



Response of planktonic cladocerans (Class: Branchiopoda) to short-term changes in environmental variables in the surface waters of the Bay of Biscay

Jean d'Elbée^{a,*}, Yann Lalanne^b, Iker Castège^c, Noelle Bru^{d,e}, Frank D'Amico^{b,e}

^a Laboratoire d'Analyses de Prélèvements Hydrobiologiques LAPHY, 1341 chemin d'Agerrea, 64210 Ahetze, France

^b UNIV PAU & PAYS ADOUR, UFR Sciences & Techniques de la Côte Basque, Département d'Ecologie, Parc Montaury, 64600 Anglet, France

^c Centre de la Mer, Plateau de l'Atalaye, 64200 Biarritz, France

^d Laboratoire de Mathématiques et de leurs Applications de Pau UMR CNRS 5142, UNIV PAU & PAYS ADOUR, 64000 Pau, France

^e Fédération de Recherche sur les Milieux Aquatiques – MIRA, UNIV PAU & PAYS ADOUR, UFR Sciences & Techniques de la Côte Basque, Département d'Ecologie, Parc Montaury, 64600 Anglet, France

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ABSTRACT

From January 2001 to December 2008, 73 surface plankton samples and 45 vertical profiles of sea temperature, salinity, dissolved oxygen and pH were collected on a monthly basis from a single sampling station located in the Bay of Biscay (43°37'N; 1°43'W) (North-East Atlantic). Two types of North Atlantic Oscillation (NAO) indexes were included in the data set and submitted to a Canonical Correspondence Analysis and Spearman non-parametric test. Significant breaks and levels in time series were tested using a data segmentation method.

The temperature range varies from 11 °C to 25 °C. It begins to rise from April until August and then decline. Low salinity values occur in mid-spring (< 34 PSU) and high values (> 36 PSU) in autumn. Dissolved oxygen mean values were around 8 mg/l. In summer, when temperature and salinity are high, surface water layer is always accompanied with a significant deoxygenation, and the process reverses in winter. pH mean values range was 7.78–8.33. Seasonal and inter-annual variations of the two NAO indexes are strongly correlated to one another, but do not correlate with any hydrological or biological variable.

Five of the seven cladocerans species which are present in the Bay of Biscay were found in this study.

There is a strong pattern in species succession throughout the year: *Evadne nordmanni* is a vernal species, while *Penilia avirostris* and *Pseudevadne tergestina* occur mainly in summer and autumn. *Evadne spinifera* has a maximum abundance in spring, *Podon intermedius* in autumn, but they both occur throughout the year. However, for some thirty years, the presence of species has tended to become significantly extended throughout the year. During the 2001–2008 period, there was a noticeable decline and even a disappearance of the categories involved in sexual reproduction as well as those involved in parthenogenesis, in favor of non-breeding individuals.

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1. Introduction

Of the 600 currently recorded cladoceran species in the world (Onbé, 1999), only eight are marine and seven of them are present in the Bay of Biscay (Alcaraz, 1981; d'Elbée and Castel, 1995). Despite the low number of marine species, compared to other groups such as copepods, many authors (Alonso, 1996; Egloff et al., 1997; Onbé, 1999) have stressed the importance of studying these species due to their position in the pelagic ecosystem. These

studies highlighted several aspects of their biology: seasonal succession of species, rapid population growth, alternating phases of sexual and asexual reproduction. However, cladoceran studies in the Bay of Biscay are scarce. In 1976, Alcaraz (1981) began studying successions of species and their abundances on the Spanish Cantabrian coast. In 1979, Villate and Orive (1981) analyzed the interactions between environmental variables and the development of cladocerans in the Estuary of Plencia near Bilbao. More recently, studies have been conducted in the Arca-chon Basin and the nearby neritic zone (d'Elbée and Castel, 1995). The aim of this work is to add to current knowledge about the population dynamics of these microcrustaceans in the Bay of Biscay: variations of abundance alongside seasonal succession of

* Corresponding author. Tel.: +33 559 22 12 80.
E-mail address: laphy@wanadoo.fr (J. d'Elbée).

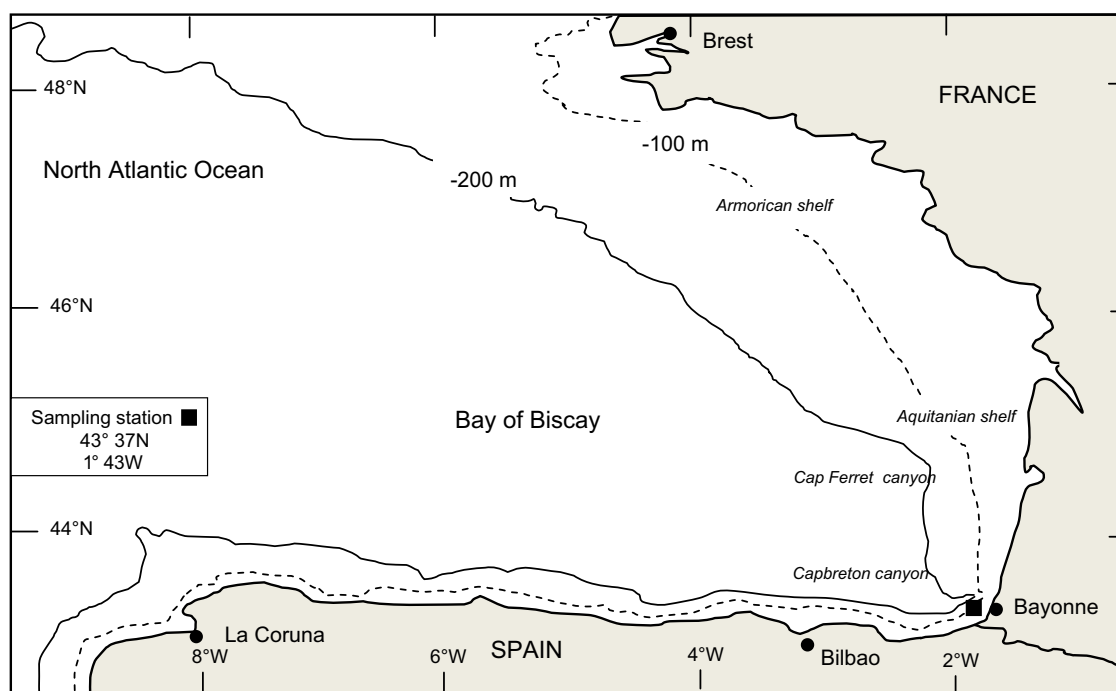


Fig. 1. Location of the sampling station (dark square) in the southern Bay of Biscay.

the species are described and compared with the aforementioned studies.

However, none of the previous studies extended longer than one annual cycle. Our study was carried out over eight years with a monthly sampling frequency, which allowed us to clarify some features of the ecology of these cladocerans, and investigate the role of climatic and environmental variables in the development of these populations on a quasi-decadal scale. Finally, some aspects of parthenogenetic and gamogenetic reproduction of these species are presented for the first time in this geographical area.

2. Material and methods

2.1. Study area

The single sampling station (43°37'N; 1°43'W) for plankton and hydrological data was located in the Bay of Biscay on the southern border of Capbreton canyon at 20 km (≈ 10.7 nm) from the coast, near the city of Bayonne (Fig. 1). Water depth at the sampling site was around 540 m. The planktonic community at this site is highly diverse and well-balanced between surface and deep water influences (d'Elbée, 2001; d'Elbée et al., 2009).

2.2. Field and laboratory work

From January 2001 to December 2008 (i.e. 96 months), 73 plankton samples were collected on a monthly basis from this station. All months have therefore not been sampled because of logistical constraints and unfavorable meteorological conditions (Table 1). The sampling surveys were carried out by the vessel "Haize Hegoa" (30 m length) belonging to the French Coast Guard (Douanes françaises). Plankton was always sampled at the same time of day (between 0900 and 1000), using a WP2-type net with 200 μ m mesh size. Horizontal hauls were collected at 2 m below the sea surface and the net was towed at a speed of 0.5 m s⁻¹. The volume of water filtered through the net was estimated with a

Table 1

Distribution of the 73 plankton samples during the study period (January 2001–December 2008). Months with plankton sampling only are shown with one asterisk (*), those with additional hydrological data are shown with two asterisks (**).

	2001	2002	2003	2004	2005	2006	2007	2008	Total
January		*	*		**	**	**	**	6
February	*	*	*	**		**		**	6
March		*	*	**	**	**			5
April			*	**	**	*	**	**	6
May	*	*	*	**		**	**	**	7
June	*	*	*			**		**	5
July	*	*	*	**		**	**	**	7
August	*			**	*			**	4
September	*	*	*	**	**	**	**	**	8
October			*		**	**	**		4
November	*	*		**	**	**	**	**	7
December	*	*	**	**	**	**	**	**	8
Total	8	9	10	9	8	11	8	10	73

General Oceanics flowmeter. Plankton was preserved in 4% sea-water formalin following Griffiths et al. (1976).

In addition, from December 2003 to December 2008, after the sampling of plankton, we used a YSI 556 MPS multiparametric probe to measure four hydrological variables: temperature (°C), salinity (PSU), dissolved oxygen (mg/l) and pH, at seven depths: 0.5 m, 1 m, 2 m, 3 m, 5 m, 10 m, and 15 m. Thus, during this period, 45 months were sampled (Table 1).

Plankton samples were sorted in the laboratory, using a LEICA/WILD M10 stereo microscope. When concentrations were high, subsamples were taken with a Motoda box. Identification of cladocerans species was carried out using specialized literature (Alonso, 1996; Margaritora, 1985; Onbé, 1999). For each species, we distinguished the four following categories: males, parthenogenetic females (bearing parthenogenetic eggs or embryos), gamogenetic females (with resting eggs) and non-breeding females without any eggs (Marazzo and Valentin, 2004a; Atienza et al., 2008). Abundances were expressed as number of individuals (N) per m³ of water (N m⁻³).

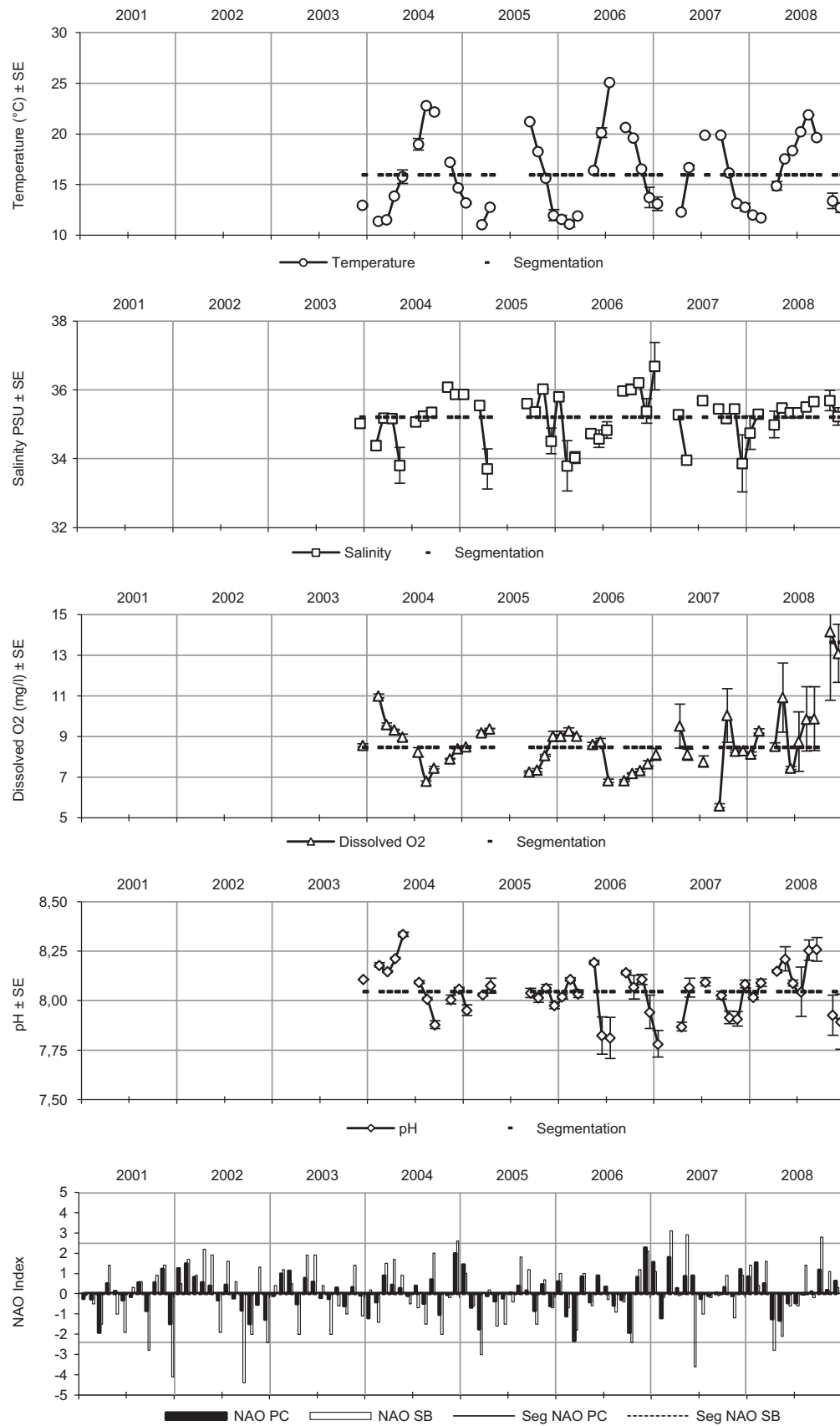


Fig. 2. Inter-annual fluctuations of hydrological variables (monthly mean values $\pm$ SE), NAO climatic indexes and segmentation during 2001–2008 period.

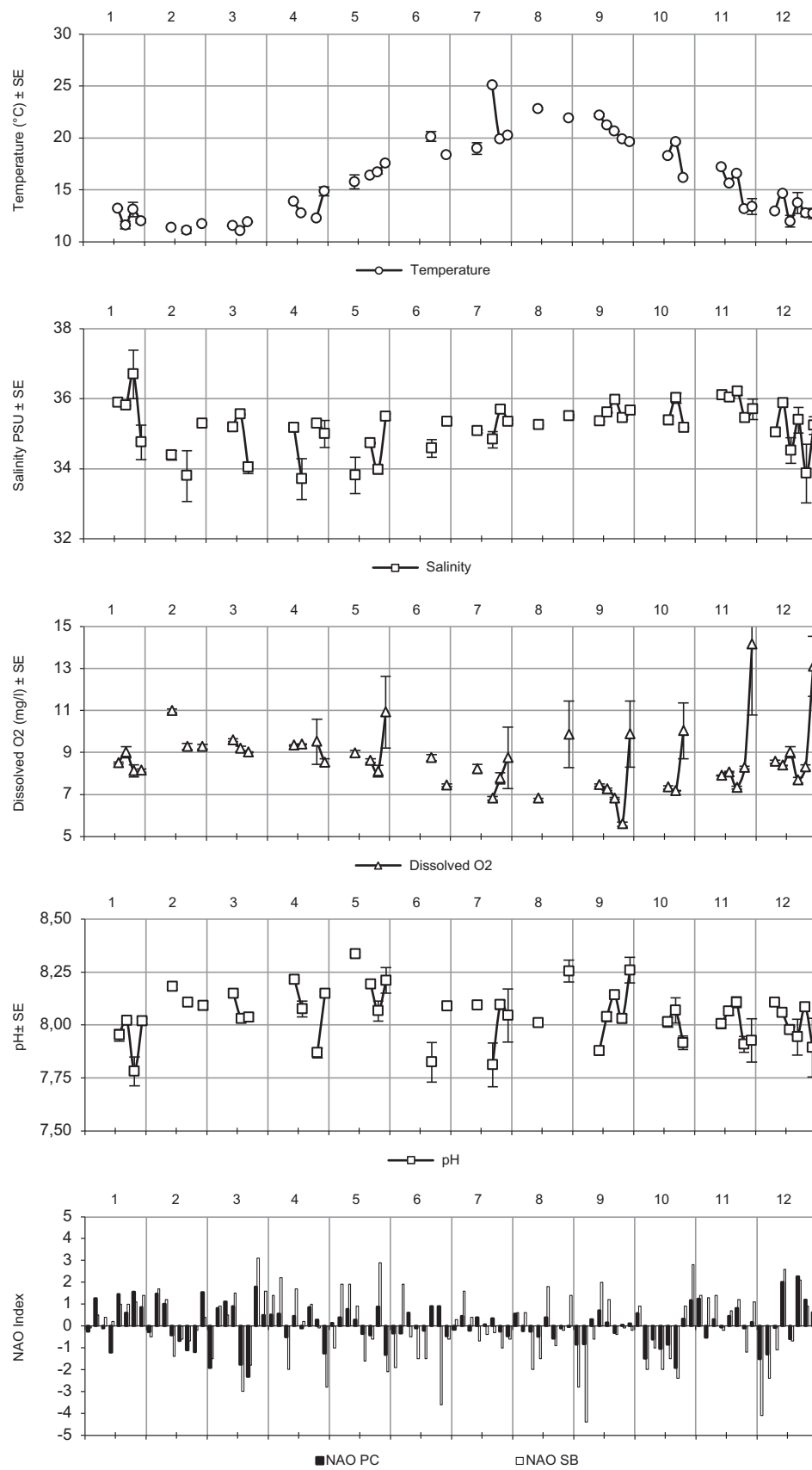


Fig. 3. Seasonal fluctuations of hydrological variables (monthly mean values $\pm$ SE) and NAO climatic indexes during 2001–2008 period.

2.3. Using NAO indexes

To see if the monthly and annual fluctuations in species abundance were correlated with climatic changes in the North-Eastern Atlantic including the Bay of Biscay, two types of North Atlantic Oscillation (NAO) indices were used: (1) the winter (December–March) station-based index (NAO SB), based on the difference of normalized sea level pressure (SLP) between Lisbon (Portugal) and Stykkisholmur/Reykjavik (Iceland) (<http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based>) and (2) the Principal Component based index (NAO PC), which gives the time series of the leading Empirical Orthogonal Function (EOF) of SLP anomalies over the Atlantic sector, 20–80°N, 90°W–40°E (<http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-pc-based>). The data set used extends over the 2001–2008 study period (96 months).

2.4. Mathematical and statistical analysis

Graphs and statistical analysis of the data were undertaken using Excel v7, StatBox v. 6.0s and R software. Sampling fluctuations around the mean abundances were described by their standard error (SE). ($SE = SD/\sqrt{n}$ with SD: standard deviation and n : sample size). Spearman's rank correlation ρ between monthly abundance species, hydrological variables and NAO indexes were performed using the Spearman non-parametric test.

To assess the significant breaks and levels changes in the studied hydrological and biological time series (73 months during the 2001–2008 period), a segmentation procedure (Hubert et al., 1989) was used. It is an iterative procedure with successive cutting of the sample based on the statistical tests of comparison of means. This procedure has been used to test inter-annual fluctuations in the mean level of the hydrological and biological dataset. The calculations were done using Khronostat software, available at: <http://www.hydrosciences.org/spip.php?article239>.

Canonical Correspondence Analysis (CCA) was performed using two contingency tables, the first including the biological variables (monthly estimated abundances of the species) $\times$ 45 months (December 2003–December 2008), the second with the four hydrological variables (monthly mean values of T (°C), salinity, dissolved oxygen and pH on the water column) and the two climatic indexes (NAO PC and NAO SB) $\times$ 45 months. Before performing CCA, all the abundance data were log-transformed and standardized.

3. Results

3.1. Hydrological and climatological data

Between December 2003 and December 2008, the four hydrological variables (temperature, salinity, dissolved oxygen and pH)

were subject to inter-annual and seasonal fluctuations (Figs. 2 and 3). To assess these changes, three parameters were considered: firstly, their monthly value averaged over the water column sampled from the surface to 15 m; secondly, the standard error reflecting the intensity of the gradient, and thirdly Hubert's segmentation values to show significant breaks or levels in the inter-annual fluctuations of hydrological time series dataset (Fig. 2). Spearman's rank correlation matrix was also used to understand the relationships between hydrological variables (Table 2).

3.1.1. Temperature

During the 2003–2008 period, water temperature ranged between 11 °C and 25 °C (Fig. 2). Winter water temperatures – in December and January – are higher than in early spring in February and March when minimum temperatures are found. Temperatures begin to increase in April until August and then decline. In the water column, the temperature gradient is never accentuated (low values of SE) (Fig. 3). The segmentation procedure of Hubert did not reveal any significant breaks in inter-annual fluctuations of this parameter.

3.1.2. Salinity

The salinity range lies between 33 PSU and 36 PSU. Low values occur in mid-spring in April and May while high values occur in autumn (November). This increase in salinity occurs throughout the summer with inter-annual variations lower than those of other periods (Fig. 3). Freshening surface waters may be significant, thus increasing the salt gradient, especially during winter and spring.

3.1.3. Dissolved oxygen

Dissolved oxygen mean values were around 8 mg/l, but in late 2008 (from June to December), the oxygen gradient (high values of SE) and its average value through the water column both increased strongly to a maximum of 14 mg/l. Moreover, Hubert's segmentation procedure revealed two offset values in November and December 2008 (Figs. 2 and 3). Temperature, salinity and dissolved oxygen have synchronized temporal evolutions: in summer, when temperature and salinity are high, the surface water layer is always deoxygenated and the process reverses in winter (Fig. 3). These observations are confirmed by the two significantly negative correlations, one between temperature and dissolved oxygen, the other between the latter and salinity (Table 2).

3.1.4. pH

The pH mean values range was 7.78–8.33. Inter-annual fluctuations are irregular, and as for temperature and salinity, Hubert's segmentation procedure did not reveal any significant breaks

Table 2

Spearman's rank correlation ρ between monthly abundance species, hydrological variables and NAO indexes. The analysis was performed using Spearman's test. In bold, significant values ($p < 0.05$).

	<i>E. spinifera</i>	<i>E. nordmanni</i>	<i>P. intermedius</i>	<i>P. avirostris</i>	<i>P. tergestina</i>	NAO PC	NAO SB	pH	T (°C)	O ₂	S (‰)
<i>E. spinifera</i>	1										
<i>E. nordmanni</i>	−0.33	1									
<i>P. intermedius</i>	−0.08	0.70	1								
<i>P. avirostris</i>	0.55	−0.16	−0.09	1							
<i>P. tergestina</i>	0.58	−0.16	−0.04	0.39	1						
NAO PC	−0.14	−0.11	−0.22	−0.08	−0.06	1					
NAO SB	0.00	−0.11	−0.07	−0.13	0.08	0.84	1				
pH	−0.05	0.36	0.26	−0.05	0.11	−0.27	−0.13	1			
T (°C)	0.43	−0.42	−0.42	0.47	0.27	−0.10	0.00	0.01	1		
O ₂	−0.36	0.34	0.35	−0.47	−0.12	−0.02	0.02	0.21	−0.55	1	
S (‰)	0.44	−0.33	−0.41	0.30	0.42	0.11	0.12	−0.15	0.27	−0.29	1

during the 2004–2008 period (Fig. 2). Moreover, pH is not correlated with any of the three other hydrological parameters (Table 2). In the water column, the pH gradient is often insignificant, but occasionally more pronounced, especially in 2007 and 2008.

3.1.5. NAO indexes

Seasonal and inter-annual variations of the two NAO indexes are significant and irregular. They are strongly correlated to one another, but do not correlate with any hydrological variable

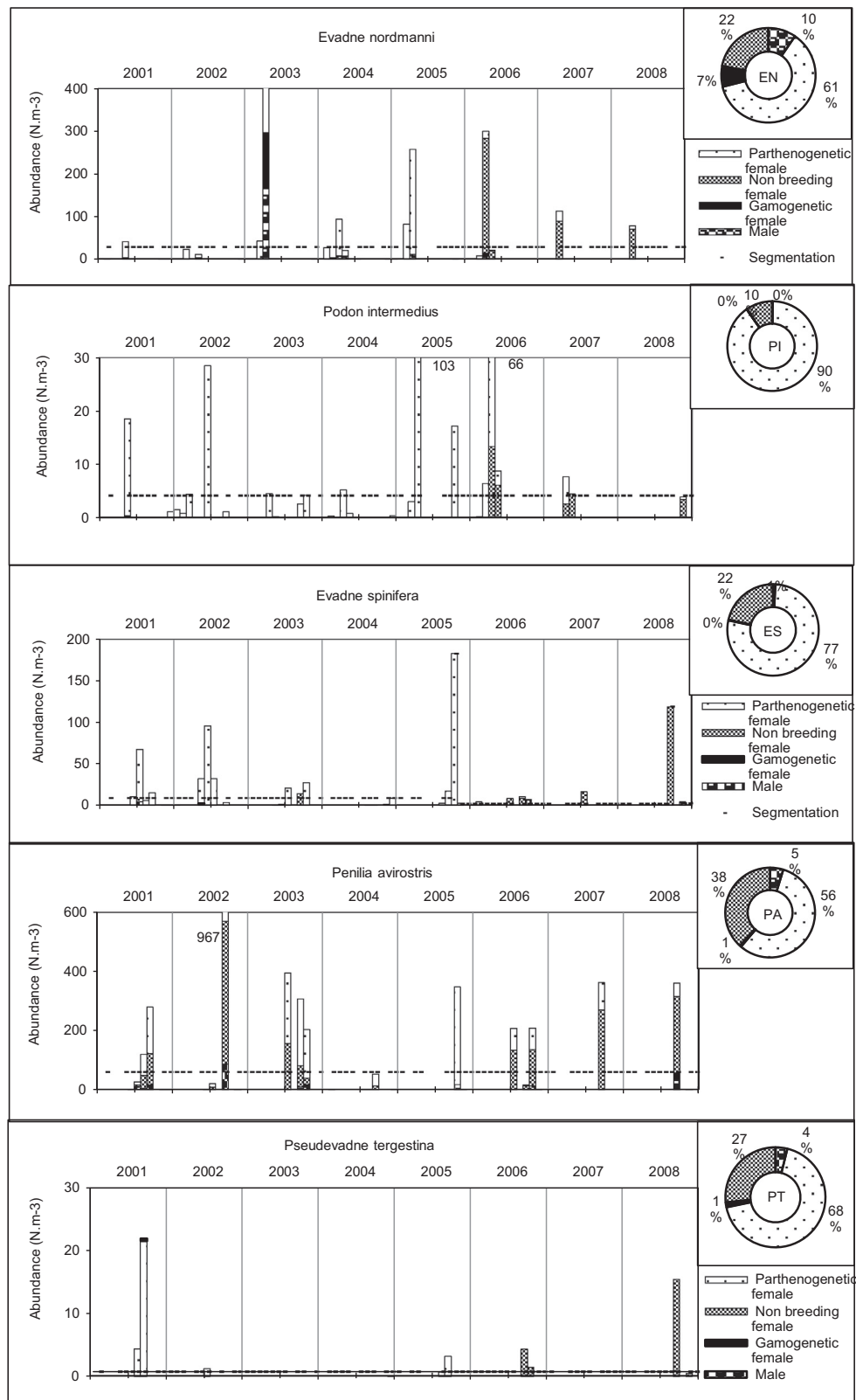


Fig. 4. Inter-annual fluctuations of monthly abundance values, proportions of the different sexual forms (top right) of the five cladoceran species, and segmentation during the 2001–2008 period.

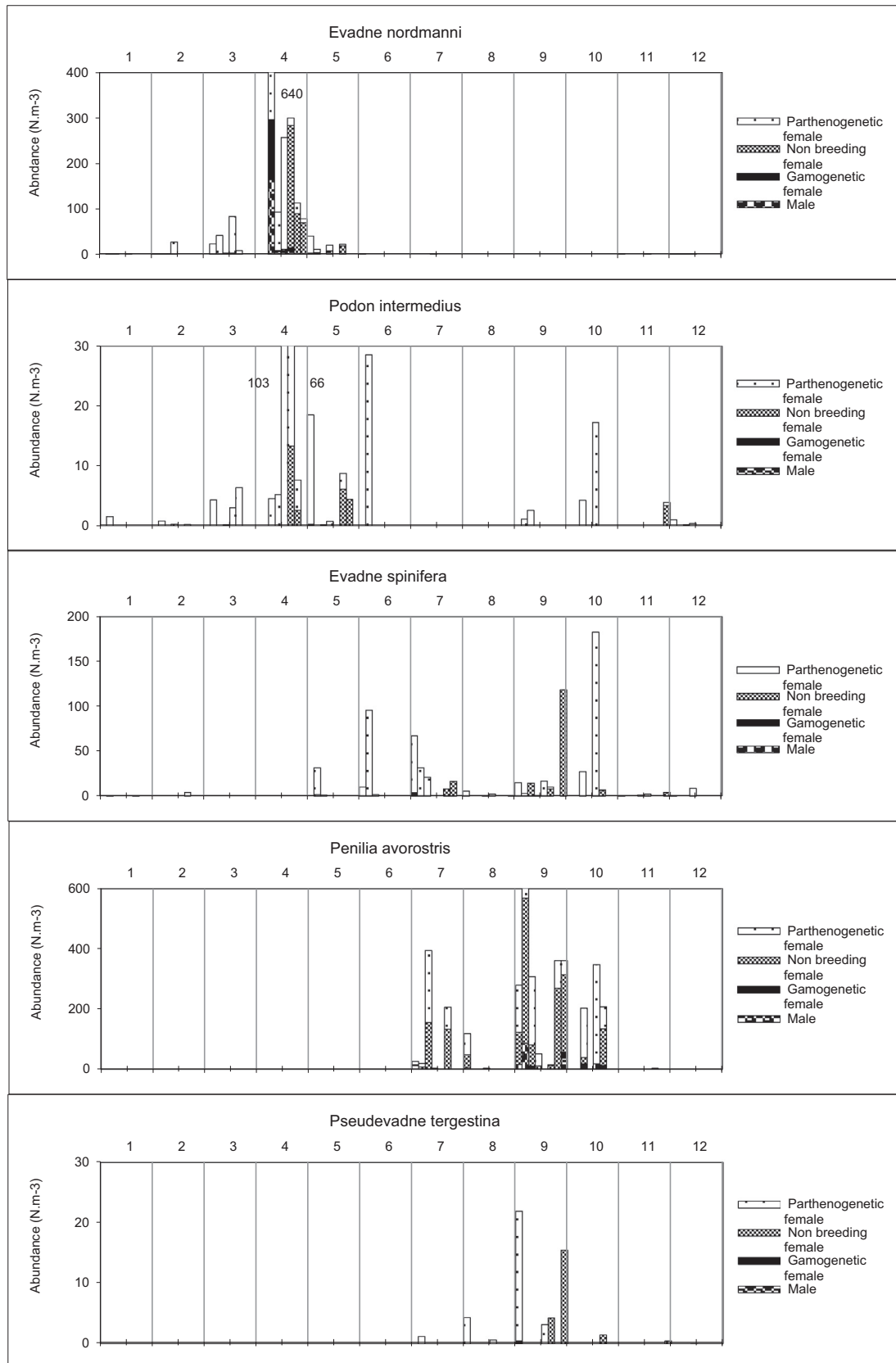


Fig. 5. Seasonal fluctuations of monthly abundance values of the five cladoceran species during the 2001–2008 period.

(Table 2). Levels calculated by the segmentation procedure are very close to 0 (0.057 for NAO PC; 0.049 for NAO SB) and showed no break (Fig. 2).

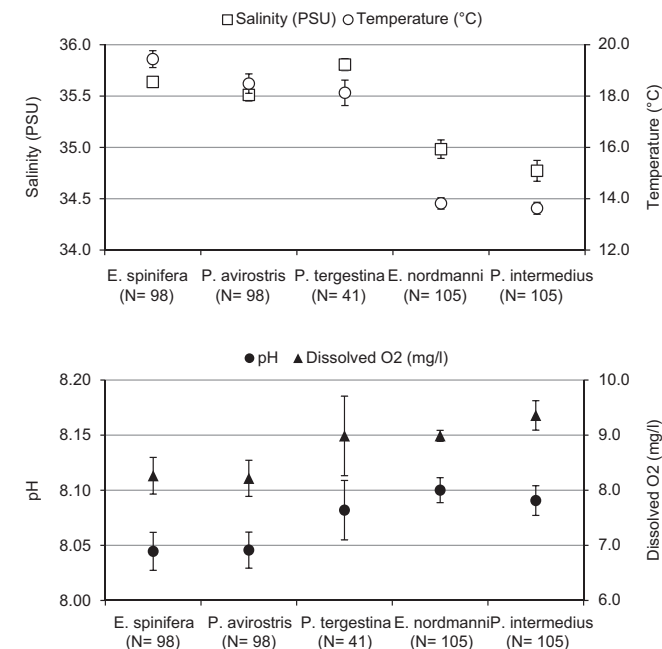


Fig. 6. Optimal values of hydrological variable for the five cladoceran species (N=number of values of each variable for which the species occurs).

3.2. Biological data

3.2.1. Abundances and temporal successions of the species

Five of the seven cladoceran species (Class: Branchiopoda) which are present in the Bay of Biscay were found in this study: *Evadne nordmanni* Lovén, 1836, *Podon intermedius* Lilljeborg, 1853, *Evadne spinifera* P.E. Müller, 1857, *Penilia avirostris* Dana, 1849, and *Pseudevadne tergestina* (Claus, 1877) (Fig. 4). The two dominant species *E. nordmanni* and *P. avirostris* are ten times more abundant ($100\text{--}1000\text{ N m}^{-3}$) than the three other species ($10\text{--}100\text{ N m}^{-3}$). *P. tergestina* is particularly scarce (Fig. 4). Inter-annual abundances are quite irregular from year to year for all species, but there were no significant changes in the values (i.e. condition of stationarity is respected) of the 73 monthly abundance values for most species, except for *E. spinifera* (detection of 3 significant changes in the abundance mean values: 8.47 N m^{-3} before October 2005, 1.94 N m^{-3} after September 2008 and 1.73 N m^{-3} between these two dates).

During the year, there is species succession (Fig. 5): *E. nordmanni* and *P. intermedius* have maximum abundances values in spring. *E. spinifera* appears in May and then is present throughout the year. *P. avirostris* and *P. tergestina* have the most abundant values in summer and early autumn. From one month to another, variations in abundances are high for all species, with a factor of $\times 10$ or $\times 100$. In winter abundance values are minimal.

3.2.2. Reproduction aspects

Parthenogenetic and non-breeding females were clearly dominant for all five cladoceran species, whereas male and gamogenetic female abundances were very low and never exceeded 10% of

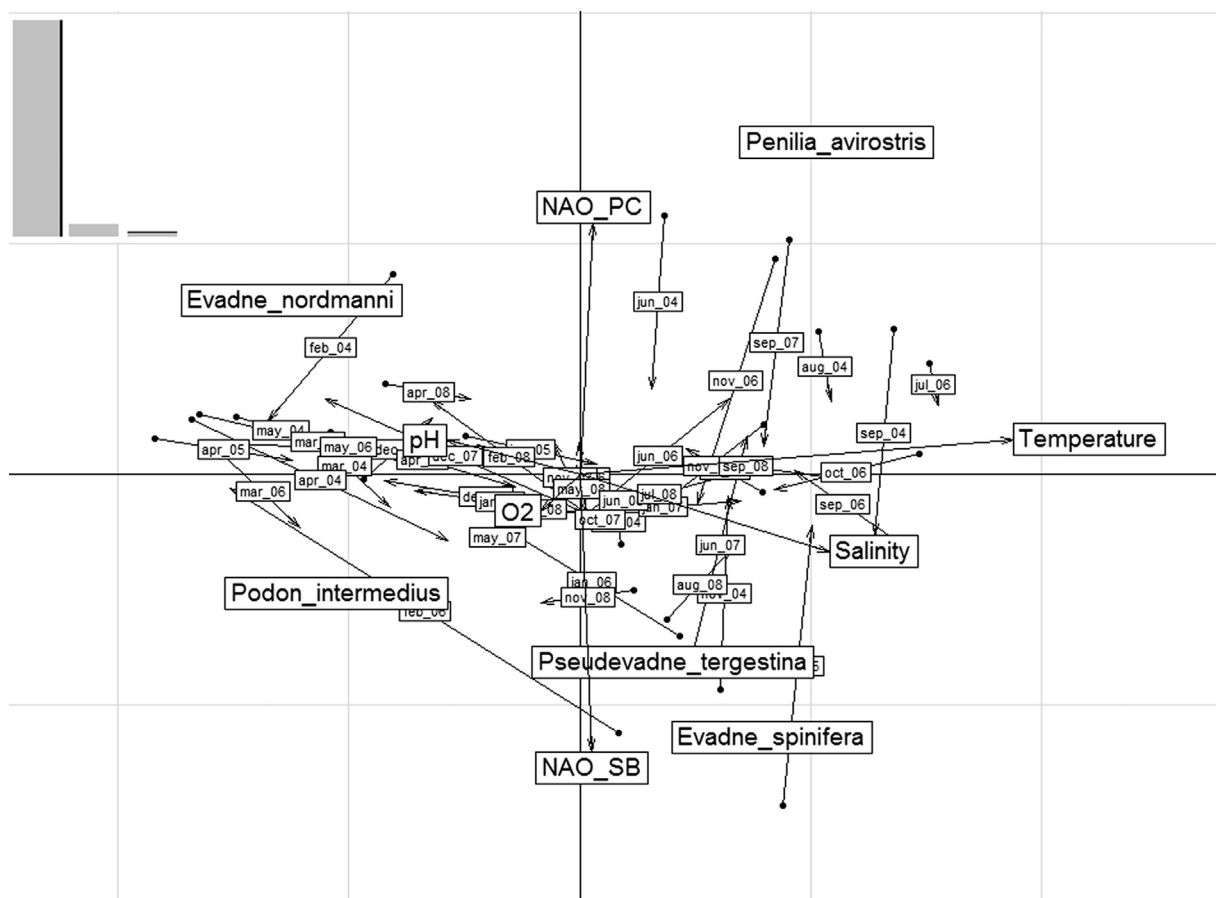


Fig. 7. Projection in the factorial plan $F1 \times F2$ of the results of Canonical Correspondence Analysis (CCA). Months and years are abbreviated (jun 04: June 2004). Top left, the histogram of the eigenvalues of the first four factors of the CCA.

the total population (Fig. 4). The proportions of these two latter categories always evolved in parallel, and take minimum values for *P. intermedius* (< 1%), the only species for which no gamogenetic female has been recorded, and maximum values for *E. nordmanni*. During the 2001–2008 period, there is a decline and even disappearance of the categories involved in sexual reproduction (i.e. males and gamogenetic females), as well as those involved in parthenogenesis, in favor of non-breeding individuals which have become dominant for all species since 2006 (Fig. 4).

During the year, these categories also undergo a particular evolution: parthenogenetic and non-breeding females are present throughout the occurrence period of each species. But sexual reproduction (male and female gamogenetic) takes place in the middle or towards the end of each seasonal occurrence period (i.e. *E. nordmanni* and *P. avirostris* in Fig. 5).

3.3. Hydrological and biological interactions

3.3.1. Species preferenda

The average of each hydrological variable was calculated each time a species occurred. These averages can be considered as optimal values for the development of the species (Fig. 6). The three species *E. spinifera*, *P. avirostris* and *P. tergestina* which have high values of thermal ($\approx 19^\circ\text{C}$) and saline (> 35.5 PSU) optima, also have low values of optima for dissolved oxygen and pH. The opposite occurs for the two other species *E. nordmanni* and *P. intermedius* whose thermal ($\approx 14^\circ\text{C}$) and saline (< 35 PSU) optima are lower, whilst pH and dissolved oxygen optima are higher.

3.3.2. CCA analysis

A Canonical Correspondence Analysis (CCA) was performed with monthly species abundance, hydrological data and the two NAO climatic indexes (Fig. 7). The first two axes show 97% (F1: 91%; F2: 6%) of variability in cladoceran assemblages. Thermophilic and halophilic species *P. avirostris*, *E. spinifera* and *P. tergestina* are on the right side of F1 $\times$ F2 factorial plan, positively correlated with the F1 horizontal axis, high temperature and salinity values, and low dissolved O_2 values, while the spring species *P. intermedius* and *E. nordmanni* are negatively correlated to F1, low temperature and salinity values and high dissolved O_2 values (Spearman's test, $p < 0.05$, Table 2). Except for pH, the F1 factorial axis represents a gradient of environmental variables on which temperature, salinity and dissolved oxygen are best correlated to each other and with the species. Finally, the two NAO indexes are well correlated with the second factorial axis F2 of CCA but this does not explain the temporal variations in species distribution or hydrological values, as shown by Spearman's test ($p > 0.05$, Table 2).

4. Discussion

4.1. Hydrological variables

4.1.1. Temperature

For twenty years, many publications have dealt with the physical structure and surface hydrology of the Bay of Biscay (González-Pola et al., 2005; Michel et al., 2009; Pingree, 1994; Planque et al., 2004, 2006; Puillat et al., 2004, 2006). In the context of global warming, temperatures have been particularly well studied over long time scales (several decades in general). These studies show an upward trend in surface water temperatures recently estimated at $\sim 0.3^\circ\text{C}$ per decade in the top 100 m of the water column, from 1986 to 2005 across the Bay of Biscay ($43\text{--}50^\circ\text{N}/1\text{--}12^\circ\text{W}$) (Michel et al., 2009) and a thermal

stratification of the water that appears in spring and then gradually disappears in autumn (Puillat et al., 2004). In the Bay of Biscay, García-Soto and Pingree (1998, 2009) have shown that the installation of thermocline and its corollary, the increase in primary production are progressive and favored by sun insolation and low wind turbulence, terms earlier in the south than in the north of the bay. In the latitudinal range $43^\circ\text{N}\text{--}50^\circ\text{N}$ ($\approx 3^\circ\text{W}$), the temporal shift in primary production can reach up to two months, and the spring bloom pulses in the southern Bay of Biscay start in February.

Compared to these studies, it seems that the duration of our study on hydrology (only four years), alongside the thickness of the surface layer sampled (down to 15 m) are insufficient to demonstrate a significant rise or drop trend in temperatures. The high speed in the appearance or disappearance of the thermal gradient observed in our work prevented the installation of a permanent thermocline at this level. Moreover, the low number of temperature measurements during June, July and August does not allow us to identify the maximum summer temperature.

4.1.2. Salinity

Our study shows that salinity gradients in the water column are particularly pronounced throughout the winter period and spring until May, and attenuated in summer. It is very likely that these gradients are modulated by changes in climatic conditions, especially by the relative importance of rainfall and evaporation over the seasons: in summer the more scattered rainfall and high evaporation tends to reduce the salinity gradient and increase the average values. The opposite occurs during the remainder of the year. Planque et al. (2004, 2006) and Puillat et al. (2004) have shown that many other factors such as river runoff, wind patterns and the occurrence of coastal upwelling continuously modulate the surface salinity gradient in the Bay of Biscay. This stratification of the sea is an important environmental variable for surface production (García-Soto and Pingree, 2009). Despite its distance from the coast (see Fig. 1), it is also a possibility that freshwater inflow of continental origin can affect measurements of salinity at some times of the year at this station, as is the case in other parts of the Bay of Biscay at varying distances from the shore (Puillat et al., 2004, 2006).

4.1.3. Dissolved oxygen and pH

The negative correlation observed between temperature and dissolved oxygen shows a predominance of the dissolution process that links these two variables together: increased summer water temperatures induced degassing of dissolved gases, most notably near the air–water interface. But unlike temperature and salinity which are modulated mainly by physical and climatic factors, the dissolved oxygen (like pH) is also affected by biological processes such as autotrophic and heterotrophic activity of planktonic organisms. Thus, the decrease of summertime dissolved oxygen levels found in this study could also be induced by high heterotrophic zooplankton activity, especially abundant in summer (Gattuso and Hansson, 2011). Even if the temperatures measured in late 2008 are lower than those of previous years, high dissolved oxygen values measured during this period cannot result only from dissolution processes. They could be the result of strong autotrophic activity located just below the air–water interface. This activity leads to an increase of pH (Riebesell and Tortell, 2011), which is observed in May, August, and September 2008, but not in the following three months. The high values of dissolved O_2 not linked to a decrease in pH could result from improper measurement with the multiparameter probe just below the air–water interface during bad weather.

4.2. NAO climatic indexes

Some authors (Pingree, 2002, 2005; Garcia-Soto and Pingree, 2012, Fig. 7) have shown links between hydrological variables, especially sea surface temperature SST and the evolution of the NAO index in Eastern North Atlantic, for ocean scale circulation and winter conditions in the North Sea. More recently, Garcia-Soto and Pingree (2012) have analyzed the relations between SST and two climatic indexes: the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO) during the last 150 years (1854–2010) in the Bay of Biscay. The AMO index explains ~25% of the inter-annual variability of the annual SST, while different indices of the NAO explain $\leq 1\%$ of the long-term record. NAO is a high frequency climate mode while AMO can modulate low frequency changes.

We have shown that during the 2001–2008 period, taking into account the NAO indexes values as explanatory variables of hydrological (and biological cf. below) data provides little information about the temporal evolution of the parameters studied. Great irregularity in the inter-annual and seasonal variations of the two NAO indexes prevents linkages or correlations with any of the hydrological and biological variables. It is likely that the study area, which is reduced to a single station, and the shortness of the time series, do not allow for the acquisition of sufficient data to compare and correlate these with longer time series covering the whole Bay of Biscay (Garcia-Soto and Pingree, 2012; Planque et al., 2004, 2006).

However, these explanations of scale do not provide a full explanation: Villate et al. (2008) showed that on the Spanish Cantabrian coast, strong correlations could exist between hydrological data, climate (using the NAO index) and phytoplankton abundances on time series just as short and a sample area just as small as that of our study.

NAO is unlikely to work well at small scale as NAO reflects wind at large scale (from atmospheric pressure field) and local winds will differ even with the same value of NAO. We intend to use wind speed and direction as an environmental variable in future analyses in place of NAO. Levels of the two NAO indexes calculated by the segmentation procedure are very close to each other because of their similar variations during the 2001–2008 period.

4.3. Succession, sustainability and dominance in cladocerans populations

Five of the seven species which make up the cladoceran fauna in the study area (Alcaraz, 1981; d'Elbée and Castel, 1991, 1995; Villate and Orive, 1981) were found. The two non-observed species *Pleopsis polyphemoides* (Leuckart, 1859) and *Podon leuckarti* (Sars, 1861) are both located in coastal environments, or even strictly estuarine ones (Alonso, 1996; d'Elbée and Castel, 1995; Onbé, 1999; Saito and Hattori, 2000) and therefore do not have a sufficiently extensive distribution to be present at our sampling station.

The cladocerans successions during the year described in this work broadly confirm the aforementioned studies concerning the ecology of these planktonic crustaceans in the Bay of Biscay. However, the presence of the species has inclined to become significantly extended during the year. In 1976, on the Spanish Cantabrian coast, close to our sampling station, Alcaraz (1981) found that the presence of each species did not exceed two or three months, whereas our data show a doubling or tripling of this duration within the year.

This population sustainability affects all species: *P. avirostris* which was strictly a summer species in 1976 (July–August) became a summer-autumnal species (July–October) during our study period 2000–2008. The vernal (March–May) *P. intermedius*, and

the summer (June–September) *E. spinifera* in 1976 had both become present almost all year around during 2000–2008 period.

The winter season seems particularly affected by this recent sustainability of cladocerans populations, since they were absent during the cold season thirty years ago in the southern Bay of Biscay (Alcaraz, 1981; Villate and Orive, 1981). In the North Sea, Johns et al. (2005) made the same observation that we did on the thermophilic species *P. avirostris*. Its limited presence in October 1990 had extended from July to November fourteen years later in 2004. This was recently observed in the south-eastern Bay of Biscay for other planktonic organisms such as copepods (Villate et al., 1997) and ichthyoplankton (d'Elbée et al., 2009).

It should be noted that this sustainability is accompanied by significant changes in species dominance: in 1976, *P. avirostris* was clearly a minority species (Alcaraz, 1981), then it became dominant from the 80s onwards (d'Elbée and Castel, 1991, 1995), which also supports our present study. On the North East Atlantic scale, other groups such as planktonic copepods (Beaugrand and Goberville, 2010), coccolithophorids (Hays et al., 2005), dinoflagellates and diatoms (Hinder et al., 2012) have undergone similar changes. All these authors describe general global warming as the major cause for these phenomena, which also affect the biogeography of species. Furthermore, these changes in dominance of species are often accompanied by increased values of abundances, with the appearance of almost monospecific populations (Attrill et al., 2007; Johns et al., 2005). However, in our work extending over eight years, no significant increase in cladocerans populations was found.

4.4. Reproduction aspects

The low proportion of the gamogenetic phase observed in our study (< 10% of the total) has already been observed before among the cladocerans (Atienza et al., 2008; Miyashita et al., 2011; Saito and Hattori, 2000; Wong et al., 2004, 2008), but it varies depending on the species (Egloff et al., 1997). The lack of *P. intermedius* gamogenetic female, and the very low proportion of males also observed in Brazilian populations in 2008 by Miyashita et al. (2011), shows a retraction of this phase throughout the study period 2000–2008 in the Bay of Biscay. Even for those species whose gamogenetic phase is longer (e.g. *E. nordmanni*), the trend is similar. Many authors have shown that unfavorable environmental conditions such as low values of temperature, salinity and dissolved oxygen (Atienza et al., 2008; Marazzo and Valentin, 2004a; Onbé, 1999; Pöllupüü et al., 2010) promote the emergence of the gamogenetic phase. These unfavorable conditions have not been observed in our study. Therefore, other reasons should be considered.

4.5. The role of predation

The presence of asexual or sexual forms is also modulated by predation, which acts on the most visible forms, that is to say, particularly but not exclusively on the pregnant females (Marazzo and Valentin, 2004a; Miyashita et al., 2011). Chaetognaths and fish larvae are often cited as cladocerans predators (Marazzo and Valentin, 2004b; Wong et al., 2004). Cladocerans populations react by changing their nyctemeral migration and breeding cycle rhythm. Thus, gravid females remain in deep areas during the day, and/or release their eggs or embryos before rising to the surface at dawn (Onbé, 1999; Saito and Hattori, 2000; Wong et al., 2004, 2008). In our study, samples were always taken in the early morning (see Section 2), and it is possible that these two processes explain, at least from 2006, the significant increase in non-breeding females which can be considered as parthenogenetic females having released their eggs or embryos before their ascent

to the surface. Moreover, we find in our study that, for all species, mean annual abundances of these parthenogenetic females have been decreasing from 2006 onwards.

4.6. The role of environmental variables

Many environmental factors modulate the dynamics and development of marine Cladocerans populations (Christou and Stergiou, 1998; Marazzo and Valentin, 2004b; Onbé, 1999). Among them, temperature and salinity are often seen as predominant (Christou and Stergiou, 1998), and this is also the result obtained by our CCA analysis. The latter shows that despite a trend towards the perpetuation of the species throughout the year (see above), there is still a clear alternation between winter populations with *E. nordmanni* and *P. intermedius*, and summer populations with *P. avirostris*, *E. spinifera* and *P. tergestina*. This is what also demonstrates high values of correlations between species of these two populations (Table 2). However, strong positive or negative correlations between species and measured environmental variables highlight their dominant role in structuring populations of cladocerans.

5. Conclusion

This work allows us to highlight some particular features of the temporal evolution of cladocerans populations in the Bay of Biscay, and to compare our results with earlier data (Alcaraz, 1981; d'Elbée and Castel, 1991, 1995; Villate and Orive, 1981). Significant changes were observed especially in maintaining populations throughout the year, and also changes in species dominance. Temperature and salinity are prominent environmental variables most likely to explain the temporal evolution of populations of cladocerans. On the scale of the thin water layer under the air-water interface, the variability of the gradients is high with great variability. Although we did not notice any significant trends in the temporal evolution of any hydrological variables during these eight years of monitoring, many authors have already shown these trends over longer time series and on a larger scale in the Gulf of Biscay (González-Pola et al., 2005; Michel et al., 2009; Pingree, 1994; Planque et al., 2004, 2006). It is clear that the changes highlighted in this work are strongly modulated by the regional and global climate change described by these afore-mentioned authors.

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References

- Alcaraz, M., 1981. Ciclo anual de los Cladóceros y Ostráceros planctónicos en la plataforma continental de Vizcaya (Punta Endata). Invest. Pesq. 45, 3–16.
- Alonso, M., 1996. *Crustacea Branchiopoda*. Coll. Fauna Iberica no. 7. Museo Nacional de Ciencias Naturales. Consejo Superior de Investigaciones Científicas. Madrid, 486 pp.
- Atienza, D., Saiz, E., Skovgaard, A., Trepal, I., Calbet, A., 2008. Life history and population dynamics of the marine Cladoceran *Penilia avirostris* (Branchiopoda: Cladocera) in the Catalan Sea (NW Mediterranean). J. Plankton Res. 30 (4), 345–357.
- Attrill, J.M., Wright, J., Edwards, M., 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol. Oceanogr. 52 (1), 480–485.
- Beaugrand, G., Goberville, E., 2010. Conséquences des changements climatiques en milieu océanique. [VertigO]. La revue électronique en sciences de l'environnement, no. 8. (<http://id.erudit.org/iderudit/045530ar>).
- Castège, I., Hémerly, G. (Coords), 2009. Oiseaux marins et cétacés du golfe de Gascogne. Répartition, évolution des populations et éléments pour la définition des aires marines protégées. Biotopie Eds, Mèze; M.N.H.N., Paris editions, 176 pp (Coll. Parthénope).
- Christou, E.D., Stergiou, K.I., 1998. Modelling and forecasting the fortnightly Cladoceran abundance in the Saronikos Gulf (Aegean Sea). J. Plankton Res. 20 (7), 1313–1320.
- d'Elbée, J., Castel, J., 1991. Zooplankton from the continental shelf of the southern Bay of Biscay exchange with Arcachon Basin, France. Ann. Inst. Oceanogr. 67, 35–48.
- d'Elbée, J., Castel, J., 1995. Evolution spatio-temporelle du zooplancton dans le Bassin d'Arcachon: le rôle des variables de milieu. Cah. Biol. Mar. 36, 33–45.
- d'Elbée, J., 2001. Distribution et diversité des copépodes planctoniques dans le Golfe de Gascogne. In: Elbée (d'), J., Prouzet, P. (Coord.) (Eds.), Océanographie du Golfe de Gascogne. Vlle Colloq. Int., Biarritz, 4–6 avril 2000. Ifremer ed., Actes Colloq., 31, pp. 147–156.
- d'Elbée, J., Castège, I., Hémerly, G., Lalanne, Y., Mouches, C., Pautrizel, F., D'Amico, F., 2009. Variation and temporal patterns in the composition of the surface ichthyoplankton in the southern Bay of Biscay (W. Atlantic). Cont. Shelf Res. 29, 1136–1144.
- d'Elbée, J., Prouzet, P., 2001. Océanographie du Golfe de Gascogne. Vlle Colloq. Int., Biarritz, 4–6 avril 2000. Ifremer ed., Actes Colloq., 31, 369 pp.
- Egloff, D.A., Fofonoff, P.W., Onbé, T., 1997. Reproductive biology of marine Cladocerans. Adv. Mar. Biol. 31, 79–168.
- García-Soto, C., Pingree, R.D., 1998. Late autumn distribution and seasonality of chlorophyll-a at the shelf-break/slope Region of the Armorican and Celtic shelf. J. Mar. Biol. Assoc. UK 78, 17–33.
- García-Soto, C., Pingree, R.D., 2009. Spring and summer blooms of phytoplankton (SeaWiFS/MODIS) along a ferry line in the Bay of Biscay and western English Channel. Cont. Shelf Res. 29 (8), 1111–1122.
- García-Soto, C., Pingree, R.D., 2012. Atlantic Multidecadal Oscillation (AMO) and sea surface temperature in the Bay of Biscay and adjacent regions. J. Mar. Biol. Assoc. UK 92, 213–234.
- Gattuso, J.-P., Hansson, L., 2011. Ocean acidification: background and history. In: Gattuso, L., Hansson, L. (Eds.), Ocean Acidification. Oxford University Press, pp. 1–20. (325 pp).
- González-Pola, C., Lavín, A., Vargas-Yáñez, M., 2005. Intense warming and salinity modification of intermediate water masses in the southeastern corner of the Bay of Biscay for the period 1992–2003. J. Geophys. Res. 110, C05020, <http://dx.doi.org/10.1029/2004JC002367>.
- Griffiths, F.B., Fleminger, A., Kimor, B., Vannucci, M., 1976. Shipboard and curating techniques, Zooplankton Fixation and Preservation. In: H.F., Steedman (Ed.), Monographs on Oceanographic Methodology UNESCO, Paris, pp. 17–19.
- Hays, G.C., Anthony, J., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol. 20, 337–344.
- Hémerly, G., D'Amico, F., Castège, I., Dupont, B., d'Elbée, J., Lalanne, Y., Mouchès, C., 2007. Detecting the impact of oceanic-climatic changes on marine ecosystems using a multivariate index: the case of the Bay of Biscay (North Atlantic-European Ocean). Global Change Biol. 14, 1–12.
- Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes in marine dinoflagellate and diatom abundance under climate change. Nat. Climate Change 2, 271–275.
- Hubert, P., Carbonnel, J.-P., Chaouche, A., 1989. Segmentation des séries hydro-météorologiques: applications à des séries de précipitations et débits de l'Afrique de l'ouest. J. Hydrol. 110, 349–367.
- Johns, D.G., Edwards, M., Greve, W., Sjöhn, A.W.G., 2005. Increasing prevalence of the marine cladoceran *Penilia avirostris* (Dana, 1852) in the North Sea. Helgol. Mar. Res. 59, 214–218, <http://dx.doi.org/10.1007/s10152-005-0221-y>.
- Marazzo, A., Valentin, J.-L., 2004a. Reproductive aspects of marine cladocerans *Penilia avirostris* and *Pseudevadne tergestina* (Crustacea, Branchiopoda) in the outer part of Guanabara Bay, Brazil. Braz. J. 64 (3A), 543–549.
- Marazzo, A., Valentin, J.-L., 2004b. Population Dynamics of *Pseudevadne tergestina* (Branchiopoda: Onychopoda) in Guanabara Bay, Brazil. Braz. Arch. Biol. Technol. 47 (5), 713–723.
- Margaritora, F.G., 1985. Cladocera. Fauna d'Italia. Caldini ed., Bologna, 400 pp.
- Michel, S., Vandermeersch, F., Lorange, P., 2009. Evolution of upper layer temperature in the Bay of Biscay during the last 40 years. Aquat. Living Resour. 22, 447–461.

- Miyashita, L.K., Gaeta, S.A., Rubens, M., Lopes, R.M., 2011. Life cycle and reproductive traits of marine podonids (Cladocera, Onychopoda) in a coastal subtropical area. *J. Plankton Res.* 33 (5), 779–792.
- Onbé, T., 1999. Ctenopoda and Onychopoda. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*, vol. 1. Backhuys Publishers, Leiden, pp. 797–813.
- Pingree, R., 1994. Winter warming in the southern Bay of Biscay and Lagrangian eddy kinematics from a deep-drogued Argos buoy. *J. Mar. Biol. Assoc. UK* 74, 107–128.
- Pingree, R., 2002. Ocean structure and climate (Eastern North Atlantic): in situ measurement and remote sensing (altimeter). *J. Mar. Biol. Assoc. UK* 82, 681–707.
- Pingree, R., 2005. North Atlantic and North Sea climate change: curl up, shut down, NAO and Ocean Colour. *J. Mar. Biol. Assoc. UK* 85, 1301–1315.
- Planque, B., Lazure, P., Jegou, A.-M., 2004. Detecting hydrological landscapes over the Bay of Biscay continental shelf in spring. *Clim. Res.* 28, 41–52.
- Planque, B., Lazure, P., Jegou, A.-M., 2006. Typology of hydrological structures modelled and observed over the Bay of Biscay shelf. *Sci. Mar.* 70 (1), 43–50.
- Põllupüü, M., Simm, M., Ojaveer, H., 2010. Life history and population dynamics of the marine cladoceran *Pleopsis polyphemoides* (Leuckart) (Cladocera, Crustacea) in a shallow temperate Pärnu Bay (Baltic Sea). *J. Plankton Res.* 32 (10), 1459–1469.
- Puillat, I., Lazure, P., Jégou, A.-M., Lampert, L., Miller, P.I., 2004. Hydrographical variability on the French continental shelf in the Bay of Biscay, during the 1990s. *Cont. Shelf Res.* 24 (10), 1143–1163.
- Puillat, I., Lazure, P., Jégou, A.-M., Lampert, L., Miller, P.I., 2006. Mesoscale hydrological variability induced by northwesterly wind on the French continental shelf of the Bay of Biscay. *Sci. Mar.* 70 (1), 15–26.
- Riebesell, U., Tortell, P.D., 2011. Effects of ocean acidification on pelagic organisms and ecosystems. In: Gattuso, J.-P., Hansson, L. (Eds.), *Ocean Acidification*. Oxford University Press, pp. 99–121. (325 pp).
- Saito, H., Hattori, H., 2000. Diel vertical migration of the marine Cladoceran *Podon leuckarti*: variations with reproductive stage. *J. Oceanogr.* 56, 153–160.
- Villate, F., Orive, E., 1981. Abundancia y distribución de las poblaciones de Cladoceros en el estuario de Plencia. *Invest. Pesq.* 45 (2), 327–336.
- Villate, F., Moral, M., Valencia, V., 1997. Mesozooplankton community indicates climate changes in a shelf area of the inner Bay of Biscay throughout 1988 to 1990. *J. Plankton Res.* 19, 1617–1636.
- Villate, F., Aravena, G., Iriarte, A., Uriarte, I., 2008. Axial variability in the relationship of chlorophyll a with climatic factors and the North Atlantic Oscillation in a Basque coast estuary, Bay of Biscay (1997–2006). *J. Plankton Res.* 30 (9), 1041–1049.
- Wong, C.K., Ji, C., Nip, H.M.T., 2004. Diel cycle in the percentage abundance of parthenogenetic females with embryos of different developmental stages in four species of marine cladocerans. *J. Plankton Res.* 26 (9), 1095–1103.
- Wong, C.K., Li, V.C.Y., Chan, A., 2008. Diel cycles of reproduction and vertical migration in the marine Cladocerans *Pseudevadne tergestina* and *Penilia avirostris*. *J. Plankton Res.* 30 (1), 65–73.