Biogeosciences Discussions

Zooplankton communities fluctuations from 1995 to 2005 in the Bay of Villefranche-sur-Mer (Northern Ligurian Sea, France)

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Abstract

An integrated analysis of the pelagic ecosystems of the Ligurian Sea is performed combining time series of different zooplankton groups (small and large copepods, chaetognaths, appendicularians, pteropods, thaliaceans, decapods larvae, other crustaceans, other gelatinous and other zooplankton), chlorophyll-*a* and nutrients, seawater salinity, temperature and density and local weather at the Point B coastal station (Northern Ligurian Sea). From January 1995 to December 2005, a shift in most variables occurred ca. 2000. From 1995 to 2000 winters were wet and mild resulting in lower winter sea surface density. These years showed lower than average nutrients and zooplankton concentrations while phytoplankton biomass was higher. After 2000, winters were colder and dryer resulting in higher sea surface density. Nutrients and zooplankton showed higher concentrations while phytoplankton was lower than average. The ca. 2000 shift was observed for most zooplankton groups with a one year delay for certain groups. The observed patterns suggest that the pelagic ecosystem trophic state is mostly set by the winter forcing on the convection that upwells nutrients to the surface sustaining the spring bloom. However, low phytoplankton concentrations in higher nitrate and zooplankton conditions during the well mixed years suggest that phytoplankton is controlled by grazers. The proposed mechanisms of convection regimes hold for most of the time series, but specific years with contradicting patterns needed to be explained by other factors. The limitation of phytoplankton growth by the light availability in spring/summer was then proposed as a secondary driving force that can moderate or even reverse the winter forcing. Finally, the eleven years of observation did not reveal a clear link with the North Atlantic Oscillation, suggesting a more complex dynamics linking large scale climate to Ligurian Sea ecosystems or that the length of the plankton monitoring is not yet sufficient to detect those links.

1 Introduction

Plankton, because of their rapid response to ecosystem variability, their non-exploitation as commercial species and their amplification of subtle changes through non-linear processes, had been pointed out to follow the effect of climate variability (Taylor et al., 2002; Perry et al., 2004; Hays et al., 2005). Notably, the use of long-term plankton time-series can be a key tool to detect those changes (Perry et al., 2004; Alheit and Bakun, 2010; Mackas and Beaugrand, 2010). Recently, temperature changes have been suggested to cause regime shifts in plankton ecosystems. For example, 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, Reid et al., 2001, 2003; Beaugrand, 2004). Regarding Mediterranean plankton, very few studies on long-term variation have been conducted, due to the paucity of long-term time series (Mazzocchi et al., 2007). Recently, it has been highlighted the appearance of regime shifts with turning points in 1987 in two northern Mediterranean coastal ecosystems (Adriatic and Ligurian Sea) and their synchrony with changes in the Atlantic ocean and the Baltic and Black seas (Conversi et al., 2010). The authors pointed out the positive trend of surface temperature in the Northern Hemisphere as the main forcing for the concomitant changes in such far and diverse locations. In the Balearic Sea (Fernàndes de Puelles et al., 2007, studied period: 1994–2003) a decrease of zooplankton abundance was observed from 1995 to 1998, a recovery of mainly all groups was then observed from 2000. Such an inter-annual variability was linked to the NAO forcing. In its positive phase, the NAO drive colder temperature during winter months enhancing the southward spread of rich northern Mediterranean waters in the Balearic Sea (Fernàndes de Puelles et al., 2007; Fernàndes de Puelles and Molinero, 2008). From a joint study of six zooplankton time series in the Mediterranean Sea a synchronous cooling and warming affecting the zooplankton community was observed between Trieste, Naples and Villefranche-sur-Mer, with, again, a main turning point in 1987 from high to low

abundances of zooplankton (Berline et al., 2010) – yet, no significant links with large scale climate indicators such as the NAO were found. Other studies in the Ligurian Sea, based on a long time series (1963–1993) have also suggested that the pelagic ecosystem was heading toward a more regenerated system dominated by jellyfish in the early 1990's (Molinero et al., 2008). A more recent study from the same time series extended until 2003 revealed that the zooplankton and mainly copepods recovered their initial concentrations after 2000 suggesting a quasi decadal cycle (Garcia-Comas et al., 2010). Such a recovery around year 2000 was also observed by Berline et al. (2010) in Villefranche-sur-Mer and Naples, and by Fernàndes de Puelles et al. (2007) in the Balearic Sea. The higher abundance of zooplankton were correlated to dry and cold winter resulting in high winter mixing. Dry and cold winters lead to an increase in surface density increasing the winter convection and as suggested by the authors, enhancing nutrients replenishment and strengthening the spring bloom. The positive effect of dry winters was observed on the entire zooplankton community suggesting that it was controlled by it's resource. This hypothesis of a strong "bottom-up" control initiated by the intensity of the winter convection is also supported by observations in the southern and central Ligurian Sea (Goffart et al., 2002; Nezlin et al., 2004; Marty and Chiavérini, 2010) with, yet, not consideration of the zooplankton. In addition, the limitation of phytoplankton growth by light in the Mediterranean Sea was suggested as a possible additional factor of inter-annual variability (Arnone, 1994; Duarte et al., 1999; Nezlin et al., 2004; Morán and Estrada, 2005).

The aim of the present work is to extract the main causes of inter-annual variability of zooplankton in the Ligurian Sea and to test whether hypotheses formulated by Garcia-Comas et al. (2010) and Molinero et al. (2005, 2008) fit the observed dynamic. Yet, in oligotrophic seas, such as the Mediterranean, changes in environmental conditions and plankton occurs at short time scales (Underwood, 1989; Bustillos-Guzmán et al., 1995; Fernàndes de Puelles et al., 2007). Therefore, temporal studies based on monthly sampling or less (e.g., Goffart et al., 2002; Molinero et al., 2005, 2008; Garcia-Comas et al., 2010; Marty and Chiavérini, 2010) can miss important changes.

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Here we are analyzing a new time series, weekly sampled with a WP2 net, covering 1995 to 2005, independent from the work of Molinero et al. (2008) and Garcia-Comas et al. (2010). Sample analysis was done using the ZooScan instrument (Gorsky et al., 2010), using it, abundance and biovolume for 10 zooplankton groups was produced (small and large copepods, chaetognaths, appendicularians, pteropods, thaliaceans, decapods larvae, other crustaceans, other gelatinous and other zooplankton). This dataset is used together with chlorophyll-*a* biomasses, nitrates concentration, sea water temperature, salinity and density and meteorological data (temperature, precipitations, and solar irradiance) for a combined analysis of different part of the ecosystem.

2 Materials and methods

2.1 Sampling site and environmental datasets

The Bay of Villefranche-sur-Mer is located in the Northern part of the Ligurian Sea (NW Mediterranean Sea, Fig. 1). The monitored station, called Point B (Fig. 1), is located at the entrance of the Bay (43°41.10′ N, 7°18.94′ E; 85 m water depth). All basic physical, hydrological, chemical and biological parameters have been sampled weekly since 1995. Further information about this station is available at http://www.obs-vlfr.fr/Rade. The environmental variables selected for the analysis are: nitrate (NO_3 µmol L^{-1}), chlorophyll-*a* (µg L^{-1}), sea water temperature (°C), salinity (psu) and density (σ_θ), air temperature (°C), precipitation (mm d^{-1}) and irradiance (J cm^{-2} d^{-1}). Water for nitrate and chlorophyll-*a* analysis was sampled by Niskin bottles at 6 different depths, i.e. surface, 10, 20, 30, 50 and 75 m depth – depth averaged values (0–75 m depth) were used in our analysis. Nitrates were analyzed by colorimetry (Aminot and Kérouel, 2004) with an autoanalyzer Technicon Alliance, chlorophyll-*a* was determined by spectrometry and fluorimetry (Strickland and Parsons, 1977). A Seabird SBE25 CTD was used for weekly sea water temperature, salinity and density analysis of the water column. In the present work, mean values of temperature, salinity and density of the upper layer were used

(10 to 40 m depth, see Sect. 3.2.2). All these environmental measurements fit the quality controls and protocols of SOMLIT (http://www.domino.u-bordeaux.fr/somlit_national) and SO-RADE (http://www.obs-vlfr.fr/Rade). Local weather was provided daily by Meteo-France at a meteorological station, the Sémaphore, located on Cap-Ferrat at 138 m height and 1.2 kilometer away from Point B.

2.2 Zooplankton data

The net samples used in this study were collected weekly from February 1995 until December 2005 aboard the *NO Sagitta* and *NO Vellele*. Sampling was carried out vertically between 60 m and the surface with a WP2 net (mesh size of 200 µm, mouth aperture of $0.25\,\mathrm{m}^2$). The resulting time series included 489 samples (7–8 weeks were missing per year on average) and contained a total of $\approx 600\,000$ objects digitized with the ZooScan imaging system (http://www.zooscan.com) developed at the "Laboratoire d'Océanographie de Villefranche-sur-mer" (Gorsky et al., 2010). The zooplankton sampling was carried out in the frame of the RADE-ZOO program (http://www.obs-vlfr.fr/Rade/RadeZoo/RadZoo/eng/RadeZoo_eng/Home.html).

Each sample was gently separated into two subsamples with a 1000 µm mesh. Then each subsample was fractionated separately with the Motoda box. Since small objects are generally more abundant than large ones, they were fractionated more. Separation of small and large objects and subsequent separate image acquisition of the two size classes prevents underestimation of large rare objects (Gorsky et al., 2010). This procedure, WP2 and ZooScan, enables to quantitatively record objects from $0.032\,\mathrm{mm}^3$ which is equivalent of a spherical diameter larger than ca. 350 µm (Vandromme et al., 2010). Images were analyzed by dedicated imaging software called ZooProcess http://www.zooscan.com. Several variables were measured from each extracted object such as "Major": primary axis of the best fitting ellipse for the object, and "Minor": secondary axis of the best fitting ellipse for the object. From the Minor and Major axes, an equivalent apparent elliptical biovolume ("EBv") was estimated: $\mathrm{EBv} = 4/3 \cdot \pi \cdot (\mathrm{Major}/2) \cdot (\mathrm{Minor}/2)^2$.

All other variables (see Appendix 4 in Gorsky et al., 2010) were utilized for the automatic classification of objects which was performed using the free software "Plankton Identifier" (Gasparini, 2007) based on Tanagra data mining software (Rakotomalala, 2005). Unknown objects were automatically sorted into categories defined in a learning set (Gorsky et al., 2010; Vandromme et al., 2010). To assess the performance of the classifier, recall and contamination rates were computed for each category on randomly chosen samples. The recall rate was the proportion of positive cases that were correctly identified and the contamination rate was defined as being 1-precision, where precision is the proportion of the predicted positive cases that were correct (Gorsky et al., 2010).

The zooplankton was successfully separated from non-living objects with a recall rate of 0.94 and a contamination rate of 0.04 (Vandromme et al., 2010). However this is mainly due to the efficient classification of copepods (recall rate of 0.92 and contamination of 0.02). However these rates decrease for large objects and a manual separation of objects larger than $0.724\,\mathrm{mm}^3$ in "EBv" was proposed (more or less 1.5 mm length). In the present work, all objects larger than this value were visually identified from non-living objects and classified into nine zooplankton categories: appendicularians, chaetognaths, copepods, decapods larvae, other crustaceans, gelatinous, pteropods, thaliaceans and other zooplankton (Fig. 2 for examples of thumbnails). These large organisms (i.e. $>0.724\,\mathrm{mm}^3$ "EBv") account for an average of 42% of the total zooplankton apparent biovolume. Adding the small copepods automatically classified, ten zooplankton categories were defined. Percentages concerning these categories and representative species are given in Table 1. These percentages must be taken with precaution because they stand for percentages of the apparent biovolume which is different from biomass, especially when comparing crustaceans and jellies. Yet the present work focalizes on the variation of these groups and not on their absolute concentration in the field. Biases in the evaluation of their biovolume were supposed constant throughout the time lag considered.

2.3 Analysis

Results will focus on the description of seasonal and inter-annual variation on first the zooplankton compartment and then the environment, including nitrates, chlorophyll-*a*, water column physics and meteorological variables. Graphs and analyses were made using Matlab R2009b[®] (the Mathworks Company, inc.) and SigmaStat 3.5[®] (Systat Software, inc.). Anomalies were computed on regularized data with linear interpolation to fill scarce gaps in time series. Correlations were Spearman rank order correlations referred to as r_s with the corresponding *p* value. Cumulative sums (Ibañez et al., 1993) enable a fast representation of shifts dates and were computed as the first differences of anomalies. Finally, timing of start and maximum of peaks were recorded from smoothed time series following the method of Mieruch et al. (2010) with a visual control of results.

Next, to assess the effect of light limitation on the ecosystem a combination of the model of light attenuation in the water column of Lacroix and Grégoire (2002) and Raick et al. (2005) developed for the central Ligurian Sea and of the model of phytoplankton growth of Andersen and Nival (1988) developed for the bay of Villefranche-sur-Mer was used. The light attenuation is formulated as follows

$$I_z = I_{z=0} \cdot (1 - \text{albedo}) \cdot \exp\left[-\int_0^z K_{ext}(z)\,dz\right] \tag{1}$$

with $K_{ext}(z) = K_{water}(z) + K_{chl}[\text{Chl}(z,t)]$. Units and values used are the same as in Lacroix and Grégoire (2002) and Raick et al. (2005). I_z is the irradiation at depth z, K_{ext} is the light attenuation coefficient and depends on the attenuation by the water (K_{water}) and by the phytoplankton shadowing (K_{chl}) which is calculated from the measured quantity of chlorophyll-*a*. The light limitation on phytoplankton growth (I_l) is then calculated as

$$I_l = 2 \cdot (1 + \beta_l) \cdot \frac{(I_z/I_s)}{(I_z/I_s)^2 + 2 \cdot \beta_l \cdot (I_z/I_s) + 1} \tag{2}$$

Values of β_I and I_s (the optimal irradiance) are taken from Andersen and Nival (1988) and I_z comes from Eq. (1).

3 Results

3.1 Zooplankton community dynamics

The global average of zooplankton biovolume was 113 mm^3 m^{-3} and the abundance was 937 # m^{-3}. The poorest year in term of total biovolume was 1998 (66 mm^3 m^{-3}) whereas the richest one was 2004 (201 mm^3 m^{-3}). the less abundant year was 1995 (448 # m^{-3}) and the most abundant one was 2000 (1468 # m^{-3}). The maximum biovolume and abundance occurred generally from March to May (Fig. 3c, d). Weeks of start and maximum of the spring peak were recorded from abundance time series (see Table 2). Spring peak started during week 7.3 ± 2.3, and was maximum during week 11.5 ± 2.7, i.e. an average of 4.2 weeks after the start. The earliest years were 1997, 2001 and 2002 with a start on week 4, and the earliest maximum was for years 2001 and 2002 (week 7) and 1997 (week 10). A second peak in late summer/early autumn was only observed for years 2002, 2003 and 2005 – it was of the same order than the spring peak for year 2002 only.

Following the anomalies of biovolume and abundance (Fig. 3a, b), a clear opposition appears between years before and after ca. 2000. During the first period the average biovolume was 67.2 mm^3 m^{-3} and the average abundance was 614.9 # m^{-3}. For the second period these values almost doubled (1.93 and 1.77, respectively) to reach 130.0 mm^3 m^{-3} and 1089.6 # m^{-3}. Years with the maximum annual biovolume were 2001, 2000, 2004 and 2003, followed by years 2005, 2002 and 1996 which were close to the average, then years 1998, 1995, 1999 and 1997 were the lowest. According to annual abundance means, the pattern was almost similar (Fig. 3b), yet anomaly of year 1999 increase and anomaly of year 2004 decrease when considering abundance instead of biovolume. This highlight changes in the average mean size, with year

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1999 showing the smallest organisms with an average of 0.063 mm^3, and year 2004 showing the largest, almost 2.44 times larger, with an average of 0.154 mm^3. The maximum value of the spring peak followed a similar pattern varying between a minimum of 270 and a maximum of 1685 mm^3 m^{-3} in 1998 and 2004 according to biovolume, and between a minimum of 3676 and a maximum of 17 750 # m^{-3} in 1997 and 2001 according to abundance (from weekly samples). From 1995 to 1999, the average value of the annual maximum was 5144 $\pm$ 323 # m^{-3} whereas it was 11 796 $\pm$ 3623 # m^{-3} for the second period.

In addition, zooplankton taxonomic groups abundance globally changed from year 2000, with larger concentrations after. The exact years of these changes are reported on Fig. 4a–c with the computation of cumulative sum on yearly means for each category. Most groups changed from negative to positive anomalies in 2001 (2000 for small copepods and pteropods, 2002 for thaliaceans, 2003 for large copepods). However, from year 2000, some differences appeared among the different categories. The biggest difference was between year 2000 and years 2001 to 2005. Years 2001 to 2005 were globally abundant in all different taxonomic groups whereas year 2000 were abundant in copepods but showed negative anomalies of abundance of decapods larvae, chaetognaths, appendicularians, thaliaceans and gelatinous predators.

3.2 Environmental variability

3.2.1 Nitrates and chlorophyll-*a*

Nitrates (NO$_3$) concentration (Fig. 5a) were on average of 0.44 µmol L^{-1} with the minimum in 1996 (0.18 µmol L^{-1}) and the maximum in 2003 (0.70 µmol L^{-1}). Strong negative anomalies occurred from 1995 to 1998 and in 2001, whereas strong positive anomalies occurred from 2002 to 2005, and 1999 and 2000 were close to the mean. The annual cycles as monthly means are presented on Fig. 5c. Nitrates concentration was at maximum from January to March/April (i.e. ∼ weeks 1 to 13) with maximum values reaching about 2.7 µmol L^{-1} (in 2003 from the weekly data). On these winter/spring

peaks, start and maximum were measured for each year and reported in Table 2. The start of peak of nitrates concentration occurs on average on week 2 ± 1.8, the earliest start was recorded for year 1998 with a peak starting on week 50 (mid-December) of the previous year and the latest was recorded for year 1999, with a start during week 5. The maximum of the nitrates concentration was on average at 7.1 ± 3.6 weeks, i.e. around five week after the start. The earliest and latest maximums were also for years 1998 and 1999 with a maximum during the first and eleventh weeks of the year respectively. A high variability occurred for years before 2000 with years 1995 and 1999 having a maximum during weeks 10 and 11, and years 1996, 1997 and 1998 during weeks 3, 2, 1 which are the first three earliest nitrates concentration maximums. After this winter/spring maximums, no second peak, at the end of summer and early autumn were observed except, to some extent, in 2001, 2002 and 2005. In 2005, this second peak is even higher than the first one.

The chlorophyll-a concentrations (Fig. 5b) were on average $0.301 \, \mu g \, L^{-1}$ with years 1995 to 2000 above this mean and years 2001 to 2005 below this mean. Year 2004 was the year with the minimum mean of chlorophyll-a ($0.229 \, \mu g \, L^{-1}$), and year 1995 was the year with the maximum ($0.385 \, \mu g \, L^{-1}$). Through the year, chlorophyll-a was maximum on average from February to April/May (i.e. $\approx$ weeks 6 to 22). The start and maximum of the chlorophyll-a spring bloom (Table 2) were on average at 5.5 ± 2.2 and 10.2 ± 2.8 weeks respectively, i.e. 3.5 and 3.1 weeks after the start and maximum of the NO_3 peaks. The earliest start of the chlorophyll-a peak was observed during the third week for years 1997, 2000 and 2002, and the latest start was for year 2005 during the ninth week. Earliest maximum of chlorophyll-a was for year 2001 and occurred during the fifth week, which is also the week of the start. The latest chlorophyll-a peak was for year 1996 and occurred during the fourteenth week. Second peaks in late summer/early autumn cannot be identified for the different years even if years 1995, 1996 and 2002 seem to have one.

3.2.2 Hydrology

From average yearly variation of density it appears that the density maximum occurs between the 4 and 17 weeks of the year reaching densities between 28.5 and $29\,\sigma_\theta$. During this period the water column was almost homogeneous from the surface to 80 m depth with an almost constant differences of $0.0879\,\sigma_\theta$ between the surface layer (0–10 m) and the bottom layer (70–80 m) with a gradual increase – yet, density anomalies between all layers are significantly correlated (minimum r_s of 0.9834 and a maximum p value of $9.5\ 10^{-9}$). Within this work, the layer 10–40 m was chosen since surface processes will be analyzed (i.e. the winter convection, see Sect. 4.2). However, due to the strong observed correlation between all layers, another choice will not have changed the results and conclusions.

Year 2005 presented the greatest positive anomaly (Fig. 6c) with a mean density of $28.79\,\sigma_\theta$ whereas year 1997 was the lowest ($28.41\,\sigma_\theta$). Years 1997, 1998 and 2001 were far below the mean, years 1995, 1999, 2000, 2004 and 2005 were above the mean, and years 1996, 2002, and 2003 were close to the mean. Density is a function of temperature and salinity and was significantly correlated to both of them (density vs. temperature: $r_s = -0.923$, $p < 0.001$; density vs. salinity: $r_s = 0.972$, $p < 0.001$). Years with high densities observed in winter corresponded to low water temperature (below the mean of 13.60 °C) and high salinity (above the mean of 38.04 psu) and vice versa for years with low winter densities (Fig. 6a, b). Taking the equation of state of seawater (Millero and Poisson, 1981) it appears that the amplitude of variation of winter means of temperature (1.25 °C) accounts for a variation of density of about $0.39\,\sigma_\theta$ (for a fixed salinity of 38 psu and a T_0 temperature of 13.5 °C), and that variation in winter means of salinity (0.4 psu) accounts for a variation of density of about $0.31\,\sigma_\theta$ (fixed temperature of 13.5 °C and S_0 salinity of 38 psu) whereas the variation of winter means of density is of $0.5\,\sigma_\theta$. Thus temperature and salinity should be both considered to account for the observed density variations.

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3.2.3 Local weather

The late autumn/winter time (i.e. from November of the previous year until March of the mentioned year) precipitation, air temperature and solar irradiance means are presented on Fig. 7a–c. The average temperature through this period was 11.13 °C, with a maximum for year 1998 (11.89 °C) and a minimum for 1999 (10.56 °C). The coldest winters were 1995, 1999 and 2005, whereas the warmest were 1997, 1998 and 2001. The precipitation were an average of 2.40 mm d^{-1} during this period, with a maximum in 2001 and 5.15 mm d^{-1} on average and the minimum for 2000, with an average of 0.87 mm d^{-1}, almost 6 times less than in 2001. The driest winters were 1995, 1999, 2000, 2002, 2004 and 2005 and the rainiest were 1996, 1997 and 2001. Temperatures and precipitations during winter are correlated ($r_s = 0.629$, $p = 0.026$). The mean solar irradiance was 882 J cm^{-2} d^{-1} with the maximum for year 1999 (975 J cm^{-2} d^{-1}) and the minimum for 1996 (760 J cm^{-2} d^{-1}). Winters 1995, 1998, 1999, 2000 and 2002 were the sunniest and winters 1996, 2001 and 2004 the less sunny.

The spring/summer climate was also studied (April to August, Fig. 7d–f). The average temperature during this period was 19.85 °C, year 2003 being far warmer than the others (21.69 °C, on average), and year 2004 being the coldest (19.25 °C). Precipitations during springs/summers were on average of 1.23 mm d^{-1}, with 1995, 1998, 2000, 2002 and 2004 being rainy (maximum for 2002 and 2.02 mm d^{-1}), and 1996, 2001, 2003 and 2005 being the driest (minimum for 2001 and 0.57 mm d^{-1}). The springs/summers showed an average solar irradiance of 2247 J cm^{-2} d^{-1} with years 2000 to 2005, except 2002, being sunny. 2003 was the sunniest year (2365 J cm^{-2} d^{-1}). Years 1995 to 1999 and year 2002 showed below average irradiance with 1999 being the less sunny (2137 J cm^{-2} d^{-1}).

3.2.4 Light availability and phytoplankton growth in spring/summer

The average light perceived in the water column (average from 0 to 75 m depth) from April to August for the eleventh years is 435 J cm^{-2} d^{-1}, with years 1995, 1996 and

1999 the lowest (respectively 373, 391 and 393 J cm^{-2} d^{-1}) and year 2001 the highest (547 J cm^{-2} d^{-1}), far ahead of year 2003, the second highest (459 J cm^{-2} d^{-1}). Years 1995 to 1999 are below the mean whereas years 2000 to 2005 are above. The light limitation factor (Eq. 2) follow a similar pattern, with an average value of 0.623, a minimum for years 1995, 1996 and 1999 (respectively 0.536, 0.566, 0.572) and the maximum for years 2001 and 2003 (0.692 and 0.673).

4 Discussion

4.1 Previous analysis of the pelagic ecosystem in the NW Mediterreanean Sea

Previous time series analysis on different components of the plankton communities at Point B highlighted the correspondence between changes in the abundance and/or composition of some key species and the shift in the local climate that occurred in the late 1980's (Molinero et al., 2005, 2008). In those studies, jellyfish seemed to out compete chaetognaths and to be detrimental to copepods, which abundance dropped from the late 1980's. The authors proposed a trophic reorganization due to oligotrophication related to increasing stratification driven by water warming in the 1990's. However, Garcia-Comas et al. (2010) found by analyzing 10 more years of the same time series but at the community level, that total copepods and chaetognaths recovered almost the abundance of the 1980's by year 2003 while jellyfish remained abundant. Instead of a long term trend, the authors proposed a quasi decadal fluctuation driven by changes in winter mixing intensity acting through the input of nutrient and phytoplankton production. They suggested that dry years in the 1980's and from 1999 to 2003 would increase surface salinity in winter and hence density close to deep values causing deep winter convection in the coastal Ligurian Sea. The authors proposed that zooplankton would benefit of higher phytoplankton biomass. However, their study lacked observations of nutrients and phytoplankton. A recent study in the open sea site of the Ligurian Sea (Dyfamed) support the hypothesis of a link between climate variability

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and notably precipitations and phytoplankton production and composition (Marty and Chiavérini, 2010). Convection as deep as 2000 m has been reported by Marty and Chiavérini (2010) to occur from winter 1999 to 2006 (except for 2001 and 2002). Deep convection brought to the surface high load of nutrients that triggered an intense phytoplankton bloom of mainly diatoms (Marty and Chiavérini, 2010). In addition, in the coastal zone of the Bay of Calvi (northern Corsica, Ligurian Sea), the phytoplankton blooms were reported to decrease from 1978 to 1998 as possible consequence of lower mixing related to a salinity decrease and temperature increase, which was appointed to entail less nutrient replenishment (Goffart et al., 2002). The poor sampling frequency (only 5 years in a 20 years time series) prevented the author to determine the detailed controlling factors. But surface salinity appears to be the main determinant to structure the pelagic ecosystem or part of it as in this work and in other studies in the NW Mediterranean sea for medusae (Goy, 1997; Buecher et al., 1997), dolioliids (Menard et al., 1997), zooplankton (Garcia-Comas et al., 2010) and phytoplankton (Marty and Chiavérini, 2010).

In order to further understand the pelagic ecosystem functioning, we have analyzed a zooplankton time series obtained with a different net (WP2 net instead of the Juday Bogorov as in Molinero et al., 2008; Garcia-Comas et al., 2010) and more complete data on climatology, hydrology, nutrients and phytoplankton. In the light of the new data provided by the extension of the zooplankton time series of Molinero et al. (2008, 1967–1993) by Garcia-Comas et al. (2010, 1974–2003) and the present work (1995–2005), it appears that the pelagic ecosystem in the Ligurian Sea may have recovered in the first years of 2000 the condition of the 1980's. The projected oligotrophication of the pelagic ecosystem did not occurred. Instead, there seems to be oscillations, yet the length of the zooplankton time series is not long enough to disentangle the effects of long-term zooplankton changes due to climate from inter-annual variability.

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4.2 Winter forcings on the ecosystem

In the NW Mediterranean Sea "winter convection" (e.g., Schott et al., 1993; Marshall and Schott, 1999; Soriano et al., 2004; Vage et al., 2009) occurred during continuous cooling and saltening of the surface water by atmospheric forcing during winters (Leaman and Schott, 1991; Bethoux et al., 1998, 2002). This results in increased density and allows surface water to sink into the deep layer, mixing the water column. A shift in sea water salinity was observed in the present study, with less saline winter waters occurring at the beginning of the observed period until 2000 (minimum in 1997 and 1998), whereas higher salinity were observed from 2001 to 2005 (maximum in 2005). An average difference of about 0.3 psu was observed over these years for winter months. This increased salinity was mainly related to a decrease in freshwater inputs, both due to a decrease of precipitations (present data) and rivers flow in the NW Mediterranean Sea (e.g., Skliris et al., 2007; Ludwig et al., 2009; Marty and Chiavérini, 2010; Vargas-Yanez et al., 2010). Observed anomalies of precipitations in the Bay of Villefranche-sur-Mer during winters tend to confirm this hypothesis with wetter winters mainly in 1996, 1997, 1998 and 2001, corresponding to years with low anomalies of surface water salinity. However, the increase of salinity alone appears not sufficient to explain the observed increase of winter surface density and the temperature must also be taken into account (see Sect. 3.2.2). This appears particularly visible for year 2001, which showed low densities but close to average salinities anomalies, yet the sea water temperature was the highest of the time series. Considering the whole time series, however, anomalies of sea water salinity and temperature are strongly correlated ($r_s = -0.888$, $p < 0.001$) alike anomalies of precipitations and air temperatures ($r_s = 0.629$, $p = 0.026$). Air temperature and precipitations seem to determine the intensity of the winter convection in the observed ecosystem and are both strongly correlated to the winter water density ($r_s = -0.804$ and -0.783 respectively, $p < 0.001$ for both cases).

The main consequence of an increase in winter convection is a stronger replenishment of nutrients through a deepening of the mixed layer (e.g., Gačić et al., 2002;

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Backhaus et al., 2003; Nezlin et al., 2004; Katara et al., 2008; Marty and Chiavérini, 2010). This affirmation is supported by the observed strong correlation ($r_s = 0.726$, $p = 0.006$) between winter surface density and nitrates. Marty and Chiavérini (2010) observed in the central Ligurian Sea an increase of nitrate concentration in Febru-
5 ary of about 3 times between years with low and high convection. In the present work, years 1997/1998, which showed the lowest convection, were almost 7 times lower in nitrate concentration in February than years 2005, which showed the highest convection. From the literature, such increase in nitrates and more generally nutrients availability at the end of winters were always related to a significant increase in phytoplankton
10 productivity, and mainly diatoms in the Ligurian Sea (Goffart et al., 2002; Nezlin et al., 2004; Marty and Chiavérini, 2010). In addition, the favorable conditions (dry and cold winters) and the quality of phytoplankton (i.e. more diatoms) have had a positive effect on the whole zooplankton identified taxonomic groups (Fig. 4, except for year 2000, see Sect. 4.3). Such positive forcing across different trophic levels were already ob-
15 served at various locations (e.g., Aebischer et al., 1990; Frederiksen et al., 2006), and also after recent studies at the same location (Garcia-Comas et al., 2010).

A striking results of the time series analysis is a clear opposite patterns in the inter-annual variability between nitrate concentrations and phytoplankton and also phyto-plankton and zooplankton (Figs. 3a, b and 5a, b). This temporal dynamic stands odd
20 in the common conceptual model that favorable nutrient conditions result in high phy-toplankton concentration. The opposite inter-annual variability between phytoplankton and zooplankton in periods with high nutrient concentrations strongly suggest that graz-ers control primary producers. Therefore in addition to the "bottom-up" control hypoth-esis raised by Garcia-Comas et al. (2010), we suggest that "top-down" control by zoo-
25 plankton may be important to explain the observed variability of phytoplankton. Even if "top-down" control of phytoplankton by zooplankton at both seasonal and inter-annual scales is an accepted phenomenon (Graneli and Turner, 2002; Sommer and Sommer, 2006; Wiltshire et al., 2008), such a strong "top-down" control decreasing the whole phytoplankton community stocks has rarely been observed either in field's studies or

in mesocosm experiments (Micheli et al., 1999; Shurin et al., 2002; Feuchtmayr et al., 2004; Borer et al., 2005; Sommer, 2008). According to these studies, the coupling depends mainly on the sustained co-existence between zooplankton feeding on different parts of the phytoplankton size spectrum. This can be the case in oceans where, for example, a long-term coexistence of tunicates and copepods is observed, or in lakes with a co-existence of copepods and *Daphnia* (Sommer, 2008). Copepods alone will feed only on large phytoplankton (thus decreasing the competitive pressure on small phytoplankton), or will feed on microzooplankton (thus decreasing the grazing pressure on phytoplankton); while filter-feeders (thaliaceans, appendicularians and also pteropods here) will feed on the whole phytoplankton sizes (Sommer, 2008). The co-existence and high abundance of filter-feeders and copepods after 2000 may explain the decline of phytoplankton stocks. Yet, year 2000 appears as an exception with high concentrations of nitrates, chlorophyll-*a* and zooplankton – the low abundance of filter-feeders during these year (only pteropods were present) may explain this particularity. This strong control of phytoplankton through zooplankton grazing was not observed in the central (Marty and Chiavérini, 2010), nor in the southern Ligurian Sea (Goffart et al., 2002) – nutrients and chlorophyll-*a* being positively correlated. This is potentially due to lower zooplankton biomasses in those locations compared to the present site – 15–30 mgDW m^{-3} in Dyfamed, (Gasparini et al., 2004); 45–105 mgDW m^{-3} in Calvi, Corsica, (Hecq et al., 1981; Brohée et al., 1989; Skliris et al., 2001); compared to 20–700 mgDW m^{-3} in Point B (Vandromme et al., 2010). Phytoplankton appears to be grazed faster than it is growing, hiding the "bottom-up" control (i.e., nutrients to phytoplankton), which can only be evidenced by rate measurements.

Finally, changes in timing of water column stratification, nitrate concentrations peaks, chlorophyll-*a* blooms and zooplankton peaks (Table 2) were not correlated to any inter-annual variability in annual anomalies of nitrate concentrations, chlorophyll-*a* or zooplankton. The maximum of zooplankton, despite its variability, was always between 0 and 2 weeks after the maximum of phytoplankton, suggesting that zooplankton growth is not determined by other factors than the phytoplankton development.

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The "match-mismatch" hypothesis (Cushing, 1990; Edwards et al., 2002; Edwards and Richardson, 2004; Durant et al., 2007; Bakun, 2010; Ji et al., 2010) is, then, not supported by the present observations. A "match-mismatch" occurs when the time of appearance of different trophic levels are conditioned by different driving forces (Durant et al., 2007). Even if the "match-mismatch", among other ecological mechanisms, reviewed in Bakun (2010), occurs possibly at smaller scales of analysis (both temporal, spatial or taxonomic) in the Bay of Villefranche-sur-Mer, the interplay of "bottom-up" and "top-down" controls seems sufficient to explain the main observed inter-annual variability.

4.3 Effect of spring/summer irradiation and other patterns

The "bottom-up" control caused by nutrient replenishment by intense winter convection does not seem sufficient to explain the case of years 1995, 1999 and 2001. Indeed winter convection during 1995 and 1999 were among the strongest observed in the eleventh years, yet, zooplankton concentrations were low. The opposite situation was observed during year 2001 with a particularly weak winter convection but high concentration of zooplankton. These three years correspond to years in which the winter convection strength anomalies and spring/summer irradiation are opposed. For all the remaining years a strong winter convection corresponded to high spring/summer irradiation and vice-versa. In addition, positive correlations were observed between zooplankton and spring/summer irradiance ($r_s = 0.734$, $p = 0.005$ and $r_s = 0.706$, $p = 0.009$ respectively for zooplankton biovolume and abundance) – the spring/summer irradiation being the only parameter which show a significant correlation with zooplankton.

A way through which solar irradiation may affect the ecosystem productivity is by light limitation on phytoplankton growth as suggested by previous studies (Andersen and Nival, 1988; Sciandra et al., 1997; Duarte et al., 1999; Nezlin et al., 2004; Morán and Estrada, 2005). The calculated irradiation values (Eq. 1, Sect. 3.2.4) do not reach saturation of phytoplankton growth generally observed (Geider et al., 1998; MacIntyre et al., 2002). Using a light limitation model (see Sect. 2.3) it appears that 1995, 1996

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and 1999 were the three more limited years and 2001 was the less limited. Since the model of Andersen and Nival (1988) is multiplicative, any decrease in the light limitation factor will have an effect on phytoplankton growth. In addition, the light attenuation model does not consider the turbidity from terrestrial discharge. This may be important

5 in this coastal setting (Duarte et al., 1999) and would further decrease the available light in the water column. There is a need of the addition of suspended particles concentration to the light attenuation model and of new measurements of available light in the water column. Additional experiments of light limitation on phytoplankton species from the sampling site will be also needed to validate this hypothesis.

10 Another inter-annual variability was observed in the time-lag between the appearances of the different taxonomic groups (see Fig. 4). It appears that most of the large groups increased in 2001 whereas smaller zooplankton, mainly copepods, increased one year before. Such a time-lag was already observed at the same location by Garcia-Comas et al. (2010) in the 1981/1983 and 1999/2000 switches. The reason for the time

15 lag is not truly understood but seems to be a constant feature in the studied area and also in various location in the world (e.g. Cloern and Jassby, 2010). A possible explanation lies in different reproductive strategies among the different taxonomic groups. Some may respond immediately through an increase fecundity/natality (small copepods). Other groups may respond with a certain time-lag because of longer generation

20 time (euphausiids, amphipods) or by the production of diapause eggs enabling a more strong initiation the following year. Yet, the time lag of responses of the different groups can explain the particularity of the year 2000 in which the herbivorous community was mainly composed of copepods and not of filter-feeders, reducing the "top-down" control on phytoplankton from zooplankton previously mentioned (Sect. 4.2).

25 ### 4.4 Conceptual scheme

On the basis of the new data by Garcia-Comas et al. (2010) and this work we propose an explanation whereby the climate forcing modifies the dynamics of zooplankton groups in the NW Mediterranean Sea in four patterns (Fig. 8). In winter, precipitations

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and temperatures controlled the strength of the winter convection. Years 1996, 1997, 1998 and 2001 showed weak winter convection due to high winter precipitations and/or temperatures. Years 1995, 1999, 2000 and 2005 showed strong winter convection, related to low precipitations and/or low temperatures in winter. Years 2002, 2003 and 2004 were intermediate. The strength of the winter convection controls the availability in nitrates, and thus phytoplankton growth. In spring/summer light limitation, can counteract or reinforce the effect of winter convection. Years 1995, 1996, 1997, 1998, 1999 and 2002 had an unfavorable spring/summer climate. In the case of years 1996, 1997, 1998 and 2002 this may have positively moderate the weak (or intermediate) winter convection assuming that nutrients were not limiting even. For year 1995 and 1999 the unfavorable spring/summer climate (i.e. low irradiance and high precipitations) may have negatively moderate the positive effect of the strong winter convection. By contrast, years 2000, 2001, 2003, 2004 and 2005 a favorable spring/summer climate. Especially for year 2001 which was weak as regards winter convection but high as regards zooplankton concentrations. This suggests again an important role of the spring/summer climate. In addition high abundance of zooplankton during the previous year would have an impact on some taxonomic groups of zooplankton – especially the large ones (see Sect. 4.3). This gives an explanation of the peculiarities of year 2000 which had high abundance of copepods but low abundance of gelatinous zooplankton (mainly filter-feeders) changing characteristics of the "top-down" control from zooplankton to phytoplankton. Yet this global scheme do not take microplankton into account due to a lack of data. This could possibly modify the proposed hypotheses about the global functioning of the presented ecosystem since they are known to contribute to the grazing of phytoplankton, to represent a food resource for small copepods (especially in the bay of Villefranche-sur-Mer) and to contribute to the recycling of nutrients (Nejstgaard et al., 2001; Klaas et al., 2008). Yet, considering or not the microplankton will not modify the positive link between the presence of copepods only and the increase of chlorophyll-*a*. The presence of copepods feeding on large phytoplankton decrease the competitive pressure for small phytoplankton and the chlorophyll-*a* increase. This

is similar to the presence of copepods feeding on microplankton and so decreasing the grazing pressure on phytoplankton by microplankton, which result also in an increase of chlorophyll-*a* even if the link is different. A global decrease of phytoplankton can only be reached by the presence of filter-feeders. Further studies will have, however, to deal with the microplankton to assess its role in the global functioning of Ligurian Sea coastal ecosystems.

In summary, dry, cold late autumns and winters are beneficial for phytoplankton growth and zooplankton development that ultimately control the biomass of phytoplankton by grazing. All groups of zooplankton are present and their concentrations are further increased if previous year was favourable or if light conditions are increased. These factors seem to set the ecosystem dynamics for the whole year. Continuing the long-term monitoring of these variables is needed to confirm the propose dynamics before any attempt to forecast ecosystem state is made.

4.5 links with the North Atlantic Oscillation (NAO)

As was suggested by several studies in the Western Mediterranean Sea, ecosystems fluctuations seem linked to large scale atmospheric patterns and more specifically the NAO (e.g., Molinero et al., 2005, 2008; Fernàndes de Puelles et al., 2007; Conversi et al., 2010, . . .). Particularly, strong (*sensu* Fernàndes de Puelles and Molinero, 2008, i.e. $\pm > 1$) positive phase of the NAO are known to generally drive colder and drier winters over the Western Mediterranean and vice-versa for strong negative phases (Hurrell, 1995; Stenseth et al., 2003; Hurrell and Deser, 2010). In the present time series, strong NAO+ occurred in 1995, 1999, 2000 and 2005 and strong NAO− in 1996, it was also low in 2001. Yet, no significant relationships were found between the NAO and the zooplankton total abundance and biovolume. Similar results were found in Berline et al. (2010) and in Garcia-Comas et al. (2010) where no significant links between any climate indicator and Ligurian Sea *zooplankton dynamics* were found. Yet, some significant links were found between the local environment and the NAO in Garcia-Comas et al. (2010). For the periods presently studied (1995–1999 poor and

2000–2005 rich in zooplankton), this appears to be mainly due to years 1995, 1999 and 2001. Surprisingly, these years in which the spring/summer climate moderated, or even reversed, the predicted effect of the winter convection (see Sect. 4.3), were years with strong NAO+ (1995 and 1999) or ≈ strong NAO– (2001). This lack of correlation can be due to the interplay between various climate indicators and also local climate drivers in the control of coastal zooplankton dynamics. The length of the time series used, 11-years, may also be not long enough to detect significant links.

5 Conclusions

From the present work an eleven years time-series of the Ligurian Sea including zoo-plankton, chlorophyll-*a*, nitrates concentration, hydrology and local weather with weekly values was analyzed. It is presently the most complete time series analyzed in this area. It was found that,

- A recovery at ca. 2000 of the ecosystem from low zooplankton abundances that occurred in the 1990's was found, with quasi decadal fluctuation from low to high zooplankton abundances confirming hypothesis by Garcia-Comas et al. (2010). Such a shift in ca. 2000 was also observed at diverse locations and for other components of ecosystems (e.g. Batten and Welch, 2004; Fernàndes de Puelles et al., 2007; Payne et al., 2009; Cloern and Jassby, 2010; Goberville et al., 2010; Marty and Chiavérini, 2010; Berline et al., 2010).

- A one-year time lag was observed in the recovery of large zooplankton groups compared to smaller one.

- A clear opposite trend in the inter-annual dynamic of nitrates and zooplankton vs. chlorophyll-*a* was observed suggesting a strong "top-down" control of phytoplankton by zooplankton.

- The main driving factor of these fluctuations is the strength of the winter convection mainly determined by winter precipitations and temperature. The main consequence being a stronger replenishment in nutrients which affects zooplankton through a "bottom-up" control.

- A second driving factor was proposed, i.e. the light limitation of phytoplankton growth in spring/summer, which moderated or even reversed the system initiation of the winter convection.

- Correlations between NAO and zooplankton were insignificant. This can be due to the moderation effect of the spring/summer climate.

A monitoring of microbial and phytoplanktonic communities is underway to perform a real "end to end" analysis of the presented ecosystem. This will allow to test some of the proposed hypothesis and deepens the analysis. In addition, further works will have to include measurements of growth rates of phytoplankton and zooplankton, pigments concentration as a proxy to monitor phytoplankton communities and also light availability in the water column to investigate the light limitation hypothesis. The development of zooplankton models coupled to phytoplankton and environment are also underway to achieve a deeper analysis of the main driving forces of the long-term dynamic.

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Table 1. Large zooplankton categories ($>0.724\,\text{mm}^3$), percentage of abundance ("Ab.")/apparent elliptical biovolume ("EBv") of these categories among zooplankton of this size range (for indication only), representative species or groups and dominant diet considered in this work. The category "Copepods (small)" comes from copepods automatically sorted from 0.032 to $0.724\,\text{mm}^3$ and the percentage given applies on zooplankton of this size range only. The large zooplankton (i.e., $>0.724\,\text{mm}^3$) represent 1.8 and 31.5% of total zooplankton abundance and apparent biovolume, respectively.

Taxonomic groups	%Ab./EBv	Representative species	Dominant diet
Copepods (small)	61.4/46.5	*Acartia* spp*., Oithona* spp*., Clausocalanus* spp*., Paracalanus* spp*., Oncea* spp*., Farranula rostrata* . . .	microplanktono-phage/herbivores
Appendicularians	1.2/0.5	*Oikopleura albicans, Fritillaria pelucida* . . .	filter-feeders
Chaetognaths	6.1/4.4	*Sagitta inflata*	carnivores (copepods)
Copepods (large)	12.7/4.8	*Centropages* spp*., Temora stylifera, Calanus minor, Calanus gracilis, Pleuromamma* spp*., Candacia* spp*., Euchaeta marina* . . .	omnivores
Decapods larvæ	3.3/2.4	Zoé, Protozoé and Metazoé larvæ of mostly crabs, langoustine and lobsters	omnivores
Crustaceans (other)	5.1/3.2	Euphausiids (*Meganyctiphanes norvegica, Nyctiphanes couchii*) and mysidacea	omnivores
Gelatinous predators	19.6/34.1	ctenophores (*Beroe* sp*., Pleurobrachia* sp. . . .), siphonophores (*Muggia* sp*., Lensia* sp*., Agalma elegans* . . .), Medusæ (Ephyrula of *Pelagia noctiluca, Rhopanolema velatum, Liriope Tetraphylla, Solmissus albecans* . . .) . . .	carnivores
Pteropods	4.7/9.3	*Cavolinia inflexa, Creseis laciculata* . . .	filter-feeders/suspensivores
Thaliaceans	6.9/12.8	*Thalia democratica, Salpa fusiformis, Dolioleta gegenbauri, Doliolum nationalis, Pyrosoma atlanticum* . . .	filter-feeders
Zooplankton (other)	1.7/1.2	fish larvæ, annelids . . .	mixed

Table 2. Timing (week number) of starting and maximum of seasonal variables, i.e. the nitrates (NO_3), the chlorophyll-*a* (chl-*a*), the zooplankton total abundance (Zoo.) and the stratification of the water column (Strat.).

Year	NO_3		chl-*a*		Zoo.		Strat.	
	start	max	start	max	start	max	start	max
1995	3	10	6	11	9	12	17	29
1996	2	3	6	14	10	15	14	31
1997	1	2	3	8	4	10	20	32
1998	−2	1	5	10	7	11	16	33
1999	5	11	8	12	8	12	18	35
2000	3	5	3	13	8	15	15	36
2001	1	9	5	5	4	7	17	34
2002	1	9	3	7	4	7	17	30
2003	2	8	8	10	7	12	19	34
2004	2	10	4	9	9	11	19	33
2005	4	10	9	13	10	14	17	32
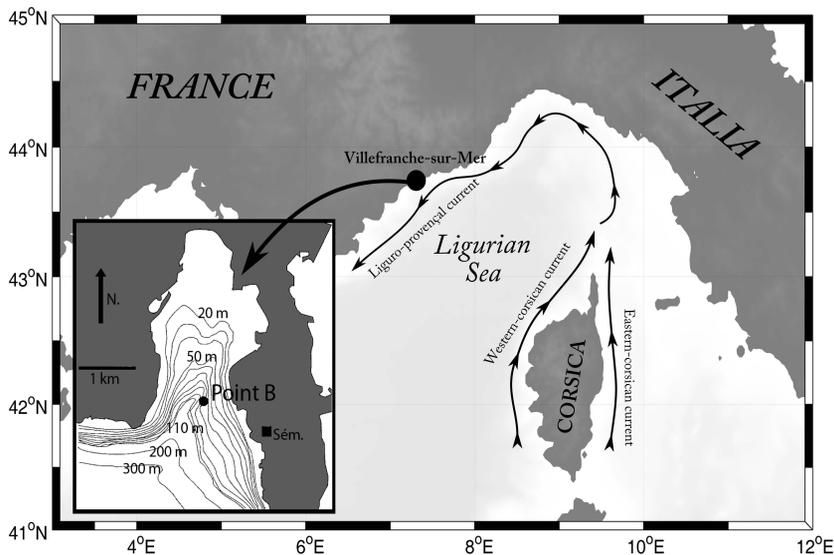
Fig. 1. Location of the sampling site (Pt. B) in the Ligurian Sea and the meteorological station Sémaphore (Sém.) situated in Cap Ferrat 1.2 km from Point B. The cyclonic circulation of the Ligurian Sea with the Liguro-Provençal Current, the Western Corsican Current and the Eastern Corsican Current are also shown on this map. The central zone of the Ligurian Sea is separated from more coastal areas by the frontal zone.
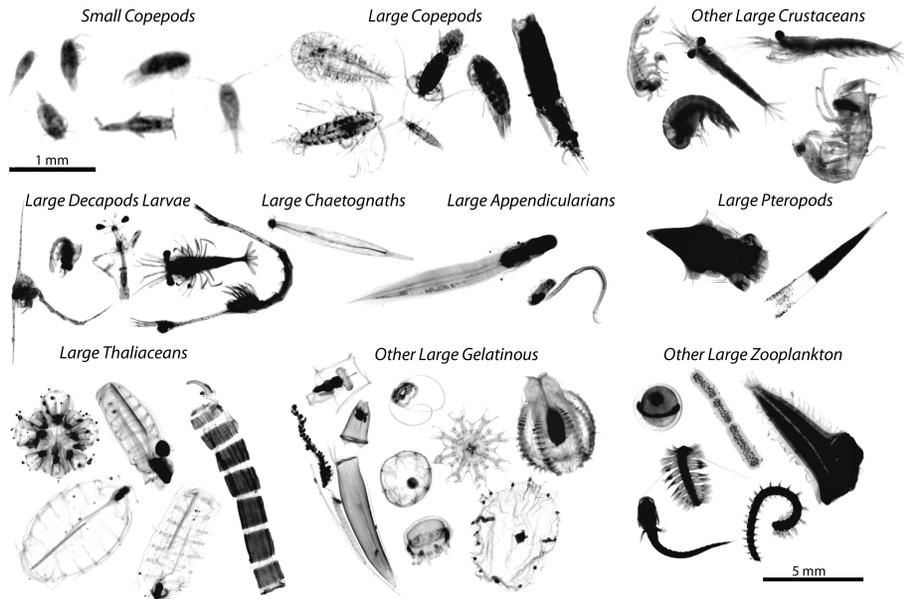
Fig. 2. Example of thumbnails directly issued from the ZooScan/ZooProcess of the ten identified zooplankton taxonomic groups. All thumbnails have the same scale (bottom right corner) except the small copepods which have their own scale on top left.
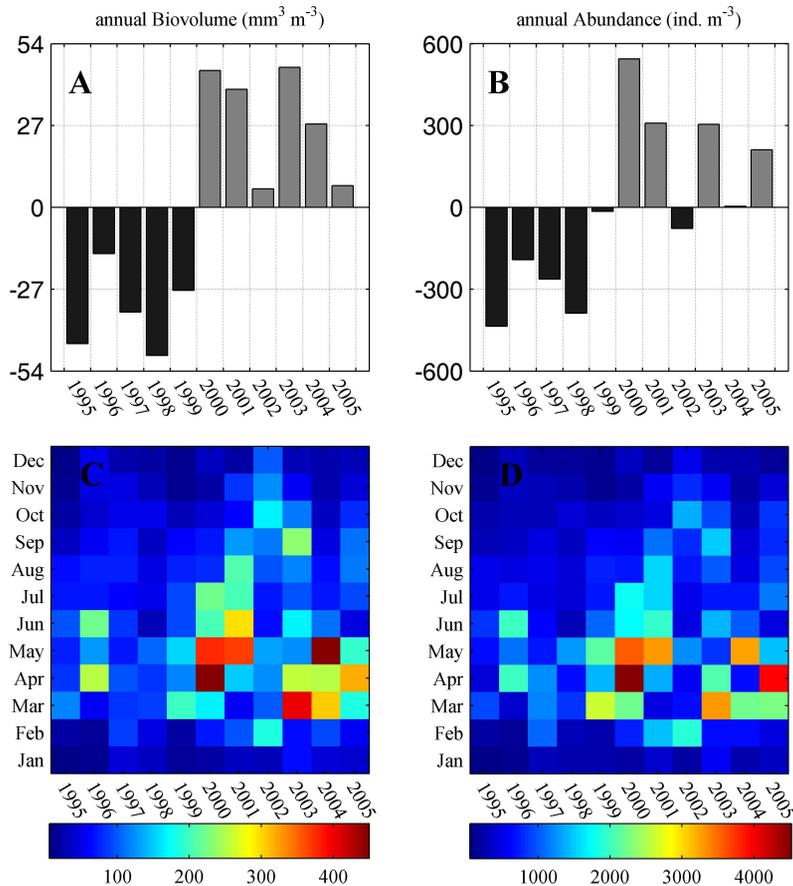
Fig. 3. Dynamic of total zooplankton biovolume (in mm^3 m^{-3}) and abundance (in # m^{-3}) from 1995 to 2005. **(A)** annual anomalies of total biovolume; **(B)** annual anomalies of total abundance; **(C)** monthly values of total biovolume; **(D)** monthly values of total abundance.
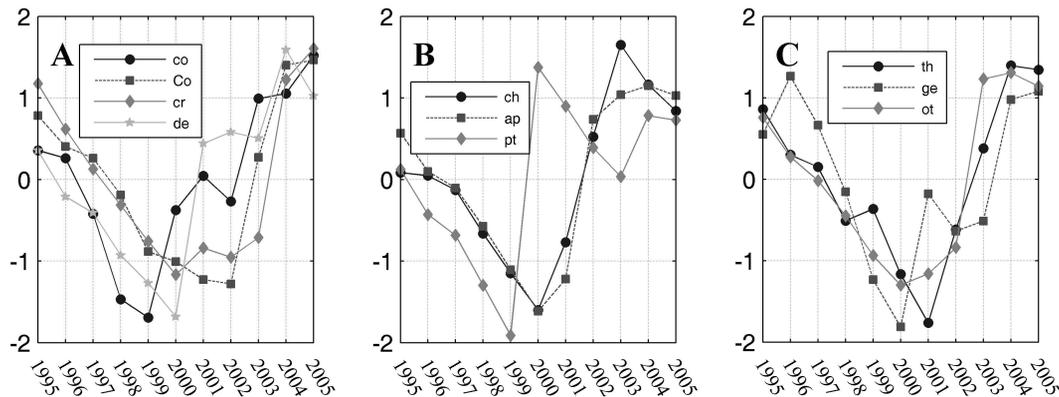
Fig. 4. Cumulative sum of annual anomalies of the ten identified taxonomic groups: **(A)** co for small copepods, Co for large copepods, de for decapods larvae, cr for other crustaceans; **(B)** ch for chaetognaths, ap for appendicularians, pt for pteropods; **(C)** th for thaliaceans, ge for gelatinous predators, ot for other zooplankton. Small copepods account only for individuals between 0.032 and $0.724 \, \text{mm}^3$ whereas the other groups account for individuals larger than $0.724 \, \text{mm}^3$. The cumulative sum method was first used in ecology by Ibañez et al. (1993), a negative slope means a negative anomaly and vice-versa.

Fig. 5. Dynamic of nitrates (NO_3) in $\mu mol\,L^{-1}$ and chlorophyll-a in $\mu g\,L^{-1}$. **(A)** annual anomalies of NO_3; **(B)** annual anomalies of chlorophyll-a; **(C)** monthly values of NO_3; **(D)** monthly values of chlorophyll-a.
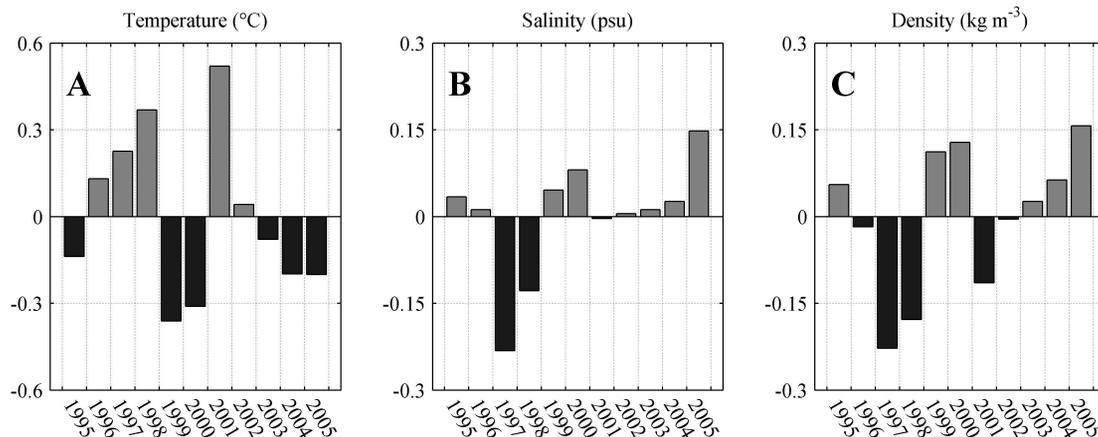
Fig. 6. Annual anomalies of hydrological characteristics of the water column (averaged from 10 to 40 m) during the winter period, i.e. from the 4 to the 17 weeks which showed the maximum values of sea water surface density (unpresented data). Anomalies of **(A)** density (in σ_θ), **(B)** sea temperature (in °C) and **(C)** salinity (in psu).
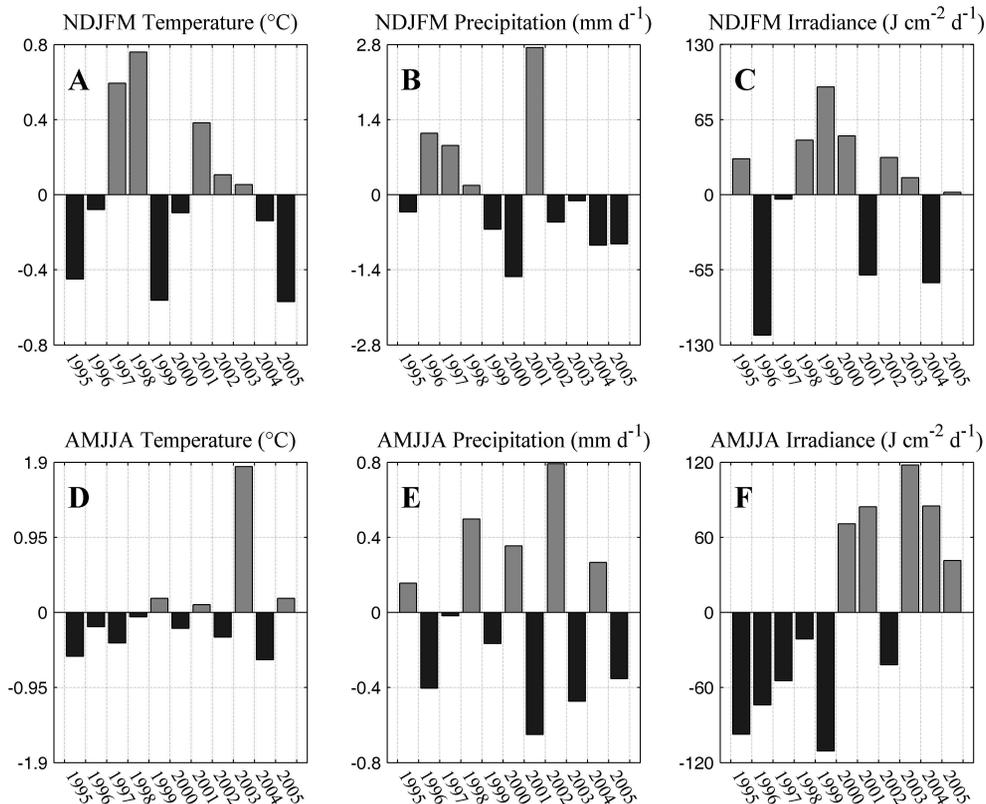
Fig. 7. Annual anomalies of climatic variables measured at the Sémaphore station (see Fig. 1): air temperature in $°C$ (**A** and **D**), precipitation in $mm\,d^{-1}$ (**B** and **E**) and solar irradiance in $J\,cm^{-2}\,d^{-1}$ (**C** and **F**). A, B and C report anomalies from autumn and winter months, i.e. from November of the previous year to March of the current year (NDJFM). And D, E and F report anomalies from spring and summer months, i.e. from April to August of the current year (AMJJA).
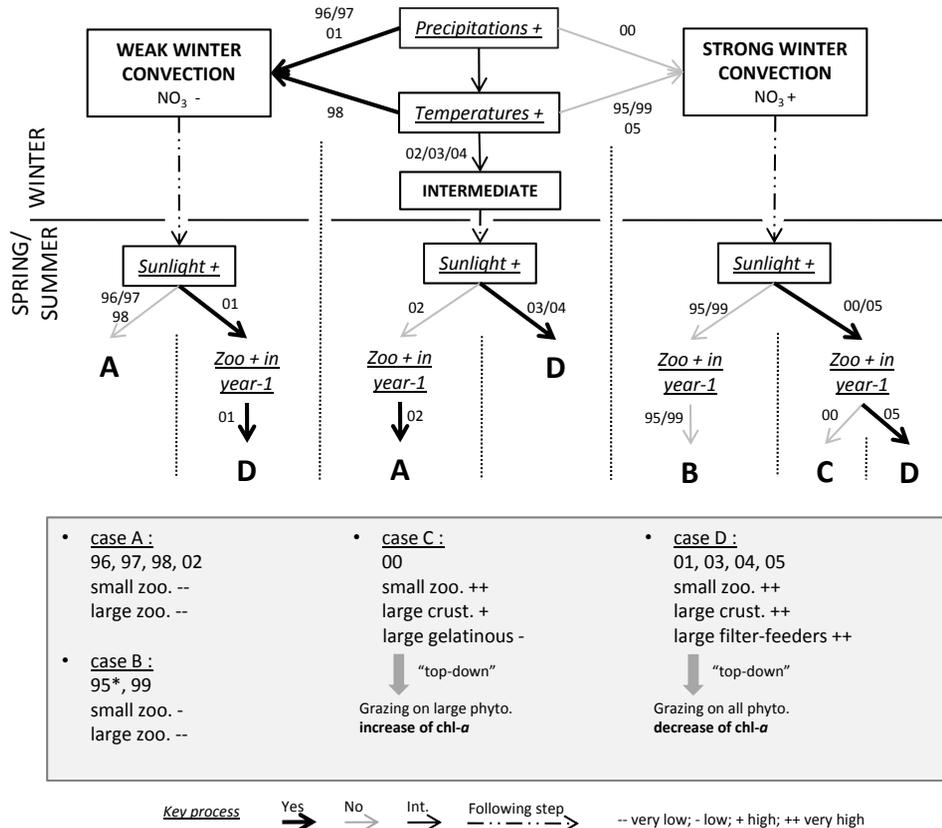
Fig. 8. Proposed general scheme of Ligurian Sea ecosystems dynamics, see Sect. 4.4 for details. The legend of line and boxes is at the bottom of the scheme (Int. is for intermediate). (*) the quantity of previous year zooplankton can not be verified, however from Garcia-Comas et al. (2010) the beginning of the 1990's were low in zooplankton.