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Changes in the distribution of copepods in the Gironde estuary: A warming and marinisation consequence?

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ABSTRACT

The Gironde is the largest estuary of South-West Europe and is one of the best monitored estuarine systems in the world. This macrotidal estuary is characterized by a low biodiversity in both oligo- and mesohaline zones. Its zooplankton community is constituted by only five major species, three calanoid copepods (including one invasive species) and two mysids. Retrospective analyses have already documented a warming associated to a phenomenon of marinisation. Here, we investigate the influence of both marinisation and warming on the spatial distribution and the abundance of copepods (i.e. *Eurytemora affinis*, *Acartia bifilosa* and neritic species) in the Gironde estuary. We modelled the environmental envelope of the copepods as a function of salinity and temperature to demonstrate that the alteration of their longitudinal distribution in the estuary between 1975 and 2003 was the result of both changing temperature and salinity. Although the upstream movement of neritic species was mostly related to salinity, we show that the augmentation of both temperature and salinity was at the origin of the upstream progression of both *A. bifilosa* and *E. affinis*. These results suggest that the distribution of copepods can be affected by both anthropogenic forcing and climatic change, which modulate the physic-chemistry of the Gironde estuary.

1. Introduction

The effects of climate change on marine ecosystems have become unequivocal since recent years (Hatun et al., 2009; Cloern et al., 2010). Changes concern all biological compartments and are altering the biodiversity of both marine and estuary ecosystems (Attrill and Power, 2002; Halpern et al., 2008; Goberville et al., 2010). Estuarine ecosystems, which have an undeniable economic value (e.g. fishing ground, important tourism, industrial, and traffic area (Costanza et al., 1997)), at the interface between marine and freshwater systems, constitute complex environments characterised by great ecological and biological values (e.g. habitat for many species, nursery, refuge or growth area (Blaber and Blaber, 1980; Haedrich, 1983; Beck et al., 2001)). Consequences of Global Change on these environments have also been recently documented. Two processes are frequently described: a marinisation, i.e. an increased intrusion of marine waters (David et al., 2005) and a surface water warming with a possible incidence on the estuary hydrological properties (Scavia et al., 2002; Goberville et al., 2010).

Temperature and salinity are important parameters since they govern both the spatial and temporal changes occurring along an estuary (Pritchard, 1967; Elliott and McLusky, 2002). Changes in the thermal regime have often profound consequences for the dynamic regime of coastal ecosystems (Scavia et al., 2002; Goberville et al., 2010). Temperature effects on biological processes were first described by Arrhenius (1889) as leading the kinetics of many metabolic reactions (e.g. speed of enzymatic reaction, increase in metabolism). Temperature has also well-known ecological effects on reproduction, locomotion, feeding rates and species interaction (Magnuson et al., 1979; Mauchline, 1998; Beaugrand and Reid, 2003), the influence of this parameter ramifying throughout the trophodynamics of the ecosystem (Kirby and Beaugrand, 2009).

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The spatial distribution of a species along an estuary is mainly linked to salinity (Elliott and Hemingway, 2002; Vilas et al., 2009) since the salinity preferendum differs from a species to another. Salinity changes indeed can induce osmotic stress that increases the risk of mortality of individual species and lead in some cases to a reduction in inter-specific competition (Vilas et al., 2009). Effects of salinity on zooplankton organisms were particularly documented for copepods having vertical migrations in water bodies with different characteristics (Sautour and Castel, 1995).

Recently, a long-term increase in salinity has been described in the Gironde estuary (David et al., 2005). In the present state of knowledge, it has been described as a response to a general reduction of freshwater discharges, due to both climate change and anthropogenic forcings. One of the anthropogenic factors is the increase of water pumping in the upstream watershed, with strong effects on river flow (Delpech personal communication). This salinity rise has been termed marinisation (David et al., 2005). The associated reduction in river flow has led to an upstream shift in the Maximum Turbidity Zone (MTZ, (Sottolichio and Castaing, 1999; David et al., 2005)) with a resulting upstream movement of brackish waters that could also imply changes in the spatial distribution of zooplankton due to the MTZ movement, which is known to be a physical barrier for some species such as *Eurytemora affinis* (e.g. ovigerous females (Castel, 1995)) or can disturb both their survival and fecundity rates (Sautour and Castel, 1995; Gasparini et al., 1999). Some studies on European estuaries have already documented significant changes in zooplankton distribution ranges. For example, Appeltans et al. (2003) reported a spatial shift in the population of the calanoid copepod *E. affinis* from brackish water towards lower salinities in the Schelde estuary that coincided with an increase in oxygen concentration in the freshwater zone.

In this paper, we investigate the spatial distribution of the main copepod taxa (i.e. *Eurytemora affinis, Acartia bifilosa* and neritic species) in relation to recent marinisation and changes in temperature in the Gironde estuary. We model the environmental envelope of the copepods as a function of salinity and temperature to demonstrate that the alteration of their longitudinal distribution in the estuary between 1975 and 2003 was the result of both changes in temperature and salinity.

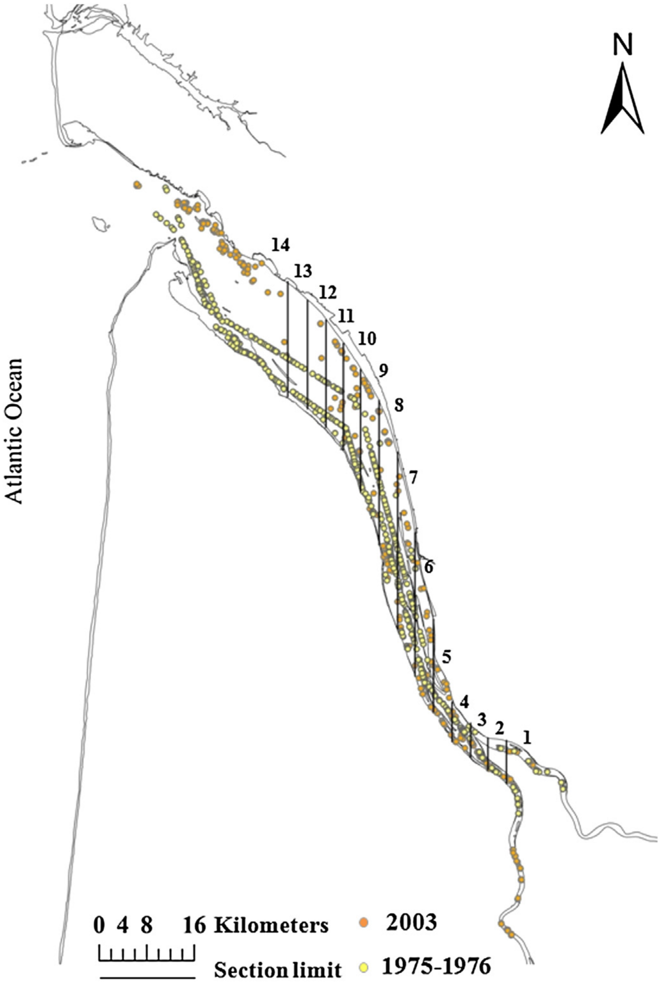

Fig. 1. Map of the Gironde estuary and sampling stations (campaign 1975–76 in yellow dots and campaign 2003 in orange dots) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

2. Materials and methods

2.1. The Gironde estuary

The Gironde estuary (latitude 45°20′N, longitude 0°45′W), considered as the largest South-Western European estuary, covers an area of about 625 km^2 at high tide (Fig. 1, (Boigontier and Mounié, 1984; Lobry et al., 2003)). This estuary is 70 km long, beginning at the junction of the rivers Dordogne and Garonne, draining 71,000 km^2 (Jouanneau and Latouche, 1981) with a mean flow ranging from 250 m^3 s^{-1} (August–September) to 1500 m^3 s^{-1} (January–February). The upstream limit of the salinity intrusion was estimated between 40 and 75 km from the inlet depending upon the river-flow. The Gironde is also one of the most turbid European estuaries with a mean concentration of suspended matter higher than 500 mg l^{-1} in the MTZ (Sautour and Castel, 1995). Because of this high turbidity, the Gironde estuary is characterized by a reduced primary production compared to other similar systems (i.e. the Schelde or the Ems (de Jonge and Van Beusekom, 1992; Heip et al., 1995)).

2.2. Biological models

Due to the light-limitation of autochthonous primary production, the Gironde estuary is often described as heterotroph (Irigoien and Castel, 1997). Primary consumers (zooplankton) are considered as playing a key role in the Gironde estuary trophic food web and consequently in the carbon cycle (David et al., 2006; Lobry et al., 2008). Moreover because of their short life cycle and generation time, these organisms have also been described as good bio-indicators as they exhibit rapid response to climate change (David, in press).

Regarding the zooplankton estuarine diversity, it is composed of 5 dominant species including 3 calanoid copepod species (*Eurytemora affinis, Acartia bifilosa*, and *Acartia tonsa*) (Castel, 1993; David et al., 2005, 2007). The copepod *E. affinis* was described upstream from the maximum of turbidity zone (MTZ) and both Acartidae were documented more downstream in the poly- and meso-haline parts of the estuary (Castel, 1995; Sautour and Castel, 1995). Another zooplankton community is being found in the polyhaline zone of the Gironde estuary with reduced densities but a high diversity: neritic copepods (e.g. *Calanus helgolandicus*, *Paracalanus parvus*, *Pseudocalanus elongatus*, *Centropages hamatus*, *Oithona similis*, and *Euterpina acutifrons*) originated from the estuary plume (i.e. the Bay of Biscay (D'Elbée and Castel, 1991)). We focused our study on copepod species as they dominate the zooplankton in the Gironde estuary (Sautour and Castel, 1995).

2.3. Databases

2.3.1. Environmental and zooplankton data

2.3.1.1. Long-term time series. Time series of environmental and zooplankton data (1978–2009) were provided by the "Blayais" nuclear power plant monitoring programme. Different environmental parameters (water temperature, salinity, dissolved dioxygen, suspended particulate matter (SPM), chlorophyll *a*, and nitrogen oxides concentrations, current speed and river discharge) and biological parameters (3 zooplankton species abundances (ind m^{-3})) were monitored from March 1978 to November 2009. Samples were collected 9 times a year at Station E (median point in the estuary located at 52 km downstream from Bordeaux city). Only these long-term data were considered (even if data were available for 2 other stations; see Castel, 1995) in order to consider the longest time series period (32 years versus 24 and 12 years respectively for stations E, K, and F). Sampling was carried out at 1 m below the surface and 1 m above the bottom at 3 h intervals during a tidal cycle (high and low tide, flood and ebb tide).

2.3.1.2. Monitoring surveys of years 1975–76 and 2003. Environmental and zooplankton data were provided by two distinct monitoring campaigns with different sampling strategies. The monitoring of 1975–76 (monitoring of the reference state of the Gironde estuary before the establishment of the 'Blayais' nuclear power plant) was monthly performed at 8 stations (respectively at kilometre points 'KP' 20, 35, 42, 52, 62, 67, 78, and 89 from Bordeaux city) at 1 m below the surface and 1 m above the bottom at 3 h intervals during a tidal cycle (high and low tide, flood and ebb tide). Due to some missing data, we gathered years 1975 and 1976 by averaging same months values. For the second monitoring (2003), the sampling strategy was to sample along an upstream-downstream transect each 3 salinity units at 1 m below the surface and 1 m above the bottom. The parameters in common to both campaigns (used for the different data analyses) were: water temperature, salinity, SPM, chlorophyll *a* and phaeopigments concentrations.

2.3.2. Local meteorological parameters

Monthly data of local air temperature (°C) and cumulated precipitation (millimetre per month), measured at Pauillac meteorological station (kilometre point 52 downstream from Bordeaux city – nearest meteorological station from the median point of the estuary), were provided by the Méteo France Centre of Mérignac for the period 1975–2009 (35 years).

2.4. Data analyses

2.4.1. Data pre-treatment

Due to a difference in the sampling strategies of the years 1975–76 and 2003 monitoring, the two campaigns data bases were first homogenised by computing the theoretical position at high tide of all sampled water bodies to get rid of the impact of tidal water movement on zooplankton position. We used the hydro-sedimentary model SIAM 3D (Brenon and Le Hir, 1999) applied to the Gironde estuary (Sottolichio et al., 2000) to get current speed curves plotted against time per sections of similar hydrodynamics and every 10 tidal coefficient units. We integrated the model curve equation to find the distance covered by the water bodies between their sampling moment and the corresponding high tide moment. The theoretical positions of each water bodies at high tide were finally obtained by trigonometry and are presented in Fig. 1.

2.4.2. Characterization of the temporal variations of environmental conditions

2.4.2.1. Characterization of years 1975–76 and 2003 regarding to environmental conditions. A standardized Principal Components Analysis (PCA) was performed on annual means of different environmental parameters (water temperature, salinity, dissolved oxygen, suspended matter, chlorophyll *a*, and phaeopigments concentrations) for the period 1975–2009 (except year 1977 that was not monitored). Local precipitations and river discharge were used as supplementary variables, as indicators of local hydrology, these parameters being also strongly correlated to chlorophyll *a* and nutrients concentrations (see Goberville et al., 2010). The first principal component (PC1 ENV) scores were plotted against time.

2.4.2.2. Spatial pattern of annual salinity, temperature, and copepods annual abundance in 1975–76 and 2003. In order to characterize the difference of spatial pattern of salinity, temperature, and copepods abundance, annual means were computed per estuary section of about 5 km (14 sections in total) for years 1975, 1976 (common mean for both years 1975 and 1976) and year 2003. Corresponding standard deviations were also computed for each value.

2.4.3. Characterisation of the environmental envelope

Using raw data of salinity and temperature of both years 2003 and 1975–76 (homogeneised databases), we modelled the abundance of each species or taxonomic group as a function of both temperature and salinity. We examined graphically the relationships between the abundance of each taxon and environmental variables (not shown). When a maximum of abundance flanked by two decreasing slopes was detected, we applied a Gaussian function. Such function is often used to model the ecological niche sensu Hutchinson (Fort et al., 2012). When such a maximum was not found, we modelled the abundance of the species as a function of the environmental parameter using a linear function. All methods were computed using the MATLAB language.

2.4.3.1. The statistical model for E. affinis. We tested that the abundance of *Eurytemora affinis* (as $\log_{10}(x+1)$) 'E' was the sum of a linear relationship with salinity 'S' and a Gaussian relationship with water temperature 't', as follows:

$$E = M_{E\mathrm{obs}} \times e^{-\left(\frac{(t-u)^2}{2s^2}\right)} + aS + C$$

with a the coefficient of proportionality and C the constant of the linear relationship between *E. affinis* and salinity *S*, *u* and *s* the thermal optimum and thermal tolerance of *E. affinis*, respectively. The linear relationship between *E. affinis* and salinity *S* determines the maximum of abundance of *E. affinis* at its thermal optimum.$M_{E\mathrm{obs}}$ is the observed maximum density for *E. affinis*. The coefficients $M_{E\mathrm{obs}}, a, C, u,$ and *s* were found by minimising the sum of squares of the residuals assessed by calculating the differences between observed and predicted abundance of *E. affinis* ($\log_{10}(x+1)$):

$$F(M_{E\mathrm{obs}}, a, C, u, s) = \sum_{i=1}^{n} [L_i - f(M_{E\mathrm{obs}}, a, C, u, s;\ S_i, t_i)]^2$$

with *n* the number of observed data (312 observations). Therefore, the degree of freedom was equalled to df = 312 observations − 3 parameters = 309.

2.4.3.2. The statistical model for A. bifilosa. The abundance of *Acartia bifilosa* (as $\log_{10}(x+1)$) 'A' was modelled as the product of a Gaussian relationship with water temperature t, and a Gaussian relationship with salinity S, as follows:

$$A = M_{Aobs} \times e^{-\left(\frac{(t-u)^2}{2s^2}\right)} \times e^{-\left(\frac{(S-\mu)^2}{2\sigma^2}\right)}$$

with M_{Aobs} the maximum density observed for *A. bifilosa*, u and s the thermal optimum and thermal tolerance of *A. bifilosa*, and μ and σ the salinity optimum and salinity tolerance respectively. The coefficients M_{Aobs}, u, s, μ, and σ were found by minimising the sum of squares of the residuals assessed by calculating the differences between observed and predicted abundance of *A. bifilosa* ($\log_{10}(x+1)$):

$$F(M_{Aobs}, a, C, u, s) = \sum_{i=1}^{n} [L_i - f(M_{Aobs} a, C, u, s;\ S_i, t_i)]^2$$

with n the number of observed data (252 observations). Therefore, the degree of freedom equalled to df = 252 observations − 4 parameters = 248.

2.4.3.3. The statistical model for neritic copepods. The abundance of neritic copepods (as $\log_{10}(x+1)$) 'N' was modelled as the sum of a linear relationship with water temperature t and a Gaussian relationship with salinity S, as follows:

$$N = M_{Nobs} \times e^{-\left(\frac{(S-\mu)^2}{2\sigma^2}\right)} + at + C$$

with a the coefficient of proportionality and C the constant of the linear relationship between neritic copepods and water temperature, u and s the salinity optimum and salinity tolerance of neritic copepods, respectively. The linear relationship between neritic copepods and water temperature determines the maximum of abundance of neritic copepods at its salinity optimum. M_{Nobs} is the maximum density of neritic copepods. The coefficients M_{Nobs}, a, C, u, and s were found by minimising the sum of squares of the residuals assessed by calculating the differences between observed and predicted abundance of neritic copepods ($\log_{10}(x+1)$):

$$F(M_{Nobs}, a, C, u, s) = \sum_{i=1}^{n} [L_i - f(M_{Nobs}, a, C, u, s;\ S_i, t_i)]^2$$

with n the number of observed data (312 observations). Therefore, the degree of freedom was equalled to df = 312 observations − 3 parameters = 309.

In each case (for the three taxa), a validation step consisted in estimating the relationship between modelled and observed abundance using the Pearson coefficient of determination (Fig. 5).

2.4.4. Upstream movement prediction

Annual abundances were computed per section along the estuary for all taxa for both years 1975–76 and 2003 in order to compare these estimations to the raw data and to test whether modelled abundance as a function of temperature and salinity could explain the observed movement of the three species or taxonomic group. We also computed the mean weighted distance distribution (centroid) for the three taxa and both periods in order to qualify their potential movement (see the method in Yanicelli et al., 2006).

3. Results

3.1. Long-term changes in environmental conditions

The first three principal components (PC1, PC2 and PC3) of the principal components analysis performed on environmental parameters (Fig. 2) explained respectively 42.8, 22.3% and 19.4% of total variance (84.5% in total). The first principal component (PC1) was negatively related to water temperature and positively related to suspended particulate matter and dissolved oxygen. PC2 was positively related to chlorophyll *a* concentrations. The third principal component (19.4%) was negatively related to salinity (better represented on the variables factor map PC1 − PC3, see Appendix 1).

Long-term changes in PC1 were examined (Fig. 2). The first component reflected the main changes of the estuarine system: a warming of the estuary associated to a decrease in turbidity and oxygen saturation. Whereas the first years of the time series (1975–1976) were characterized by lower temperatures (and salinity, PC3 not shown) and higher concentrations in chlorophyll *a*, recent years

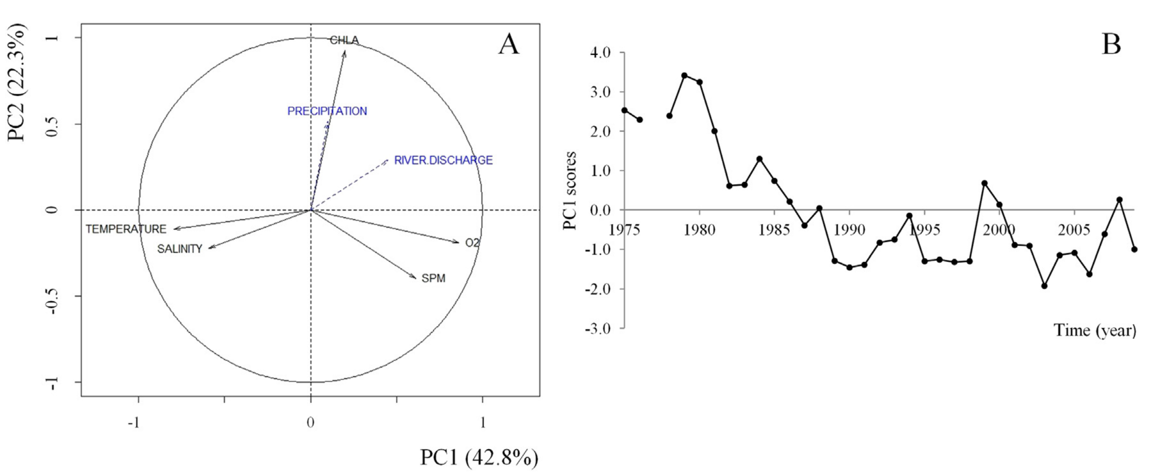

Fig. 2. Principal Components Analysis on environmental parameters: variables correlation circle (A). Local precipitations (precipitation) and river discharge (Flow) were used as supplementary variables; active variables were water temperature (T), salinity (S), dissolved oxygen (O_2), suspended matter (SPM) and chlorophyll *a* (CHLA) concentrations. (B) Long-term changes in the first principal component.

(2003–2009) were characterized by higher temperatures (and salinity, PC3 not shown) and associated to reduced precipitation and river discharges.

3.2. Longitudinal changes in annual salinity and copepod abundance in 1975–76 and 2003

Annual salinity and temperature values were higher in 2003 for all sections of the estuary even if this trend was more perceptible in the upstream sections for temperature data and in the downstream sections for salinity (Fig. 3).

Annual abundances in both *Eurytemora affinis* and *Acartia bifilosa* increased in the upstream sections where these species were found in 1975–76 and decreased in its downstream sections between 1975-76 and 2003. Neritic copepods increased in densities in 2003 compared to 1975–76. In 2003, neritic copepods were recorded up to the fourth estuarine section (~45 km downstream from Bordeaux city or 55 km upstream from the mouth of the Gironde estuary).

3.3. Statistical models

The examination of the potential relationships between the abundance of each taxon and both key environmental parameters (e.g. temperature and salinity; Fig. 5) suggested: (i) Gaussian interactions between *Eurytemora affinis* and temperature (with an optimum around 15 °C), neritic copepods and salinity (optimum ~ 29 P.S.U.), and *Acartia bifilosa* and both parameters (thermal optimum ~ 20 °C and salinity ~ 16 P.S.U.), and (ii) linear relationships between *E. affinis* and salinity, and neritic copepods and temperature (Fig. 5).

Our models explained respectively 59%, 69%, and 67% of the total variance of the abundances of *Eurytemora affinis*, *Acartia bifilosa*, and neritic copepods for both years 1975–76 and 2003 (Fig. 5). Our model misestimating was mainly related to the non-prediction of zero abundance.

3.4. Upstream movement prediction

Globally our models did estimate upstream movements of the estuarine copepods (see also the centroids computed that globally shifted upstream for the three taxa). Increased densities were estimated in the upstream sections (oligo- and mesohaline areas) where the taxa were already present (but in lower abundances) in 1975–76. In the polyhaline area, an important progression upstream was predicted for the neritic copepods, but the modelled abundances (Fig. 6) were underestimated compared to raw data (See Fig. 4). This is related to the difference between the linear regression (between neritic copepods abundance raw data and predicted data) and the bisector; the slope of regression line being less important than the one of the bisector.

4. Discussion

Climatic variability and climate change particularly influence both coastal ecosystems and estuaries (Halpern et al., 2008; Goberville et al., 2010, 2011). More specifically, previous studies already pointed out the alteration of the Gironde estuary due to the combined influence of anthropogenic forcing and climate change (David et al., 2005; Goberville et al., 2010; Etcheber et al., 2011; Pasquaud et al., 2012). David et al. (2005) first described a long-term marinisation process that-is-to-say the salinity increase as if the Gironde system was moving upstream. This marinisation was associated to a reduction in river discharge and river run-off, originating from the Garonne and Dordogne rivers. This phenomenon has probably been exacerbated by the increasing demand in irrigation (Delpech personal communication) that in turn led to an upstream shift of the MTZ (Sottolichio and Castaing, 1999; David

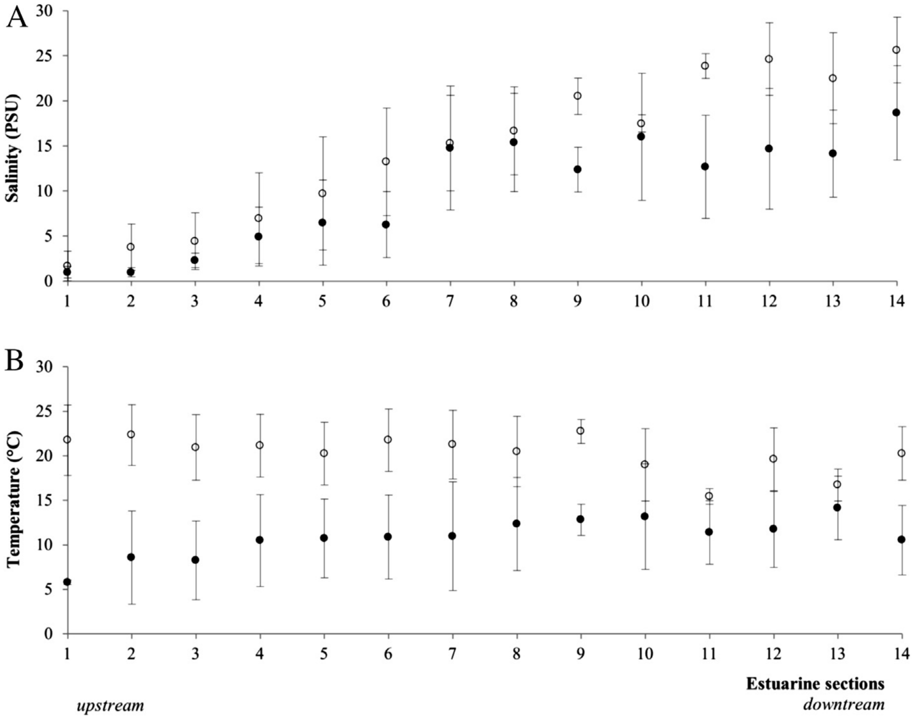

Fig. 3. Spatial variability in annual salinity (A) and temperature (B) from the estuary upstream sections (1) to the downstream estuary sections (14): white dots for year 2003 and black dots for year 1975–1976.

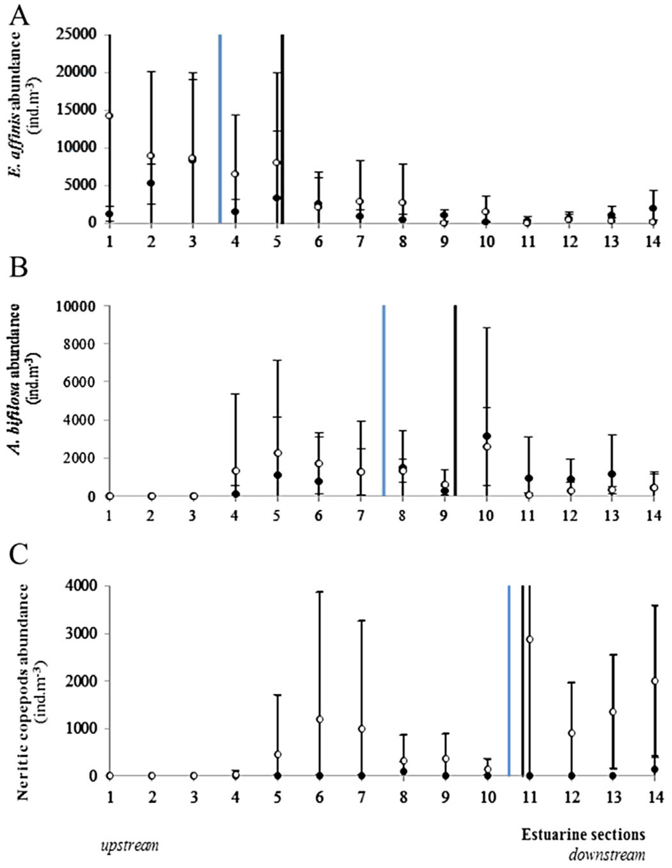

Fig. 4. Spatial variability in the annual abundance of (A) *Eurytemora affinis*, (B) *Acartia bifilosa*, and (C) Neritic copepods from the estuary upstream sections (1) to the downstream estuary sections (14): white dots for year 2003 and black dots for year 1975–1976. Species centroids computed per period (1975–76 in black and 2003 in blue) were superimposed (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

et al., 2005). As a consequence reduced turbidities were noticed in the middle and downstream parts of the estuary (data not shown) with possible consequences on biological compartments (data not published). Some other effects not yet elucidated, are related to changes on the asymmetry of the tide, partly due to the anthropogenic deepening of the upstream Garonne in the years 60s (Castaing et al., 2006). The relative impact of changes on the tide are still under investigation (Sottolichio et al., 2011), but it is expected that they may contribute to the enhanced trapping of suspended sediment and the general upstream shift of the salinity front and the TMZ.

The distribution of the copepod *Eurytemora affinis*, one of the two native estuarine copepod species, seemed to be associated to temperate water (near 15 °C) and low values of salinity (near 0 P.S.U.). These results are in accordance with literature indicating that *E. affinis* is found in the whole oligohaline estuarine areas (Von Vaupel-Klein and Weber, 1975; Gyllenberg and Lundquist, 1979; David et al., 2005) and associated to water temperatures ranging from 9 °C to 14.9 °C (between March and June, during the maximum of biomass period) depending on the considered estuary (e.g. Ems estuary, Schelde, and Gironde estuary) according to Sautour and Castel (1995). These estimated ranges of tolerance values are also supported by physiological studies that documented that shorter species development time (e.g. eggs incubation time, generation time; see for instance Vuorinen, 1982; Bradley, 1975) are associated to temperature around ~14 °C (Escaravage and Soetart, 1993) and increasing development rates to rising temperature (from 8 to 17 °C). Our results also illustrated an upstream displacement of *E. affinis* population that is in agreement with the observations of Appeltans et al. (2003) and especially the capacity of *E. affinis* to colonize upstream areas (Appeltans et al., 2003) as its maximum abundance zone seems to have shifted. We also stressed the importance of two ecological parameters conditioning *E. affinis* distribution (water temperature and salinity, both being important, see Appendix 2A) but we did not take into account the dissolved oxygen, although this species progression in freshwaters was already observed in response to improved oxygen concentrations (Tackx et al., 2004). Etcheber et al. (2011) estimated oxygen saturation in the Gironde estuary between 40 and 100%, with episodic critical values under 20% only observed in Bordeaux city during the ebb phase in summer, in the MTZ. However, considering the fact that the estuarine turbidity maximum (ETM) may act as an entrapment zone for zooplankton, as it appeared in a study of the Chesapeake Bay (Roman et al., 2001) and was also characterized by Modéran et al. (2010) as an ecotone (as it is an environmentally stressful zone/barrier between freshwater and a salinity gradient zone), turbidity may be considered as an additional important factor controlling the longitudinal distribution of this species in the Gironde estuary (Sautour and Castel, 1995). Actually, as high turbidities are located more upstream (Etcheber et al., 2011), we cannot exclude the hypothesis that the population of this species would be localized just upstream of the turbidity maximum as a result of both hydrodynamic processes and survival (Sellner and Bundy, 1987; Gasparini et al., 1999) as it was hypothesized by Castel (1993).

Acartia bifilosa, was the dominant copepod species in the Gironde estuary in the mesohaline area, seaward of the maximum turbidity area until 1999 (Irigoien and Castel, 1995; Sautour and Castel, 1995; David et al., 2005). It was preferentially found in more downstream estuarine sections (at 52 km downstream from Bordeaux city, (David et al., 2005)). This is also observed in other estuaries (Soetaert and Van Rijswik, 1993; Mouny and Dauvin, 2002; Vieira et al., 2003). In a recent study (unpublished), we also showed that the occurrence of this species (and the ones of the mysid *Mesopodopsis slabberi*) is closely linked to increasing temperature and salinity. Our work indicates a shift in *A. bifilosa* distribution due to both the marinisation and warming trends, but it also highlights an upstream displacement of the population. The evaluation of the importance of the two considered ecological factors (see Appendix 2B) revealed that both temperature and salinity parameters explained the movement of *A. bifilosa* towards more upstream sections with a possibly more pronounced and conditioning water temperature effect. This species also experienced a phenological change with a production period occurring one month earlier than before as a result of *Acartia tonsa* establishment (David et al., 2007). Therefore, we can wonder if *A. tonsa* could not have influenced *A. bifilosa* spatial distribution. This hypothesis seems being supported by Aravena et al. work (2009). Thus, Aravena et al. documented noticeable changes in another Acartia species, *A. clausi.* Its distribution in the estuary of Bilbao shifted in response to *A. tonsa* successful colonization since 2003.

Considering the neritic copepods, for which a maximum of abundance was expected in the estuarine plume (as they are mainly found in the Bay of Biscay (Sautour and Castel, 1999), we show both their increasing abundances (between 1975 and 2003) and their upstream progression in the estuarine system. These results have to be nuanced as the dominant species (in terms of density) composing the neritic taxonomic group in 2003 (not the case in 1975–76) was *Euterpina acutifrons* and this species represented an average percentage of 66.8% of total neritic copepods abundance (with a range between 0 and 100%). Nevertheless an intermediate

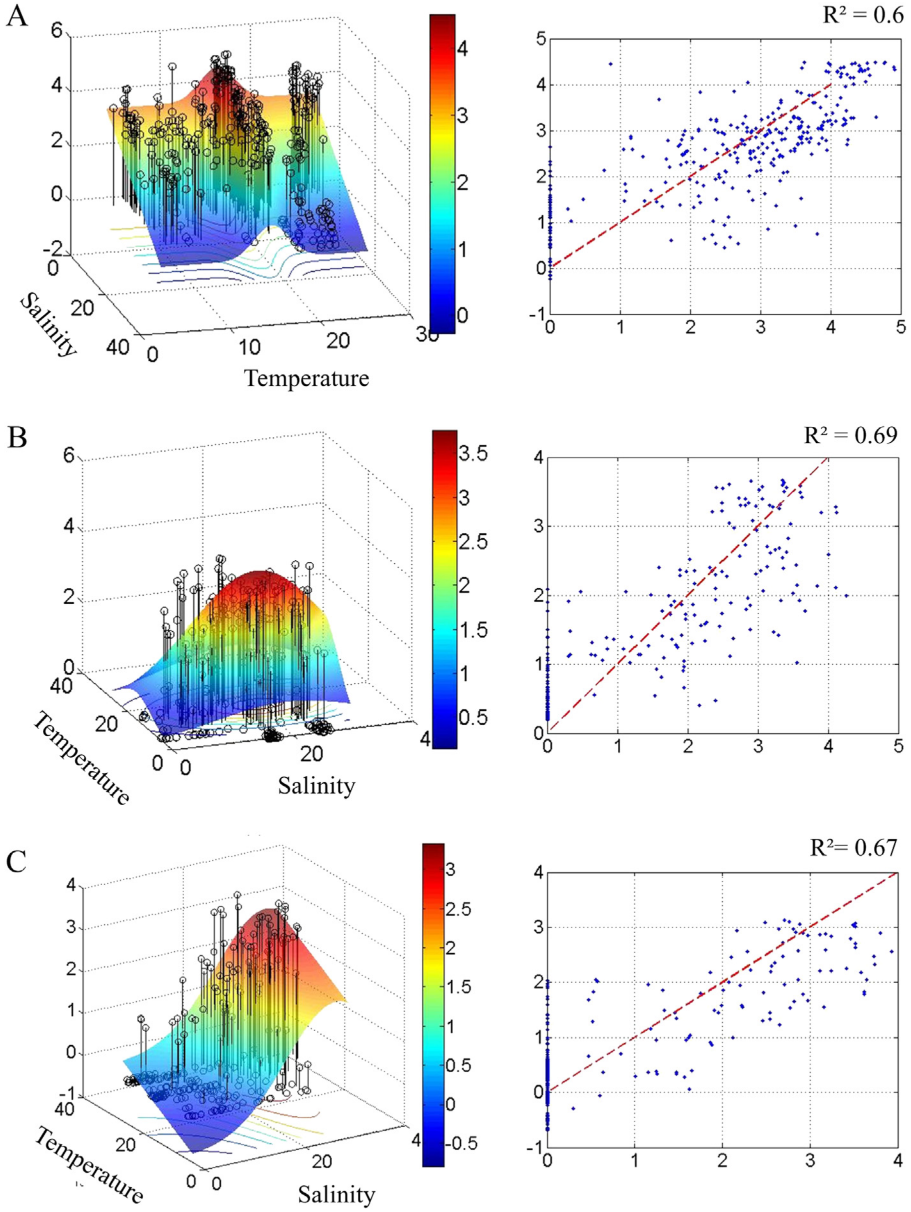

Fig. 5. Abundance of (A) *Eurytemora affinis*, (B) *Acartia bifilosa*, and (C) Neritic copepods as a function of both annual salinity and temperature (left). Estimated species abundances were plotted against raw data and both the bisector and the Pearson coefficient of determination were superimposed (right).

position between marine and estuarine conditions was assigned to this species by Goncalves et al. (2010). However comparing to more marine ecosystems such as the Bay of Marennes-Oléron (Sautour and Castel, 1995), we referred to this species as neritic (as originally found in the Bay of Biscay). This point has to be considered regarding the important upstream progression of neritic copepods observed between 1975 and 2003 (as neritic copepods were found until 55 km upstream from the mouth of the Gironde estuary) but this does not contest the increased abundances of neritic copepods into the estuary. Besides the more important ecological parameter that would condition their longitudinal distribution is salinity (see Appendix 2C).

These results really support our hypothesis of a response of all three taxonomic groups to the warming and the marinisation process of the Gironde estuary and highlight the importance of salinity as a key factor controlling the spatial distribution of the zooplankton along the estuary. However, our work also suggests the importance of a second ecological factor, water temperature as temperature also explained the upstream movement of *Eurytemora affinis* and to a lesser extent the movement of *Acartia bifilosa* and the group of neritic copepods.

Our observations suggest a movement of the taxa to remain within their respective environmental envelope. Indeed copepods transport is mainly related to water bodies movement as they have no sufficient swimming aptitude to get rid of water bodies circulation. However if copepods had moved passively, we would have expected their upstream movement to be strongly and essentially driven by salinity. Because copepods perform vertical migrations, we cannot completely discard the fact that instead of being distributed in a passive way with water bodies (Castel and Veiga, 1990), this taxonomic group might use the hydrodynamics of the estuary (e.g. water discharge (Peitsch et al., 2000)) to progress

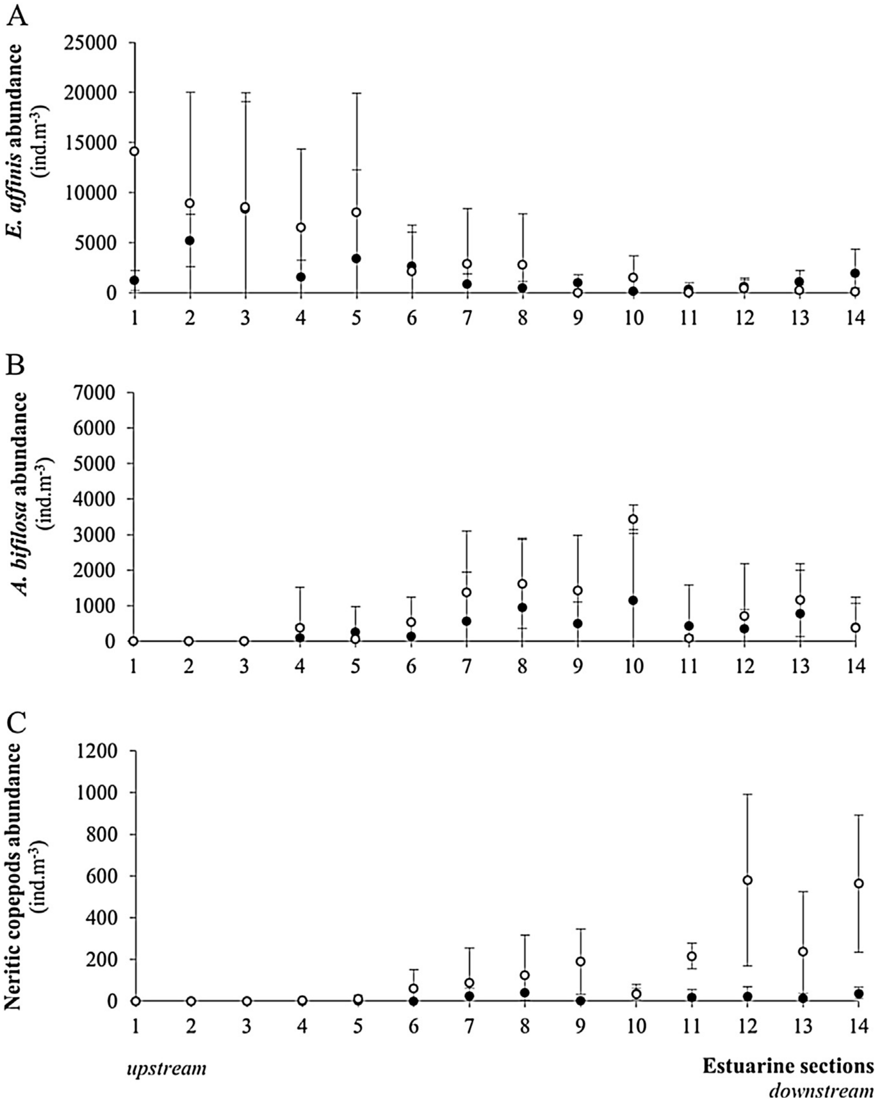

Fig. 6. Spatial variability in the predicted annual abundance of (A) *Eurytemora affinis*, (B) *Acartia bifilosa*, and (C) Neritic copepods from the estuary upstream sections (1) to the downstream estuary sections (14): white dots for year 2003 and black dots for year 1975–1976.

upstream along the estuary. This hypothesis is in agreement with Seuront (2006) who provided evidence of an endogenous behavioural adaptive strategy for *Eurytemora affinis* independent of its circadial activity (Hough and Naylor, 1992). Thus, Seuront (2006) highlighted that increased salinity increased swimming activity of both males and non-ovigerous females of *E. affinis*. Furthermore Hills (1991) used a sinusoidal model, which demonstrated that copepods, by their diel vertical migration, may control their horizontal distribution in systems characterized by strong tidal movements. However, Kimmerer et al. (1998) concluded that despite diel differences in *E. affinis* vertical distribution, suggesting an active migration, this would be insufficient to reverse species seaward transport. Thus, they hypothesized that *E. affinis* spatial gradient would be mainly linked to its predation by *Potamocorbula amurensis*. Furthermore, the hydrodynamics hypothesis cannot be reasonably evocated alone regarding the generation time of copepods (~1 month) and the time scale we used, even though an effect could have been detected at a long-term scale. An alternative hypothesis may result in a combination of different processes dealing with species plasticity or acclimatisation to environmental changes but also resulting from species reproduction success, survival, competition, resource availability, and predation. With the exception of some neritic copepods, species were already present in upstream sections but in low/residual abundances. Thus, species movement may suggest that they have found more suitable conditions to develop or have even been displaced by new established species (e.g. *A. tonsa*, see Aravena et al., 2009). Temperature and salinity may indeed affect many physiological processes, acting on copepods reproduction, locomotion, feeding rates, osmoregulation and species interaction (Magnuson et al., 1979; Castel, 1993; Sautour and Castel, 1995; Mauchline, 1998; Elliott and Hemingway, 2002; Beaugrand and Reid, 2003; Vilas et al., 2009); the consequences and mechanisms of this longitudinal shift need therefore further investigations. However our results and model predictions have also to be linked with the observations of Pasquaud et al. (2012) who found an increased number of marine migrant fish species in the estuary. Their results left open the question of the new potential preys they could have found. Our concordant results address therefore the issue of the induced changes in the Gironde trophic food web resulting from the movement of these different taxa. Indeed, the movement of all or part of the trophodynamics of the estuary can lead to important changes in the distribution of their predators/preys and may induce strong consequences on the whole food web (Durant et al., 2007). Biogeographical shifts (Perry et al., 2005) or even match/mismatch responses are likely to occur (Murawski, 1993; Durant et al., 2007). Trophic cascades and amplifications previously observed in other systems (Kirby and Beaugrand, 2009), might also alter the ecosystem.

5. Conclusions

In conclusion, by modelling the environmental envelopes of the neritic copepods and both dominant copepod native species, *Acartia bifilosa* and *Eurytemora affinis*, we pointed out an alteration in copepods spatial distribution between 1975 and 2003. The models which considered only 2 climate-driven parameters (water temperature and salinity) provided coherent estimations with raw data. This emphasizes the importance of both descriptors relative to the marinisation and the warming of the Gironde estuary. Our result showed an upstream progression of neritic species that appear to be mostly due to salinity while for both dominant copepod native species the upstream movement comes from the augmentation of both temperature and salinity. The consequences of copepods longitudinal distribution changes have to be fully investigated while also considering predators. This would allow a more global view of the ecosystem changes involved as some alterations of the Gironde trophic food web are already expected.

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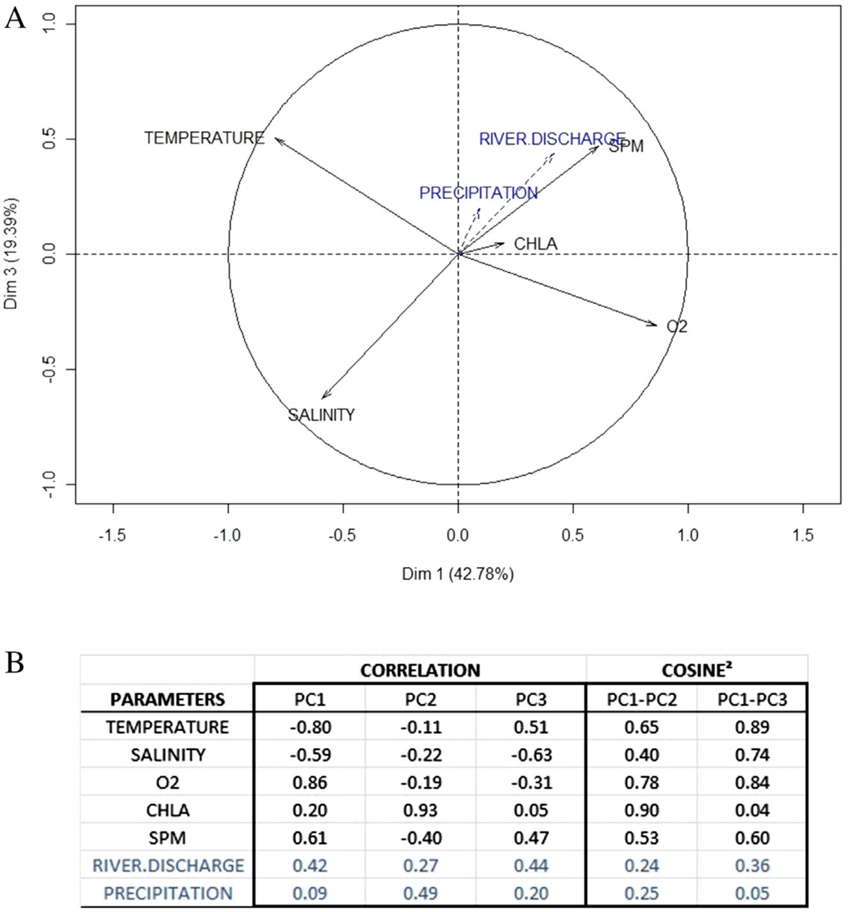
Appendix A



	CORRELATION			COSINE²	
PARAMETERS	PC1	PC2	PC3	PC1-PC2	PC1-PC3
TEMPERATURE	-0.80	-0.11	0.51	0.65	0.89
SALINITY	-0.59	-0.22	-0.63	0.40	0.74
O2	0.86	-0.19	-0.31	0.78	0.84
CHLA	0.20	0.93	0.05	0.90	0.04
SPM	0.61	-0.40	0.47	0.53	0.60
RIVER.DISCHARGE	0.42	0.27	0.44	0.24	0.36
PRECIPITATION	0.09	0.49	0.20	0.25	0.05

Fig. A1. Principal Components Analysis on environmental parameters: variables correlation circle (A; Factor map: PC1 – PC3). Local precipitations (PRECIPITATION) and river discharge (RIVER DISCHARGE) as supplementary variables and water temperature (T), salinity (S), dissolved oxygen (O_2), suspended matter (SPM) and chlorophyll *a* (CHLA) concentrations as active variables. (B) Table of correlations between first principal components (PC1, PC2, and PC3) and environmental parameters and cumulative squared cosine for PCs 1–2 and 1–3.

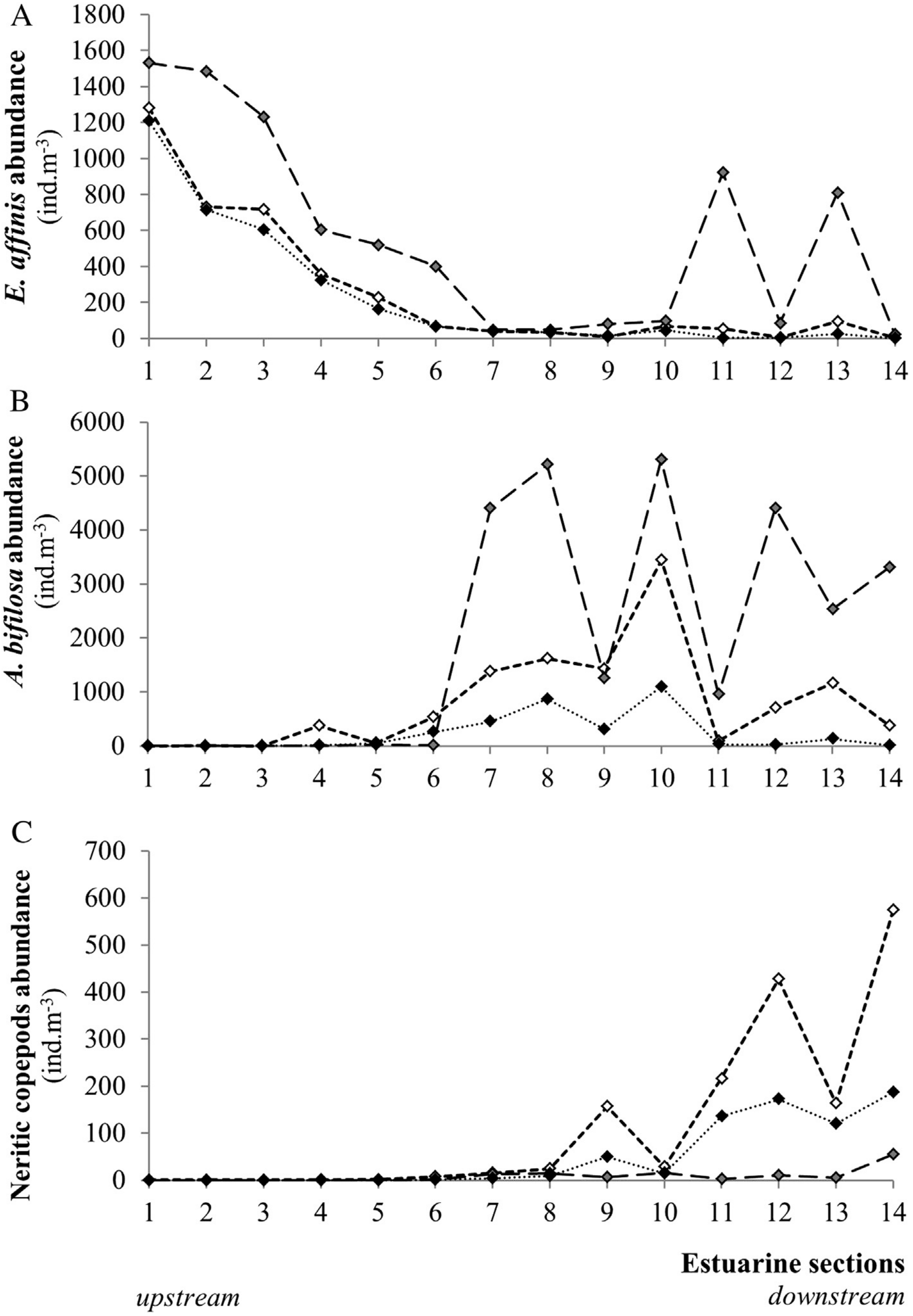


Fig. A2. Spatial variability of predicted annual abundance of (A) *Eurytemora affinis*, (B) *Acartia bifilosa*, and (C) Neritic copepods from the estuary upstream sections (1) to the downstream estuary sections (14): white dots for predicted data of year 2003, grey dots for predicted data computed with salinity values of year 1975–1976 and temperature values of year 2003, and black dots for predicted data computed with temperature values of year 1975–1976 and salinity values of year 2003.

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