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Long-term changes on estuarine ciliates linked with modifications on wind patterns and water turbidity

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Abstract :

Planktonic ciliates constitute a fundamental component among microzooplankton and play a prominent role in carbon transport at the base of marine food webs. How these organisms respond to shifting environmental regimes is unclear and constitutes a current challenge under global ocean changes. Here we examine a multiannual field survey covering 25 years in the Bahía Blanca Estuary (Argentina), a shallow, flood-plain system dominated by wind and tidal energy. We found that the estuary experienced marked changes in wind dominant regimes and an increase in water turbidity driven from the joint effect of persistent long-fetch winds and the indirect effect of the Southern Annular Mode. Along with these changes, we found that zooplankton components, i.e. ciliates and the dominant estuarine copepod Acartia tonsa, showed a negative trend during the period 1986–2011. We showed that the combined effects of wind and turbidity with other environmental variables (chlorophyll, salinity and nutrients) consistently explained the variability of observed shifts. Tintinnids were more vulnerable to wind patterns and turbidity while showed a loss of synchrony with primary productivity. Water turbidity produced a dome-like pattern on tintinnids, oligotrichs and A. tonsa, implying that the highest abundance of organisms occurred under moderate values (~50 NTU) of turbidity. In contrast, the response to wind patterns was not generalizable probably owing to species-specific traits. Observed trends denote that wind-induced processes in shallow ecosystems with internal sources of suspended sediments, are essential on ciliate dynamics and that such effects can propagate trough the interannual variability of copepods.

Highlights

► Planktonic ciliate's abundance decreased over the last 25 years in a shallow estuary. ► Decreasing cell abundance was linked to changes in wind dominant regimes and increased water turbidity. ► Tintinnids were more vulnerable to wind patterns and turbidity and lost synchrony with primary productivity. ► Interannual variability of the copepod *Acartia tonsa* followed the changes in ciliate community. ► Erosive processes in shallow estuaries impact on the interannual dynamics of ciliates and such effects can cascade-up to copepods.

Keywords : Tintinnids, Oligotrichs, *Acartia tonsa*, Wind, Turbidity, Estuaries

Introduction

In coastal ecosystems, tintinnids and oligotrichs (hereafter collectively referred to as 'ciliates'), constitute a fundamental component among microzooplankton and play a prominent role in carbon transport at the base of marine food webs (Keller and Hood 2011, Mitra et al. 2014, Legendre and Rivkin 2015). They rapidly synchronize productivity patterns due to their short generation time and graze an average of 60 % of daily primary production and 10 % of daily bacterial production (Steinberg and Landry 2017), while representing nearly 30 % of copepods diet (Calbet and Saiz 2005). In spite of their relevance in both trophic dynamics and carbon fluxes, ciliate's responses to environmental drivers remain elusive due to the lack of sustained long-term surveys and synoptic approaches (Clamp and Lynn 2017). Empirical evidence has shown a prominent role of temperature and food on ciliate's dynamics, however, the long-term response of these organisms is shaped by a variety of additional drivers (Dolan and Gallegos 2001, Aberle et al. 2013, López-Abbate et al. 2015). Hence, we urgently need sustained field observations that integrate ecological responses of natural communities to multi-scale drivers (Heger et al. 2014). Sustained observations of wide-varying environments are critical to understand underlying mechanisms shaping the structure and function of plankton communities (Boyd and Hutchins 2012) and to detect non-linearities (Kreyling et al. 2018). This information will ultimately facilitate the anticipation of inefficient carbon transfer toward higher trophic levels (Wohlers et al. 2009).

Among shallow estuaries, surface winds have an important influence on the seasonal pattern of plankton (Reynolds 2006). This influence is driven by physical processes such as waves, currents, microscale turbulence and particles resuspension (Scully et al. 2005, Li and Li 2011, Whipple et al. 2018). Microscale turbulence induced by surface winds, for

instance, reduces the sinking velocity of suspended organisms and can enhance prey capture and nutrient uptake (Kiørboe and Saiz 1995, Barton et al. 2014, Pécseli et al. 2014). In addition, the transport of inorganic nutrients toward illuminated layers produced by wind-driven water mixing, regulates phytoplankton growth and availability (Kiørboe 2008). In flood-plain estuaries, wind-induced currents and wind waves are among the most important factors that favour sediment resuspension in the water column, and profoundly interfere with the light penetration (Weir and McManus 1987, Brand et al. 2010, Bever et al. 2018). A high concentration of suspended particles, in turn, can restrict ciliate reproduction (Jack and Gilbert 1993), while handling-limited predation by the interference of inedible suspensoids with prey uptake has been observed in planktonic filter feeders such as cladocerans (Laspoumaderes et al. 2017).

Located in the SW Atlantic Ocean, the Bahía Blanca Estuary is a shallow, flood-plain estuary dominated by wind and tidal energy (Piccolo and Perillo 1990). In the last decades, the region has experienced climate-driven environmental changes encompassing warmer winters and extreme dry periods (Aravena and Luckman 2009, Guinder et al. 2010), along with persistent positive anomalies of the Southern Annular Mode (SAM). Such anomalies are associated with stronger than normal westerlies over the mid-high-latitudes and weaker westerlies in the mid-latitudes (Marshall 2003). Concurrently, water turbidity has shown a positive trend in the last 15 years, presumably as a response to wind shifts and the lateral erosion of salt marshes associated with sea level rise (Pratolongo et al. 2013, López-Abbate et al. 2017). Modelling approaches revealed the emergence of both, wind speed and water turbidity, as dominant factors driving the decline of chlorophyll concentration in recent years (López-Abbate et al. 2017), however, the interannual response of phagotrophic plankton has been so far overlooked. Ciliates contribute with the highest carbon biomass

within estuarine microzooplankton during the entire annual cycle. Experimental approaches have revealed that these organisms are the preferred food source of the dominant copepod *Acartia tonsa* (Diodato and Hoffmeyer 2008). This omnivorous species cohabits with ciliates during most of the year whereas it may reach up to 90 % of total mesozooplankton abundance during the warm season, concurrent with the highest annual concentration of tintinnids (Hoffmeyer 2004). In turn, *A. tonsa* is one of the main food sources of planktivorous fish (López Cazorla et al. 2011). The aim of this study is to quantify the interannual response of ciliates to environment drivers, with emphasis on wind patterns and water turbidity. For this purpose, we have employed a unique multiannual data set in the SW Atlantic Ocean that covered the abundance of micro- (ciliates community) and meso-zooplankton (*A. tonsa*) along with an exhaustive environmental data set. To quantify the effect of multiple drivers on ciliates and *A. tonsa*, we used Boosted Regression Trees (BRT). The analyses are organized in the following steps: 1) exploration of top-down and bottom-up interactions, 2) testing of the hypothetical cause-effect models, 3) identification of dominant drivers according to the amount of explained deviance and 4) comparison of the partial response of zooplankton groups to wind patterns and water turbidity.

Materials and Methods

Study area

The Bahía Blanca Estuary (38°42'-39°25'S, 61°50'-62°22'W) is located in a temperate, semiarid region at the northern boundary of Patagonia in the SW Atlantic coast, Argentina. Mesotidal setting and wind-driven mixing prevents stratification during most of the year (Perillo et al. 2001). The depth of the estuary ranges between 1 and 24 m, while the mean

value is about 10 m (Perillo et al. 2001). Half of the estuarine basin consists of extensive low-slope tidal flats densely fragmented by tidal courses (Perillo 2009) oriented NW–SE (Fig. 1). The feature promotes an intense interaction between the water column and the bottom layers, whose first 3-4 m are composed by a massive deposit of unstructured mud (Pratolongo et al. 2017). Predominant NW winds run parallel to the estuarine main channels and produce high energy wind waves that enhances the erosion of tidal flats (Perillo and Sequeira 1989, Pratolongo et al. 2010). Grain size in the lower mudflats are in the very coarse to fine silt range (mode of 32 µm), while suspended sediments size in the water column varies between 1 and 50 µm (mode of 10 µm) (Guinder et al. 2015, Zapperi et al. 2017).

The main estuarine channel is periodically dredged since 1958, while the harbour basin in the inner reach is water-jettied to prevent sediment deposition. The dredged volume increased 11-fold after 1999 due to the deepening and widening of the access channel. Currently, dredging operations are executed along an area of 20 km long and 190 m width and attain a regular depth of 13.5 m (López-Abbate et al. 2017). As a result, the volume of sediment extraction by dredging significantly increased from a yearly mean of 240,714 m^3 in 1958-1998, to 2,657,919 m^3 in 1999-2011. In addition, the development of urban centres fostered point-source nutrient loading, which can sporadically exceed the tolerance of microzooplankton due to the toxic effect of ammonium (López-Abbate et al. 2015).

Biological data

Microzooplankton samples were taken from the surface layer using a van Dorn Bottle (2.5 l) in the inner zone of the estuary (Puerto Cuatreros, 38º-50'S, 62º20'W) (Fig. 1), at a monthly frequency during discontinuous periods from 1986 to 2011. The quantification of

137 ciliates was done by settling a variable volume (10-50 ml, depending on sediment and
138 plankton concentration) of preserved seawater sample (neutral Lugol's iodine, f.c. 10 %) in
139 Utermöhl chambers during 24 h. The entire chamber was analysed under a Wild M20
140 inverted microscope (Hasle 1978). We here focused on tintinnids and oligotrichs since they
141 represent the most abundant groups within microzooplankton in the Bahía Blanca Estuary
142 (Pettigrosso 2003, Barría de Cao et al. 2005). A total of 178 samples were analysed for the
143 quantification of tintinnids, while 97 samples were analysed for the quantification of
144 oligotrichs. Samples for tintinnids quantification were taken at a monthly or biweekly
145 frequency during the following periods: April 1986 to May 1989, June 1995 to April 1997,
146 March 2002 to March 2004, October 2006 to February 2008 and July 2008 to April 2011.
147 Samples for oligotrichs quantification were also taken at a monthly or biweekly frequency
148 during the following periods: February 1994 to February 1995, January 2007 to February
149 2008, July 2008 to April 2011. Tintinnids were identified to the species level, while
150 oligotrichs were in some cases identified to the genus level while in other cases they were
151 counted as a whole. From 1978 to 2009, samples for chlorophyll *a* analysis were taken
152 uninterruptedly at the same location, on a fortnightly basis. Chlorophyll *a* concentration
153 was quantified by the extraction with acetone (90 %) at a controlled room temperature and
154 then refrigerated in the dark at 4 °C for 24 h. Then the samples were centrifuged and the
155 supernatant separated. The pigment concentration was determined by spectrophotometry
156 (Jenway 6715 UV–Vis) using the equations of Lorenzen (1967). To assess predator-prey
157 links we also included data on the dominant copepod species, *A. tonsa,* which is a key
158 component of the estuarine food web. Adults of *A. tonsa* were obtained from
159 mesozooplankton samples collected at a monthly frequency during the following periods:
160 July 1979 to August 1980, August 1982 to September 1983, July 1990 to August 1991,

April 2002 to November 2002, January 2007 to February 2008, July 2008 to December 2010 and January 2015 to December 2015. Samples were collected with subsurface horizontal tows using a 200 µm mesh plankton net and 0.30 m mouth diameter equipped with a Hydrobios flowmeter and towed for 10 min at a constant speed of 2 knots. Surface sampling bias was minimized by reproducing the sampling protocol and the subsequent sample treatment throughout the studied period. Samples were fixed (4 % formalin) and analysed under a Wild M5 stereoscopic microscope using a Bogorov chamber following the methodology proposed by Boltovskoy (1981).

Environmental data

Water temperature (°C), salinity and turbidity (NTU) were measured simultaneous to biological sampling using a digital multi-sensor Horiba U-10. Likewise, samples for the determination of dissolved inorganic nutrients were taken from the surface layer using a van Dorn Bottle (2.5 l) at a monthly frequency. Nitrate, nitrite, phosphate and silicate concentrations were determined following the methods described in Spetter et al. (2015). The sum of nitrate and nitrite was expressed as the concentration of dissolved inorganic nitrogen (DIN). Data on wind speed and direction were provided by the National Weather Service (http://www.smn.gov.ar). Hourly data were available for the period 1991-2015 while previous to 1991 (1978-1990) data were recorded every three hours.

The region is influenced by large-scale atmospheric phenomena such as SAM and El Niño Southern Oscillation (ENSO) (Vera et al. 2004, Menéndez and Carril 2010). The SAM-Marshall index, based on the difference of mean sea level pressure between the latitudes 40°S and 65°S, was selected for the analysis as it reduces the influence of spurious trends of reanalysis products (Marshall 2003). The temporal evolution of ENSO was assessed by

185 the SST averaged anomaly in the Niño 3.4 region (Niño 3.4 index) in the central-east
186 region of the Tropical Pacific Ocean (5°N–5°S, 170°–120°W) (Trenberth 1997). The
187 atmospheric variables used to assess indirect effect of climate modes on wind patterns were
188 air temperature and sea level pressure. Monthly record covered the northern SW Atlantic
189 coast including the estuarine area and extending from -35.0 to -42.5 °N and from 295.0 to
190 302.5 °E. Regional atmospheric variables as well as the standardized modes of atmospheric
191 variability were obtained from the Climate Diagnostics Center (NCEP/NCAR) reanalysis
192 fields.
193
194 *Data analysis*
195 *Identification of trends in biological data*
196 Owing to the different frequency and time-coverage of time series, all records were
197 screened and averaged to obtain monthly values prior the analysis. To evaluate the
198 influence of co-occurring environmental drivers on the interannual response of ciliates and
199 the copepod *A. tonsa*, we first analysed the general trend of tintinnids and oligotrichs
200 abundance by fitting a linear model on monthly records as a function of time. The long-
201 term variability of log-transformed abundance of the three zooplankton groups and wind
202 speed were also fitted to linear models to compute the yearly rate of change. In addition, the
203 long-term trend of individual tintinnid's species was displayed in a heat map using the
204 annual mean of log-transformed abundance. The phenology of tintinnids, whose sampling
205 frequency allowed a more detailed examination, was evaluated using Generalized Additive
206 Model (GAM). For this purpose, we compared the annual cycle using mean monthly
207 records as a function of time (months) during two periods: 1986-2002 and 2003-2011.
208 These periods were selected considering the significant breakpoint on the chlorophyll *a*

time series noticed in 2002 (López-Abbate et al. 2017) and assuming a bottom-up linkage between tintinnids and chlorophyll.

Interconnection between climate modes, regional atmospheric variability and water turbidity

Wind patterns along the period 1991-2015 were visualized through annual wind roses with the R-function plot.windrose (R Development Core Team 2014). Hourly data were employed to plot the frequency of wind speed and direction by year. Records previous to 1991 were not plotted due to lower than hourly data frequency. The percentage of 'calms', defined as the fraction of zero wind speed along the year, was calculated by the windRose function from the R-package openair. To improve the visualization of long-term trends, annual means of wind speed, wind direction and water turbidity were fitted as a function of time by a GAM. Yearly records in the period 1978-2015 were fitted with a logit link function using the R-package mgcv.

To explore correlations between water turbidity and wind patterns with climate variables of interest operating at regional and global scales, we constructed a path model (SEM). We first constructed the theoretical model by ranking the explanatory variables, from global (ENSO, SAM), regional (air temperature and sea level pressure) and local scale variables (precipitation, wind speed, wind direction and SST), to the response variable (water turbidity), thus assuming causal relationships. ENSO and SAM signals are known to co-vary during austral summer (Fogt et al. 2011), therefore they were set as covariates in the model. Path coefficients were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1000 replicates), while the Chi-square values were used to

assess the robustness of models (Alsterberg et al. 2013). Path analysis was performed using the R-package lavaan.

Influence of environmental drivers on plankton groups

Once defined the long-term modifications on ciliate community, we identified the environmental variables driving such changes by means of Regression Tree Models. Regression Trees are non-linear predictive models that can be used when data have lots of features which interact in nonlinear ways. The method is based on the partition of the predictor space into rectangles until data fragments can fit simple models. Predictors and split points are chosen to minimize prediction errors, which is calculated as the sum of squared errors between the predicted values and the actual values (Breiman et al. 1984, De'ath and Fabricius 2000). We here used Boosted Regression Tree (BRT) which combines simple models (trees) to gain predictive power (Elith et al. 2008). The number of times a predictor is selected for splitting and the amount of explained deviance, allow to rank predictive variables according to their relative importance. The R-packages gbm and dismo were employed for the construction of BRT. Models were trained by setting the log-transformed abundance of tintinnids and oligotrichs as the response variables, and chlorophyll *a* concentration, wind speed, wind direction, salinity, turbidity and dissolved inorganic nutrient concentration (DIN, phosphate and silicate) as the explanatory variables. Given the positive correlation between ciliates and chlorophyll *a* concentration with the abundance of *A. tonsa* (Diodato and Hoffmeyer 2008), we assumed that the ecological interaction among groups was dominated by the bottom-up control exerted upon the copepod. Thus we constructed an additional model using the abundance of *A. tonsa* as the response variable and the concentration of ciliates and chlorophyll *a*, wind speed, wind

direction, salinity and turbidity as the explanatory variables. The lack of data regarding the loss of *A. tonsa* by fish predation, as well as other unobservable factors, can significantly reduce the predictive power of models. In BRT, pre-selection of variable is not required since the model largely ignores non-informative predictors when fitting trees (Elith et al. 2008). Sea surface temperature (SST), nevertheless, was not included to avoid spurious up-weighting due to autocorrelation. The marked seasonality of ciliates and *A. tonsa*, may further contribute to the up-weighting of SST in BRT models. Model fitting was evaluated by the cross-validation deviance and standard error. Given that wind speed, wind direction and turbidity explained more than 29% of variance when predicting the abundance of zooplankton groups, we examined the partial response of tintinnids, oligotrichs and *A. tonsa* to these three predictors.

Results

Long-term dynamics of ciliates

The mean monthly abundance of tintinnids along the time series was 3416 cell l^{-1} (Table S1), while the monthly abundance of oligotrichs was lower and averaged 1403 cell l^{-1} (Table S2). The assessment of the long-term variation of ciliates showed a negative interannual trend (Fig. 2). Tintinnids declined at a yearly rate of 2.8 % ($p<0.001$, $R^2=0.735$), corresponding to a decrease of ~97.8 cell l^{-1} yr^{-1}, while oligotrichs declined at a yearly rate of 1.6 %, although the trend was not significant ($p=0.221$, $R^2=0.281$). Likewise, the abundance of the copepod *A. tonsa* also showed a negative trend ($p=0.005$, $R^2=0.605$) and a yearly rate of decline of 3.3 %. A total of 11 tintinnid species showed a negative trend, including the dominant species *Tintinnidium balechi*, while *Tintinnopsis brasiliensis* and *T.* sp. showed a positive trend, and *Metacylis* aff. *mereschkowskyi*, *T. buetschlii*, *T.*

buetschlii var. *mortensenii*, *Favella taraikaensis Leprotintinnus pellucidus* and *T. amphora* showed only occasional occurrence (Table S1, Fig. 3). The most abundant species within ciliates throughout the time series was *T. balechi*, which represented an average of 27 % of total abundance and revealed a steeper rate of decline (4.3 %, p=0.008, R^2=0.425, data not shown) compared with total tintinnid abundance. The percentage decline represented a decrease of 52.4 ind l^{-1} yr^{-1}. The annual cycle of tintinnids before and after 2003 revealed the loss of the spring pulse that followed the winter phytoplankton bloom in recent years (Fig. 4).

Trends in environmental conditions

Wind speed showed a slowdown rate of 0.4 m s^{-1} y^{-1} since 1998 to date (linear regression model: p<0.001, R^2=0.680), which represents a decline of 32.7 % (Fig. 5, Fig. 6a). During the period 1986-2002, wind speed averaged 6.51 m s^{-1} while the mean annual wind speed in the following period (2003-2015) was 5.71 m s^{-1}. Mean annual wind direction showed higher persistence toward of NW quadrant since the 1978 to date (linear regression model: p<0.001, R^2=0.480) (Fig. 5, Fig. 6a). In addition, the percentage of calm periods declined at a yearly rate of 2 % since the beginning of the time series (linear regression model: p<0.001, R^2=0.509). Water turbidity increased accordingly after 1999 (Fig. 6a) at a yearly rate of 4 % (p<0.001, R^2=0.745), while SEM revealed that in the period 1978-2011, it responded to the direct effect of wind speed, wind direction and SST and to the indirect effect of SAM and ENSO (X^2=450.49, df=12, p<0.001, Fig. 6b). Mean annual SST and salinity was 15.7 °C and 33.2 respectively, and both variables evidenced no linear trends along the time series. Positive trends were observed in the mean annual concentration of DIN (p=0.002, R^2=0.290) and phosphate (p<0.001, R^2=0.470), while no evident trend was

observed in the concentration of silicate. Mean annual concentration of DIN, phosphate and silicate was 6.90, 2.07 and 90.37 µM respectively, while the yearly rate of DIN and phosphate increase was 1.1 and 0.8 % respectively.

Environmental drivers of ciliates and A. tonsa abundance

BRT yielded evidence of the response of tintinnids (R^2=0.528), oligotrichs (R^2=0.982) and *A. tonsa* (R^2=0.435) to environmental variables. The ranking of driver importance (Fig. 7) revealed that the optimal predictors of tintinnid abundance were turbidity, wind speed, wind direction and DIN, which explained 25.9, 22.3, 14.0 and 13.1 % of total tintinnids variability, respectively. Predictors that better explained the variability of oligotrichs were phosphate (34 %), silicate (26.5 %), wind speed (25.1 %) and turbidity (12.2 %), while the variability of *A. tonsa* was mostly predicted by tintinnid abundance (27.0 %), salinity (18.7 %), turbidity (12.2 %) and wind direction (11.7 %). Taken together, wind speed, wind direction and turbidity explained 62.2, 39.4 and 29.8 % of tintinnids, oligotrichs and *A. tonsa* variability, respectively. Partial dependence plots (Fig. 8) revealed that tintinnids and *A. tonsa* adults showed a saturating relationship with wind speed, with a threshold value near 25 m s^{-1}. Similarly, tintinnids and *A. tonsa* adults showed a binomial-like relationship with winds direction, i.e., the highest abundance values occurred in concurrence with winds coming from the SE quadrant and lowest abundance values in concurrence with winds coming from the NW quadrant. A dome-like pattern to water turbidity was register in all zooplankton groups, with the highest abundance values occurring at nearly 50 NTU.

Discussion

Ciliates and A. tonsa interannual response

During the studied period (1986–2009), we identified a progressive decline of tintinnids and *A. tonsa* adults and a less obvious decline on oligotrichs concentration. Parallel to the negative trend of zooplankton groups, phytoplankton community showed a drastic erosion of seasonal peaks and a shift from the typical unimodal productivity pattern to a bimodal regime (López-Abbate et al. 2017). Along the time series, two tintinnids species, *Tintinnopsis brasiliensis* and *T.* sp., showed a positive trend. The oral diameter of these species ranges from 56 to 90 µm, which is above the mean oral diameter of the estuarine tintinnids (mean <40 µm). The oral area is proportional to prey encounter rate, and a wider encounter radius may confer a competitive advantage against species with narrower oral area constrained to a smaller prey size spectrum (Dolan 2010). The loss of the winter phytoplankton bloom in the last three decades, produced a loss of synchrony between tintinnids and primary producers, and changed the seasonal pattern of resource availability for higher trophic levels. In turn, the abundance of the dominant copepod *A. tonsa*, showed a significant positive relationship with tintinnids, denoting that the ecological interaction among groups was dominated by the bottom-up control exerted upon the copepod. In addition, the type of interaction confirmed by our model, allows to confidently attribute the negative trend of tintinnids to environmental factors. Tintinnids are a relevant prey item among estuarine copepod's diet (Dolan and Gallegos 2001), and during warm months in the Bahía Blanca Estuary, tintinnids represent nearly 78 % of total particles filtration by the copepod *A. tonsa* (Diodato and Hoffmeyer 2008). Our results revealed that environmental factors produced cascade-up effects, from phytoplankton to copepods, and imply a high probability that such effects resonate into the dynamics of planktivorous fish that prey on *A. tonsa* (López Cazorla et al. 2011). The disclosure of long-term patterns further highlights

351 the importance of sustained ocean observation systems to discriminate directional trends on
352 ciliates and to identify clues regarding the loss of functional diversity.
353
354 *Long-term patterns of wind and water turbidity*
355 Regional wind patterns evidenced a shift toward low intensity but highly persistent NW
356 winds in the last 25 years. Local winds over the South Atlantic are modulated by the
357 intensity and displacement of the South Atlantic subtropical anticyclone (Venegas et al.
358 1996, Palma et al. 2004). In the last decades, this anticyclone revealed a slight southward
359 movement (Dragani et al. 2010) and caused wind pattern modifications over the region
360 (Simionato et al. 2005, Brendel et al. 2017). At the interannual time scale, the southward
361 displacement of the anticyclone tends to be associated with positive phases of SAM (Sun et
362 al. 2017). Such large scale atmospheric variability was superimposed with the variability of
363 local winds as suggested by our SEM model, in which both wind speed and wind direction
364 showed teleconnections with SAM through the effect of sea level pressure anomalies. At
365 longer timescales, the non-annular component of SAM produces contrasting spatial
366 responses on SST and could also influence local wind patterns (Yeo and Kim 2015). In
367 fact, a noticeable inflection in both wind speed and direction was perceived around 1999
368 (Fig. 6a), in concurrence with the decadal shift on SAM spatial structure.
369 Although the increase of water turbidity is generally attributed to an increase in wind speed
370 (Bever et al. 2018), in geomorphologically complex systems, other attributes such as the
371 prevailing wind direction also come into play. The prominent role of wind direction on
372 water turbidity revealed by the data, can be interpreted as the potential of winds cardinally
373 aligned with the estuarine main channels to produce longer fetch and high energy wind
374 waves (Perillo and Sequeira 1989, Pratolongo et al. 2010). High energy wind waves boost

375 the lateral erosion of wide expansions of tidal flats and promote the mobilization of soft
376 sediments to the water column thereby contributing to increase water turbidity (Piccolo et
377 al. 2008). Among estuaries with strong interaction across coastal forms (i.e. saltmarshes
378 and flood-plains) and the water column, wind attributes capable of producing wind waves
379 are thereby better descriptors of water turbidity than wind velocity alone (Cho 2007,
380 Reisinger et al. 2017). The simultaneous intensification of bottom shear stress due to the
381 expansion of the dredged area may additionally amplify the effect of changing wind
382 patterns on water turbidity (López-Abbate et al. 2017).
383 The significant positive effect of SST on turbidity denotes the recurrent seasonal pattern of
384 this variable, which typically shows maximum values during the warm months. This
385 seasonal pattern is echoed by the dynamics of the borrowing crab, *Neohelice granulata*,
386 which produces an intense sediment destabilization within tidal flats and a conspicuous
387 mobilization of soft sediments toward the water column during summer (Zapperi et al.
388 2016). The present rate of sea level transgression into the estuarine basin may also affect
389 the positive trend of water turbidity (Lanfredi et al. 1988). Sea level rise presently causes an
390 intense lateral erosion of saltmarshes which already experienced a 33 % loss of its area
391 since 1967 (Pratolongo et al. 2013). Marsh boundary erosion along with the 50 % loss of
392 shrub-like steeps area due to the settlement of human infrastructure (Pratolongo et al.
393 2013), likely stimulated the continuous transport of mud deposits to the adjacent water
394 column.
395
396 *Partial response of zooplankton groups to wind patterns and water turbidity*
397 Long-term evaluation of environmental and biotic data revealed a prominent role of wind
398 and water turbidity as underlying drivers of the decline of zooplankton groups, especially

tintinnids. In turn, the consistent increase on water turbidity resulted from the joint effect of wind patterns and the indirect effect of SAM in the last two decades. Further external forces may improve the consistency of predictive models constructed here. For instance, behavioural retention, migration and horizontal advection, are important factors that drive the spatial distribution of ciliates and their assessment requires a detailed three-dimensional observation of biota.

Partial dependence plots, denoted that wind speed produced a logistic-like pattern in the concentration of tintinnids and *A. tonsa*, while oligotrichs evidenced a dome-like pattern. Wind mixing is one of the most important drivers that determines three-dimensional distribution of plankton in shallow environments (Moreno-Ostos et al. 2008, Cardoso and Motta Marques 2009, Zhou et al. 2015). Additionally, wind-driven water turbulence may enhance or reduce prey encounter depending on the size of organisms, sensory strategies and behavioural traits (Pécseli et al. 2014). Ambush feeders such as *A. tonsa* when offered motile prey, are more dependent on turbulence to effectively encounter prey than motionless predators, while suspension feeders that create feeding currents, such as most ciliates, are less dependent on turbulence (Kiørboe and Saiz 1995). However, turbulence also affects ciliate's growth and sinking rate and their response is thereby less generalizable (Martínez et al. 2017). Fast-sinking tintinnids with agglomerated lorica, would be more dependent on wind-induced turbulence than slower sinking oligotrichs to retain suspended populations. The broad majority of the tintinnid species found in the estuary display agglutinated minerals, mostly sediments, covering the surface of their lorica, and this particular trait could underlie the specific response of both tintinnids and oligotrichs to wind speed.

Tintinnids and *A. tonsa* showed the strongest dependence on wind direction and evidenced a negative relationship with winds coming from the NW quadrant. In the Bahía Blanca Estuary, NW winds are effective impellers of erosive wind waves, and water turbidity can thereby be described as a function of wind direction (Piccolo et al. 2008). Accordingly, the response of plankton to wind direction is likely mediated by water turbidity, although wind direction may also affect the vertical distribution and retention of organisms. Wind-induced internal waves, for instance, reduce the likelihood of sedimentation losses (Hingsamer et al. 2014). Waves generated by NW winds across the estuary have relatively small wavelengths implying that the turnover due to waves only occurs in the upper 2-3 m (Perillo and Sequeira 1989). The confinement of turbulence mixing within the upper layers likely intensifies the sedimentation of rapidly sinking plankton such as tintinnids. Our models, however, are based on the abundance of organisms at the surface layer, and do not provide evidence on the sedimentation of organisms or the compensatory dynamics such as vertical migration. NW winds are further directed toward the mouth of the estuary and can intensify the ebb-oriented transport of suspensoids toward the shelf area. Outflowing winds are known to produce the horizontal advection of plankton and the local exclusion of cells (Wolfe et al. 2015), and may be an additional factor driving the negative trend of tintinnids and *A. tonsa* to NW winds.

Water turbidity produced a dome-like pattern in zooplankton groups denoting that the highest abundance values occur under moderate levels of turbidity. Increased concentration of suspended sediments in the size range of zooplankton prey, limits prey encounter rate and handling (Boenigk and Novarino 2004). In fact, experimental data revealed that water turbidity reduced the growth and survival of heterotrophic nanoflagellates owing to the interference of mineral suspensoids with the uptake of prey rather than to the physical

damage of cells (Sommaruga and Kandolf 2014). In particular, the mean oral diameter of the 20 tintinnid species reported in the Bahía Blanca Estuary was 41 µm, suggesting that the size spectrum of prey are below 10-15 µm (Dolan et al. 2012). The prey size spectrum of tintinnids fall well between the size range of suspended sediments in the Bahía Blanca Estuary, which varies between 1-50 µm while the modal value is 10 µm (Guinder et al. 2015). Above 50 NTU, water turbidity produced a negative effect on zooplankton groups, denoting that this factor may be considered as an ecological disturbance. Maximum zooplankton biomass, however, occurred at intermediate values of water turbidity, revealing that tintinnids, oligotrichs and *A. tonsa* are able to successfully coexist under this scenario. Optimal coexistence of functional groups at the average scale gradient of disturbance (i.e. water turbidity), partly supports the Intermediate Disturbance Hypothesis, which states that species diversity is maximized when disturbance intervals are intermediate (Connell 1978). Optimal disturbance interval depends on the generation time of the exposed organisms (Gaedeke and Sommer 1986), which in this case ranges between days to hours, and coincides with the time-lag needed to wind and tides to produce observable shifts in water turbidity (Perillo 1995).

At the long temporal scale, water turbidity may have produced a detrimental effect on ciliates by reducing the ratio between inedible suspensoids and phytoplankton, and forcing ciliates to an additional energy expenditure to sort inedible particles. Mixotrophic oligotrichs, however, are less sensitive to water turbidity and likely constitute the trophic link between bacteria and higher trophic levels due to the exclusion of light limited phytoplankton and filter feeders (Sommaruga and Kandolf 2014, Kammerlander et al. 2016). The close link between oligotrichs and inorganic nutrients revealed by BRT denotes that higher inorganic nutrient concentration in the last years may have mitigated the low

concentration of prey availability. Wind-induced processes can thereby influence the food web organization by changing the spatial distribution of plankton and the ratio between edible and inedible particles.

Human activities at coastal areas are restricting the ability of coastal wetlands to compensate the effect of climate change, and projection based on the IPCC mean sea level rise scenario revealed that 20 % of salt-marsh area will be lost by 2100 (Craft et al. 2009). The cumulative effect of sea level rise along with intense land use and limited ecosystem feedbacks, will enhance the erosion of coastal margins and the mobilization of soft sentiments toward the adjacent water column (Kirwan and Megonigal 2013). Shallow ecosystems with internal sources of suspended sediments, are thereby highly vulnerable to erosive processes. Our results provide quantitative evidence on the long-term response of pelagic ciliates to growing water turbidity and further revealed that ciliates can propagate such effects trough the interannual variability of copepods.

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Figure and table captions

Figure 1. Map of the Bahía Blanca Estuary, SW Atlantic Ocean, showing the location of the sampling site at the inner estuary close to "Puerto Cuatreros". Main tributaries, sewer

494 discharge points, industrial and port areas (grey area) and the main urban centers (orange
495 area) are also shown. Dredging operations take place periodically in the port area and in the
496 Principal Channel.
497
498 **Figure 2.** Long-term changes of tintinnids, oligotrichs (cell l^{-1}, upper and mid panels,
499 respectively) and *Acartia tonsa* (ind m^{-3}, lower panel) abundance. Significant trends are
500 indicated by a linear fit and confidence interval at 95 %. R^2 and p-values are indicated
501 inside the plots.
502
503 **Figure 3.** Mean annual log-transformed abundance (cell l^{-1}) of tintinnid species over the
504 time series. Years with incomplete monthly observations (1986-1989, 1996-1997 and 2004-
505 2006) were averaged together. Negative trend was observed in almost all species except for
506 *Tintinnopsis brasiliensis* and *T.* sp. that showed a positive trend. Scale bar denotes the value
507 of tintinnid abundance.
508
509 **Figure 4.** GAM estimates of mean monthly log-transformed abundance (cell l^{-1}) of
510 tintinnids in the periods 1986-2002 (blue dots) and 2003-2011 (red dots) denoting the loss
511 of the spring peak following the winter phytoplankton bloom in recent years. R^2 and p-
512 values are indicated inside the plots.
513
514 **Figure 5.** Annual wind roses in the period 1991-2015 showing the frequency of wind speed
515 and direction (%). Plots denotes the decreased prevalence of wind coming from the NE, SE
516 and SW quadrants. Mean wind velocity decreased after 2000 and the relative persistence of

517 NW winds intensified over the time series. Scale bar at the right side of the plots denotes
518 wind speed (ws).
519
520 **Figure 6.** a) Annual mean of wind speed (upper panel), wind direction (mid panel) and
521 turbidity (lower panel) in the Bahía Blanca Estuary over the period 1978–2011. b) Path
522 diagrams showing significant ($p<0.05$) interconnections between climate and
523 environmental drivers and water turbidity. At each significant path the positive (blue) and
524 negative (red) effects are represented by the standardized coefficients. The variables used in
525 SEM were: SAM-Marshall index (SAM), Niño 3.4 index (N3.4), seal level pressure (SLP),
526 air temperature (Air Temp), precipitation (PP), wind speed (ws), wind direction (wd), sea
527 surface temperature (SST) and turbidity (turb).
528
529 **Figure 7.** The ranking of explanatory variable importance driving the response of tintinnids
530 (left panel) and oligotrichs (right panel) abundance. The variables used in the BRT model
531 were wind speed (ws), wind direction (wd), turbidity (turb), chlorophyll concentration
532 (chla), salinity (sal), dissolved inorganic nitrogen (DIN), phosphate (P) and silicate (Si). R^2
533 values are indicated inside the plots.
534
535 **Figure 8.** Partial dependence plots for wind speed (ws), wind direction (wd) and turbidity
536 as depicted by BRT of zooplankton groups: a) tintinnids, b) oligotrichs and c) *Acartia*
537 *tonsa*. Percentage of explained variance of each predictor is shown between parentheses.
538
539 **References**

Aberle, N., K. G. Schulz, A. Stuhr, A. M. Malzahn, A. Ludwig, and U. Riebesell. 2013. High tolerance of microzooplankton to ocean acidification in an Arctic coastal plankton community. Biogeosciences **10**:1471-1481.

Alsterberg, C., J. S. Eklöf, L. Gamfeldt, J. N. Havenhand, and K. Sundbäck. 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. Proceedings of the National Academy of Sciences:201303797.

Aravena, J. C. and B. H. Luckman. 2009. Spatio□temporal rainfall patterns in Southern South America. International Journal of Climatology **29**:2106-2120.

Barría de Cao, M. S., D. Beigt, and C. Piccolo. 2005. Temporal variability of diversity and biomass of tintinnids (Ciliophora) in a southwestern Atlantic temperate estuary. Journal of Plankton Research **27**:1103-1111.

Barton, A. D., B. A. Ward, R. G. Williams, and M. J. Follows. 2014. The impact of fine□scale turbulence on phytoplankton community structure. Limnology and Oceanography: Fluids and Environments **4**:34-49.

Bever, A. J., M. L. MacWilliams, and D. K. Fullerton. 2018. Influence of an observed decadal decline in wind speed on turbidity in the San Francisco Estuary. Estuaries and Coasts.

Boenigk, J. and G. Novarino. 2004. Effect of suspended clay on the feeding and growth of bacterivorous flagellates and ciliates. Aquatic Microbial Ecology **34**:181-192.

Boltovskoy, D. 1981. Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. Instituto Nacional de Investigación y Desarrollo Pesquero Mar del Plata.

Boyd, P. W. and D. A. Hutchins. 2012. Understanding the responses of ocean biota to a complex matrix of cumulative anthropogenic change. Marine Ecology Progress Series **470**:125-135.

Brand, A., J. R. Lacy, K. Hsu, D. Hoover, S. Gladding, and M. T. Stacey. 2010. Wind-enhanced resuspension in the shallow waters of South San Francisco Bay: Mechanisms and potential implications for cohesive sediment transport. Journal of Geophysical Research: Oceans **115**.

Breiman, L., J. Friedman, C. Stone, and R. Olshen. 1984. Classification and Regression Trees. CRC Press, New York.

Brendel, A. S., M. S. Dutto, M. C. Menéndez, M. A. H. Cisneros, and M. C. Piccolo. 2017. Wind Pattern Change Along a Period of Coastal Occurrence Variation of a Stinging Medusa on a SW Atlantic Beach. Anuário do Instituto de Geociências - UFRJ **40**:303-315.

Calbet, A. and E. Saiz. 2005. The ciliate-copepod link in marine ecosystems. Aquatic Microbial Ecology **38**:157–167.

Cardoso, L. d. S. and D. d. Motta Marques. 2009. Hydrodynamics-driven plankton community in a shallow lake. Aquatic Ecology **43**:73-84.

Clamp, J. C. and D. H. Lynn. 2017. Investigating the biodiversity of ciliates in the 'Age of Integration'. Eur J Protistol **61**:314-322.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

Craft, C., J. Clough, J. Ehman, S. Joye, R. Park, S. Pennings, H. Guo, and M. Machmuller. 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Frontiers in Ecology and the Environment **7**:73-78.

Cho, H. J. 2007. Effects of prevailing winds on turbidity of a shallow estuary. International Journal of Environmental Research and Public Health **4**:185-192.

De'ath, G. and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology **81**:3178–3192.

Diodato, S. L. and M. S. Hoffmeyer. 2008. Contribution of planktonic and detritic fractions to the natural diet of mesozooplankton in Bahía Blanca Estuary. Hydrobiologia **614**:83-90.

Dolan, J. R. 2010. Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. Acta Protozoologica **2010**:235-244.

Dolan, J. R. and C. L. Gallegos. 2001. Estuarine diversity of tintinnids (planktonic ciliates). Journal of Plankton Research **23**:1009-1027.

Dolan, J. R., R. W. Pierce, E. J. Yang, and S. Y. Kim. 2012. Southern ocean biogeography of tintinnid ciliates of the marine plankton. J Eukaryot Microbiol **59**:511-519.

Dragani, W. C., P. B. Martin, C. G. Simionato, and M. I. Campos. 2010. Are wind wave heights increasing in south-eastern south American continental shelf between 32°S and 40°S? Continental Shelf Research **30**:481-490.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology **77**:802-813.

Fogt, R. L., D. H. Bromwich, and K. M. Hines. 2011. Understanding the SAM influence on the South Pacific ENSO teleconnection. Climate Dynamics **36**:1555-1576.

Gaedeke, A. and U. Sommer. 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. Oecologia **71**:25-28.

Guinder, V. A., M. C. López-Abbate, A. A. Berasategui, V. L. Negrin, G. Zapperi, P. D. Pratolongo, M. D. Fernández Severini, and C. A. Popovich. 2015. Influence of the winter phytoplankton bloom on the settled material in a temperate shallow estuary. Oceanologia **57**:50-60.

Guinder, V. A., C. A. Popovich, J. C. Molinero, and G. M. Perillo. 2010. Long-term changes in phytoplankton phenology and community structure in the Bahía Blanca Estuary, Argentina. Marine Biology **157**:2703-2716.

Hasle, G. R. 1978. The inverted microscope method. Pages 88-96 *in* A. Sournia, editor. Phytoplankton Manual. UNESCO, Paris.

Heger, T. J., V. P. Edgcomb, E. Kim, J. Lukes, B. S. Leander, and N. Yubuki. 2014. A resurgence in field research is essential to better understand the diversity, ecology, and evolution of microbial eukaryotes. J Eukaryot Microbiol **61**:214-223.

Hingsamer, P., F. Peeters, and H. Hofmann. 2014. The consequences of internal waves for phytoplankton focusing on the distribution and production of Planktothrix rubescens. PLoS One **9**:e104359.

Jack, J. D. and J. J. Gilbert. 1993. The effect of suspended clay on ciliate population growth rates. Freshw Biol **29**:385-394.

Kammerlander, B., K. A. Koinig, E. Rott, R. Sommaruga, B. Tartarotti, F. Trattner, and B. Sonntag. 2016. Ciliate community structure and interactions within the planktonic food web in two alpine lakes of contrasting transparency. Freshw Biol **61**:1950-1965.

Keller, D. P. and R. R. Hood. 2011. Modeling the seasonal autochthonous sources of dissolved organic carbon and nitrogen in the upper Chesapeake Bay. Ecological modelling **222**:1139-1162.

Kiørboe, T. 2008. A mechanistic approach to plankton ecology. Princeton University Press.

Kiørboe, T. and E. Saiz. 1995. Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. Marine Ecology Progress Series **122**:135-145.

Kirwan, M. L. and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. Nature **504**:53.

Kreyling, J., A. H. Schweiger, M. Bahn, P. Ineson, M. Migliavacca, T. Morel-Journel, J. R. Christiansen, N. Schtickzelle, and K. S. Larsen. 2018. To replicate, or not to replicate – that is the question: how to tackle nonlinear responses in ecological experiments. Ecol Lett **0**.

Lanfredi, N. W., E. E. D'Onofrio, and C. A. Mazio. 1988. Variations of the mean sea level in the southwest Atlantic Ocean. Continental Shelf Research **8**:1211-1220.

Laspoumaderes, C., M. S. Souza, B. Modenutti, and E. Balseiro. 2017. Glacier melting and response of Daphnia oxidative stress. Journal of Plankton Research **39**:675-686.

Legendre, L. and R. B. Rivkin. 2015. Flows of biogenic carbon within marine pelagic food webs: Roles of microbial competition switches. Marine Ecology Progress Series **521**:19-30.

Li, Y. and M. Li. 2011. Effects of winds on stratification and circulation in a partially mixed estuary. Journal of Geophysical Research: Oceans **116**.

López-Abbate, M. C., J. C. Molinero, V. A. Guinder, M. S. Dutto, M. S. Barria de Cao, L. A. Ruiz Etcheverry, R. E. Pettigrosso, M. C. Carcedo, and M. S. Hoffmeyer. 2015. Microplankton dynamics under heavy anthropogenic pressure. The case of the Bahia Blanca Estuary, southwestern Atlantic Ocean. Mar Pollut Bull **95**:305-314.

López-Abbate, M. C., J. C. Molinero, V. A. Guinder, G. M. E. Perillo, R. H. Freije, U. Sommer, C. V. Spetter, and J. E. Marcovecchio. 2017. Time-varying environmental control of phytoplankton in a changing estuarine system. Science of The Total Environment **609**:1390-1400.

López Cazorla, A., R. Pettigrosso, L. Tejera, and R. Camina. 2011. Diet and food selection by Ramnogaster arcuata (Osteichthyes, Clupeidae). Journal of fish biology **78**:2052-2066.

Lorenzen, C. J. 1967. Determination of chlorophyll and pheo-pigments: Spectrophotometric equations. Limnology and Oceanography **12**:343-346.

Marshall, G. J. 2003. Trends in the Southern Annular Mode from observations and reanalyses. Journal of Climate **16**:4134-4143.

Martínez, R. A., A. Calbet, and E. Saiz. 2017. Effects of small-scale turbulence on growth and grazing of marine microzooplankton. Aquatic Sciences **80**:2.

Menéndez, C. G. and A. F. Carril. 2010. Potential changes in extremes and links with the Southern Annular Mode as simulated by a multi-model ensemble. Climatic change **98**:359-377.

Mitra, A., K. J. Flynn, J. M. Burkholder, T. Berge, A. Calbet, J. A. Raven, E. Granéli, P. M. Glibert, P. J. Hansen, D. K. Stoecker, F. Thingstad, U. Tillmann, S. Våge, S. Wilken, and M. V. Zubkov. 2014. The role of mixotrophic protists in the biological carbon pump. Biogeosciences **11**:995-1005.

Moreno-Ostos, E., L. Cruz-Pizarro, A. Basanta, and D. G. George. 2008. The influence of wind-induced mixing on the vertical distribution of buoyant and sinking phytoplankton species. Aquatic Ecology **43**:271-284.

Palma, E. D., R. P. Matano, A. R. Piola, and L. E. Sitz. 2004. A comparison of the circulation patterns over the Southwestern Atlantic Shelf driven by different wind stress climatologies. Geophysical Research Letters **31**.

Pécseli, H., J. Trulsen, and Ø. Fiksen. 2014. Predator–prey encounter and capture rates in turbulent environments. Limnology and Oceanography: Fluids and Environments **4**:85-105.

Perillo, G. M. 1995. Geomorphology and sedimentology of estuaries. Elsevier.

Perillo, G. M. E. 2009. Tidal courses: classification, origin and functionality. Pages 185–210 *in* G. M. E. Perillo, E. Wolanski, D. R. Cahoon, and M. M. Brinson, editors. Coastal Wetlands: An Integrated Ecosystem Approach. Elsevier, Amsterdam.

Perillo, G. M. E., M. C. Piccolo, E. Parodi, and R. H. Freije. 2001. The Bahia Blanca Estuary, Argentina. Pages 205-217 *in* U. Seeliger and B. Kjerfve, editors. Coastal Marine Ecosystems of Latin America. Springer Berlin Heidelberg, Berlin, Heidelberg.

Perillo, G. M. E. and M. E. Sequeira. 1989. Geomorphologic and sediment transport characteristics of the middle reach of the Bahia Blanca estuary (Argentina). Journal of Geophysical Research: Oceans **94**:14351-14362.

Pettigrosso, R. E. 2003. Planktonic ciliates Choreotrichida and Strombidiida from the inner zone of Bahía Blanca Estuary, Argentina. Iheringia, Série Zoolgia **93**:117-126.

Piccolo, M., G. Perillo, and W. Melo. 2008. The Bahía Blanca Estuary: an integrated overview of its geomorphology and dynamics. Pages 221-232. IST Scientific Publishers, Lisbon (Portugal).

Piccolo, M. C. and G. M. E. Perillo. 1990. Physical characteristics of the Bahia Blanca estuary (Argentina). Estuarine, Coastal and Shelf Science **31**:303-317.

Pratolongo, P., C. Mazzon, G. Zapperi, M. J. Piovan, and M. M. Brinson. 2013. Land cover changes in tidal salt marshes of the Bahía Blanca estuary (Argentina) during the past 40 years. Estuarine, Coastal and Shelf Science **133**:23-31.

Pratolongo, P., M. J. Piovan, D. G. Cuadrado, and E. A. Gómez. 2017. Coastal landscape evolution on the western margin of the Bahía Blanca Estuary (Argentina) mirrors a non-uniform sea-level fall after the mid-Holocene highstand. Geo-Marine Letters **37**:373-384.

Pratolongo, P. D., G. M. E. Perillo, and M. C. Piccolo. 2010. Combined effects of waves and plants on a mud deposition event at a mudflat-saltmarsh edge in the Bahía Blanca estuary. Estuarine, Coastal and Shelf Science **87**:207-212.

R Development Core Team. 2014. R: A language and environment for statistical computing.

Reisinger, A., J. C. Gibeaut, and P. E. Tissot. 2017. Estuarine suspended sediment dynamics: Observations derived from over a decade of satellite data. Frontiers in Marine Science **4**.

Reynolds, C. S. 2006. The ecology of phytoplankton. Cambridge University Press.

Scully, M. E., C. Friedrichs, and J. Brubaker. 2005. Control of estuarine stratification and mixing by wind-induced straining of the estuarine density field. Estuaries **28**:321-326.

Simionato, C. G., C. S. Vera, and F. Siegismund. 2005. Surface wind variability on seasonal and interannual scales over Río de la Plata area. Journal of Coastal Research **21**:770-783.

Sommaruga, R. and G. Kandolf. 2014. Negative consequences of glacial turbidity for the survival of freshwater planktonic heterotrophic flagellates. Sci Rep **4**:4113.

Spetter, C. V., C. A. Popovich, A. Arias, R. O. Asteasuain, R. H. Freije, and J. E. Marcovecchio. 2015. Role of nutrients in phytoplankton development during a

winter diatom bloom in a eutrophic South American estuary (Bahía Blanca, Argentina). Journal of Coastal Research **31**:76-87.

Steinberg, D. K. and M. R. Landry. 2017. Zooplankton and the ocean carbon cycle. Ann Rev Mar Sci **9**:413-444.

Sun, X., K. H. Cook, and E. K. Vizy. 2017. The South Atlantic Subtropical High: Climatology and Interannual Variability. Journal of Climate **30**:3279-3296.

Trenberth, K. E. 1997. The definition of el nino. Bulletin of the American Meteorological Society **78**:2771-2778.

Venegas, S. A., L. A. Mysakand, and D. N. Straub. 1996. Evidence for interannual and interdecadal climate variability in the South Atlantic. Geophysical Research Letters **23**:2673-2676.

Vera, C., G. Silvestri, V. Barros, and A. Carril. 2004. Differences in el nino response over the southern hemisphere. Journal of Climate **17**:1741-1753.

Weir, D. and J. McManus. 1987. The role of wind in generating turbidity maxima in the Tay estuary. Continental Shelf Research **7**:1315-1318.

Whipple, A. C., R. A. Luettich, J. V. Reynolds-Fleming, and R. H. Neve. 2018. Spatial differences in wind-driven sediment resuspension in a shallow, coastal estuary. Estuarine, Coastal and Shelf Science **213**:49-60.

Wohlers, J., A. Engel, E. Zollner, P. Breithaupt, K. Jurgens, H. G. Hoppe, U. Sommer, and U. Riebesell. 2009. Changes in biogenic carbon flow in response to sea surface warming. Proc Natl Acad Sci U S A **106**:7067-7072.

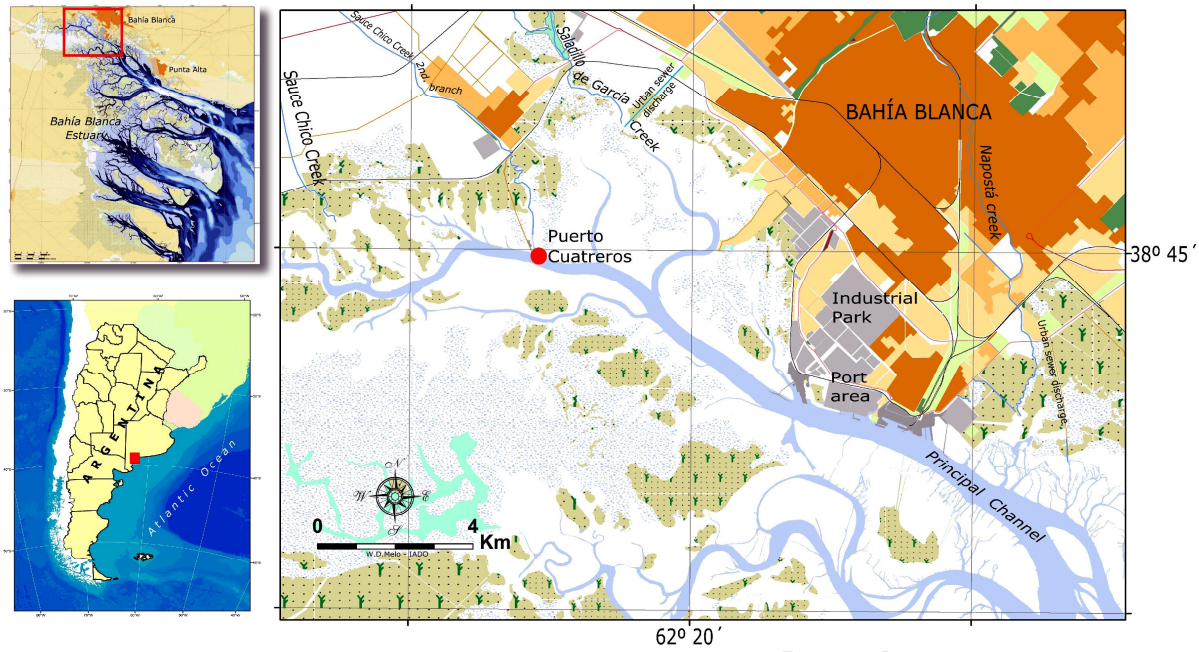
Wolfe, A. M., S. E. Allen, M. Hodal, R. Pawlowicz, B. P. Hunt, and D. Tommasi. 2015. Impact of advection loss due to wind and estuarine circulation on the timing of the spring phytoplankton bloom in a fjord. ICES Journal of Marine Science **73**:1589-1609.

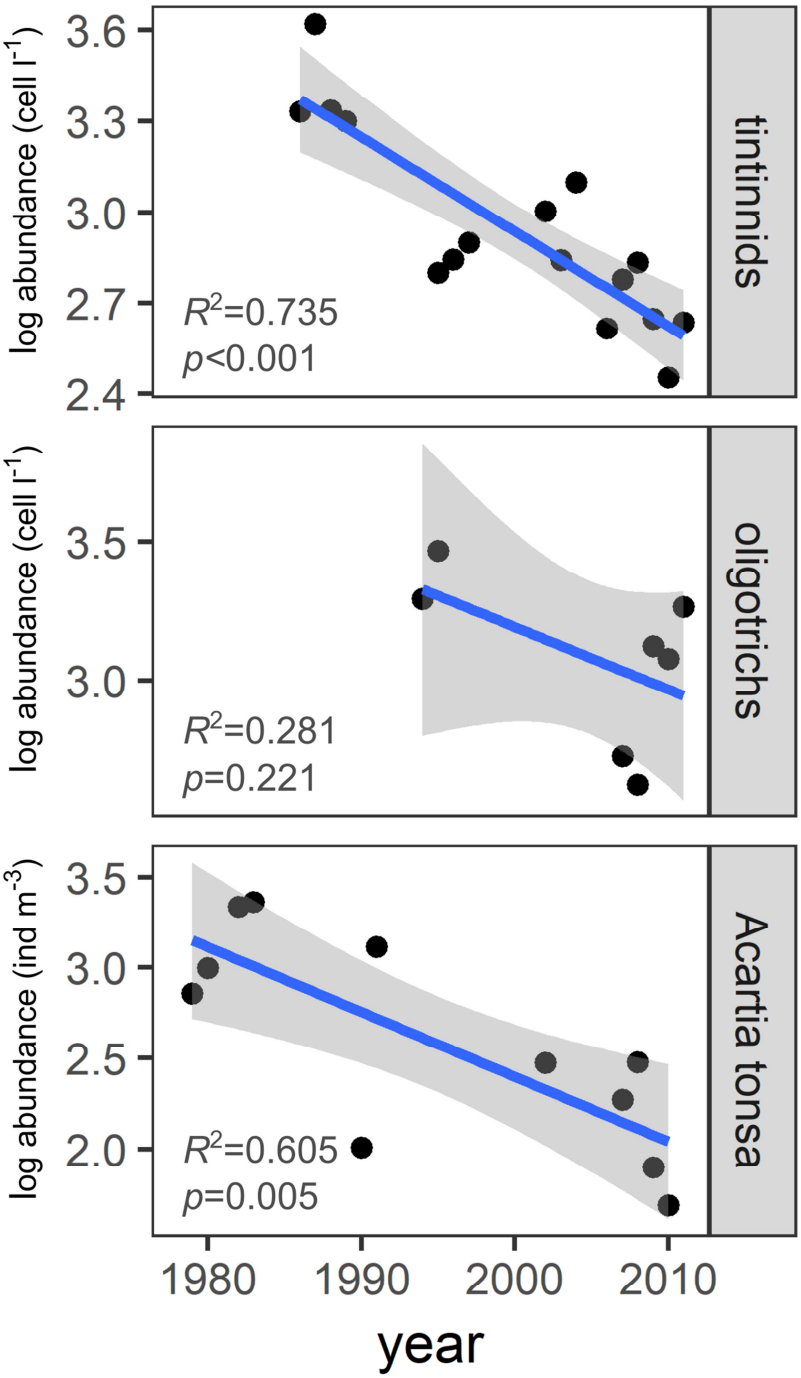
Yeo, S.-R. and K.-Y. Kim. 2015. Decadal changes in the Southern Hemisphere sea surface temperature in association with El Niño–Southern Oscillation and Southern Annular Mode. Climate Dynamics **45**:3227-3242.

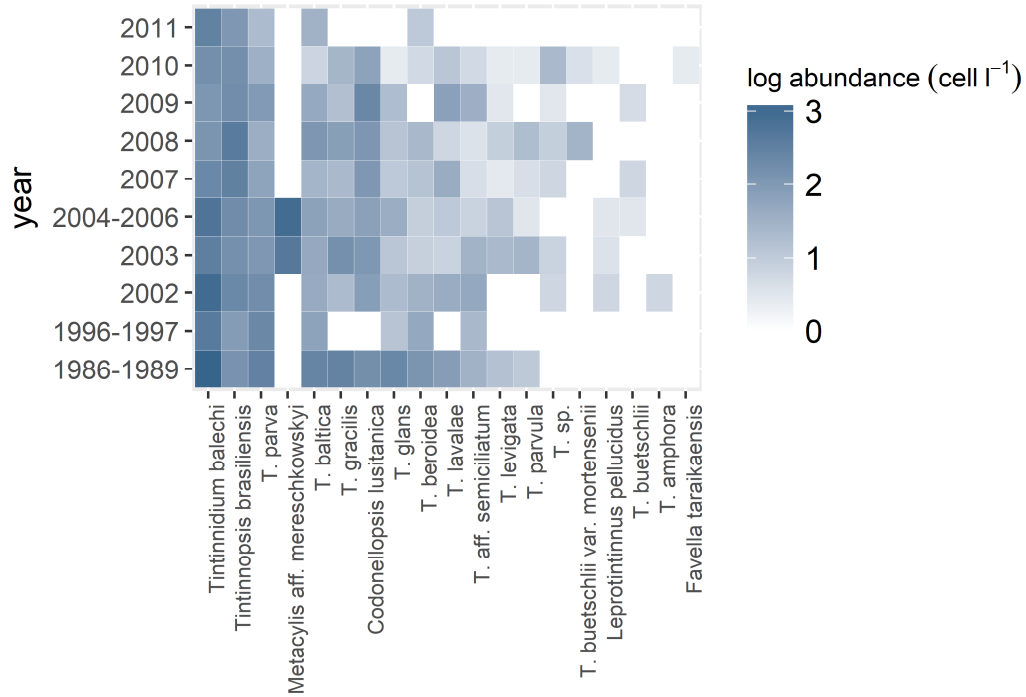
Zapperi, G., M. J. Piovan, and P. Pratolongo. 2017. Community structure and spatial zonation of benthic macrofauna in mudflats of the Bahía Blanca Estuary, Argentina. Journal of Coastal Research **0**:null.

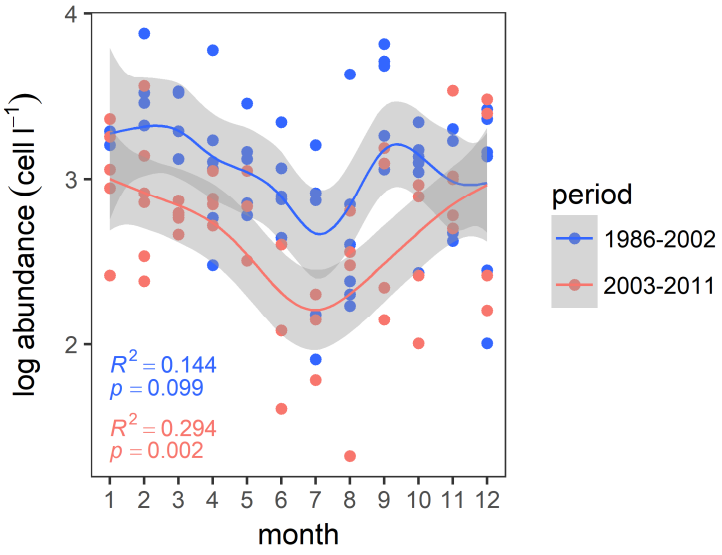
Zapperi, G., P. Pratolongo, M. J. Piovan, and J. E. Marcovecchio. 2016. Benthic-Pelagic coupling in an intertidal mudflat in the Bahía Blanca Estuary (SW Atlantic). Journal of Coastal Research **32**:629-637.

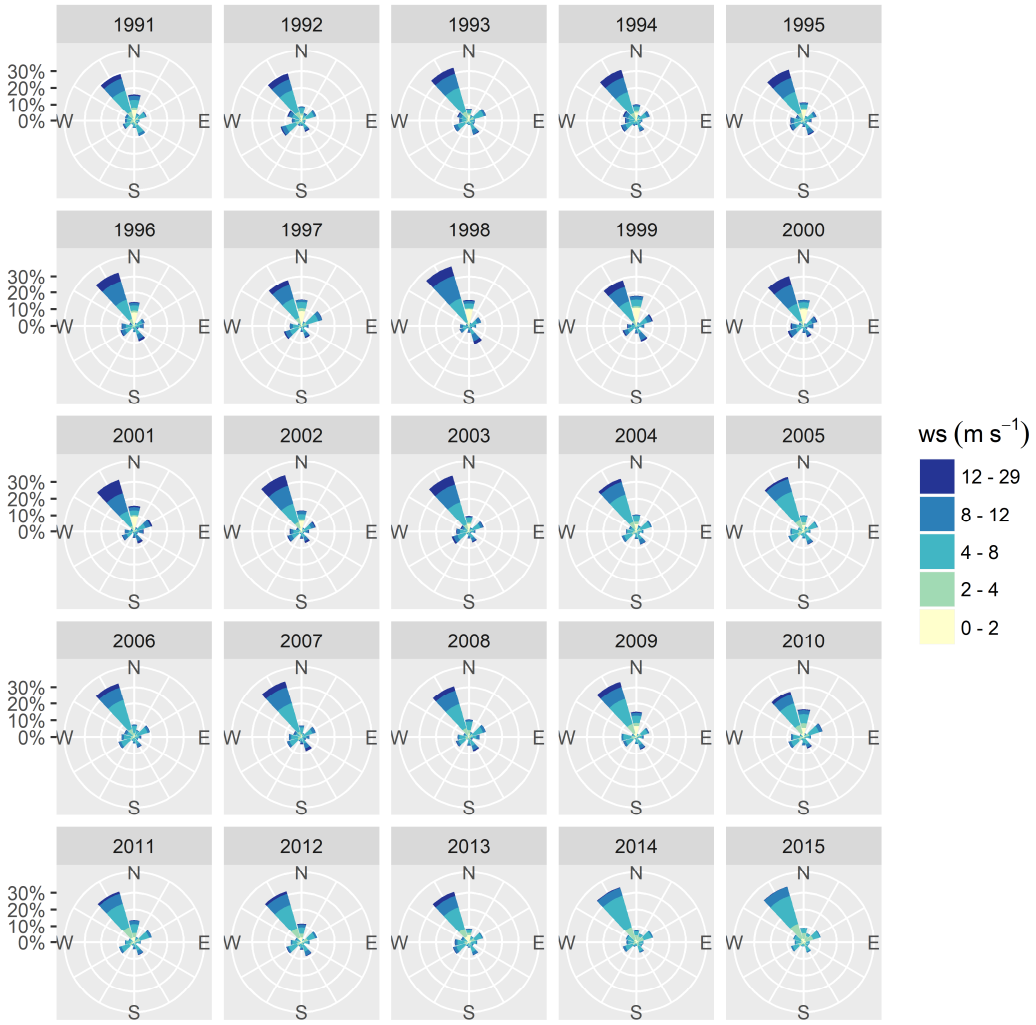
Zhou, J., B. Qin, C. Casenave, X. Han, G. Yang, T. Wu, P. Wu, and J. Ma. 2015. Effects of wind wave turbulence on the phytoplankton community composition in large, shallow Lake Taihu. Environmental Science and Pollution Research **22**:12737-12746.

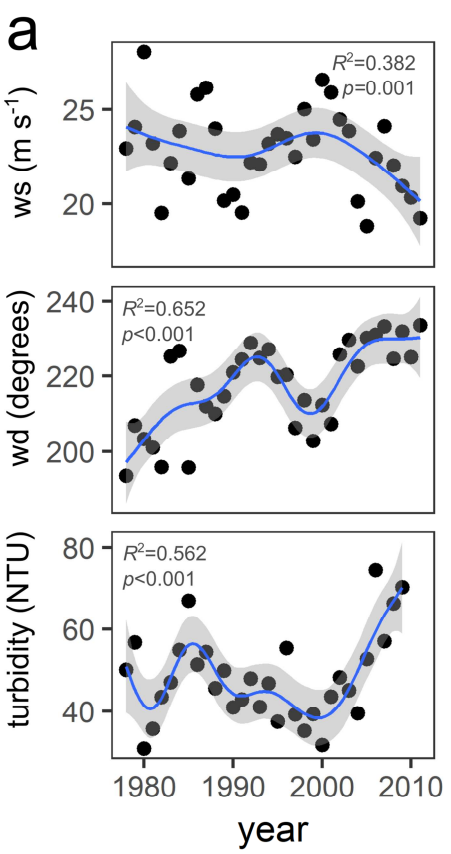


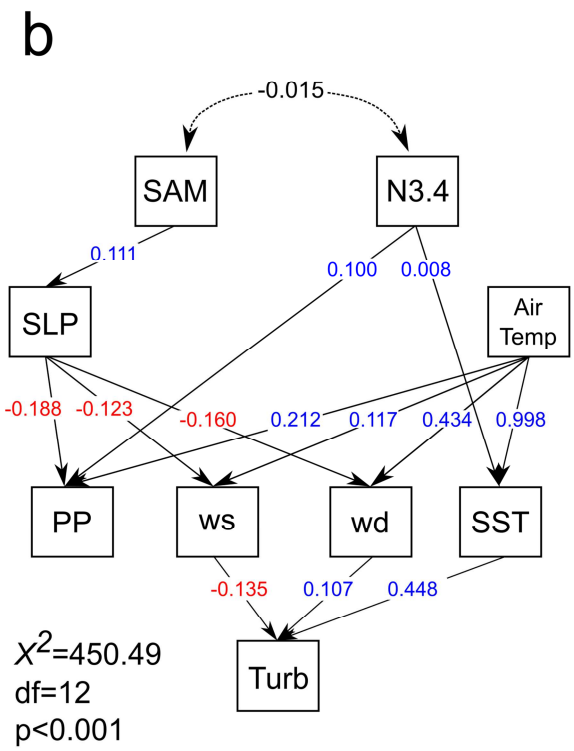

log abundance (cell l-1)
3.6
3.3
3.0
2.7
2.4
R2=0.735
p<0.001
tintinnids
log abundance (cell l-1)
3.5
3.0
R2=0.281
p=0.221
oligotrichs
log abundance (ind m-3)
3.5
3.0
2.5
2.0
R2=0.605
p=0.005
Acartia tonsa
1980
1990
2000
2010
year

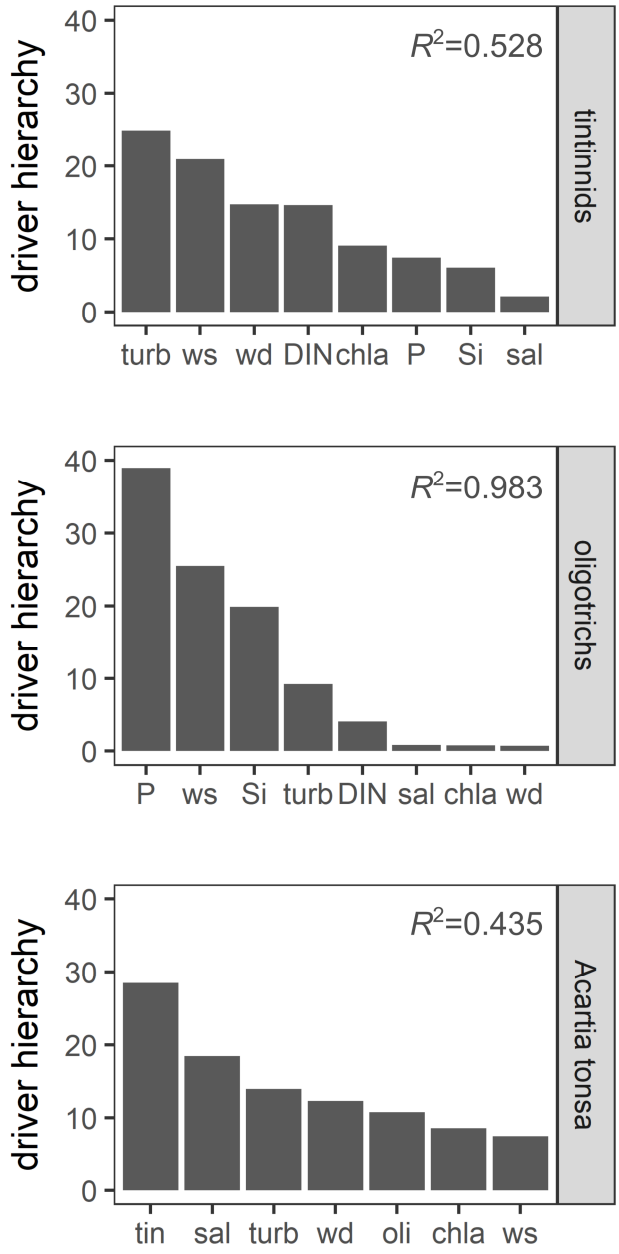


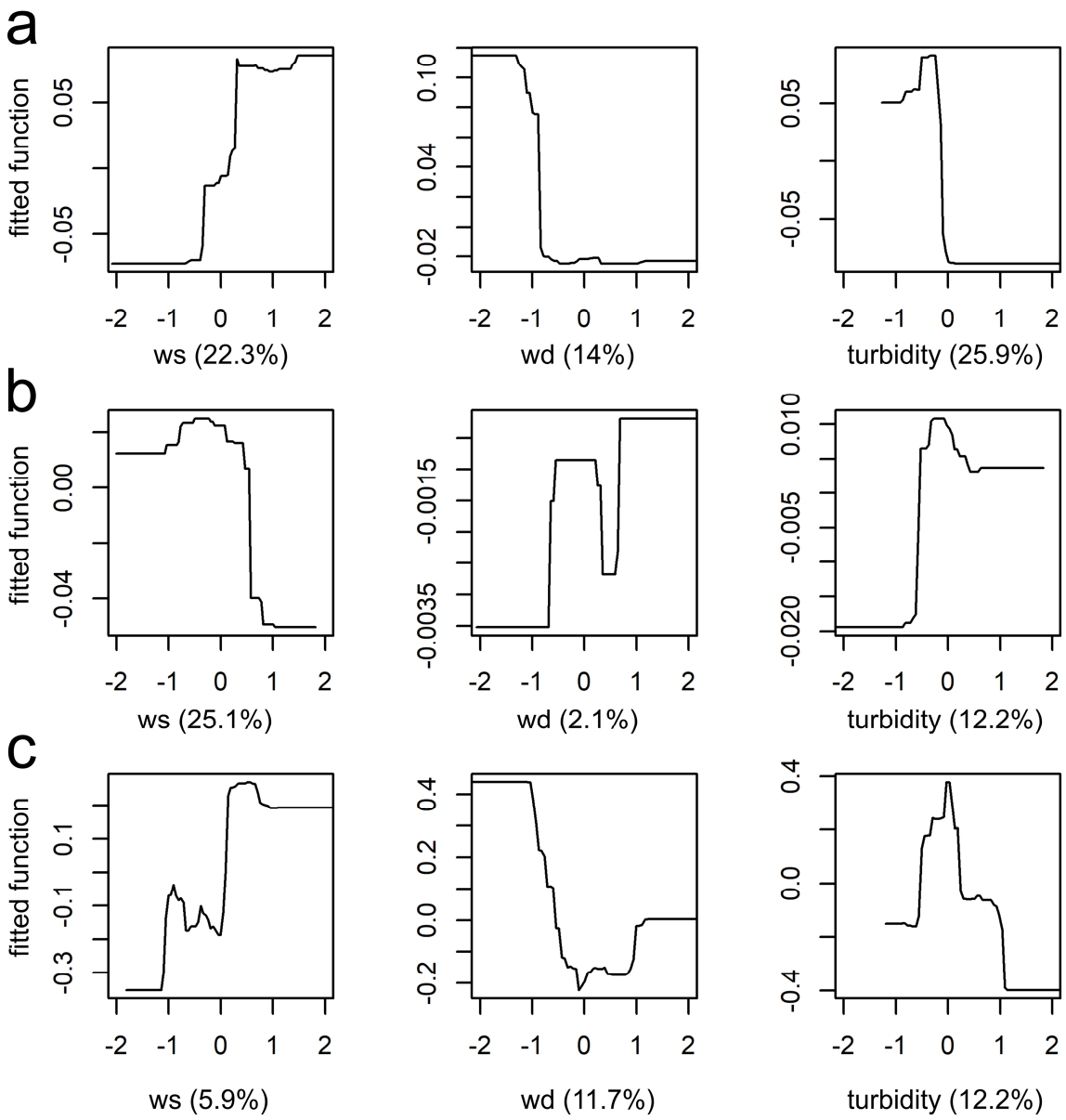











a
fitted function
-0.05
0.05
-2 -1 0 1 2
ws (22.3%)
-0.02
0.04
0.10
-2 -1 0 1 2
wd (14%)
-0.05
0.05
-2 -1 0 1 2
turbidity (25.9%)
b
fitted function
-0.04
0.00
-2 -1 0 1 2
ws (25.1%)
-0.0035
-0.0015
-2 -1 0 1 2
wd (2.1%)
-0.020
-0.005
0.010
-2 -1 0 1 2
turbidity (12.2%)
c
fitted function
-0.3
-0.1
0.1
-2 -1 0 1 2
ws (5.9%)
-0.2
0.0
0.2
0.4
-2 -1 0 1 2
wd (11.7%)
-0.4
0.0
0.4
-2 -1 0 1 2
turbidity (12.2%)

-Planktonic ciliate´s abundance decreased over the last 25 years in a shallow estuary.

-Decreasing cell abundance was linked to changes in wind dominant regimes and increased water turbidity.

-Tintinnids were more vulnerable to wind patterns and turbidity and lost synchrony with primary productivity.

-Interannual variability of the copepod *Acartia tonsa* followed the changes in ciliate community.

-Erosive processes in shallow estuaries impact on the interannual dynamics of ciliates and such effects can cascade-up to copepods.