Zooplankton long-term changes in the NW Mediterranean Sea: Decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes?

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A B S T R A C T

Copepod, chaetognath, decapod larva, siphonophore and jellyfish monthly abundances, from 1974 to 2003 at Point B (northwestern Mediterranean), were obtained with the ZooScan. Principal component analysis (PCA) was performed on zooplankton, and another PCA on local environment. Almost-decadal periods (1974–1982, 1983–1991, 1992–1999, and 2000–2003) were distinguished in the 1st PC of zooplankton, and that of local environment (1974–1980, 1981–1991, 1992–1998, and 1999–2003). The 1st PC of local environment was correlated with winter North Atlantic Oscillation (NAO) until early 1990s. In early 1980s, all groups increased and the majority of the decade abundances were above the long-term average for most groups. In the 1990s, all decreased, and in early 2000s they increased. This synchrony suggests bottom-up control as main mechanism structuring these groups. The 1980s were characterized by low winter temperature and high salinity. We hypothesize that phytoplankton production was favored during that decade due to increased nutrient uprise to surface by strong winter vertical mixing. In the 1990s salinity decreased probably to the detriment of vertical mixing and carrying capacity of the system. These results stress the role of salinity as physical forcing on water-column stability, in the NW Mediterranean, and the importance of winter conditions to determine the state of pelagic ecosystems.

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1. Introduction

Changes in climatic conditions may alter the structure and dynamics of pelagic ecosystems (IPCC, 2007) and plankton are good indicators of those climate changes (Hays et al., 2005). Notably, temperature changes have been suggested to cause regime shifts in plankton ecosystems. For example, in the North Pacific shifts between a cool high-productivity system and a warm low-productivity system have appeared about every 10 years with turning points in 1977, 1989 and 1998 (Hare and Mantua, 2000; Mackas et al., 2007; Peterson and Schwing, 2003). In the Atlantic Ocean, a regime shift from cold to warm biotopes, with a turning point in 1987, has been described and related to the North Atlantic Oscillation (NAO) and surface temperature anomalies in the Northern Hemisphere (NHT) (Beaugrand and

Ibanez, 2004; Reid et al., 2001, 2003). A regime shift, synchronous to the one in the North Sea in the late 1980s, has also been reported in the marine ecosystems of the central Baltic and related to temperature increase and salinity decrease (Alheit et al., 2005). A critical thermal boundary of 9–10 °C has been appointed to provoke the regime shifts in the North Atlantic (including the North Sea) and in the Baltic Sea (Beaugrand et al., 2008). This thermal boundary would affect organisms for being a thermal physiological threshold for many species and for a related decrease of seasonal stability with temperature. Regarding Mediterranean plankton, very few studies on long-term variation have been conducted, due to the paucity of long-term time series. Yet, recently the appearance of regime shifts with their turning points in 1987 in two northern Mediterranean coastal ecosystems and their synchrony with changes in the Atlantic ocean and the Baltic and Black seas has been highlighted (Conversi et al., 2010). The authors pointed to the positive trend of surface temperature in the northern hemisphere as the main forcing for the concomitant changes in such far and diverse locations.

The Mediterranean Sea, a semi-enclosed basin connected to the Atlantic Ocean, has been proposed as a suitable model to investigate

climate change and anthropogenic effects on marine ecosystems (Duarte et al., 1999; Turley, 1999). Several studies, mainly performed in the western Mediterranean basin, revealed long-term changes in the hydrographic and meteorological conditions, with warming water, less rainfall and lower wind-speed trends from the early 1980s (Bethoux et al., 1990; Trigo et al., 2000; Vargas-Yáñez et al., 2008). Increasing temperature and salinity have modified water circulation and dense water formation (Astraldi et al., 2002; Herbaut et al., 1997; Samuel et al., 1999). These hydrographic changes have been related to the NAO by its effect on local atmospheric forcing (Rixen et al., 2005; Tsimplis and Josey, 2001; Vignudelli et al., 1999). Results from two zooplankton time series in the northwestern Mediterranean have shown that interannual abundance patterns fitted the interannual pattern of the winter NAO (Fernández de Puelles and Molinero, 2007; Molinero et al., 2005, 2008).

The longest Mediterranean zooplankton time series is the one conducted since 1966, without interruption, at Point B in the Bay of Villefranche (Ligurian Sea, northwestern Mediterranean). Molinero et al. (2005) studied the abundance of several copepod, jellyfish and siphonophore target species from 1967 to 1993 at Point B. The authors proposed a cascade of links between the large-scale climate pattern occurring in the North Atlantic, and the local climate variability governing the northwestern Mediterranean. The sequence of events appeared to be driven by the long-term temperature anomalies that in turn played a key role in the top-down control of copepods by jellyfish. Further research on the same long-term pelagic time-series, with chaetognath temporal evolution included in the analyses, suggested that a regime shift had taken place in 1987 in the Ligurian Sea (Molinero et al., 2008). According to the authors, the system evolved towards a more regeneration-dominated ecosystem in which jellyfish controlled copepods and chaetognaths by predation and competition, respectively. Thermal stratification was appointed to be the main force ruling zooplankton composition, and a community dominated by gelatinous zooplankton was predicted due to water warming in the 1990s (Molinero et al., 2008). Such shifts in community structure deserve more attention because they may indicate a general trend of changes in the dynamics of pelagic ecosystems forced by global warming (Perry et al., 2004). For example, global warming has been appointed to be detrimental to primary production in low and mid-latitude marine ecosystems due to enhanced thermal stratification that entails less nutrient input into the trophic layer (Behrenfeld et al., 2006; Sarmiento et al., 2004).

The main aim of the present work was to undertake the analysis of the Point B time series well beyond the published results (10 recent years added) and to compare the resulting assessments to those made in the previous studies. The methodology applied in our work differs from that of Molinero et al. (2005, 2008) in several aspects. (1) We analyzed the abundance of broad zooplankton groups (e.g., total copepods, total chaetognaths) to check if the long-term changes reported in their work for some target species up to 1993 were also observed when considering the whole community. Monthly abundance of copepods, decapod larvae, chaetognaths, carnivorous medusae (hereafter named jellyfish) and siphonophores were analyzed for the period from 1974 to 2003 (30 years). (2) To accelerate and standardize the time-series construction, the zooplankton community was analyzed using the ZooScan digital imaging system (Gorsky et al., 2010; Grosjean et al., 2004), coupled with automated and semi-automated object recognition. Finally, (3) in addition to analyzing the results obtained by PCA performed on average annual values of original variables, as was done in the previous studies, we also present monthly data to observe the temporal variability at different seasons.

2. Materials and methods

2.1. Zooplankton datasets

The sampling site (Point B, 43° 41 N; 7° 19E) is situated at the entrance of the Bay of Villefranche, in the Ligurian Sea (northwestern Mediterranean) (Fig. 1). The site is affected by hydrographic–climatic variability such as the Ligurian Current flow, wind patterns and by open sea conditions due to a narrow continental shelf and the presence of a submarine canyon (~2000 m depth) in front of the bay. Zooplankton sampling at Point B has been performed since 1966 on a daily basis (from Monday to Friday), with few exceptions, over a bottom depth of 80 m (water column sampled: 0–75 m).

The plankton samples analyzed in this study belong to the same sample collection studied by Molinero et al. (2005, 2008). Vertical hauls were performed with a Juday-Bogorov net (330 μm mesh size and 0.5 m opening diameter) from 75 m depth to the surface. Daily samples were pooled in a single beaker on a weekly basis. Organisms were preserved by formol fixation (2.5%) buffered with borax (Sodium Borate) until saturation. Samples corresponded to the period 1974–2003. The period from 1966 to 1973 could not be included due to dubious metadata that needed validation and thus those samples were not scanned at the moment of this study. With few exceptions, one sample per month (the sample of the week that included the 15th of each month) was analyzed. Out of the 360 months corresponding to the 30-year time series, 17 non-continuous months were missing, and 18 extra samples corresponding to the previous and following week of extreme values were analyzed to verify outliers. In total, 359 samples were digitized.

The constancy of the sampling strategy makes our datasets homogeneous and comparable over time. Moreover, results can be compared with those of Molinero et al. (2005, 2008) for sharing the same sampling methodology. Underestimation of the copepod small-size fraction (e.g., nauplii, copepodites, *Oithona sp.* and *Oncaea sp.* adults) is likely to be expected with the 330 μm mesh-size used (Calbet et al., 2001). In addition, jellyfish and siphonophores often require a larger mesh-size to avoid damage of their gelatinous bodies (Molinero et al., 2005), and therefore their abundance estimates could be biased by the net sampling. By pooling daily samples weekly, variability due to small-scale patchiness is reduced.

2.1.1. Zooplankton digitization

Preserved zooplankton samples were analyzed with the ZooScan digital imaging system (http://www.zooscan.com), developed in the Laboratory of Oceanography of Villefranche (LOV) (Gorsky et al., 2010; Grosjean et al., 2004). The ZooScan provides standardized measurements (i.e., steady image quality and parameterized measures) of abundance and body size of the zooplankton contained in preserved net samples.

Each sample was first separated in two size-fractions (200–500 μm and >500 μm). Separation in two size-fractions prevented misrepresentation of rare large organisms in the scanned subsample caused by excessive dilution during the splitting process. Each fraction was split with a Motoda Plankton Splitter (Motoda, 1959) until the subsample was diluted enough to allow separation of all organisms in the scanning tray (~1000 objects per scan). The two sub-samples were digitized with the ZooScan at 2400-dpi resolution and the resulting images had $17,500 \times 7000$ pixels (i.e., each pixel was equivalent to $10.58\ \mu m^2$).

2.1.2. Automatic and semi-automatic taxonomic recognition

The digital dataset consisted of 718 raw images (i.e., two images corresponding to two size-fractions per sample) with ~1000 objects per image. The whole ZooScan processing, from the image scanning to the acquisition of the data matrix, was done with the Zooprocess software. Automatic recognition by supervised-learning was performed with the Plankton Identifier software. For details on the methodology of the ZooScan integrated system see Gorsky et al. (2010).

Each object was characterized by several size, shape and gray level related measures. The learning set (i.e., collection of objects arranged in different categories) created to act as reference for the automatic
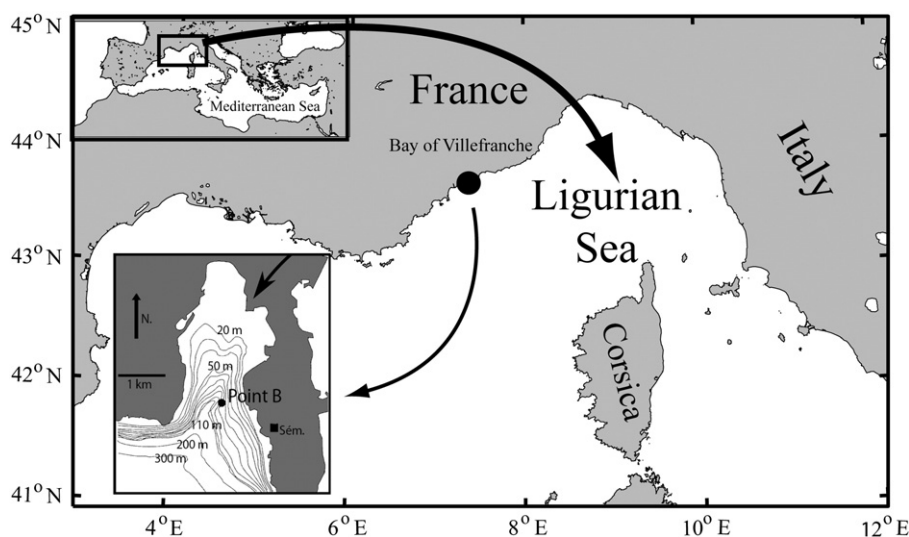
Fig. 1. Location of the Ligurian Sea in the Western basin of the Mediterranean Sea, and Point B sampling site at the entrance of Villefranche Bay.

classifier consisted of 13,100 objects. To avoid recognition biases related to temporal variability, the objects integrating the learning set were randomly and equitably picked from 8 non-consecutive years of the time series, and with all months equally represented. The automatic classifier consisted of 26 categories (17 biological and 9 detritus and artifact categories), and the supervised-learning algorithm used was the Random Forest algorithm (Breiman, 2001). This algorithm is suitable for zooplankton image recognition (Bell and Hopcroft, 2008; Gorsky et al., 2010; Grosjean et al., 2004). The recognition accuracy, estimated from a cross-validation (2 folds, 5 trials), applied on the learning set was very satisfactory for copepods; 96% of copepods were recognized (recall) although 19% (1-precision) of the copepod category corresponded to contamination (i.e., objects from other categories misclassified as copepods). Accuracy was less good for the other zooplankton groups analyzed in this work (top-10 automatic classification of categories in Table 1).

To verify the proficient accuracy of copepod automatic recognition, automatic estimates were compared to the true copepod abundance in 60 samples independent of the learning set (i.e., test set) and belonging to five non-consecutive years (Fig. 2). Although there was a slight overestimation of copepods by automatic recognition (i.e., most estimates slightly above the 1:1 linear relationship) due to contamination, the relationship was not significantly different from 1:1 (1000 Bootstrap trial, 5% confident interval, slope = [0.95 1.05]), and there

was a close linear fit between the true counts and the automatic estimates ($r^2 = 0.95$, $n = 60$, $p < 0.01$). Thus, copepod standing stocks can be monitored by automatic classification from ZooScan images.

The automatic classification of chaetognaths, decapod larvae, jellyfish and siphonophores was manually validated (i.e., semi-automatic recognition as defined in Gorsky et al., 2010). Sorted objects were visually examined and misclassified organisms were rearranged in the four groups. Jellyfish and siphonophores were manually sorted from the single gelatinous zooplankton category. In the case of colonial siphonophores, only the first bell was taken into account and considered as a single individual. The decapod larvae time series, not considered in the study of Molinero et al. (2005, 2008), was added to the analysis to represent meroplankton.

2.2. Hydrographic and meteorological datasets

Water temperature and salinity were measured weekly at Point B at 0, 10, 20, 30, 50 and 75 m depths. Before 1991 temperature was measured with a reversing thermometer while salinity was estimated with an induction salinometer (Etienne et al., 1991). From 1991 onwards these measurements were conducted by means of a Seabird

Table 1
Automatic-recognition accuracy on the top-10 categories respect to classification success. Recall (proportion of objects well recognized among all objects belonging to a certain category) and 1-Precision (proportion of objects wrongly assigned to a certain category by automatic recognition) are calculated from cross-validation (2 folds, 5 trials) applied on the learning set.

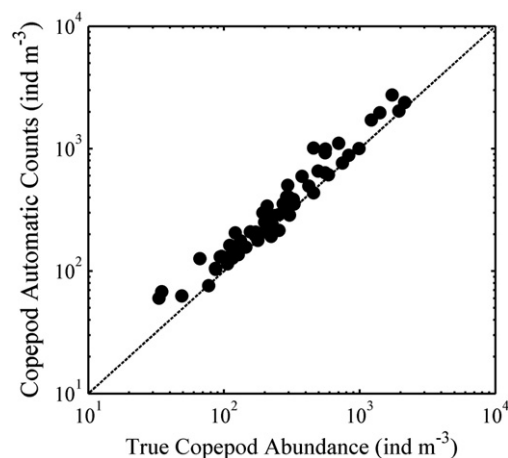| Groups	Recall	1-Precision
Copepod	0.96	0.19
Appendicularia	0.87	0.22
Appendicularia tail	0.85	0.08
Pteropoda Cavolinia	0.81	0.18
Gelatinous Zooplankton	0.81	0.25
Chaetognatha	0.77	0.12
Cladocera Penilia	0.71	0.29
Cladocera	0.66	0.38
Jellyfish A. hemistoma	0.64	0.19
Decapod larvae	0.48	0.31

Fig. 2. Relationship between the true abundance of copepods in the samples and the automatic estimates.

SBE25 CTD. Water density was calculated from salinity, temperature and sampling-depth (Fofonoff and Millard, 1983; Millero et al., 1980). In addition, nitrate (NO_3) concentration was available from 1992 for same depths and frequency as temperature and salinity. Water was sampled with Niskin bottles, filtered onto 47-mm GF/F Whatman fiber filters and concentration was estimated using standard colorimetric techniques.

Local meteorology was provided by Meteo France, the French national weather organization. Atmospheric pressure, irradiance and precipitation daily measurements were recorded at a station next to Nice airport (43°39′12″N, 7°12′00″E, 4 m above sea level). A methodological bias, due to a change in the position of the Nice airport anemometer in 1989, prompted us to use wind speed measurements from the Cap Ferrat semaphore station (43°41′00″N, 7°19′42″E, 138 m height) instead. The Cap Ferrat station was not operational from August 1991 until December 1996. Missing data were estimated by type II regression between the wind speed recorded at Nice airport from 1989 (after the anemometer relocation) and the wind speed registered at Cap Ferrat. Both speeds were previously recalculated for a 10 m height from sea level. The linear regression ($r^2 = 0.72$) obtained from 5478 daily observations was:

$$\text{Wind speed}_{C.F.} = 0.68335 \times \text{Wind speed}_{N.A.} - 2.78.$$

After the gap was filled, the Ekman depth was calculated from wind speed using the formula reported by Cushman-Roisin (1994).

Winter NAO (December–March mean value) was calculated from the monthly time series provided by the Climate Prediction Center (CPC) of the National Oceanic and Atmospheric Administration (NOAA) (http://www.cpc.noaa.gov). We opted for this dataset because it is based on the orthogonally rotated principal component analysis (RPCA) which takes into account spatial coverage of the teleconnection and so it is less sensitive to changes in the position of the centers of action (Barnston and Livezey, 1987).

2.3. Data analysis

Data analyses were performed with Matlab® 7.0 (The Mathworks, Inc., Natick, MA). All datasets were regularized to one sample per month. Monthly environmental values were the average of daily (meteorology) or weekly (hydrography) data. In the case of zooplankton abundance, monthly values were those of the week containing the 15th of each month (week 2 or 3 of each month). Missing values were predicted by Eigen-Vector Filtering (EVF) (Colebrook, 1978; Ibanez and Conversi, 2002; Ibanez and Etienne, 1992).

A stepwise statistical method was applied to synthesize temperature and salinity information at the six depths, without missing the main pattern of temporal changes (Escoufier, 1973; Robert and Escoufier, 1976). The aim of this method is to search for linear combinations of m variables (m<p, p being the total number of variables, in this case six depth temporal profiles) such that the temporal pattern of the resulting combination (1st PC of m variables) is as close as possible to the original pattern of p variables (1st PC of the p variables) (see Appendix A for detailed explanation). For both T and S, 20 m and 50 m depths were retained. These two depths represent the layers above and below the seasonal thermocline.

Seasonal patterns were represented by depicting monthly values in a plot in which the x-axis corresponded to the year, the y-axis to the month of each observation, and the color (z) represented the value of the variable. Zooplankton abundance was transformed to its natural logarithm (log (abundance + 1)) to better see the whole range of changes. Interannual changes were presented by computing the annual normalized anomalies. Annual mean values were centered by subtracting the arithmetic average of the 30 annual mean values, and then reduced by dividing each of the annual centered mean values by the standard deviation of those 30 annual mean values.

A boxplot was used to show differences between NO_3 concentration at surface during high density events and during the rest of the February to March period, when the highest annual density records occurred. The central mark of each box represents the median of the data distribution, whiskers are 1.5 times the interquartile range and crosses indicate outliers. Boxplots were notched to represent a robust estimate of the uncertainty about the medians for box to box comparison. The comparison was done with a Mann–Whitney–Wilkoxon test which is the non-parametric equivalent of a Student's t-test.

To obtain the general modes of zooplankton and environmental conditions, a principal component analysis (PCA) (Jollife, 2002) was performed on the annual mean values of zooplankton abundances (i.e., copepods, decapod larvae, chaetognaths, siphonophores and jellyfish), and another PCA was performed on the hydro-climate annual-mean conditions (i.e., water temperature and salinity, atmospheric pressure, rainfall, irradiance and Ekman depth). The PCA analyses were performed on centered and reduced anomalies. To distinguish the main periods in both environmental and zooplankton general modes (1st PCs), the cumulative sum (cusum) of the deviations from the mean was computed. Periods were individualized by the turning points of the curve. By this method, the sign and steepness of the slopes reflects the deviation of a period from the time-series mean value (Ibanez et al., 1993).

Co-variation of the winter NAO and the 1st PC of local environment was established by calculating the Bravais–Pearson correlation coefficient accounting for the reduction of degrees of freedom due to autocorrelation (Chelton, 1984; Pyper and Peterman, 1998). Following Kirby and Beaugrand (2009), a sliding correlation analysis (10-year window) was applied to monitor the temporal stability of the relationship between both signals. Correlations were calculated on periods of 10 years by moving one year at a time from the first 10 years until completing the time series. To asses the sensitivity of the method to the window size, analyses with five-year and 15-year windows were tested, and results gave the same conclusions.

3. Results

3.1. Zooplankton changes

All the studied groups (i.e., copepods, jellyfish, siphonophores, chaetognaths, and decapod larvae) had rather similar long-term changes during the 30-year study (Fig. 3). In the 1980s (from 1983), most of the annual concentrations were above or close to the long-term average. At the beginning of the 1990s concentrations decreased, and during the 1990s annual values were below the long-term average except for two years in the case of gelatinous zooplankton. From 2000, the groups presented higher concentrations than in the late 1990s. Despite the common long term pattern, while copepods and decapod larvae displayed high concentrations from 1982–1983 to 1991–1992 (Fig. 3A and B), the high concentration period of the other groups were more restricted. In the case of siphonophores and jellyfish, high abundances appeared one year later, in 1984 (Fig. 3D and E). For chaetognaths, siphonophores and jellyfish, the period of high concentration ended earlier, in 1989–1990 (Fig. 3C–E). In addition, copepods and chaetognaths showed a short period of concentration above the average in the mid 1970s (Fig. 3A and C) not recorded for the rest of the groups.

At seasonal scale, the different groups did not show the same pattern. Copepod common seasonal feature was a recurrent spring peak for the whole time series (Fig. 4A). Yet, there was a relatively high interannual variability in the seasonal cycle of this group. Indeed, the spring peak spread out from late winter to early summer depending on the period. From 1976 to 1979, a high annual peak was recorded in summer that was not present in the rest of the time series. Regarding the autumn season, a peak was recorded from 1983
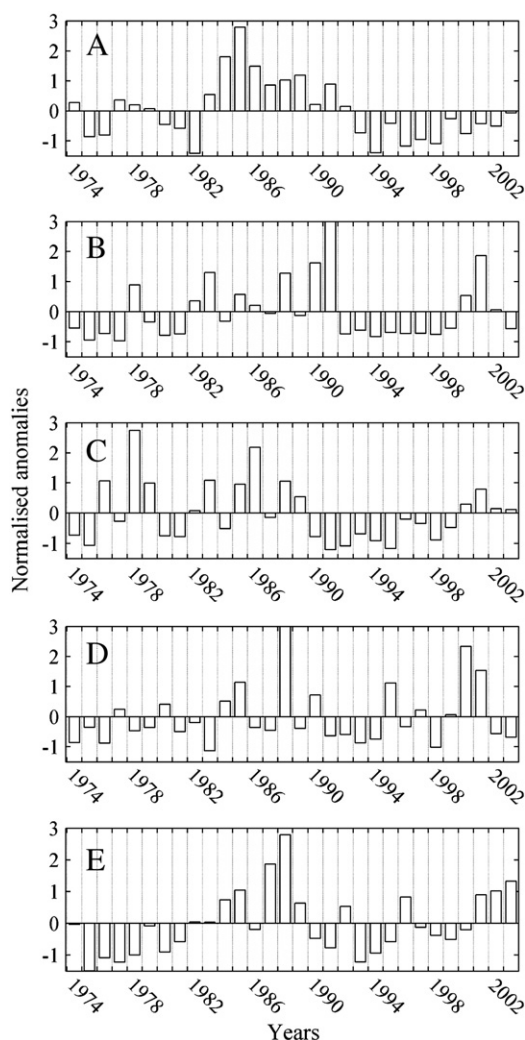
Fig. 3. Normalized anomalies of the mean annual abundance of (A) copepods, (B) decapod larvae, (C) chaetognaths, (D) siphonophores and (E) jellyfish, at Point B from 1974 to 2003.
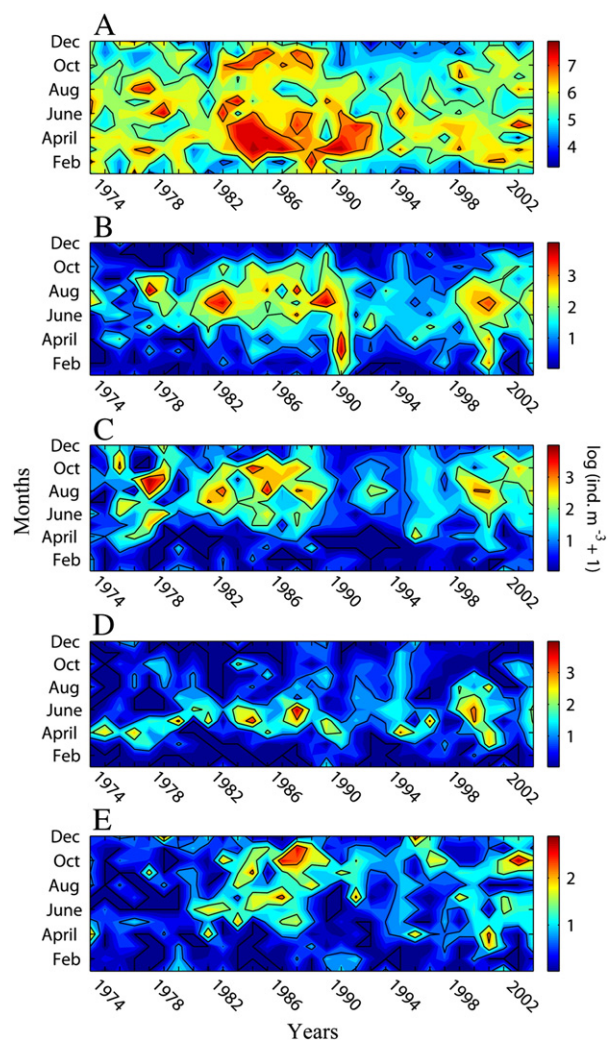

Fig. 4. Seasonal and interannual variability of log (abundance + 1) of (A) copepods, (B) decapod larvae, (C) chaetognaths, (D) siphonophores and (E) jellyfish, at Point B from 1974 to 2003.

to 1989; it disappeared in the 1990s and reappeared, less marked and more spread out, in the 2000s. Decapod larvae usually peaked in summer, from July to August, and were poorly represented in winter and late autumn (Fig. 4B). Chaetognath seasonal cycle consisted of a single peak occurring between August and October and only in the mid-1970s high abundances were registered earlier in summer (Fig. 4C). Compared to the other groups, the siphonophore seasonal cycle was quite constant along the 30-year time series, with narrow peaks taking place in spring, from April to June depending on the year (Fig. 4D). Finally, jellyfish were usually rare in winter and early spring, and sporadic peaks spread from April to November (Fig. 4E).

The three first PCs of the PCA accounted for 78% of zooplankton abundance variability (Table 2A). The 1st PC represented 44% of total variance, and all groups contributed with similar factor loadings and same direction to the creation of this axis (range of contribution 0.40–0.50). Thus, the 1st PC represented a smoothed pattern of interannual changes of all the studied groups. The 2nd PC (19%) reflected an opposition of copepods, decapod larvae and chaetognaths to siphonophores and jellyfish abundance patterns. In the first three groups, the decrease between the 1980s and the 1990s was the most marked long-term pattern in their time series, whereas for the gelatinous

zooplankton the most marked pattern during the 30 years was the lowest presence records in the 1970s (Figs. 3 and 4).

3.2. Environmental changes

The 30-year mean temperature and its standard deviation were 16.9 ± 0.5 (°C) at 20 m depth, and 15 ± 0.4 (°C) at 50 m depth. Before 1983, annual mean temperature was below the long-term average, except in 1977 (Fig. 5A). From 1983 to 1990, it was above the average except for 1984–1985 and 1988. From 1991 to 1993, annual mean temperature was again below the average, with values similar to those recorded before 1983. From 1995 temperature was constantly above the long-term average.

The 30-year mean salinity and its standard deviation were 38 ± 0.1 at 20 m depth, and 38 ± 0.1 at 50 m depth. Before 1980, annual mean salinity was below the long-term average, except for the 1975–1976 years (Fig. 5B). From 1980 to 1988, salinity was above the average. Inside this period, the 1983–1985 annual mean salinity was lower than adjacent years. From 1989 to 1998, annual mean salinity was lower than the long-term average, except for 1991 and 1994–

1995 when mean records were slightly above the average. From 1999, annual mean salinity was above the long-term average except for 2002.

The 30-year mean winter density (February–March mean) and its standard deviation were 28.7 ± 0.2 (kg m^{-3}) at 20 m depth, and 28.9 ± 0.2 (kg m^{-3}) at 50 m depth. Before 1980, winter density was below the long-term average, except for the 1975–1976 period (Fig. 5C). From 1980 to 1993, winter density was above the average, except for 1983 and 1990. The highest records of the 30-year time series occurred from 1981 to 1987. From 1994 to 1998, winter density was below the long-term average, except for 1995–1996 that presented density values close to the average. From 1999 winter density was above the average, except for 2001.

Each year, the classic thermal seasonal cycle of temperate zones was observed (Fig. 6A). Thermocline formation occurred at the beginning of summer, and water column remained stratified until autumn. The lowest minimal winter temperatures of the time series at 20 m depth were observed from 1979 to 1987. Annual maximal temperature, in summer, was below the long term average during the 1970s. The 1980s showed the highest annual temperature amplitude of the time series. In addition, summer thermal stratification occurred one month earlier from the mid-1980s as indicated by the 19 °C isoline at 20 m depth. Salinity annual minimum was usually recorded in spring and the maximum in autumn/winter (Fig. 6B). From 1981 to 1986, winter salinity was higher than in the rest of the studied period. Density presented the combination of temperature and salinity patterns (Fig.6C). The density pattern showed that stratification onset tended to occur earlier in the year. From 1980 to 1988, winter water at 20 m depth was denser than in the rest of the time series.

Every year, highest sea water density records at 20 m depth occurred between February and March (Fig. 6C). In the 1980s, 60% of those monthly cases presented values above 28.85 kg m^{-3} at 20 m depth, while in the 1990s it decreased to 20% of the cases. In the studied area, winter waters with 28.85–29.05 kg m^{-3} density are usually observed as deep as 200–350 m depth near the coast (Stemmann et al., 2008). From 1992 to 2003, period of nitrate measurements at Point B, water with density higher than 28.85 kg m^{-3} had significantly higher surface nitrate concentration than water with density lower than 28.85 (Fig. 7). The null hypothesis of equal medians was rejected ($p < 0.00001$) when applying a Mann–Whitney–Wilkoxon test.

The three first synthetic axes (PCs) created by PCA accounted for 73% of the variance of environmental conditions (Table 2B). The 1st PC accounted for 33% of the general variability. It was mainly driven by salinity (0.47–0.5 contribution), with precipitation opposing it. Still,
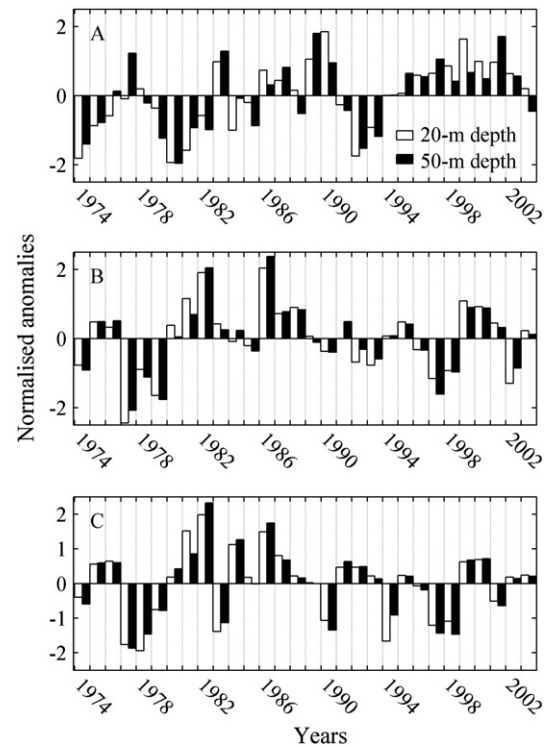

Fig. 5. Normalized anomalies, at Point B from 1974 to 2003, of mean annual (A) temperature, (B) salinity and (C) winter density, at 20 and 50-meter depth.

the rest of original variables contributed in positive direction to the construction of this axis (range of contribution 0.20–0.36). The 2nd PC (26%) mainly reflected the temperature signal. Interannual normalized-anomalies of the winter NAO and the environmental 1st PC significantly co-varied ($r = 0.54/p = 0.005$) (Fig. 8A). Yet the
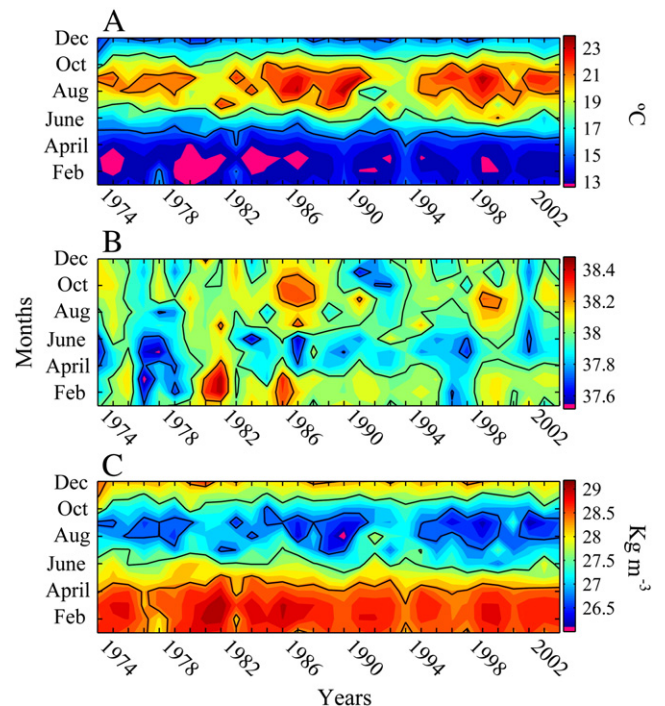
Table 2
Contribution of each variable to the first three principal components (PCs) of two PCAs conducted on (A) zooplankton abundances and (B) environmental conditions. Explained variances are indicated between brackets.

A. Zooplankton	Variables	1st PC (44%)	2nd PC (19%)	3rd PC (15%)
	Copepods	0.50	−0.24	−0.31
	Decapod larvae	0.45	−0.13	0.71
	Chaetognaths	0.40	−0.62	−0.04
	Siphonophores	0.40	0.66	0.28
	Jellyfish	0.47	0.33	−0.57
B. Environment	Variables	1st PC (33%)	2nd PC (26%)	3rd PC (14%)
	Temperature 20 m	0.27	0.54	0.14
	Temperature 50 m	0.22	0.57	0.14
	Salinity 20 m	0.50	−0.33	0.24
	Salinity 50 m	0.47	−0.32	0.36
	At.Pressure	0.36	0.11	0.08
	Precipitation	−0.38	0.03	0.20
	Irradiance	0.31	0.24	−0.65
	Ekman depth	0.20	−0.31	−0.57

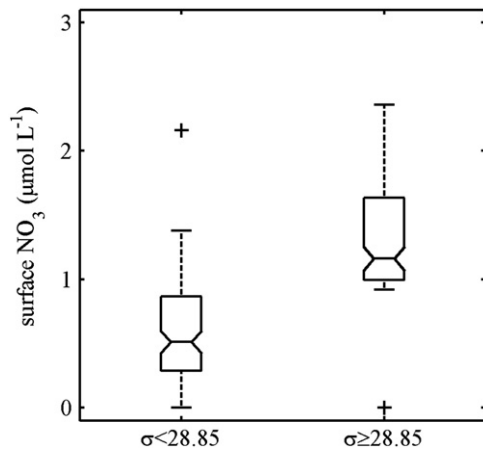Fig. 6. Seasonal and interannual variability of (A) temperature, (B) salinity and (C) density at 20 m depth.

Fig. 7. Nitrate concentration at surface in February–March (1992–2003) for water density at 20 m depth below the threshold ($\sigma<28.85$ kg m^{-3}, 60 cases), and high density water ($\sigma>28.85$ kg m^{-3}, 19 cases). The central mark of each box corresponds to the median of the monthly distribution, whiskers are 1.5 times the interquartile range and crosses indicate outliers. Median notches not overlapping indicate significant higher nitrate concentration when density exceeded 28.85 kg m^{-3}, corroborated by the Mann–Whitney–Wilkoxon test.
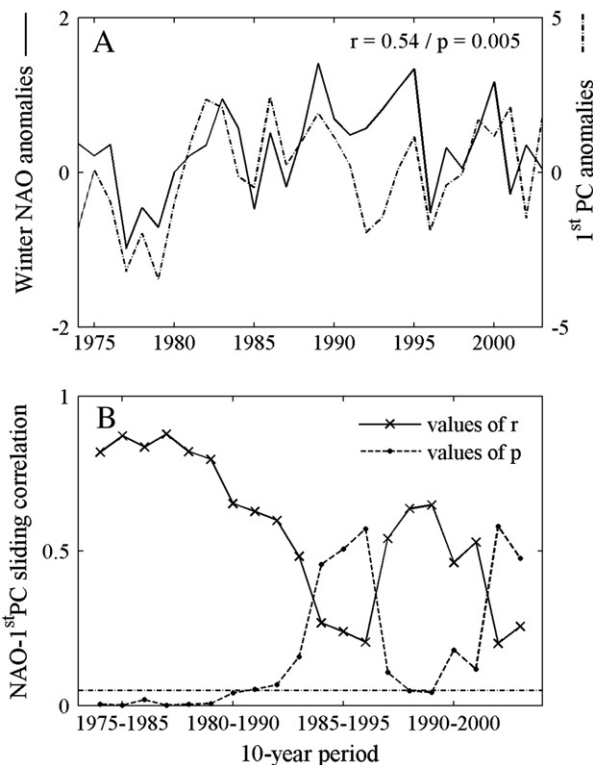

Fig. 8. (A) Correlation between the annual normalized anomalies of the winter NAO (continuous line) and the 1st PC of local environmental variables (dashed line), and (B) sliding correlation analysis of both variables using a 10-year window (the horizontal dashed line indicates the 0.05 level of significance).

correlation was not stable over the years, as reflected by the 10-year sliding correlation (Fig. 8B). The first half of the 1990s the correlation was lost (Fig. 8B) and in the early 2000s the relationship even reversed (Fig. 8A).

3.3. Environmental and zooplankton fluctuations

Cumulative sums (cusums) of the 1st PC anomalies, of both environmental (Fig. 9A) and zooplankton (Fig. 9B) datasets, showed
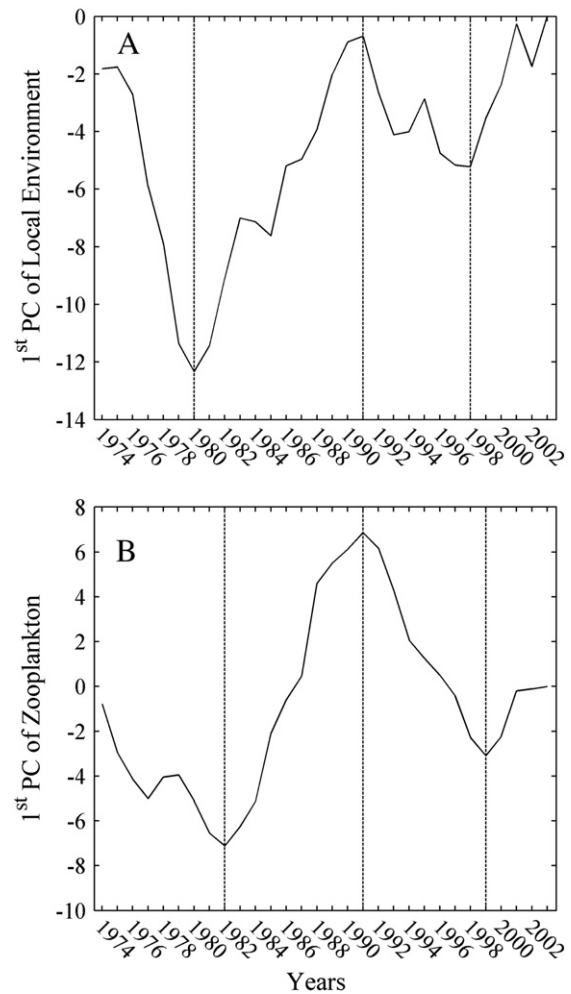

Fig. 9. Cusum of annual normalized anomalies of (A) the 1st PC of local environmental variables and (B) the 1st PC of the abundance of zooplankton groups.

striking resemblance. In both cases, four general periods could be clearly distinguished: The 1970s (until 1980 for environmental conditions and 1982 for zooplankton), the 1980s (1981–1991 for environment and 1983–1991 for zooplankton), the 1990s (1992–1998; 1992–1999) and the 2000s (from 1999 and 2000 respectively).

4. Discussion

One of the aims of the present work was to assess if the interannual zooplankton changes found in the Bay of Villefranche by Molinero et al. (2005, 2008) studying several target species (e.g., *Centropages typicus*) over the period 1967 to 1993, were also observed when studying broad zooplankton groups (e.g., total copepods). For the overlapping period (1974–1993), the interannual changes observed in chaetognath and copepod stocks were similar to those reported by Molinero et al. (2008). Concerning chaetognaths, this similarity is not surprising since in both studies individuals were counted without any species distinction. This observation confirms that our new methodology (i.e., ZooScan semi-automatic counts) gives results that can be compared with previous studies performed with traditional methodology (i.e., counts under the microscope). In the case of copepods, both patterns were similar because although in the former study the copepod signal was built with few species, those were key species of the seasonal succession of Mediterranean

copepods (i.e., *Centropages typicus* and *Acartia clausi* peak in spring, *Oithona spp.* and *Oncaea spp.* peak between summer and autumn, and *Temora stylifera* represents the autumn community) and thus they may be representative of a wide range of physiological constraints. While the chaetognath and copepod groups showed similar trends in both studies, the estimated abundance of the broad jellyfish and siphonophore groups presented here showed a different interannual pattern to the one suggested by the 1st PC computed by Molinero et al. (2005) using four medusae species (*Pelagia noctiluca*, *Liriope tetra-phylla*, *Solmundella bitentaculata*, and *Rhopalonema velatum*), two siphonophores (*Abylopsis tetragona* and *Chelophyes appendiculata*) and one ctenophore species (*Pleurobrachia rhodopissome*). Our datasets showed a decrease of jellyfish (medusae) stocks from 1989, concomitant to the disappearance of the copepod autumn peak, and a slight decrease of siphonophore abundance in the 1990s, whereas the 1st PC of jellyfish of the former study suggested a continuous increase from the beginning of the 1990s. Such contrasting results in the two studies highlight the difference between considering few target species and studying the whole community. The relative magnitude of changes in species abundance/biomass, phenology, and physiological condition is often larger than that of the changes in total biomass or abundance of broader groups (Mackas and Beaugrand, 2010). At species level covariance with climate is often stronger than at broader taxonomic levels because each species has its particular requirements depending on the niche they occupy and, if their niche breadths are narrow, slight climatic changes can critically alter their population dynamics (Parmesan, 2006; Thuiller et al., 2005). Yet, studies based on the relationship between individual species and climate have limited potential for inferring changes at the plankton ecosystem level (Beaugrand and Ibanez, 2004). Species diversity does not necessarily imply functional diversity, and effects in some species can be compensated at community level by other species with overlapping niches (Hooper et al., 2005). Thus, the analysis of broad groups, as in our study, does not substitute but efficiently complements the species level approach, and may act as an indicator of the effect of climate change on the total plankton production of an ecosystem.

Another aim of this work was to revisit the mechanisms shaping the interannual variability of zooplankton in the Ligurian Sea. In our study, the jellyfish community did not continue to increase from the early 1990s, contrary to the hypothesis of jellyfish dominance suggested by the analysis of the time series until 1993 made by Molinero et al. (2005, 2008). Nevertheless, some methodological limits impose caution while interpreting data from both studies. Jellyfish are not sampled properly with a 330 μm net, and with the frequency of one sample per month we might miss seasonal peaks. Yet, one sample contains the daily tows of a week, which diminishes the spatial and temporal variability. Supporting our results, Molinero et al. (2008) showed that not all jellyfish species continued to increase their stocks in the 1990s. Indeed, the studied species showed very variable interannual patterns, and most of them showed an increasing trend in the early 1980s followed by a decrease by the end of the 1980s (Fig. 7 in Molinero et al., 2008).

In the present study, almost decadal changes appeared rather simultaneous in the environmental and zooplankton conditions, and annual environmental conditions seemed to be, over certain periods, coupled with atmospheric alterations occurring over the Atlantic Ocean. These results suggest that pelagic ecosystems in the Ligurian Sea may vary in response to large-scale climate changes, as already highlighted by Molinero et al. (2005, 2008). The novelty of our study is that (1) changes might occur periodically every 8–9 years rather than being long term changes, (2) salinity seems to have a relevant role in those changes, and (3) in general all the studied groups seem to have a similar reaction to those changes.

The results presented by Molinero et al. (2005, 2008) prompted the authors to propose thermal stratification as the main local forcing shaping the zooplankton ecosystem at Point B. They suggested that

the rising abundance of jellyfish between 1987 and 1993 was due to increasing temperature, by means of greater water-column stability, that would have increased their survival and reproduction rates. According to the authors, stronger thermal stratification, predicted related dominance of small phytoplankton, and mainly a strong jellyfish predation-pressure in the early 1990s would have been detrimental to copepod populations by affecting their physiological thresholds, life-history traits and recruitment. In addition, in their conceptual model chaetognaths were out-competed by jellyfish for their main preys, copepods (Molinero et al., 2008). Instead of the top-down and competition control formerly stated (Molinero et al., 2005, 2008), the synchrony of our data (i.e., the same sign of long term anomalies in the studied groups, as well as similar cusum of environmental and zooplankton main modes) suggests the bottom-up control forced by climate as the main factor altering the standing-stocks of the studied zooplankton groups.

Warmer local water temperature from 1986 to 1987 was also considered by Conversi et al. (2010) as the trigger to what they defined as the late-1980s zooplankton shift at Point B and at another coastal station in the north Adriatic Sea (north central Mediterranean). The authors suggested that, due to continuous warming, this shift might not reverse to previous conditions in the near future. In our study, although we report a trend to earlier stratification from the beginning of the 1980s, the main modes of zooplankton and environmental conditions showed an almost decadal periodicity. The presence of jellyfish in the water column seems to be related to temperature, as reflected by their low records in the 1970s, when water was colder, and by their absence in the water column during the winter months. Nevertheless, although temperature continued to increase in the 1990s, the number of jellyfish decreased. Consequently, another factor apart from temperature may have controlled jellyfish standing stocks. All five zooplankton groups showed dominance of annual abundance higher than or equal to long-term average in the 1980s, and lower than average in the 1990s. The 1980s have been named the dry period, characterized by high salinity records and water temperature above the average (Fromentin and Ibanez, 1994; Ménard et al., 1994, 1997). Although annual-mean temperature values were above the long-term average, winter water was colder than average at Point B during most of the 1980s. Contrary to the former studies that focused on thermal stratification, we propose winter hydrography as the main local forcing shaping the zooplankton ecosystem, and salinity playing a key role in the intensity of winter water-column mixing at Point B, convection in deeper waters near the sampling site, and thus nutrient enrichment at Point B.

In our conceptual model, the 1980s might have been more productive than the previous and following decades due to stronger winter mixing and convection triggered by high salinity and low winter temperature, which in turn increased the input of nutrients into the photic zone. More nutrients would have entrained higher phytoplankton production and resources for grazers (i.e., copepods) and their predators (i.e., chaetognaths and gelatinous carnivores). The enhanced winter nutrient input may have set the biological production for the whole year including effects on the summer and autumn communities. The bottom-up control can thus be inferred from the comparison of copepod and chaetognath temporal patterns. Copepods are the main preys of chaetognaths in the Mediterranean Sea (Duró and Saiz, 2000; Kehayias, 2003). The chaetognath peak occurs between August and October at Point B. Our results show that the chaetognath abundance increased when an unusual mid-summer copepod peak occurred in the mid-1970s, and it dropped in the 1990s following the disappearance of the autumn copepod peak. Contrary to the 1980s situation, in the 1990s lower salinity may have probably been detrimental for the vertical input of nutrients to surface waters and thus to the annual biological production.

We are aware of the speculative nature of our hypothesis because (1) the weekly frequency of hydrographic measurements does not

allow individualizing strong mixing events due to their short temporal scale, and because (2) a time series of nutrient concentration and phytoplankton biomass is lacking at Point B for the whole studied period. Nevertheless, we have found some elements supporting our hypothesis. The frequency of winter high density events ($>28.85–29.05$ kg m^{-3}) was three times higher in the 1980s than in the 1990s. The detection of such dense waters at 20 m depth in Point B, usually observed at 200–350 m depth near the coast (Stemmann et al., 2008), suggests previous strong mixing with deep waters that would have uplifted nutrients to surface. Concordantly, we found that surface nitrate concentration was significantly higher during those high density events.

Other studies at Point B and in central and southern areas of the Ligurian Sea seem to support our hypothesis. In the southern (off Calvi, northern Corsica coast) and central Ligurian Sea, silicic acid and nitrate concentrations have increased with salinity (Goffart et al., 2002). Off Calvi, phytoplankton winter–spring bloom was high from 1979 to 1986 due to nutrient replenishment by convection, whereas from 1988 the input of nutrients was lower, and consequently phytoplankton blooms were weaker. Gómez and Gorsky (2003) obtained similar results by compiling information about the spring-peak amplitude of single-year studies in the Bay of Villefranche. The spring peak was high from 1985 to 1988, whereas it was low in all the seven non-consecutive years of study from 1988 to 1999. In addition, monthly data covering the 1995–2007 period from a sampling station 50 km offshore from Point B, over a depth of ~2000 m in the central Ligurian Sea, revealed an increasing frequency of strong winter vertical mixing and related nutrient and phytoplankton enhancement (Marty and Chiavérini, 2010). The authors hypothesized as major cause a deficit in fresh water inputs since 2003 in the western Mediterranean basin. The results presented by Marty and Chiavérini (2010) also support the possible almost-decadal periodicity of zooplankton and environmental modes presented in our study, because salinity and productivity are increasing again from the early 2000s in the central Ligurian Sea as it seems to occur at our coastal station, Point B.

Based on these results from different areas of the Ligurian Sea, we hypothesize that the 1980s might have been very productive years in the whole northwestern Mediterranean basin related to saltier and colder winter hydrographic conditions. Indeed, cold winters during the 1980s (Hurrell and VanLoon, 1997), and higher salinity during low precipitation periods, have already been reported for the north and western areas of the Mediterranean regions (Xoplaki et al., 2004). Salinity has been proposed to be a key parameter in winter convection in the western Mediterranean basin (Bethoux and Gentili, 1999; Skliris et al., 2007; Somot et al., 2006), and Rixen et al. (2005) have shown that in the Mediterranean Sea, salinity at the 0–150 m layer presented highest positive anomalies in the 1980s, whereas deep waters showed a monotonic increase from the 1950s. This common pattern in such an extended area as the western Mediterranean basin could be ultimately linked to the NAO effect on local atmospheric conditions (Hurrell, 1995; Trigo et al., 2000). Orfila et al. (2005) have shown a negative correlation between sea level anomalies in the Ligurian Sea and the NAO index at monthly-scale.

In our study, the link between stronger vertical mixing in winter and high winter NAO, during the 1980s, is supported by the significant correlation between the winter NAO and the 1st PC of local environmental conditions. A succession of mechanisms would link high winter NAO to high sea surface water density and thus strong vertical convection in the northwestern Mediterranean basin (Hurrell, 1995; Krahmann and Schott, 1998; Tsimplis and Josey, 2001). The succession of mechanisms would be as follows. During high winter NAO records, the local atmospheric pressure is high. High atmospheric pressure leads to clearer skies that entail less precipitation. Precipitation decreases cause salinity to increase. And while in summer related enhanced irradiance entails more evaporation that contributes to salinity increases in surface

waters, in winter clear skies increase sea surface heat losses, due to lack of cloud albedo, with the consequent SST decrease (Cess et al., 1992).

Nevertheless, mechanisms do not seem as clear and direct in the 30-year time series that we present here. The sliding correlation analysis between the winter NAO and 1st PC of environmental conditions at Point B showed that correlation was stronger during the first years of the time series, and that the link between both signals was lost during the first half of the 1990s. The early 1990s, although presenting the highest winter NAO values of the time series, presented low annual salinity records at Point B. In the early 2000s the sign of the correlation even reversed. The nonstationary relationship between the NAO and European surface climate has been already reported and related to changes in the location of the NAO pressure centers (Beranová and Huth, 2007; Vicente-Serrano and López-Moreno, 2008). In Marseille, close to the studied area, Beranová and Huth (2007) showed that the correlation between the winter NAO and local winter temperature and precipitation weakened when including the 1990s in the last data point of a 31-year moving window (mid-point 1984). In the case of precipitation, the relationship even became non significant for that last period included in their study. Using a time series going back to 1785, Vicente-Serrano and López-Moreno (2008) showed that the position of the centers of action changed at a decadal scale. In the early 1990s there was a strong eastward shift of the southern center of action of the NAO from over the Azores to over the Iberian Peninsula, and in the early 2000s the center moved northward between the Azores and the north of the Iberian Peninsula (Zhang et al., 2008). To our knowledge studies are lacking on the combined effect of the intensity and location of the centers of action of winter NAO on the Mediterranean hydro-climate.

5. Conclusions

With this study, we have documented almost-decadal changes in both zooplankton abundance and local climate. These changes appear rather synchronous and to a certain extent related to the winter NAO. The continuity of long-term monitoring programs will probably give us more insight into the mechanisms and links shaping zooplankton communities.

The abundance of the jellyfish community did not increase from the late 1980s despite thermal increase. In addition, all the studied groups showed anomalies of same sign between the 1980s and the 1990s which suggest that they might be mainly subjected to bottom-up control. We propose the winter physical forcing on primary production as the most significant factor to drive the changes in the annual standing stocks of copepods, chaetognaths, decapod larvae, siphonophores and jellyfish.

Salinity seems to be the driving force affecting the water-column density and thus stability. Stratification–convection processes and nutrient supply to surface waters are not only driven by temperature but also by salinity changes. At seasonal scale, winter–spring mixing in the Mediterranean Sea can trigger large blooms even if mean annual temperature is high. Although there is a general trend of sea water warming at annual average scale, high-salinity conditions in surface layers and/or cool winters may still allow strong convection and nutrient input into the photic zone.

Appendix A. Escoufier method

A stepwise statistical method was applied to synthesize temperature and salinity information in the six depth layers without missing the main pattern of temporal changes. For each variable, depth temporal profiles, and their combinations, were ranked depending on their correlation with the first principal component (1st PC) of the six sampled depth profiles (Fig. A.1).

Correlation was established by calculating the RV-coefficient (Escoufier, 1973; Robert and Escoufier, 1976) (Eq. (A.1)) between the 1st PC of the depth-profile combination matrix (X) and the 1st PC of the matrix containing all the depth profiles together (Y):

$$RV(X, Y) = TR(RYXRXY) / [TR(R2YY)TR(R2XX))]1 / 2 \qquad (A.1)$$

The RV-coefficient varies between 0 and 1. It is equal to 1 when both first PCs are proportional (same direction). Iteratively, a new depth temporal profile was added to the depth profiles previously ranked (i.e., m-1 + 1 depth of the remainder, until m = p, number of total profiles) according to the maximum RV-coefficient obtained between the 1st PC of X (m variables) and 1st PC of Y (p variables; in this case p = 6). The number of depths retained for analysis is selected by the saturation of the curve representing the maximum RV-coefficient at each cumulative combination. In our study, we chose to retain the second combination (i.e., two-depth profile) because one depth alone already presented a RV-coefficient of more than 0.9. The temporal depth-profiles retained were 20 m and 50 m (Fig. A.2); these depth-temporal profiles represent the surface and deep layers of the water column respectively.
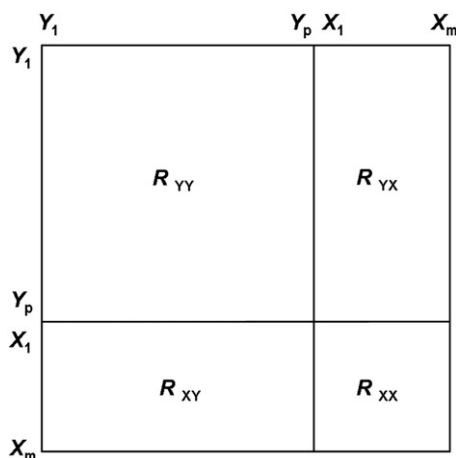

Fig. A.1. Correlation matrix between the original matrix with all depth profiles (Y) and the matrix of m profiles (X).
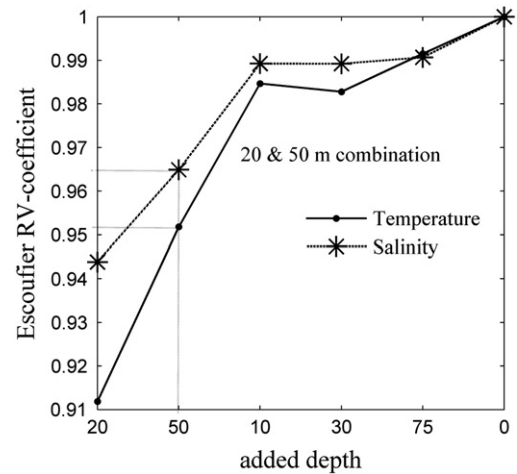

Fig. A.2. RV-coefficient (y-axis) of the cumulative combination of depth profiles with maximum RV-coefficient at each (x-axis).

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