

## ***Interactive comment on “Zooplankton communities fluctuations from 1995 to 2005 in the Bay of Villefranche-sur-Mer (Northern Ligurian Sea, France)” by P. Vandromme et al.***

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We are particularly thankful to the anonymous referee for her/his numerous comments and suggestions on our manuscript. We agree with most comments and will modify/update the manuscript accordingly. Details and answers are provided below.

### **General comments**

the manuscript “Zooplankton communities fluctuations...” by Vandromme et al. focuses on the long-term variation of zooplankton on one station in the Ligurian Sea. One major conclusion of the paper is that bottom-up processes likely play an important role in the inter-annual variation of zooplankton stocks. This challenges the view

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that physical or top-down processes control the zooplankton in the area. In its present state, the manuscript can only be seen as preliminary. I have especially problems with the presentation of data and the conclusions drawn in the discussion for the following reasons:

The originality of the manuscript is very difficult to assess. Throughout the manuscript, authors frequently refer to Garcia-Comas et al., a paper that is in review and not available for the public yet. This paper apparently provides similar data (without phytoplankton though) and one wonders what the submitted manuscript distinguishes it from the one in press.

*First, we agree with the remark. Garcia-Comas et al., was submitted in June 2010 but the review process was rather slow and it was only recently accepted in the Journal of Marine Systems (4<sup>th</sup> of April, DOI: 10.1016/j.jmarsys.2011.04.003). If the reviewer needs it, we can provide the accepted version.*

*The two papers are different and stand alone because different nets were used (Juday-Bogorov 380µm in Garcia-Comas et al., versus WP2 200µm in mesh size in our study), the time period is different (1974-2003 vs. 1995-2005), the frequency (monthly for Garcia-Comas et al., and weekly for the present manuscript) and the taxonomic determination is different (5 groups in Garcia-Comas et al., and 10 groups here). Size of the net is important because different nets collect different plankton communities: Juday-Bogorov is efficient to collect large fragile organisms such as gelatinous plankton and large crustaceans but does not collect efficiently small copepods which are really dominant in the Mediterranean Sea: for example for the common period the total abundance recorded by the Juday-Bogorov was 3.63 times less (median value) than the WP2 (1<sup>st</sup> Quartile = 2.37, 3<sup>rd</sup> Quartile = 6.03). Therefore, the present work not only supplements the observation by Garcia-Comas et al., but includes another very important size fraction of the plankton.*

*Thus the conclusions and interpretations of zooplankton cycles in the two studies are*

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*totally independent and should be seen as complementary efforts to document clearly the pelagic ecosystem variability. Our manuscript modified to show better the differences between the two works and the originality of the present work.*

Many of the conclusions, including the suggested bottom-up control and the conceptual model, are speculative and not based on original data provided in the manuscript. The manuscript provides data on standing stocks of phyto- and zooplankton, the interpretation focuses on potential mechanisms and processes for which no data or even evidence is presented. One example for this is the potential top-down control of phytoplankton by zooplankton grazing. There is little evidence for this in the literature, and the authors do not try to estimate the increased grazing pressure.

*This is a problem in many plankton time series in which only the stocks are observed while it is necessary to quantify the mass fluxes between trophic levels. Examples of top down control can be found in the literature and we give several of them here. In a recent paper (Landry et al., 2009), the in situ growth and grazing rates of phytoplankton and zooplankton were measured in the California current ecosystem. The potential control by the mesozooplankton was unexpectedly high driving shifts in the phytoplankton community between years. In another recent paper Fuchs and Franks (2010) hypothesized that an increase in nutrients could, under certain conditions, decrease the biomass of phytoplankton due to a top-down control by zooplankton. Their conclusion is based exclusively on theoretical grounds but fits well with our observations.*

*In addition, we have estimated the potential food requirement of zooplankton and compared to the primary production of phytoplankton using equations from Nival et al. (1975), Andersen and Nival (1988) and Zhou et al. (2010). It appears that the food requirements (zooplankton sampled by the WP2) represent on average 36.2% ( $\pm$  23.9%) of the primary production supporting the proposed top-down control hypothesis. The complete description of the models used to assess the grazing pressure can be given to the reviewers but will not be included in the revised manuscript because it is too*

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*long. We can send it to the reviewers.*

*We modified the discussion accordingly. Of course primary and secondary production should be measured in the future to confirm the model.*

The presentation of data is inadequate. While the discussion focuses largely on different mechanism acting seasonally (e.g. mixing in autumn/winter; light limitation in summer), the zooplankton data is presented as annual means and not even separated seasonally. The graphs suggest that some of the annual signals are caused from different seasons over time (e.g., nitrate maxima irregularly occur also in summer; similarly, the zooplankton anomaly can be driven seasonally by different groups). All in all, the authors focus too little on their data and the conclusions lack rigorous statistical support.

*Several figures present both annual means and seasonal variability (see fig. 3, 5 and 7, additionally fig. 6 focused on winter physical forcing). We agree that we could have included seasonal variation of the different zooplankton groups in the manuscript. Numerical analysis (PCA on monthly abundance of each group) was performed and showed that all zooplankton groups followed the same temporal pattern. The first component of the PCA explained 43.2% of the variance and showed a strong synchrony between all groups, even on a seasonal basis, all were positively correlated to this first PC (except for chaetognaths which appear later in the year). It clearly appears that all groups follow a similar seasonal and inter-annual trend. Student t-tests performed for each month on all values recorded in the first period (before 2000) versus second period show that the total zooplankton is significantly more abundant for each month (except February, August, November and December,) in the second period. This analysis will also be added to the revised version.*

*Since these main tendencies were also evident in the simpler analysis using the cumulative time series, we initially decided not to show the PCA result to reduce the size of the paper. Nevertheless, we have presented the PCA results in the revised manuscript.*

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Problematic is furthermore the lacking evaluation of sampling variability and how representative the chosen station is for the dynamics of the zooplankton in the Ligurian Sea (as the title suggests). Frontal systems can be important as well as advection.

*We agree with the comment which is true for all time series. Sampling variability has been evaluated in previous studies concerning the same site (Menard et al., 1997; Molinero et al., 2005, 2008; Licandro et al., 2010). These studies confirmed that averaging over one week or even one month dampens the impact of spatial/temporal heterogeneity. To check for short term spatial and temporal variability, we also compared monthly copepod abundances estimated using two nets performed on different days during each week (Juday-Bogorov and WP2 net). The comparison was made for copepods larger than 0.0525 mm<sup>3</sup> of individual biovolume (minimum size quantitatively sampled by both net calculated from Nichols and Thompson, 1991). No statistical differences were found ( $\log(WP2) = 1.037 \times \log(JB)$ ,  $r^2 = 0.9802$ ,  $p < 0.001$ ,  $N = 101$ , standardized major axis regression with the model  $y = ax$ ). The two time series are strongly correlated indicating the effect of spatial heterogeneity that advect different plankton population appear unimportant when looking at monthly dynamics.*

*In addition, because of the peculiar position of Villefranche-sur-mer, offshore waters (from the marginal zone, Sournia et al., 1990) enter the bay, thus ensuring that Point B station is representative of offshore physical conditions (see also below). Previous works on zooplankton time series have been based on the same assumption without any attempt to demonstrate it (Menard et al., 1997; Molinero et al., 2005, 2008; Licandro et al., 2010; Conversi et al., 2010). Unfortunately, there is no time series offshore. A single spatial analysis revealed that spatial variability of the copepod species composition exists between the coastal, frontal and central waters of the Ligurian sea but that the total biomass is not changed between regions (fig. 8 in Molinero et al., 2008). Therefore, we may reasonably expect the observed changes in zooplankton in the sampling site as representative of offshore changes. In the revised version, we*

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*made it clear that the HYPOTHESIS is that the observed inter-annual changes at Point B are probably occurring offshore because inter-annual environmental physical forcing are the same (see also below for the physical interpretation).*

### **Specific comments**

#### **Title**

The title is misleading as the work mostly focuses on the inter-annual variation in annual stocks. Very little detail is given to the composition of the zooplankton.

*We changed the title according to the comment: "Inter-annual fluctuations of zooplankton communities in the Bay of Villefranche-sur-mer from 1995 to 2005 (Northern Ligurian Sea, France)." Yet, the work analyzes ten different groups of zooplankton encompassing all the organisms within each group. Removing the term "communities" would also be misleading because readers would think that we treat the zooplankton as a single compartment.*

#### **Introduction**

The introduction lacks structure and should be condensed to the main hypotheses concerning the control of zooplankton in the western Mediterranean.

*The introduction was modified accordingly.*

Page 9179

- line 3: Why also?

*Editing mistake, the also will be remove.*

- line 7: The submitted paper by Garcia-Comas et al. is cited throughout the manuscript, but not available yet.

*We have answered this question above.*

Page 9180

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- line 1: Please specify what is new in the time series

*This time series is new regarding the most important aspect which is zooplankton. The net used (WP2 200µm) allows to sample small copepods which are the most abundant group in the Western Mediterranean sea (Calbet et al., 2001; Siokou-Frangou et al., 2010, p1564 for a review) and that are not sampled by the Juday-Bogorov net (Nichols and Thompson, 1991; Gallienne and Robins, 2001). For example, for the common period, the Juday-Bogorov sampled, on average, only  $31.1 \pm 21.3$  % of the abundance which was sampled by the WP2.*

*The reviewer is right that the new aspect of the present time-series was not stated clearly enough. It was modified in the revised manuscript.*

### **Material, Methods**

Page 9180

- line 12: How representative is this station for the area? Does it reflect inside bay conditions? Do fronts occur in the area, what about lateral transport and currents?

*We have analysed the CTD data from a 52km offshore time series site (DYFAMED site from 1995 to 2005). Mean seasonal values of temperature, salinity and density between 20 and 80m were compared between the coastal and open ocean sites. They show the same pattern for sea water salinity and density suggesting that the inter-annual forcing is common.*

*In addition, other authors have shown similar changes in the hydrographic properties (higher salinity, more convection and mixing in winter) of the upper Mediterranean Sea (Nezlin et al., 2004; Marty and Chiavérini, 2010; Herrmann et al., 2010), already discussed in the manuscript (except the later one published recently).*

*So we can confidently relate main changes at Point B to main changes in a larger area (i.e. Ligurian Sea) due to similar climate forcings and hydrobiological response.*

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*The revised version will include this more detailed information including the correlation between time series.*

Page 9181

- line 7: Please specify why the WP-2 net was chosen. Apparently, this has the disadvantage of being different from previous nets used to study zooplankton in this region and of sampling the small zooplankton only inadequately.

*We have answered to this point above. Briefly, the WP2 net was chosen because it samples better the small copepods. In addition, the WP2 net is a standard net used worldwide that allows intercomparisons between datasets. This point has been stressed by the ICES community (Harris et al., 2000).*

Any replicated tows in order to establish a measure of sampling variability?

*We have answered to this point above by comparing tows of different nets (WP2 and Juday-Bogorov) taken the same months. No significant statistical differences were found showing that the sampling variability appears unimportant when considering monthly dynamics. We did not replicate the samples but pooled several samples within a month in order to reduce sampling variability.*

Page 9183

- line 10: Criteria for the identification of the beginning and maxima of peaks should be given here.

*In the manuscript, we are using an approach similar to Mieruch et al. (2010). After a smoothing of the time series, the starting of peaks (bloom) is the time of the maximum increase (first differences) and the maximum of peaks is simply the time of the maximum value for each year. Because of the initial smoothing, which suppress the noise, this method gave values in agreement with visual observations of the time series. We will rewrite the section to be clearer.*

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## Results

Page 9184

line 1 ff: The discussion focuses largely on seasonal aspects of the zooplankton and ecosystem dynamics. The description of the results, however, focuses on the annual characteristics. Many interesting and important details are lost. I suggest that the authors do not only provide the anomalies of taxonomic zooplankton groups, but include the seasonal dynamics of the groups.

*We agree with this point but we wanted to keep the article focused on the inter-annual variability and not on the seasonal variability of the different groups. In the revision, we added more details on this.*

Are there any estimates of sampling variability or patchiness available during the study? How are start and maximum values defined for the estimation of timing?

*These points have been addressed above.*

Do all groups show similar timing?

*We will add results from PCA on monthly averages. The seasonality of each group was not mentioned in the paper because we found that it did not add relevant information to understand the main scheme of the pelagic ecosystem at the inter-annual scale (which is the scope of the manuscript). The strong synchrony of all groups, even on a seasonal basis is presented with the PCA results discussed above and which will be included in the revised manuscript. Only few groups such as chaetognaths have their maximum later in the year (July/August).*

How are anomalies calculated (running average or average during investigation)?

*Average during investigation with gaps filled before. Because of only few gaps a simple linear interpolation was used. It will be fully explained in the manuscript.*

With regard to processes acting in winter and summer, wouldn't it be better to show

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seasonal stocks (with estimates of seasonal variability) and their anomalies?

*Seasonal cycle of zooplankton is depicted in figure 3 (lower case). We modified the figure 4 to show the mean annual cycle of total plankton during the two periods on the same graph.*

Page 9184

- line 1 ff: Why do the authors decide to show annual averages of abundance and estimated biomass? There is little to be extracted from that, especially when the discussion focuses largely on the winter/spring conditions which are conceptually divided from the summer situation. It would be also interesting to see which groups, e.g. small copepods or large ones, respond to the suggested changes over time. Fig 3 A, B shows the annual anomalies. Information is lost here, particularly on the seasonal aspects, which play a role in the discussed changes over time.

*We show annual averages for the zooplankton because we were interested in showing the main mode of inter-annual variation. However, the seasonality is also presented (fig. 3CD) and discussed in the manuscript. We focused on the winter/spring seasons because these are key periods for the annual changes in plankton. Describing the other seasons would add more figures and text, which is not relevant to the scope of the present manuscript. We will make it clear in the revised manuscript (notably by showing that winter is key for the mixing and spring is key for growth of plankton biomass, see below). In addition it was already mentioned in the manuscript (fig. 4) that all groups are synchronous on the inter-annual scale.*

The monthly values, shown in Fig. 3 C, D consist of likely 4 estimates of abundance and biomass. I would like to see the variability within in these estimates.

*The RSD (relative standard deviation) on the mean monthly abundances is on average of 0.54 per month ( $\pm 0.31$ ). Months with highest RSD are, in order, March, January, April, February and May (average RSD > 0.6).*

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Timing of start and maxima should be shown separately for the 10 groups. The criteria for the identification should be given.

*The strong intermittency in abundance of large groups did not enable us to compute start and maxima for them with confidence. So we preferred to pool all the groups. Criteria are answered above.*

How much do the secondary peaks in late summer contribute to the anomalies? Fig. 3 D suggests that part of the positive anomalies comes from this period. This is important, because in the discussion potential mechanisms vary seasonally.

*The September and October months contribute to 11.6 % on average of the annual abundance anomaly. The maximum was in 2002 and 2003 with 22.1 and 17.4 % respectively. We clearly see a second peak for these two years on fig. 3D. Yet, except for these two years, this period is negligible compared to the April-May and June-August periods which account for 33.9 and 24.3 % of the anomaly respectively (March-April = 31.8 %; May-June = 26.5 %; July-August = 15.1 %). We added a figure in the manuscript showing the relative part of each season per year on the annual means.*

Page 9185 - line 1 ff: Data on the changes in size should also be presented on a seasonal basis. Page 9187

*We did not include this figure because no clear seasonal pattern could be extracted. A marked decrease in the plankton mean size was observed throughout the year in 1999 and 2000. This decrease in the mean size is concomitant with the increased importance of the smallest organisms (mainly small copepods).*

- line 1 ff: Fig 6 labeling and legend contradict each other with regard to what they should show. In contrast, to the biology, no seasonal data and changes over time are shown.

*We made a mistake in the legend, it was corrected. Thank you.*

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- line 1 ff: Here, data is shown for the autumn/winter. Biological data should be presented adequately.

*There is a time lag of about one month between air and sea temperatures. The impact of the weather is not immediate on the pelagic physical environment, and plankton response is also delayed by one month. This is particularly evident on cross-correlations performed between climate and hydrology. So presenting similar periods for all data would not allow description of this fundamental dynamic. In the revised manuscript we present one new figure on plankton seasonal cycle so that the reader should make the connections between seasons for the different climatic, physical and biological data.*

## **Discussion**

In their discussion, the authors review to a large part existing literature and focus on the explanation for an increase in the zooplankton abundance since 2000 and their conceptual model. Although it is a logical outcome of the work to provide a hypothesis on the potential mechanisms for the zooplankton increase, this should principally follow from own data. This is not the case, and the manuscript is not original. In contrast, the authors focus very little on their own zooplankton data, which is also inadequately presented. While the discussion concentrates on the spring time, the zooplankton is presented on an annual basis. Details in the compositional changes in the seasonal development of zooplankton are not shown, although this is important in the explanation for the lacking increase in Chla. I also miss a critical evaluation of how well the station reflects the zooplankton dynamics of the area. Do currents, advection or fronts (see for instance Molinero et al. 2008) play no role in influencing the seasonal community composition?

*The exhaustive literature review may be important in the light of contrasting results. First, the small, dominant, zooplankton collected with a WP2 net was not studied in previous works. Second, we included a larger range of new environmental variables. Finally, our observations and hypotheses concerning the important change ca. 2000*

C5399

*are strongly supported by our own data set.*

*We have addressed, and included, all the points on seasonal versus inter-annual scales and spatial variability in the revised discussion.*

-chapter 4.1 reviewing the major hypotheses concerning the causes for a change in zooplankton community composition is too long and should be condensed Problematic is that Garcia-Comas et al. is not available how do the recent results with a different net compares with the published data from the same station? It is hard to judge, therefore, if the present paper is original and provides the innovation as suggested by ' more complete data on climatology, hydrology, nutrients and phytoplankton'.

*We have explained these points above.*

- lines 16 - 26: A different net type and analysis method were used in comparison to Garcia-Comas et al. and Molinero et al. Moreover, the presented data parallels the investigation of Garcia-Comas, and only follows the work of Molinero et al. Thus, there is no overlap with Molinero et al. Before the authors can conclude that their data supports a reversal trend - for which they don't present data themselves -, they need at least to demonstrate that their data reflect a similar trend as observed in Garcia-Comas.

*Molinero et al. (2008), proposed a scenario for the changes they observed in their 1966-1993 dataset, notably with a reorganization of zooplankton community in the middle-late 1980s - early 1990s. The paper of Garcia-Comas et al. uses the same net collection and confirms that the early '90s had low zooplankton concentration. Moreover, Garcia-Comas et al. data and the time series presented here are significantly correlated for copepods of similar size. In the present paper we concentrated on another decade and emphasize the change observed ca. 2000. We show, using the WP2 time series, that oligotrophy did not persisted in the '00s. Finally, we proposed a scenario based on the winter and spring/summer forcings.*

C5400

- Lines 6 - 9: Authors state that a shift in the winter water salinity occurred with less saline water until the year 2000 and higher values in the period 2001-2005. Figure 6 shows that the anomalies in the years 1995, 1996, 1999 and 2000 were higher than 2001-2003. This is not a shift.

*The manuscript is not clear enough. We improved this part in the revised version. One of the major conclusions of the paper is that to account for the zooplankton change ca. 2000 we have to take into consideration not only the change in the winter physical conditions but also the spring/summer climate. Changes in salinity and density do not explain it fully. We did not point out any shift in the physical dynamics. We noted that the inter-annual variability showing the period of dry conditions could also contain a wet year. This was one of the main parts of the paper. We explain it better in the revised manuscript.*

*Another point concerns the use of the term shift which is commonly used in ecology to refer to modifications in the ecosystem such as strong increase of total abundance of one or several components. Yet, following the more rigorous definition of a shift by Hsieh et al. (2005), we modified it in the manuscript and are using the term "change" which is more neutral and correct (stricto sensu).*

- Lines 14 ff: Does the decreased precipitation in winter have an immediate effect on salinity or does this occur with delay (which one would expect to be the case)? From comparing Fig 6 a, b and 7 b this cannot be extracted because it is not clear what Fig 6 is showing in the different panels.

*The potential delay between precipitation and salinity is difficult to assess because the spatial scale is not local but consists of all the NW Mediterranean Sea (e.g., Goberville et al., 2010). Precipitation at Point B are intermittent and local, driving a highly variable time-series. Deficit of water in the dry year impose a more general pattern. So what we observe in the water column at Point B is the assemblage of processes acting at different time and space scales. The measure of precipitation at the Cap-Ferrat is*

C5401

*simply an indication of the inter-annual and seasonal variations of precipitations, not at the weekly scale.*

- Line 24: With the conducted sampling scheme (weekly measurements), the authors should be able to directly demonstrate the intensification of winter convection in a graph.

*We agree and are presenting a more complete description in the revised version.*

*Water column structure (density difference between surface and 75 m depth) is important to mainly determine the strength of the summer thermocline (i.e., stratification strength).*

*The way we used to assess the vertical extent of the mixing was then to focus on density values instead of density gradient. The highest is the density at Point B the deeper is the mixing offshore. We can use the frequency of occurrence of the 28.85 density value in surface waters during winter as an indicator of the strength of the mixing (It happens only in 1999, 2000, 2003, 2004 and 2005, with the most occurrence in 2005, i.e. 61.5 % of winter weeks). This value is generally found below 150 m depth in the coastal Ligurian Sea during winter (Stemmann et al., 2008). We will include this analysis in the revised version.*

- Lines 1-16: I would like to see a graph regarding the correlation of density and nitrate. Figure 5 shows only annual means, and not winter values. Which have been used to establish the correlation? The lower plot suggests little relation between density and nitrate as years with very high nitrate display only average density (e.g. 2002, 2003). So, where is the trend coming from? The figure 5 shows also that a large part of the annual nitrate signal in 2005 (the year with highest convection) occurs in September and unlikely results from winter mixing.

*The correlation between nitrate concentrations and densities taken at the same time during the winter months (January, February and March) is significant (Spearman,*

C5402

*$r=0.5634$  and  $p<0.001$ ). The winter convection explains an important part of the variability in nitrates. We agree that years 2002 and 2003 underwent medium convection but show high nitrates. In year 2005 a nitrate peak was observed in September, but values in February and March are among the highest of the time series. Hydrographic conditions are measured weekly and therefore the frequency of  $\approx 4$  sampling per month may not be enough to take into account strong events of vertical mixing because these events occur on short time scales. However, trends are significant as indicated by the Spearman correlation coefficient. We modified the revised manuscript accordingly.*

How much does nitrate reflect the availability of other nutrients, e.g., silicate, which could explain that diatoms would get more abundant?

*There is no correlation between nitrates and silicates (Spearman,  $r=0.12$ ;  $p=0.14$ ). Therefore, we hypothesized that silicate is not a limiting factor for diatoms in the present systems which tend to be confirmed by half saturation constant found in the literature (Martin-Jezequel et al., 2000) which are below observed values of silicates. In addition, Bustillos-Guzmán et al. (1995) showed that diatoms are not the most abundant group in the area and that the chlorophyll-a may more reflect nano-flagellates. Unfortunately there are no recent studies on phytoplankton community and we cannot argue that diatoms are more abundant in the second period as they are in offshore water (Marty and Chiavérini, 2010).*

- Lines 17 ff. - p. 9193: The following discussion on the paradox of low phytoplankton at high nutrient conditions and potential top down control by zooplankton focuses largely on published ideas. Although little evidence is provided in the literature (zooplankton abundance in mesocosms and at the selected station should be compared!).

*There is no mesocosm experiment available for our areas. We agree that future research should use them. We will add more details in the manuscript.*

*In Graneli and Turner (2002), they observed a trophic cascade from zooplankton to microzooplankton and to phytoplankton in mesocosms with a zooplankton community*

C5403



mainly composed of copepods and ctenophores. Biomass used ranged from 20-80  $\mu\text{gC L}^{-1}$  for copepods and 200-700 for the whole (meso)-zooplankton. At Point B, using conversion factor from Lehette and Hernández-León (2009) and Mauchline (1998), we have values ranging from about 9 to 300  $\mu\text{gC L}^{-1}$  at Point B (which is only the zooplankton taken by the WP2 net). Therefore, the values fell in the same order which support the hypothesis that concentrations of zooplankton observed at Point B could generate a trophic cascade to the phytoplankton. We also calculated the grazing pressure above and showed that it could account for 36 % of primary production. At the Dyfamed site the maximum values of zooplankton concentrations observed were about 20 times lower than in Point B using same conversion factors. This may explain why in Marty and Chiavérini (2010) they did not observed an inverse relationship between nutrients and phytoplankton.

Moreover, recent work by Fuchs and Franks (2010) provide theoretical evidence of this mechanism. It was already discussed above.

Authors conclude a potential top down control. Part of their data, however, provides evidence, that the zooplankton follows the phytoplankton with delay, as it would be expected from the duration of zooplankton lifecycles and published evidence (e.g., Smetacek, Kiørboe etc...). At this point, one would expect a thorough analysis of the winter zooplankton concentrations and their potential to keep the phytoplankton low (discussed above). However, as it looks like, zooplankton abundance is very low in winter spring, which is a counterargument for any top down control. Instead of reviewing published data and speculating about top-down effects, the authors should provide evidence.

We provide evidence in the form of data showing higher values of nitrates were mostly accompanied by higher values of zooplankton but lower values of phytoplankton at the inter-annual time scale. On average, the winter (January-February) accounts for 18.1 % of the annual anomaly of chlorophyll-a (23.2, 32.0, 13.6, 13.0 for March-April, May-August and September-December respectively). In addition, the observed decrease

C5404

of chlorophyll-a is not due to the winter-time (January-February JF). The second period (2001-2005) is lower than the first one (1995-2000) by factors of 1.14 for the JF period, 1.59 for the MA period, 1.34 for the MJJA period and 1.25 for the SOND time period. The top-down control occurred mostly in spring/summer, period with highest abundances of zooplankton. More details on these seasonal considerations are given in the revised manuscript.

In addition, estimates of primary production and zooplankton potential uptake support a top-down control since the needs of the zooplankton community are of the same order of magnitude as the phytoplankton primary production. This was also measured in the Gulf of Lion by Gaudy et al. (2003).

We cannot provide irrefutable evidence that there is a top-down control, it is a hypothesis based on observations and extrapolations, but it may be useful for future studies.

- Line 24: The criteria for start and max values in Table 2 need to be defined (especially for the start levels) see above The constant delay in the zooplankton maxima by 0-2 weeks is surprising considering that the composition changed largely during the investigation (see Fig 4). Any explanations?

The composition (fig. 4 in the manuscript) did not change much during the study period. There is a synchronous year-to-year shifts of all groups (with concomitant low and high periods). The composition changed only around year 2000 because of a time lag in the increase of small copepods and of larger organisms. Yet this did not affected the time lag in the peak of total zooplankton (which mainly represent copepods) compare to the peak of chl-a. Some papers have shown that the phenology of the phytoplankton could affect the zooplankton inter-annual variability (e.g., Edwards and Richardson, 2004; Ji et al., 2010, ...), yet, this process does not seem to be an important feature in the studied ecosystem. This is discussed in the manuscript p9193-9194.

- Which groups are "hidden" in the spring zooplankton?

C5405

*All groups are present in the spring zooplankton. Only chaetognaths peak in summer but are already present in spring.*

- The authors show mostly annual data, which surprises when the processes are discussed on a seasonal basis.

*Answered above*

- Line 7: Although the concept is okay, where is the evidence from the conducted work for both processes acting at the same time?

*We did not state that both processes act at the same time. We argued that both processes explain a part of the inter-annual variation. Looking at annual stocks of zooplankton a wet winter (driving to low convection and low nutrients inputs) could be mitigated by advantageous summer conditions. We removed in the revised manuscript the conceptual scheme since it appears to be too speculative and could lead to misunderstanding the difference between the results and hypotheses we present to explain the results.*

- Lines 10-25: Again, most of the discussion is speculative and based on literature, but not own measurements, as is its continuation on page 9195. Why should summer irradiation be important for the spring zooplankton development (as most of the biomass occurs March-May, see Figure 3)?

*First, we have calculated the spring/summer irradiation. Second, even if the maximum biomass occurs in March-May, this represents on average 46.6 % of the annual value. The period June-August represents 25.8 % which is not negligible. This last period could represent up to 41.6 % (more than March-May) as in 2001. The period for which we have calculated the spring/summer irradiation (April-August) account for 59 % of the annual means on average (April account for 16.6 % and May for 16.6 % also). These estimates suggest that climate conditions in spring and summer are not negligible in explaining the inter-annual variability of the zooplankton.*

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*A strong correlation appeared between the spring/summer irradiation and the zooplankton (In PCA made on environmental values the irradiation calculated in spring and in summer are the closest from the first PC made on zooplankton and the Spearman correlation is significant  $p < 0.05$ ). Taking into account the spring/summer irradiation (irradiation calculated in spring significantly correlated to irradiation calculated in summer, Spearman  $p < 0.01$ ) enables us to explain the inter-annual variability for years not matching with the winter control hypothesis. Molinero et al. (2005, 2008) hypothesized a summer control of the zooplankton community at Point B, with a negative effect of sunny conditions which are linked to an increase of the summer stratification. Here we do not observe the negative effect of the summer stratification and therefore we proposed an alternative hypothesis to explain the positive effect of sunnier spring/summer on the zooplankton through an indirect effect on phytoplankton growth (light limitation). This hypothesis is highly speculative since we do not have any data on in situ PAR and phytoplankton growth rate. The observation is that there is a positive effect of sunny spring/summer and that the increased summer stratification does not seem to be detrimental for copepods as argued in previous studies.*

*Nevertheless we agree with the reviewer that these arguments are speculative therefore we modified this part in the discussion.*

The conceptual model is mostly a repetition of the preceding paragraphs and should be condensed. Evidence should be provided for 'memory' effects, e.g., for the benefit of good zooplankton conditions for the succeeding year: I could have missed it, but I haven't seen any results for a correlation of zooplankton with the NAO.

*The conceptual model will be completely changed taking into account all the suggestions by both authors.*

*No significant correlations were found between the NAO and the succession of zooplankton communities in the 11-year period, neither between the NAO and the climate or hydrology at point B during the period 1995-2005. This confirm the observation of*

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*Garcia-Comas et al. (Accepted). The authors show, using a sliding correlation, that NAO was strongly correlated with the local climatic and hydrological data until the '90s and that the correlation was weaker after. Also, other studies have recently shown a non-stationary relationship between the NAO and European surface climate. It has been related to changes in the location of the NAO pressure centers (Beranova and Huth, 2007; Vicente-Serrano and Lopez-Moreno, 2008). In Marseille, close to the studied area, Beranova and Huth (2007) showed that the correlation between the winter NAO and local winter temperature and precipitation weakened when including the '90s in the last data point of a 31-year moving window (mid-point 1984). In the case of precipitation, the relationship became non significant for that last period included in their study. Using a time series going back to 1785, Vicente-Serrano and Lopez-Moreno (2008) showed that the position of the centers of action changed at a decadal scale. In the early '90s 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 '00s 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.*

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