ENO	OITN	0.284	0.011	80
PAV	OITN	-0.221	0.048	80
Biological variable	Physical variable	r	p	N
PACL	MT	0.317	0.002	93
CAL	MT	-0.270	0.009	93
OIT	φ	0.238	0.021	93
PACL	φ	0.213	0.040	93
CAL	φ	-0.294	0.004	93
CHA	φ	-0.222	0.033	93

for warm-temperate waters of spring and summer such as the small copepods Oithonidae and Paracalanidae-Clausocalanidae, the cladoceran *E. nordmanni* and appendicularians, separated from the large herbivore *C. carinatus* (Calanidae), which showed more affinity to colder winter waters (Cepeda et al. 2018 and references therein) and from the cladoceran *P. avirostris*, with more affinity for warmer waters of summer (Viñas et al. 2007). Chaetognaths presented their highest values in summer followed by lower and similar values in autumn and winter. A comparable pattern of seasonal abundance was found by

Daponte et al. (2004) in their study of an annual cycle of *Sagitta friderici*, the main chaetognath species of the EPEA station.

Copepod species smaller than 1 mm total length numerically dominated the zooplankton community throughout the year during the study period. At the EPEA station, this fraction exceeds other copepods not only in terms of abundance but also in biomass (Viñas et al. 2013). Small copepods are very abundant in temperate and tropical coastal regions (Mazzocchi and Ribera d'Alcalá 1995; Hopcroft et al. 2001; Satapoomin et al. 2004; Turner 2004; Atienza et al. 2006; Zer-

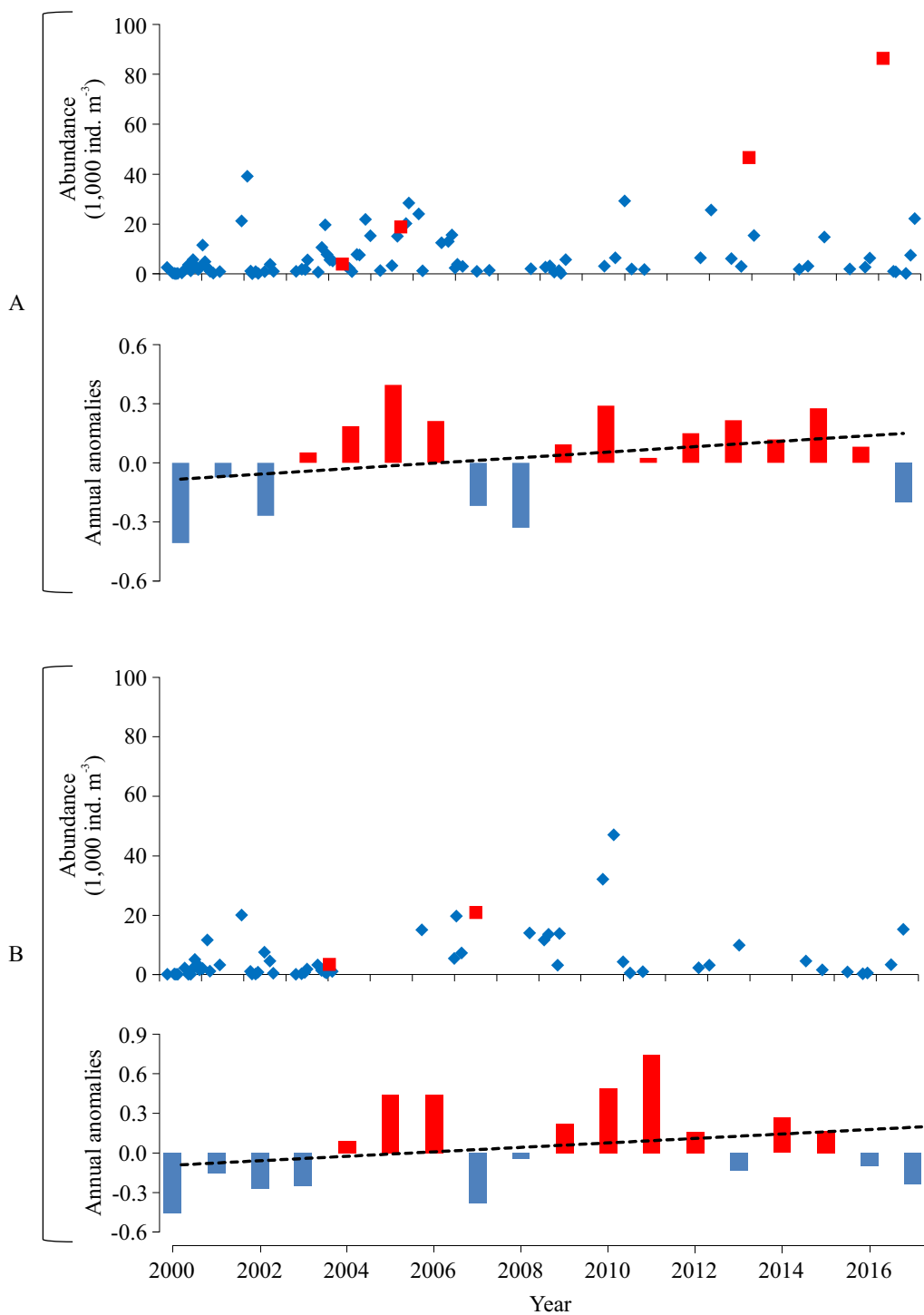


Figure 5. Interannual variation of abundance and annual anomalies of OIT (A) and OITN (B) during the period 2000-2017 at the EPEA station. Red squares: outliers. Dashed line: ns. trend.

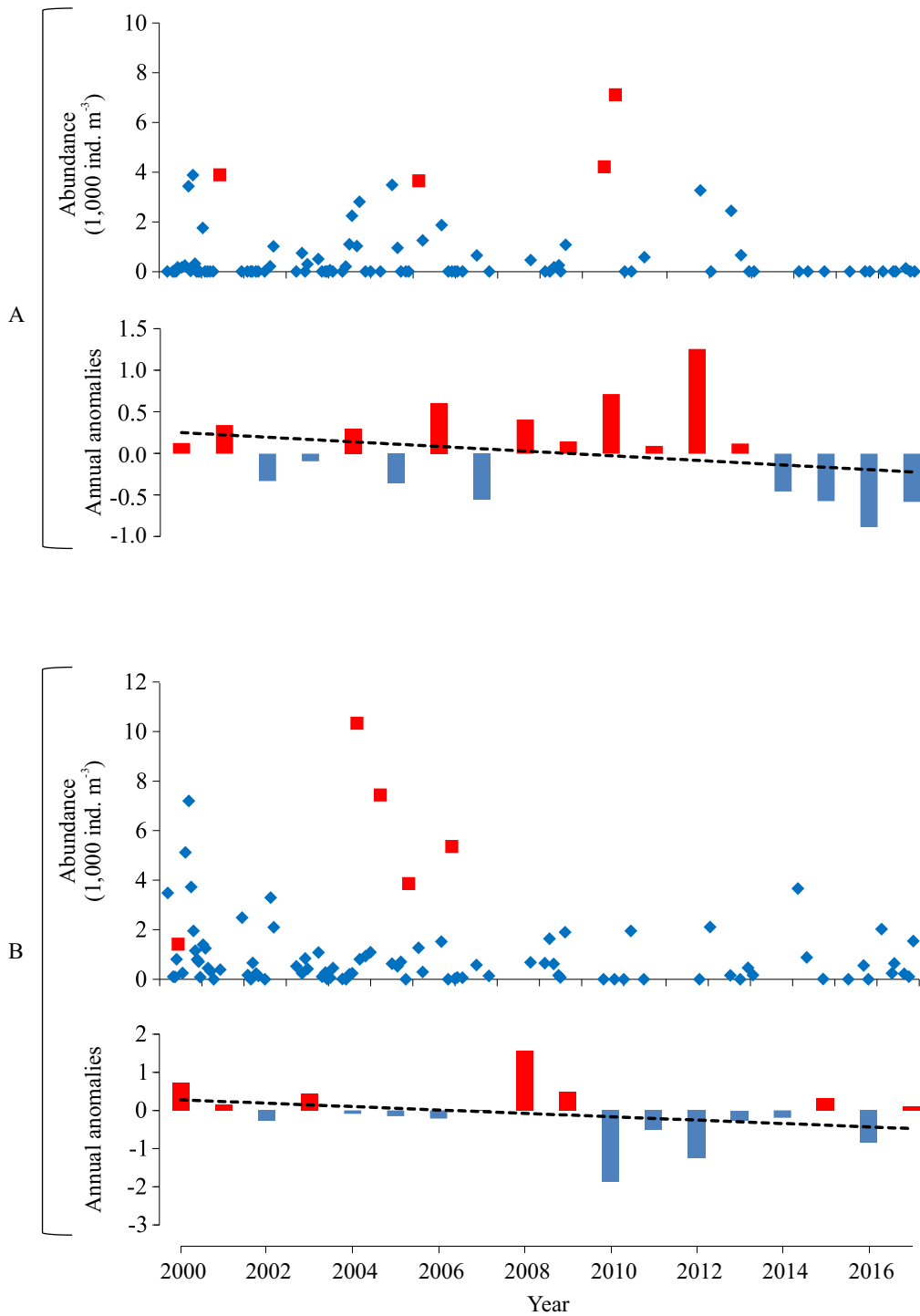


Figure 6. Interannual variation of abundance and annual anomalies of CAL (A) and LLA (B) during the period 2000-2017 at the EPEA station. Red squares: outliers. Dashed line: ns. trend.

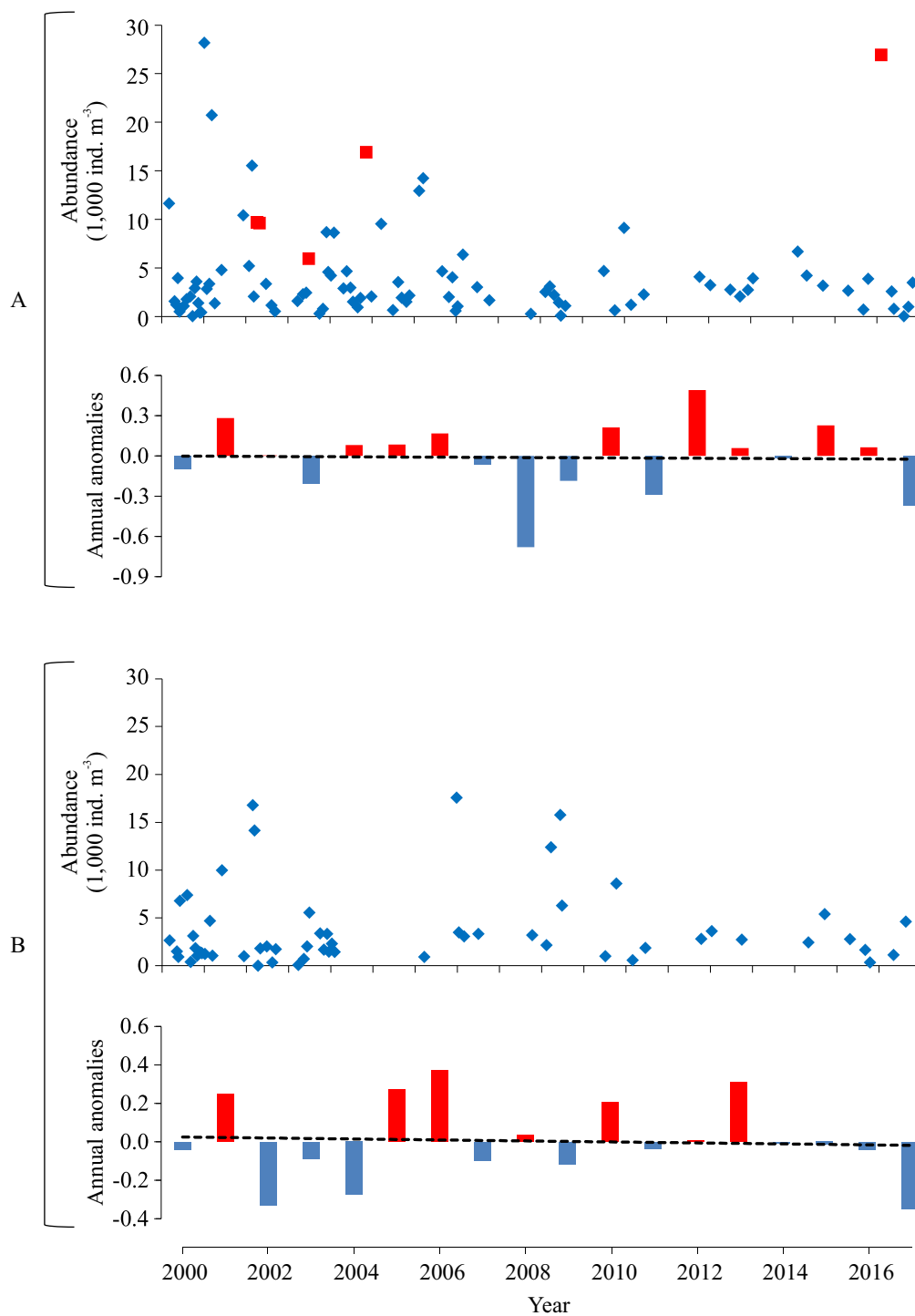


Figure 7. Interannual variation of abundance and annual anomalies of (A) PACL and (B) PACLN during the period 2000-2017 at the EPEA station. Red squares: outliers. Dashed line: ns. trend.

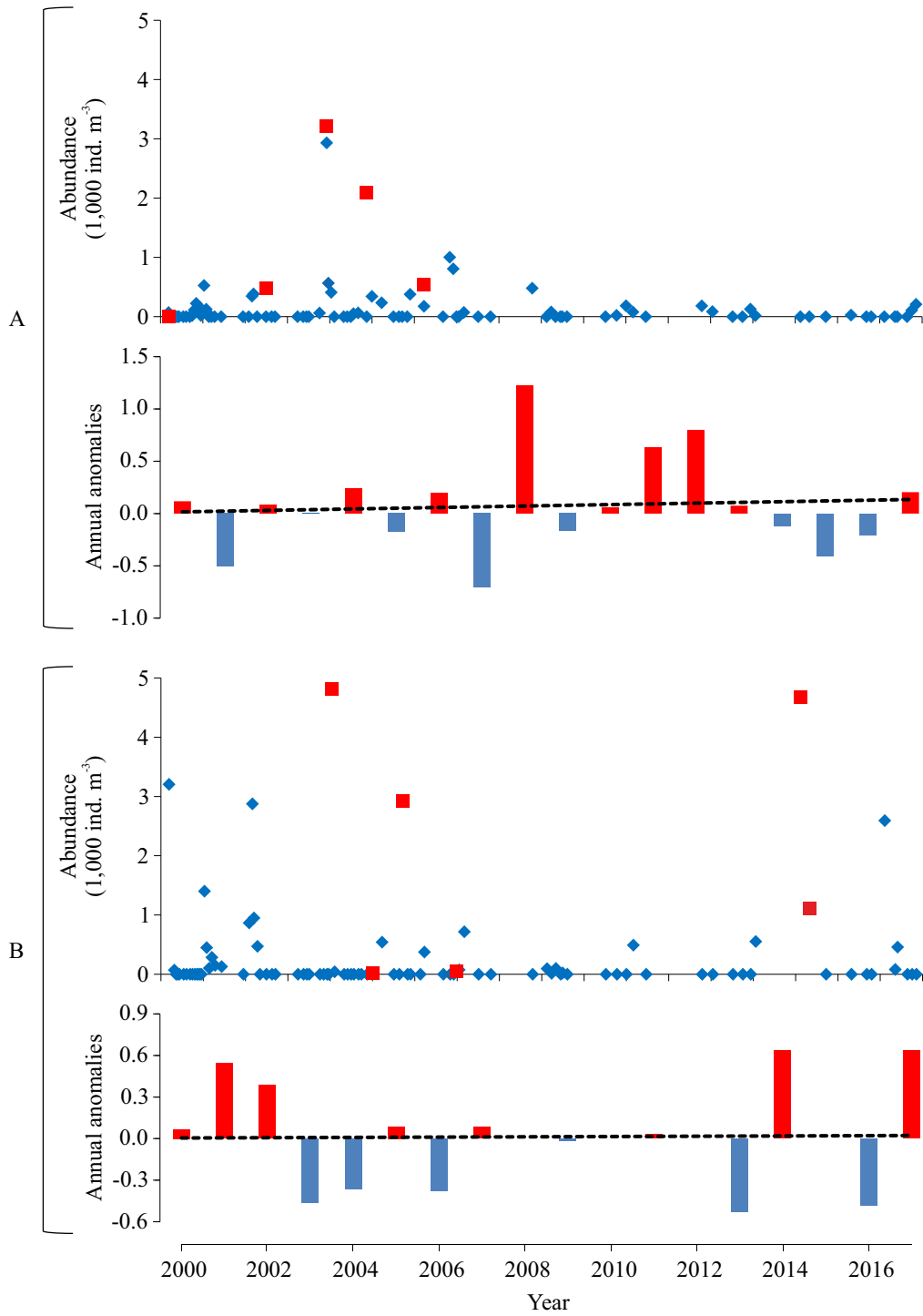


Figure 8. Interannual variation of abundance and annual anomalies of ENO (A) and PAV (B) during the period 2000-2017 at the EPEA station. Red squares: outliers. Dashed line: ns. trend.

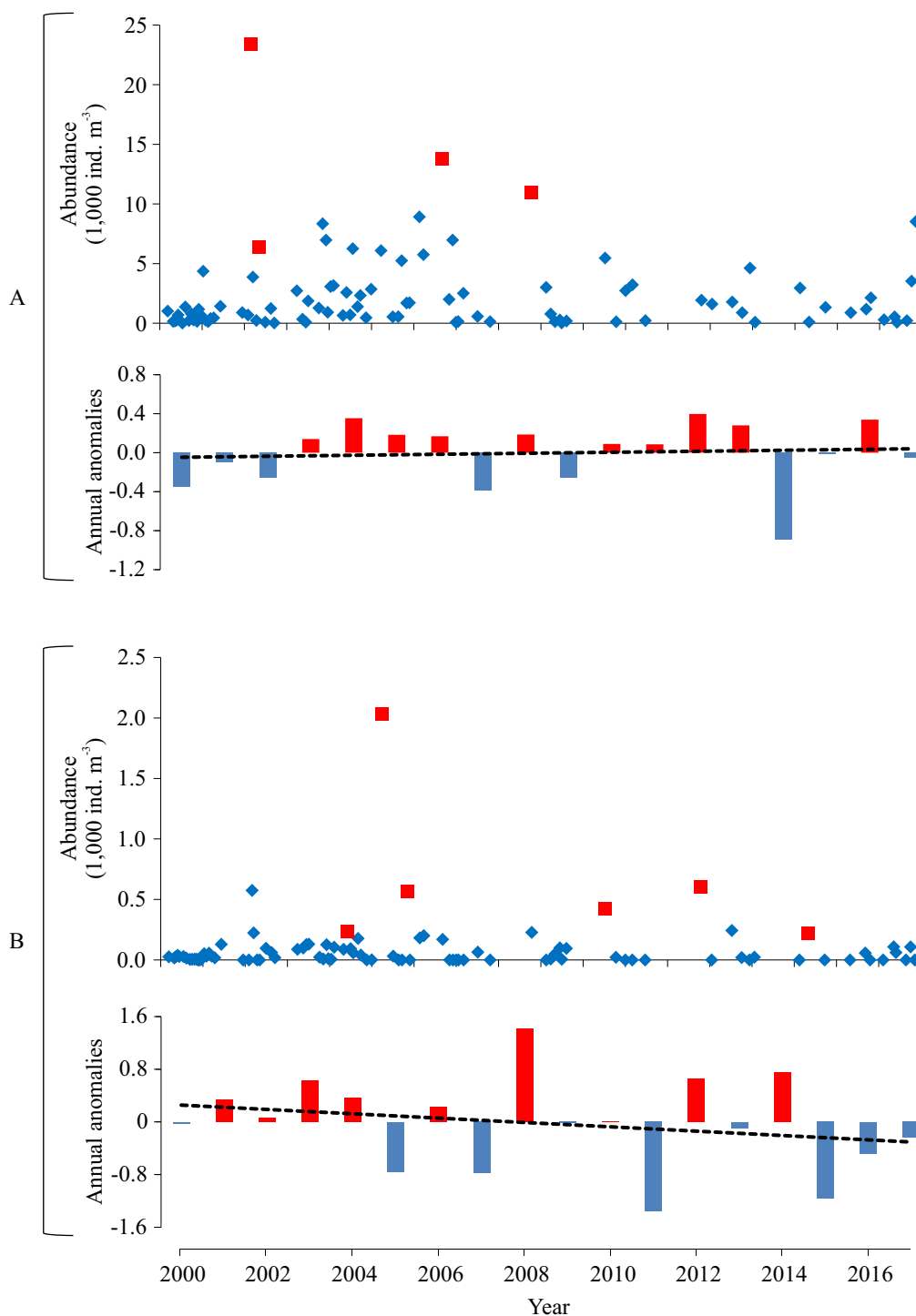


Figure 9. Interannual variation of abundance and annual anomalies of APP (A) and CHA (B) during the period 2000-2017 at the EPEA station. Red squares: outliers. Dashed line: ns. trend.

voudaki et al. 2007) including the Argentine shelf where they distribute in a large latitudinal range (Ramírez, 1981; Cepeda et al. 2018). Moreover, it was shown that small copepods and their early developmental stages dominate all marine communities (Hopcroft et al. 2001).

In the taxonomic analysis, a great percentage of adults (*ca.* 80%) of Oithonidae were identified as belonging to *O. nana* (not shown). Accordingly, the present study assumes that most of the copepodite and *nauplii* stages of Oithonidae also corresponded to this species. In coincidence with the present findings, a high abundance of *O. nana* in all seasons has been typically observed at the EPEA station (Temperoni et al. 2011; Viñas et al. 2013). The great tolerance of this species to seasonal variation of temperature might explain its ample distribution in temperate and tropical coastal waters all around the world, i.e. the Mediterranean Sea (Jamet et al. 2001), Southampton Water (Williams and Muxagata 2006), and the Argentine shelf (Cepeda et al. 2015, 2018).

The notorious numerical dominance of Oithonidae (mainly *O. nana*) all through the year is probably related to its ability to consume a wide size range of food particles including microphytoplankton, microbial heterotrophic components, and copepod *nauplii* (Paffenhöfer 1993; Turner 2004; Atienza et al. 2006; Madsen et al. 2008; Böttjer et al. 2010). An additional advantage could be the reproductive modality of this species. The egg-carrier trait might be a good strategy to prevent eggs predation, thus assuring higher survival rates and consequently more abundant populations (Kjørboe et al. 2015).

On a seasonal basis, the abundance of *O. nana* started increasing in winter and attained its highest abundance in spring. In accordance, microphytoplankton showed a similar pattern (Viñas et al. 2013; Negri et al. in preparation). During this period, adequate temperature range and food availability have probably stimulated *O. nana* females to reproduce intensively producing the highest peak of *nauplii* of the year. *O. nana* as

well as Paracalanidae, very abundant in summer, might have taken advantage of high densities of microbial components associated to the abundant picophytoplankton fraction recorded during this season. In fact, this fraction had an outstanding contribution from the end of spring up to early autumn (Ruiz et al. 2020; Negri et al. in preparation) during present period. Silva et al. (2009) reported that this fraction can reach 50-90% of the total *Chl-a* at the EPEA station during summer.

It is worth mentioning that small copepods (such as all stages of *O. nana* and Paracalanidae-Clausocalanidae) are not able to graze efficiently upon nano and picophytoplankton components. In fact, these fractions are consumed by nano- and micro-heterotrophs which are predated by protozooplankton, especially ciliates, and the latter are the main prey for small copepods. In particular, they have a greater influence on the efficiency of the trophic food webs than larger species, coupling between the primary producers, the protozooplankton, and the higher trophic levels (Zervoudaki et al. 2007).

Microbial filter-feeders *P. avirostris* and appendicularians displayed also their maximum abundance in summer. As mentioned above, this period is characterized by a strongly stratified water column with phytoplankton biomass mostly represented by nano- and picophytoplankton fractions (Silva et al. 2009; Viñas et al. 2013). *Penilia avirostris* grazes mostly on small flagellates, dinoflagellates and diatoms (Atienza et al. 2006), whereas appendicularians are major pico- and nanoplankton feeders (Flood et al. 1992; Tønnesson et al. 2005). The dominance of microbial filter-feeding such as cladocerans and larvaceans in warmer seasons is a common feature in coastal waters of the Mediterranean (Ribera d'Alcalá et al. 2004) and the Aegean and Black Seas (Siokou-Frangou et al. 2004) as well as in the Northeast Atlantic (Rodríguez et al. 2000).

In summer, chaetognaths, mostly represented by *S. friderici* (Daponte et al. 2004) also exhibit-

ed their highest abundance. It is well known that older chaetognaths prey upon appendicularians (Purcell et al. 2004) and small copepodite stages (Sato et al. 2011a), which are very abundant during this season.

Present series recorded the highest abundance of the herbivorous calanoid *C. carinatus* in cold waters of winter and spring. The high nutrient input typical of the mixing during the winter period and the starting of water column stratification in spring favor the development of the main phytoplankton bloom of the year represented mainly by the microphytoplankton fraction (Carreto et al. 1998; Negri and Silva 2003; Viñas et al. 2013). Diatoms and dinoflagellates are the main food of *C. carinatus* (Cepeda et al. 2018 and references therein).

Long term annual and seasonal variability

During the study period, a positive trend of interannual anomalies was observed in the mean temperature of the water column, but it was non-significant. However, bottom and surface temperature analysis of a longer series (19 years) in the EPEA showed a significant positive trend, as also occurred in an extended satellite-sea surface-temperature-series (Luz Clara et al. in preparation).

In support of our initial hypothesis, the abundance of Family Oithonidae (more abundant small copepods of the EPEA zooplankton community) increased during the 18 years of observation. This is clearly perceived when comparing the abundance of this species at the beginning of the series (period 2000-2001; Viñas et al. 2013) with results of the entire series between 2000 and 2017. In summer 2000, OIT abundance (adults + copepodites) was $4,428 \pm 5,816$ ind. m^{-3} on average, whereas in the total series it was $7,159 \pm 10,289$ ind. m^{-3} . In spring 2000 its abundance attained only $2,293 \pm 1,497$ ind. m^{-3} , five times less than in the present study (mean $11,793 \pm 9,200$ ind. m^{-3}). However, non-significant correlation was found between interannual anomalies of the abundance of these species and those of the

temperature during the sampling period. Duration of time-series was probably no long enough to detect such relationships in both Oithonidae and other categories of metazooplankton.

It should be noted that in coincidence with the positive trend observed in Oithonidae, concentrations of Chl_{total} and $Chl_{<5}$ showed a significant increasing trend during the present series (Silva 2011; Ruiz et al. 2020; Negri et al. in preparation). Percentage of $Chl_{<5}$ displayed a significant positive trend coincident with a significant positive tendency of pico and nanophytoplankton fractions (Negri et al. in preparation). Increasing food availability from a rich microbial food web could have favored the development of Oithonidae populations in the long-term, as it was observed in summer, on a seasonal scale.

As previously mentioned, small copepod species are the major contributor to the total copepod community abundance at the EPEA station, especially during the warmest period of the year. This is probably related to the positive and direct influence of the increasing temperature on their reproductive cycle (Uye and Shibuno 1992; Pittois et al. 2009) as well as the indirect and favorable influence of this parameter increasing the abundance of the smaller phytoplankton fraction (Negri et al. in preparation).

But not all the zooplankton species of the EPEA community seemed to be favored by the temperature increase and its possible influence upon the phytoplankton structure and phenology, among other factors. For example, a significant decreasing trend was observed in winter on the abundance of herbivorous like lamellibranch larvae and the calanoid *C. carinatus* during 2000-2017 series. The highest peak of abundance of lamellibranch larvae was recorded in August (winter). Although no information on the species composition of these larvae was available in the present zooplankton series, they probably belonged to *Mytilus platensis*, which beds are distributed in the study area (Bremec and Lasta 1998). A marked synchrony in the emission of

gametes with peaks of reproductive activity during September and October has been reported for *M. platensis* in the study area (Penchaszadeh 1980). In the present work, maximum emission of gametes corresponded to August, one month earlier than usual. One explanation for this observed decreasing anomaly could be the temperature rise on the sea surface throughout the time-series studied. In such conditions, adults of *M. platensis*, stimulated by higher temperature ranges, could have had their spawning timing earlier, which could produce a mismatch between the recently hatched larvae and the adequate phytoplankton cells that bloom later in the season. Similarly, the decreasing tendency observed in *C. carinatus* was probably due to the same causes. In both cases, fitness consequences tend to be negative when the organism is at the wrong seasonal window. In other words, as the species completes its life span within a single year, the fact of missing the best window to grow during that year prevents them from getting another chance the following year (Mackas et al. 2012). Future results of ongoing analysis of phytoplankton diversity and long-term variability of the present series (Negri et al. in preparation) would give some insight to test this hypothesis.

Perturbations to average seasonal cycles of environmental conditions, and the ability (or inability) of biota to track these variations are very important drivers of interannual variability in growth, survival, and population size (Mackas et al. 2012), as it was observed in the present work.

Small copepods represent a main food source for local fish, especially during larval stages (Viñas and Ramírez 1996; Sato et al. 2011b). If the observed increasing tendency of these species (mainly *O. nana* and members of Paracalanidae-Clausocalanidae) remains in the long term, this would expand the availability of food for fish larvae, thus favoring their growth and survival. In the study area, *Engraulis anchoita* larvae are dominant during a great part of the

year (Sánchez and Ciechowski 1995). With acoustic biomass fluctuating between one and five million tons in the period 1993-2008 (Madirolas et al 2013), this species has a superlative ecological importance because of its central role in pelagic food webs in the Argentine shelf (Leonarduzzi et al. 2010 and references therein). A recent study analyzing the same time-series denoted that density and nutritional condition of anchovy larval were higher in spring and autumn, but lower in winter (Leonarduzzi et al. 2021). Interestingly, the present work shows that higher concentrations of small copepods (all stages together) were observed in spring and summer whereas lower values corresponded to autumn. Many factors must be considered to understand larval-zooplankton relationships: real concentration of food in the larval habitat (a mean concentration in the water column is not the best approach), seasonal predators abundance (non-considered in present work) and concentration of other zooplanktonic food items (i.e. protozooplankton), among others.

Time series provide the oceanographic community with the long, high-quality data necessary to characterize the functioning of the ocean (Henson 2014) and help to unravel natural and human-induced changes in marine ecosystems (Reid and Valdés 2011). Consequently, these time-series sampling sites represent a phenomenal heritage legacy, and intergovernmental bodies such as ICES, the European Marine Board, or IOC-UNESCO strongly recommend their continuity and the establishment of new time-series based on previous findings (Valdés and Lomas 2017).

CONCLUSIONS

This work covers a time-series of 18 years in which the variability of main metazooplankton taxa of the EPEA station was studied for the first time. Results indicated that small copepods dom-

inate the metazooplankton at this station. The most abundant family, Oithonidae, showed an interannual increasing trend during the study period, whereas lamellibranch larvae and other cryophilic taxa exhibited a decreasing trend. Physical parameters (MT, MS and ϕ) did not show significant interannual trends. However, temperature exhibited a strong increasing tendency. No clear relationships were found between both long-term interannual and seasonal anomalies of taxa and those of the physical parameters, probably because of the short period analyzed. The increasing of Oithonidae abundance could be due both to the direct effect of the temperature rise on their reproductive rates and the positive influence of this parameter on the concentration of small phytoplankton fractions, an important food item for these copepods. Opposite, for other cryophilic taxa such as Calanidae and lamellibranch larvae with decreasing abundances, the increase of temperature could have had a negative effect, although the mechanisms involved are less clear. More observations are necessary to confirm these hypotheses.

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