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Short term changes in zooplankton community during the summer-autumn transition in the open NW Mediterranean Sea: species composition, abundance and diversity

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Abstract

Short term changes in zooplankton community were investigated at a fixed station in offshore waters of the Ligurian Sea (Dynaproc 2 cruise, September–October 2004). Mesozooplankton was sampled with vertical WP2 hauls (200 μm mesh-size) and large mesozooplankton, macrozooplankton and micronekton with a BIONESS multinet sampler (500 μm mesh-size). Temporal variations of total biomass, species composition and abundance of major taxa were studied. Intrusions of low salinity water masses were observed two times during the cruise. The first one, which was the most important, was associated with changes in zooplankton community composition. Among copepods, the abundance of *Calocalanus, Euchaeta, Heterorhabdus, Mesocalanus, Nannocalanus, Neocalanus, Pleuromamma* and also calanoid copepodites increased markedly. Among non-copepod taxa, only small ostracods abundance increased. After this low salinity event, abundance of all taxa nearly returned to their initial values. The influence of salinity on each zooplankton taxon was confirmed by a statistical analysis (Perry's method). Shannon diversity index, Pielou evenness and species richness were used to describe temporal variations of large copepod (>500 μm) diversity. Shannon index and Pielou evenness decreased at the beginning of the low salinity water intrusions, but not species richness. We suggest that low salinity water masses contained its own zooplankton community and passed through the sampling area, thus causing the replacement of zooplankton population.

1 Introduction

Organic carbon is synthesised by phytoplankton in the surface layer, via photosynthesis. Afterwards, a part of this carbon is exported to deep water, where it can be sequestered during many years. Intensity and quality of vertical particulate organic matter flux are related with physical and biological processes. For example, a gust of wind can generate a mixing and enrichment by nutrients of the surface layer, which can

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lead to changes in the food-web structure (Kiørboe, 1993). The biological processes which influence vertical flux are: (i) primary production, (ii) grazing by zooplankton, (iii) transfer of matter by zooplankton to deep ocean in the form of faecal pellets (Fowler and Knauer, 1986), carcasses (Turner, 2002) and vertical migrations (Longhurst, 1989; Al-Mutairi and Landry, 2001). Therefore, the structural and functional diversity of zooplankton appear as a keystone in the carbon transport to deep layers.

The multidisciplinary cruise DYNAPROC 2 (DYNAmics of the rapid PROCesses in the water column) was devoted to study carbon production and export to depth by zooplankton organisms and physical processes during the summer-autumn transition. This cruise is the continuation of DYNAPROC 1 cruise (Andersen and Prieur, 2000). During DYNAPROC 2, the sampling was performed at short time scale for all parameters, in order to study short term changes of the food-web in response to physical processes. Abundance and specific composition of zooplankton are well documented in the NW Mediterranean Sea, but the overwhelming majority of previous studies were based on monthly sampling or large scale cruises and do not address short-term changes (Vives, 1963; Hure and Scotto di Carlo, 1968; Franqueville, 1971; Sardou et al., 1996). Only two studies, Andersen et al. (2001a, b), addressed zooplankton dynamics at short time scale in the open Ligurian Sea, and these considered the late spring, period (May 1995, DYNAPROC 1 cruise).

The purpose of our study was to examine short term changes in abundance, specific composition and diversity of zooplankton community during summer-autumn transition in the open Ligurian Sea. Here, we report our results and relate variability in the zooplankton community to the environmental features and dynamics encountered.

2 Material and method

2.1 Study area

DYNAPROC 2 cruise was conducted in the central part of the Ligurian Sea (NW Mediterranean Sea) over a four-week period during the summer-autumn transition (14 September–17 October 2004). This period of time was selected in order to study the transition from stratified and oligotrophic summer conditions, to mixed and mesotrophic autumnal conditions. Sampling was done at an offshore station in the central part of the Ligurian Sea where horizontal advection is assumed to be negligible. The positioning of the Time Series Station (TSS, 28 miles offshore, 43°25 N, 8°00 E) was decided on the basis of a transect from coast to offshore waters. In addition, a grid of 16 stations centred on the TSS was sampled three times during the cruise in order to describe the hydrological environment of the TSS (Fig. 1).

2.2 Environmental data acquisition

Wind speed was measured onboard with a meteorological station (sampling every 30 s and smoothing with a moving average with a 1 h window). Between the two legs, during port call, wind speed data are taken from records by Meteo-France buoy located near the TSS, at the DYFAMED site (43°25 N, 7°52 E). CTD profiles (SBE 25) were performed with a time interval of about 3 h (255 profiles, temperature, salinity, pressure, fluorescence, O_2, irradiance). Water sampling was done with a 12 bottles rosette simultaneously to get the profiles of nutrients, chlorophyll, and others chemical parameters. In situ fluorescence was calibrated with chlorophyll-*a* concentration measured on rosette samples by HPLC. Using the method developed by Andersen and Prieur (2000), fluorescence (F, arbitrary units) was converted to chlorophyll concentration (Chl, $\mu\mathrm{g\,L^{-1}}$) with the following relationships:

$$\text{Leg 1 : Chl} = 2.0740 * (F - 0.00785) \qquad (n = 453, r = 0.97) \tag{1}$$

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$$\text{Leg 2}: \text{Chl} = 1.7807 * (F - 0.00785) \qquad (n = 466, r = 0.96) \tag{2}$$

2.3 Zooplankton sampling procedure

2.3.1 Zooplankton sampling

Short-term changes in the zooplankton community were investigated with two types of nets: (i) a multiple opening and closing net with 500 μm mesh nets, BIONESS (Sameoto et al., 1980); the sampled community corresponds therefore to large-sized copepods, macroplankton and micronekton; (ii) a WP-II net (200 μm mesh size), the sampled community corresponding to mesozooplankton (copepods mainly). The BIONESS was obliquely hauled over the 0–250 m water column (9 different strata) in the vicinity of the time-series station. WP-II sampling was performed with 0–200 m vertical tows at the time series station with a triple WP-II net: two samples were used for biomass analysis (see Mousseau et al., 2008), the third one was formalin preserved for counting and taxonomic identification.

2.3.2 Preservation, counting and taxonomic identification

Samples were preserved with 5% borax-buffered formalin-seawater before counting and identification. For copepod taxonomy, reference was made to the species inventory for Mediterranean Sea from Razouls and Durand (1991) and the web site of Razouls et al.: http://copepodes.obs-banyuls.fr. The species identification was not possible for all copepods, taxonomic determination is presented here at genus level. When the species could be recognized with absolute certainty, the name of the species is specified. Non-copepod taxa are counted at a taxonomic level of family or order.

Preserved WP-II samples were not available for the first part of leg 1 (17–22 September). Frozen samples, initially collected for biomass analysis were used for taxonomic identification. To defrost the samples, they were put in a beaker filled with room temperature water. As some organisms were damaged by the freezing, the taxonomic identification was less accurate. WP-II data from 17–22 September are also presented in this paper but these data are drawn in grey in the graphs (Figs. 4 to 7).

2.4 Data analysis

2.4.1 Abundance of zooplankton

Raw data (from BIONESS and WP-II sampling), in number of individuals per net, were standardized to number of individuals per square meter, depending on the section of the water column sampled (0–200 m for WP-II; 0–250 m for BIONESS). Abundance data from the BIONESS depth stratified hauls were integrated through the 0–250 m water column. In this study, we have separated copepods from the rest of zooplankton. For copepods, we only present the temporal abundance variation of main copepod genera, (i.e. genera whose abundance represents more than 1% of total copepod abundance). For the other organisms, we present temporal abundance variation of main non-copepod taxa, (i.e. taxa whose abundance represents more than 1% of total non-copepods abundance). However, a list of total individuals identified (copepods and other taxa) is presented in Appendix A.

2.4.2 Diversity indices

The computation of species diversity indices requires a taxonomic identification at species level. In WP-II samples, only 42% of total number of organisms could be determined at this level, making the calculation of species diversity indices impossible. In contrast, in BIONESS samples, 99% of copepods could be identified to species level. Consequently, species diversity indices were only calculated using copepod data obtained with BIONESS net.

Three different indices were computed: Shannon index (Shannon, 1948), Pielou evenness (Pielou, 1966), species richness. The comparison of these three indices will allow reveal if diversity variations are due to a change of the number of species, or a modification in the relative contributions of taxa, or a combined effect of these two parameters.

Shannon diversity index (H') was computed from Eq. (3) where s is the number of species and p_i is the relative frequency of the species i.

$$H' = -\sum_{i=1}^{s} p_i . \ln(p_i) \quad (3)$$

Pielou evenness (J) was computed by dividing H' by $\ln(s)$, as shown in Eq. (4):

$$J = H' / \ln(s) \quad (4)$$

Species richness is defined as the number of species.

2.4.3 Statistical methods

Day-night differences

Wilcoxon-Mann-Whitney test ($p \leq 0.05$) for non-paired samples was applied on zooplankton abundance and diversity data to see if there was a significant difference between night and day.

Relationship between zooplankton abundance and environmental parameters

Perry's method was used to determine if there was a relationship between zooplankton abundance and environmental parameters (Perry and Smith, 1994). This method allows identification of associations between each zooplankton group and an environmental factor (in this study, the integrated water column salinity). The range of salinity values is divided into several classes of equal amplitude, number of classes being adjusted such that no empty class exists. Frequencies of observations in each class are estimated and the cumulative distribution of frequencies is computed. The sum of zooplankton abundance from all samples in each salinity class is computed, and this distribution is also cumulated. The cumulative distribution of abundance of each zooplankton group, $g(t)$, was plotted against the cumulative distribution of salinity, $f(t)$. If these two distributions are almost similar, there is no significant dependence of this zooplankton group on the environmental parameter, whereas the greater their difference, the stronger is the association. A Monte Carlo randomization test was set after 10 000 permutations in order to test the significance of association between $g(t)$ and $f(t)$. This method is explained in detail in Perry and Smith (1994).

Relationship between zooplankton diversity and salinity

The method of cumulative sum of deviations from the mean, called "Cumsum" (Ibañez et al., 1993) is used for (i) detecting changes which occurred in the average level of a series, (ii) determining the date when changes appear, (iii) and estimating the average value of homogenous intervals. In the present study, this method was used to determine if there was a relationship between diversity among large copepods and water column salinity during the cruise.

The temporal variations of salinity and zooplankton diversity indices (day and night) are considered as three distinct chronological series. For each series $x(i)$of p values, the variable Sp, which is the cumulated sum of deviations from the mean k, is computed as shown in Eq. (5):

$$Sp = \sum_{i=1}^{p} (x_i - k) \tag{5}$$

When x_i is equal to the mean k over a period of time, the Sp curve is horizontal. When x_i remains greater than k, Sp curve shows a positive slope and inversely. So, the moments when the series is changing relatively to the mean can be detected by slope reversals.

3 Results

3.1 Meteorological and environmental conditions

Temporal variations of wind speed (Fig. 2a) was characterised by several strong wind events (>25 knots). During the first part of the cruise, two from NE occurred (17 and 25 September). At the end of the cruise there was a succession of three gust of wind from opposite directions: SW, NE and SW.

The time-depth distribution of temperature (Fig. 2b) shows highly stratified water column from the beginning of the cruise to 10 October. The thermocline was strongly marked, with a mixed-layer temperature higher than 20°C (22°C during weak wind periods). This thermocline was located at approximately 25 m depth throughout the cruise, except at the end, where it deepened to 40 m depth during the period of successive strong wind events (11–16 October). The thermocline deepening was accompanied by a strong cooling of the mixed-layer water and suggests the beginning of autumnal de-stratification.

The time-depth distribution of salinity (Fig. 2c) shows the occurrence of two intrusions of Low Salinity Water (LSW) during the cruise. This water has a coastal origin and crossed the Ligurian front along isopycnals by a barocline instability (Andersen et al., 2008[1]). The first intrusion (LSW-1), which occurred from 21 to 30 September, was very important as well as by its size and by its intensity. LSW-1 was located between 15 m and 75 m depth. The lower value recorded was less than 38.05, whereas average salinity at this depth lies between 38.30 and 38.40 outside the intrusion. The second intrusion (LSW-2), which occurred from 9 to 12 October, was weaker and restricted to the layer 20–40 m. A salinity less than 38.30 was recorded during two days, and

[1] Andersen, V., Prieur, L., and Goutx, M.: Hydrology, biology and biogeochemistry during autumn transition period (Sept. 14–0ct. 17), at a central point in the Ligurian sea, NW Mediterranean: overview of the DYNAPROC2 (DYNAmics of the rapid PROCesses) study, Biogeosciences Discuss., to be submitted, 2008.

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minimum salinity was not lower than 38.20.

The time-depth distribution of chlorophyll-*a* (Fig. 2d) shows a bimodal distribution on the vertical at the beginning of the cruise. The deeper peak (80 m depth) was mainly composed of senescent diatoms, which quickly sedimented. The upper one, which was located at about 50 m depth, was mainly composed of nanophytoplankton (Lasternas et al., 2008[2]). The 50 m peak persisted until the end of the cruise but the maximum concentration occurred at the beginning of the cruise (19–22 September). The decline coincided with the arrival of LSW-1.

3.2 Zooplankton abundance

3.2.1 Total zooplankton biomass

As temporal changes in the biomass of total zooplankton biomass are detailed in Mousseau et al. (2008)[3], we will give only few comments. Total zooplankton biomass integrated over the 0–200 m water column varied between 0.15 $g\,m^{-2}$ and 3.79 $g\,m^{-2}$ (Fig. 3). As expected, night data were generally higher than day ones, except for one point (night between 18 and 19 September). This was due to migratory organisms which are located in deep layers during day and move to the surface layer during night. In spite of a strong variability in the data, it is noticeable that average zooplankton biomass appeared higher during LSW-1.

[2]Lasternas, S., Tunin-Ley, A., Ibañez, F., Andersen, V., Pizay, M.-D., and Lemée, R.: Daily vertical abundance and diversity of microphytoplankton in NW Mediterranean Sea during the summer to autumn transition (DYNAPROC II cruise; Sep–Oct 2004), Biogeosciences Discuss., to be submitted, 2008.

[3]Mousseau, L., Lefevre, D., Andersen, V., Narcy, F., and Nival, P.: Role of the zooplankton community composition on the mineralisation and the vertical flux of organic matter at a fixed station in the Ligurian Sea, Biogeosciences Discuss., to be submitted, 2008.

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3.2.2 Abundance of major zooplankton taxa

Figures 4 to 7 present the temporal variations of abundance of major zooplankton taxa throughout the sampling period. On each figure, zooplankton abundance is overlain with the percentage of the water column occupied by LSW (<38.30).

The abundance of total copepods (adults and copepodits) sampled with WP-II varies between 10 000 and 45 000 ind m^{-2} (Fig. 4a). It reached a maximum during LSW-1, after which it nearly returns to initial values. In contrast, there were no visible effects of LSW-2 on total copepod abundance. Copepodits, which represents more than 48% of total copepod numbers, showed the same pattern as total copepods, with a maximum of 22 000 ind m^{-2} during LSW-1 (Fig. 4b). When considering abundance of adults averaged over the sampling period, the genus *Clausocalanus* ranked first, followed by *Oithona*, *Pleuromamma*, *Calocalanus* and *Neocalanus*. The sum of these five genera represents nearly 90% of the abundance of adults. *Clausocalanus* spp. was mainly *C. pergens* (43%). Its abundance did not vary a lot during the cruise but one maximum was recorded during the night between 27 and 28 September (Fig. 4c). *Oithona* spp. (61% *O. similis*) appeared to fluctuate randomly during the study period (Fig. 4d). *Pleuromamma* spp. (96% *P. abdominalis* and 4% *P. gracilis*) had a maximum around 7 October (Fig. 4e). *Neocalanus* spp. (exclusively *N. gracilis*) and *Calocalanus* spp. show a maximum of abundance during LSW-1 (Fig. 4f–g).

Most of the small copepods and copepodits collected with WP-II net in the size range 200–500 um did not appear in the BIONESS samples. Total abundance of large copepods sampled with this net, fluctuates around 500 ind m^{-2} (Fig. 5a) but shows a strong increase on 21 September, at the beginning of LSI-1 (until 3000 ind m^{-2}). Afterwards, concentrations declined until the end of LSW-1 to come back nearly to the initial values. As with WP-II samples, there was no increase of total large copepods during LSW-2. The abundance increase during LSW-1 was observed for most of the principal copepod genera, especially the dominant one: *Neocalanus* (Fig. 5b). This genus consisted of a single species, *N. gracilis* (as is WP-II samples) and represented more than 50% of total copepod numbers sampled with BIONESS net. It ranked first by average abundance, followed by *Nannocalanus* (exclusively *N. minor*), *Pleuromamma* (32% *P. abdominalis* and 68% *P. gracilis*), *Euchaeta, Scolecithricella, Heterorhabdus* and *Mesocalanus* (exclusively *M. tenuicornis*). The abundance of all these taxa clearly increased with LSW-1, except for *Euchaeta* and *Scolecithricella*, for which abundance increases were less evident (Fig. 5c–h).

Among the non-copepod taxa sampled in WP-II, the most abundant one were the appendicularians, followed by pteropods, ostracods, hyperiids, chaetognaths and euphausiids (Fig. 6a–f). For most of these taxa, abundance fluctuated randomly without any strong relationship with either LSI-1 or 2 (Fig. 6a–f). The most striking feature was the occurrence of short term abundance peaks (each time constituted with only one point): Appendicularians (night between 28 and 29 September), Pteropods (15 October), Ostracods (night between 28 and 29 September), Hyperiids (night between 19 and 20 September), Chaetognaths (25 September). These short term variations could have been related to horizontal patchiness.

Among non-copepod taxa sampled with BIONESS net, the most abundant were euphausiids (50% *Nematoscelis megalops*, 28% *Meganyctiphanes norvegica* and 14% *Stylocheiron longicorne*), followed by chaetognaths, hyperiids, ostracods and pteropods (Fig. 7a–e). As in WP-II samples, there was no clear effect of LSW-1 or 2 on these taxa. Their abundances fluctuated randomly, mostly dominated by day-night variations.

3.2.3 Day-night variations in zooplankton abundance

Vertical samples integrating zooplankton organisms over the upper layer (0–200 m) hide any migration into this depth range, so variations between day and night will reveal only taxa which are migrating out of this superficial layer during day. Among all organisms sampled with WP-II, only hyperiids and euphausiids showed a significant difference between night and day abundances (Table 1). Among large-sized organisms (BIONESS samples), the difference between day and night abundance was statistically significant for euphausiids, pteropods and hyperiids and also for the copepod genera *Euchaeta*, *Pleuromamma* and *Scolecithricella*. These organisms crossed the low salinity layer during night, confronted a 0.2 salinity decrease and did not modify their behavior.

Pteropods and the copepods *Pleuromamma* are known for their strong migratory behavior (Andersen, 2001b) but in this study, they showed a significant day-night abundance variations only in BIONESS samples. This could be the consequence of two facts: first, the large proportion of juveniles in WP-II sampled, which do not migrate out of the 0–200 m layer, and second the patchiness inducing large variability in successive samples.

3.2.4 Relationship between zooplankton abundance and salinity

The results of Perry's test, which we used to examine the relationship between salinity and abundance of the different groups, are presented in Table 2 and Figs. 8 and 9. For the groups whose day-night abundance was not significantly different, Perry's test was made by merging night and day data. In contrast, day and night data were tested separately for the others.

Most of the copepods from WP-II samples were significantly influenced by salinity (Table 2): total copepods, copepodits, *Calocalanus* and *Neocalanus*. These organisms were mainly sampled during low salinity periods (Fig. 8a). About 40% of total copepods, copepodits and *Neocalanus* were sampled in the two first salinity classes and 50% of *Calocalanus*.

As with WP-II, most of copepods sampled with BIONESS were significantly influenced by salinity (Table 2): total copepods, *Euchaeta* (day), *Heterorhabdus*, *Mesocalanus, Nannocalanus, Neocalanus* and *Pleuromamma* (day and night). 45 to 80% of these groups were sampled in the two first salinity classes (Fig. 9a–c).

The non-copepod taxa sampled with WP-II and BIONESS nets seemed less influenced by salinity. Only the small ostracods (<200 μm, WP-II samples) showed a significant relationship with salinity (Table 2). 50% of these organisms were sampled during the two first salinity classes (Fig. 8b).

3.3 Large copepods diversity

3.3.1 Day-night variations of diversity

The results of Wilcoxon-Mann-Whitney test (Table 3) showed that night values of Shannon diversity index and Pielou evenness were significantly higher than day values. However, day and night species richness were not significantly different. In other terms, during the night, Shannon index and Pielou evenness values were higher but the number of species did not change. This could have been due to the migratory taxa (*Euchaeta spp., Pleuromamma* spp. and *Scolecithricella* spp.) whose abundance were low in 0–250 m layer during day, and are increased considerably at night.

3.3.2 Temporal variations of large copepods diversity

Shannon diversity index strongly varied during the cruise, between 1.10 and 3.00 (Fig. 10). Lowest values were recorded during LSW-1, during day as well as during night. We can thus suggest that there was an impact of the LSW-1 on the copepod community structure, but this perturbation had a short duration time.

Pielou evenness varied between 0.24 and 0.64 and paralleled the Shannon diversity index. Decreases in Shannon index and Pielou evenness during LSW-1 were due to marked increases in the abundance of *N. gracilis, N. minor*, which dominated the copepod community.

The species richness (i.e. number of species) fluctuated in the range 18 to 30, with a strong random variations from day to day. It did not decrease at the beginning of LSI-1 which confirms that shifts in diversity indices reflected changes in relative abundances of taxa within a stable community.

3.3.3 Relationship between large copepods diversity and salinity

Figure 11 shows the cumulated sum of deviations from the mean (Cumsum) for salinity and night and day Shannon index. All three variables showed the same pattern: slope reversals occur at the same time, which suggests that diversity changes are related to changes in salinity. Figure 11 also suggests that the sampling period can be divided in four parts:

- Part 1 (17–20 September): slopes are positives, which means that successive values are above the mean as well as for salinity than for Shannon index.
- Part 2 (20–30 September): negative slopes, which indicate values under the mean for salinity and diversity. This is the LSW-1 period.
- Part 3 (4–9 October): slopes become positives again, which indicates the end of LSW-1. Copepods community is returning to its undisturbed state.
- Part 4 (9–16 October): slopes are close to zero. There is no effect of LSW-2. Copepods community structure comes back to its initial values; salinity and diversity are stable.

4 Discussion

4.1 Comparison with previous studies

Although NW Mediterranean zooplankton have been the object of many studies, only Andersen et al. (2001a, b) considered the short-term variations in abundance of major taxonomic groups in the central part of the Ligurian Sea. Their study took place in May 1995 (Dynaproc 1 cruise), which allows permits comparison of zooplankton community dynamics at the same place during two different seasonal transitions: late spring-summer and summer-autumn. We will present here the similarities and the differences between the two zooplankton communities observed.

In the study of Andersen et al. (2001a), total copepod abundance sampled with WP-II fluctuated between 15 000 and 50 000 ind m^2. During Dynaproc 2, the range of values is very close: 10 000–45 000 ind m^2.

The comparison of major taxa sampled during Dynaproc 1 (late spring-summer) and Dynaproc 2 (summer-autumn) reveals that the two periods shared a great number of taxa: *Clausocalanus, Euchaeta, Heterorhabdus, Neocalanus*, *Oithona* and *Pleuromamma*. Andersen et al. (2001a) reported the presence of *Calanus helgolandicus, Centropages typicus* and *Monacilla typica* among the major species during Dynaproc 1. Although these three taxa were found during Dynaproc 2, their abundance was very low (0.25% *C. helgolandicus*, 0.20% *C. typicus* and 0.03% *M. typica*). *C. helgolandicus* and *M. typica* are deep-living species (Andersen et al., 2001a), which could explain their low abundance in the 0–250 m layer. *C. typicus* is a spring species whose abundance decreases during summer (Mazzocchi et al., 2007), and it becomes rare in autumn.

Mesocalanus is the only genus which appears among the major taxa found during Dynaproc 2 but not during Dynaproc 1. The abundance of this species is low outside LSW-1 (<10 ind m^{-2}) but it increased during the salinity event. Without the increase during LSW-1, *Mesocalanus* would not have been among the major taxa in Dynaproc 2 cruise.

Large copepods diversity has calculated in the present study, for Dynaproc 2 cruise but unfortunately, Andersen et al. (2001a, b) have not calculated it for Dynaproc 1. Therefore, it is not possible to compare the dynamic of large copepods diversity between the two periods.

4.2 Impact of LSW on zooplankton community

The sampling site of Dynaproc 2 cruise was located near the permanent DYFAMED time-series station. For many years, this offshore site was thought to be protected from coastal inputs by the presence of Ligurian current flowing along the coast (Béthoux and Prieur, 1983; Sournia et al., 1990; Marty and Chiaverini, 2002). Recently, Stewart et al. (2007) formulated the possibility of lateral processes at DYFAMED site (transport of particles along isopycnals or intrusion of shelf waters to the site) to explain the disparity in their sediment traps data. The Dynaproc 2 cruise data brings some arguments in favor of shelf water intrusions hypothesis. These observations are the first ones which show clearly the dynamics of such intrusion in the central part of the Ligurian Sea.

The results of our study showed that the arrival of LSW-1 in the sampling area was associated with changes in the copepod community. These changes are summarised in Fig. 12. The temporal segmentation of the cruise was obtained from the cumsum on salinity (Sect. 3.3.3). *Nannocalanus* and large *Neocalanus* strongly increased at the beginning of LSW-1 but their abundance decreased quickly. *Euchaeta* also increased at the beginning of LSW-1 but its abundance stayed high throughout the intrusion. *Mesocalanus* increased at the middle of the intrusion but decreased immediately. The abundance increase of undetermined copepodits, *Heterorhabdus*, small *Neocalanus* and *Pleuromamma* occurred at the end of LSW-1 and had a short duration. A decrease in measures of the diversity of large copepods diversity (Shannon index and Pielou evenness) was visible only at the beginning of LSW-1.

So, we suggest that LSW-1 contained its own zooplankton community and passed through the sampling area, thus causing a community replacement. There were no taxonomic changes but rather only an abundance increase of some groups and a decrease in the diversity, in terms of evenness, of large copepods. The LSW-1 did not bring any new group of zooplankton: all taxonomic groups found during LSW-1 were also sampled outside the intrusion. Moreover, the different lags in the timing of several copepod taxa variations suggest different characteristics at the beginning, in the middle and at the end of LSW-1.

The increase of zooplankton abundance during LSW-1 cannot be explained by reproduction for two reasons. First, the increase occurred too fast and second, high abundance does not last a long time and zooplankton community comes back nearly to its initial structure a few days after LSW-1, before the end of the cruise.

Although we observed an increase in copepod abundance during LSW-1, the increase is unlikely to represent a preference for low salinity waters. Rather, zooplankton is strongly influenced by currents and hydrodynamic. Salinity is, in fact, a marker which indicates the arrival of different water masses containing different populations.

5 Conclusion

Dynaproc 2 cruise was initially devoted to study, at short time scales, how ecosystems switch from summer oligotrophy to autumnal mesotrophy in the Ligurian Sea, and notably the effect of wind forcing on mixing. Monthly data acquired since 1991 at DYFAMED station, showed that summer-autumn shift generally occurred between mid-September to mid-October (Marty and Chiaverini, 2002). In 2004 (the year of Dynaproc 2 cruise), the seasonal shift occurred late and the destratification due to gust of wind started only five days before the end of the cruise, which is too short to study its effect on zooplankton community.

However, a marked phenomenon was been recorded during the cruise: the intrusion of coastal LSW two times in the sampling area, which was thought to be protected from coastal water by Ligurian current flow. Although the authors of a recent study (Stewart et al., 2007) venture the hypothesis of such coastal intrusions existence at DYFAMED station, they have never been observed before Dynaproc 2. The cruise lasted only one month but two coastal water intrusions were observed: these phenomena may be more frequent that one can think previously.

Our study documents a marked effect of coastal LSW intrusion on the offshore zooplankton community of the Ligurian Sea, and therefore its potential effect on matter flux. So, it seems necessary to multiply high frequency studies or automatic measurements in this area in the aim (i) to determine the frequency occurrence of LSW intrusions in the central part of the Ligurian Sea, (ii) and to confirm their influence on the ecosystem.

Acknowledgements. This study was part of the PECHE project; financial support was provided by the I.N.S.U.-C.N.R.S. through the PROOF program (JGOFS-France). We thank the chief scientist, V. Andersen, for organising the DYNAPROC 2 cruise program, and the crew of the R/V Thalassa for ship operations. We thank J. Dolan for English corrections and anonymous referees for helpful comments. This paper is dedicated to our friend and colleague Valérie Andersen who prematurely passed away in March 2007.

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Table 1. Day-night variations in zooplankton abundance. Z values were calculated with a Wilcoxon-Mann-Whitney test. ns = no significant difference, * = significant difference with $p \leq 0.05$, ** = significant difference with $p \leq 0.01$.

		WP2	BIONESS
Copepods	Total copepods	0.0165^{ns}	1.4471^{ns}
	Copepodits	0.2145^{ns}	–
	Calocalanus	1.0567^{ns}	–
	Clausocalanus	1.5349^{ns}	–
	Euchaeta	–	**3.3474****
	Heterorhabdus	–	-2.7920^{ns}
	Mesocalanus	–	-0.0731^{ns}
	Nannocalanus	–	-1.2717^{ns}
	Neocalanus	0.8584^{ns}	0.3362^{ns}
	Oithona	1.6175^{ns}	–
	Pleuromamma	0.6112^{ns}	**4.8677****
	Scolecithricella	–	**1.7395***
Other groups	Appendicularians	0.1578^{ns}	–
	Chaetognaths	-1.0395^{ns}	-2.4411^{ns}
	Euphausiids	**3.2987****	**5.2477****
	Hyperiids	**3.7916****	**5.2185****
	Ostracods	0.514^{ns}	-1.5745^{ns}
	Pteropods	0.149^{ns}	**4.1368****

Table 2. Results of Perry's test, which estimate the relationship between salinity and zooplankton abundance during Dynaproc 2 cruise. ns = no significant relationship, * = significant relationship with $p \leq 0.05$, ** = significant relationship with $p \leq 0.01$.

			WP2	BIONESS
Copepods	Total copepods		**0.0015****	**<0.0001****
	Copepodits		**0.0002****	–
	Calocalanus		**0.014***	–
	Clausocalanus		0.0766^{ns}	–
	Euchaeta	day	–	**0.006****
		night	–	0.0684^{ns}
	Heterorhabdus		–	**0.0001****
	Mesocalanus		–	**<0.0001****
	Nannocalanus		–	**0.0177***
	Neocalanus		**0.0151***	**<0.0001****
	Oithona		0.4431^{ns}	–
	Pleuromamma	day	0.1152^{ns}	**0.0066****
		night		**0.0104***
	Scolecithricella	day	–	0.1432^{ns}
		night		0.3084^{ns}
Other groups	Appendicularians		0.4915^{ns}	–
	Chaetognaths		0.4734^{ns}	0.0731^{ns}
	Euphausiids	day	0.5759^{ns}	0.2049^{ns}
		night	0.309^{ns}	0.4815^{ns}
	Hyperiids	day	0.3052^{ns}	0.9292^{ns}
		night	0.8614^{ns}	0.8445^{ns}
	Ostracods		**0.0424***	0.1098^{ns}
	Pteropods	day	0.1557^{ns}	0.7318^{ns}
		night		0.2432^{ns}

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Table 3. Day-night variations in large copepods (>500 μm) diversity. Z values calculated with a Wilcoxon-Mann-Whitney test. ns = no significant difference, * = significant difference with $p \le 0.05$, ** = significant difference with $p \le 0.01$.

	Z values
Shannon index	**3.3767****
Pielou evenness	**3.4936****
Species richness	0^{ns}

Appendix A

Table A1. List of copepods species sampled with WP-II net (200 μm mesh-size) during Dynaproc 2 cruise.
++: >1% of total copepods number sampled with WP-II net
+: >0.1%
−: >0.01%
−−: >0.001%

Acartia danae	−−
Acartia negligens	−
Acartia spp.	−
Aetideus armatus	−−
Aetideus giesbrechti	−−
Aetideus spp.	−−
Calanoid copepodits	++
Calocalanus spp.	++
Centropages spp.	−−
Centropages typicus	+
Centropages violaceus	−−
Chiridius poppei	−
Clausocalanus spp.	++
Clytemnestra rostrata	−
Clytemnestra spp.	+
Copepoda nauplii	+
Corycaeidae gen. spp.	−
Corycaeus furcifer	−
Corycaeus spp.	+
Corycaeus typicus	−−
Ctenocalanus vanus	+
Eucalanus spp.	−−
Euchaeta acuta	+
Euchaeta norvegica	−−
Euchirella messinensis	−
Euchirella spp.	−−
Farranula spp.	−−

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Table A1. Continued.

Haloptilus acutifrons	– –
Haloptilus longicornis	–
Haloptilus spp.	–
Harpacticoida	–
Heterorhabdus spp.	+
Lucicutia flavicornis	– –
Lucicutia gemina	– –
Lucicutia spp.	–
Mesocalanus tenuicornis	+
Microcalanus pusilus	–
Microsetella rosea	–
Microsetella sp.	+
Mimocalanus cultifer	–
Miracia efferata	– –
Miracia minor	– –
Mormonilla minor	+
Nannocalanus minor	+
Neocalanus gracilis	+ +
Oithona similis	+ +
Oithona spp.	+ +
Oncaea mediterranea	– –
Oncaea spp.	+
Paracalanus nanus	–
Paracalanus spp.	– –
Pareuchaeta spinosa	– –
Paroithona parvula	–
Pleuromamma abdominalis	+
Pleuromamma gracilis	+ +
Ratania flava	–
Scaphocalanus curtus	+
Scolecithricella spp.	+
Scolecithrix bradyi	– –
Scolecithrix danae	– –
Spinocalanus spp.	–
Vettoria granulosa	+

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Table A2. List of copepods species sampled with BIONESS net (500 μm mesh-size) during Dynaproc 2 cruise.
++: >1% of total copepods number sampled with BIONESS net
+: >0.1%
−: >0.01%
−−: >0.001%

Acartia spp.	−−
Aetideus acutus	−−
Aetideus armatus	−
Aetideus giesbrechti	−
Aetideus spp.	−−
Arietellus minor	−−
Arietellus setosus	−−
Arietellus spp.	−−
Augaptilidae gen. sp.	−−
Augaptilus longicaudatus	−−
Augaptilus spp.	−−
Calanus helgolandicus	+
Centropages bradyi	−−
Centropages typicus	+
Centropages violaceus	−
Chiridius gracilis	−−
Chiridius poppei	+
Clausocalanus spp.	+
Corycaeus furcifer	−
Corycaeus spp.	−−
Corycaeus typicus	−−
Euaugaptilus spp.	−−
Eucalanus hyalinus	−
Euchaeta spp.	++
Euchirella messinensis	+
Gaetanus kruppi	−

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Table A2. Continued.

Haloptilus acutifrons	–
Haloptilus longicornis	+
Haloptilus spp.	– –
Haloptilus tenuis	– –
Heterorhabdus spp.	+ +
Labidocera acuta	– –
Lucicutia curta	– –
Lucicutia gemina	– –
Lucicutia spp.	– –
Mesocalanus tenuicornis	+ +
Monacilla typica	–
Nannocalanus minor	+ +
Neocalanus gracilis	+ +
Neocalanus robustior	– –
Oithona spp.	– –
Paracandacia simplex	– –
Phaenna spinifera	– –
Pleuromamma abdominalis	+ +
Pleuromamma gracilis	+ +
Pontellidae spp.	– –
Ratania flava	– –
Rhincalanus nasutus	– –
Sapphirina spp.	– –
Scolecithricella spp.	+ +
Scolecithrix bradyi	– –
Scolecithrix danae	– –
Subeucalanus pileatus	–

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Table A3. List of non-copepod taxa sampled with WP-II net (200 μm mesh-size) during Dynaproc 2 cruise.
++: >1% of total non-copepods number sampled with WP-II net
+: >0.1%
−: >0.01%
−−: >0.001%

Appendicularians	++
Chaetognaths	++
Decapods	−
Doliolids	−
Euphausiids	++
Fishs	+
Heteropods	+
Hydromedusae	+
Hyperiids	++
Mysidacea	−
Ostracods	++
Pteropods	++
Salps	−
Siphonophora destructed, parts	undetermined
Tintinnids	+

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Table A4. List of non-copepod taxa sampled with BIONESS net (500 μm mesh-size) during Dynaproc 2 cruise.
++: >1% of total non-copepod number sampled with BIONESS net
+: >0.1%
−: >0.01%
−−: >0.001%

Chaetognaths	++
Decapoda	+
Doliolids	+
Euphausiids	++
Fishs	+
Gymnosoms	−
Heteropods	−−
Hydromedusae	+
Hyperiids	++
Medusae	−
Mysids	−
Nemertea	−
Ostracods	++
Polychaeta	+
Pteropods	++
Pyrosomids	−−
Salps	−
Siphonophora destructed, parts	undetermined

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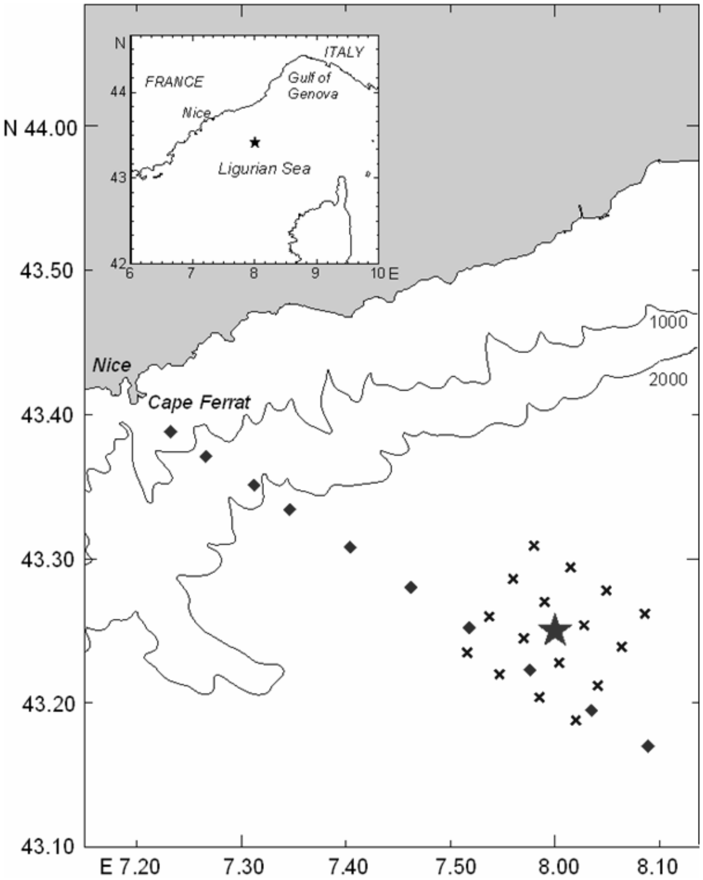

Fig. 1. Stations location of Dynaproc 2 cruise: (★) time-series station, (♦) transect of eight stations performed at the beginning of the cruise to locate the time-series station, (✕) grid of 16 stations occupied three times during the 1-month cruise.

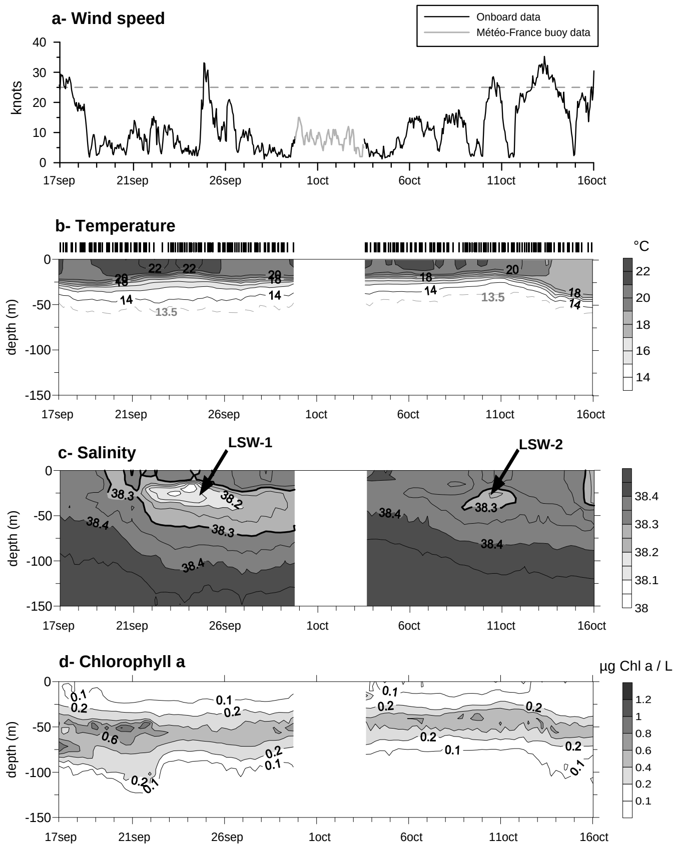

Fig. 2. Time series of meteorological and hydrological data during Dynaproc 2 cruise. **(a)** 10-m wind speed in knots. **(b)** Time-depth distribution of temperature, **(c)** salinity and **(d)** chlorophyll-*a* recorded in the 0–150 m water column during the sampling period. Periods with no data correspond to port calls between the two legs.

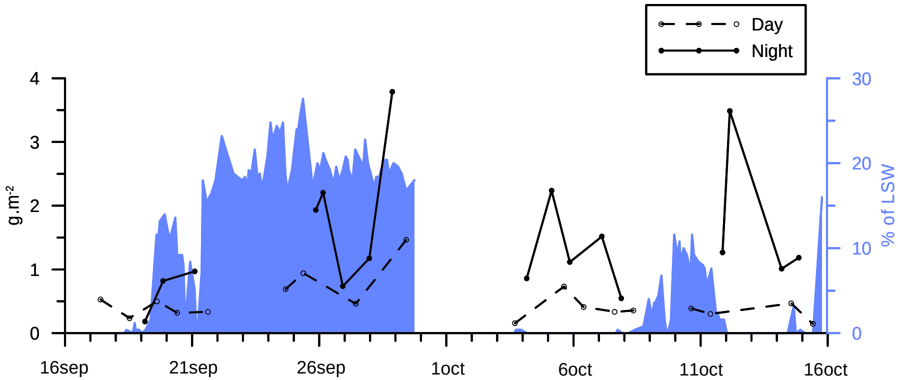

Fig. 3. In black: total zooplankton biomass sampled with WP2 during Dynaproc 2 cruise. In blue: percentage of the 0–200 m water column occupied by Low Salinity Water (LSW, <38.30).

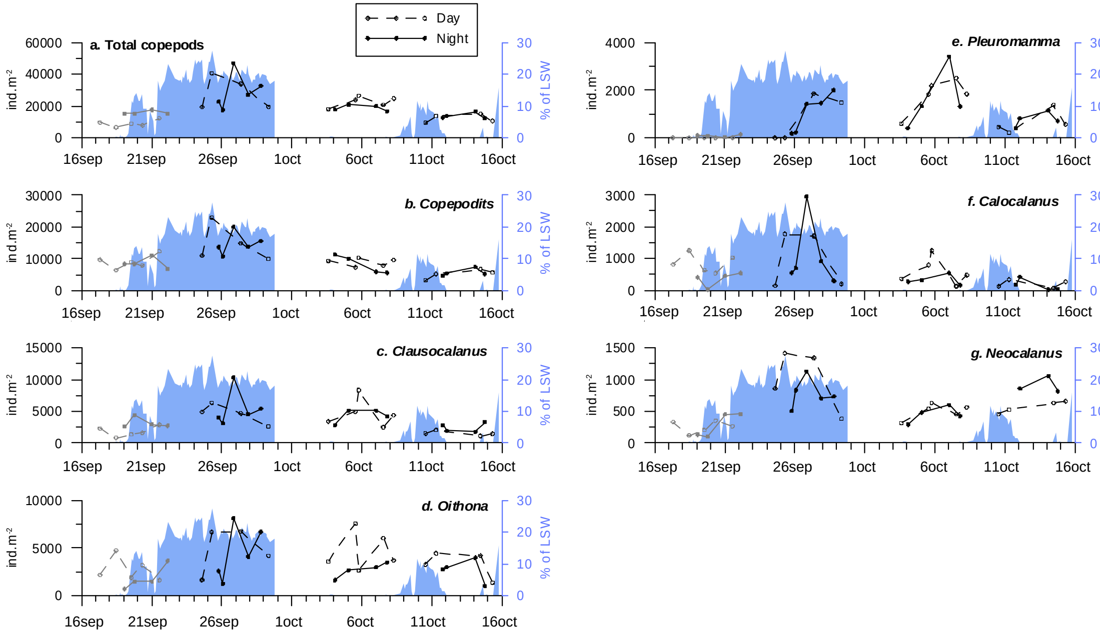

Fig. 4. Temporal variation of copepods density sampled with WP2 net during Dynaproc 2 cruise. Dashed lines: day data; continuous lines: night data. In grey: data from frozen samples. In blue: percentage of the 0–200 m water column occupied by Low Salinity Water (LSW, <38.30).

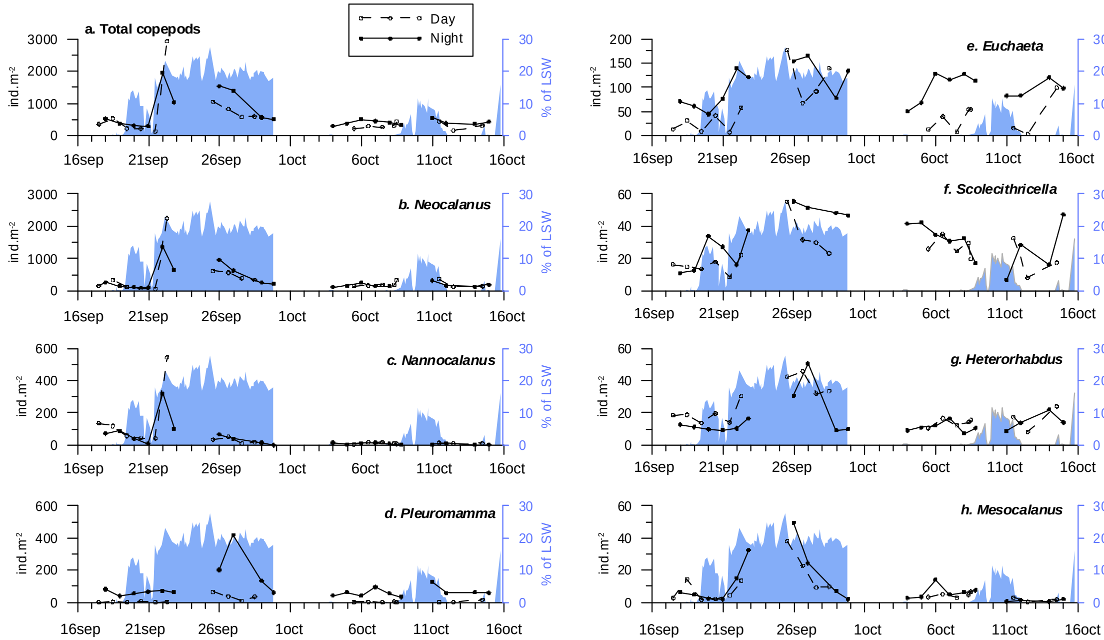

Fig. 5. Temporal variation of large copepods density sampled with BIONESS net during Dynaproc 2 cruise. Dashed lines: day data; continuous lines: night data. In blue: percentage of the 0–250 m water column occupied by Low Salinity Water (LSW, <38.30)

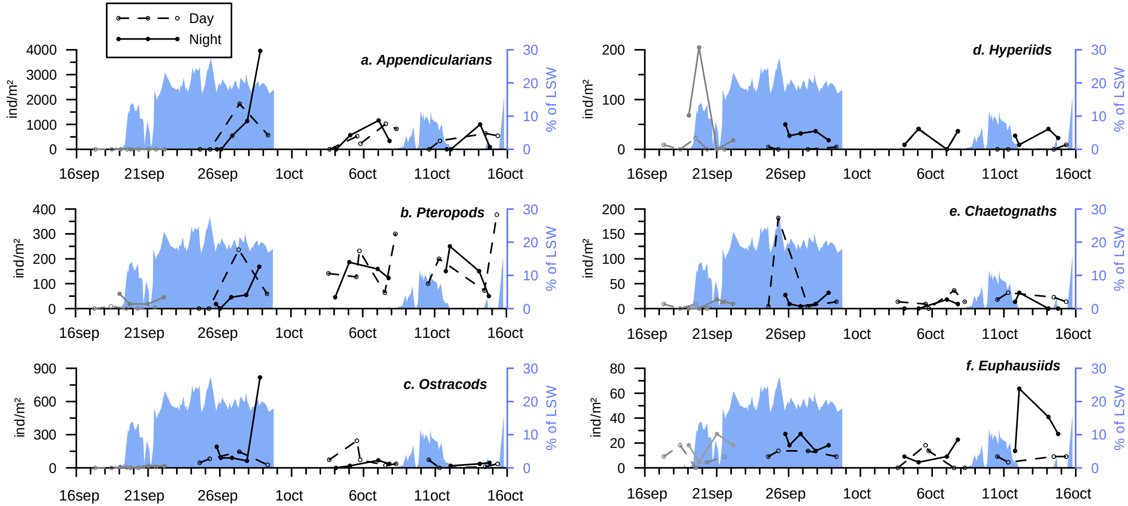

Fig. 6. Temporal variation of major non-copepods groups sampled with WP2 net during Dynaproc 2 cruise. Dashed lines: day data; continuous lines: night data. In grey: data from frozen samples. In blue: percentage of the 0–200 m water column occupied by Low Salinity Water (LSW, <38.30).

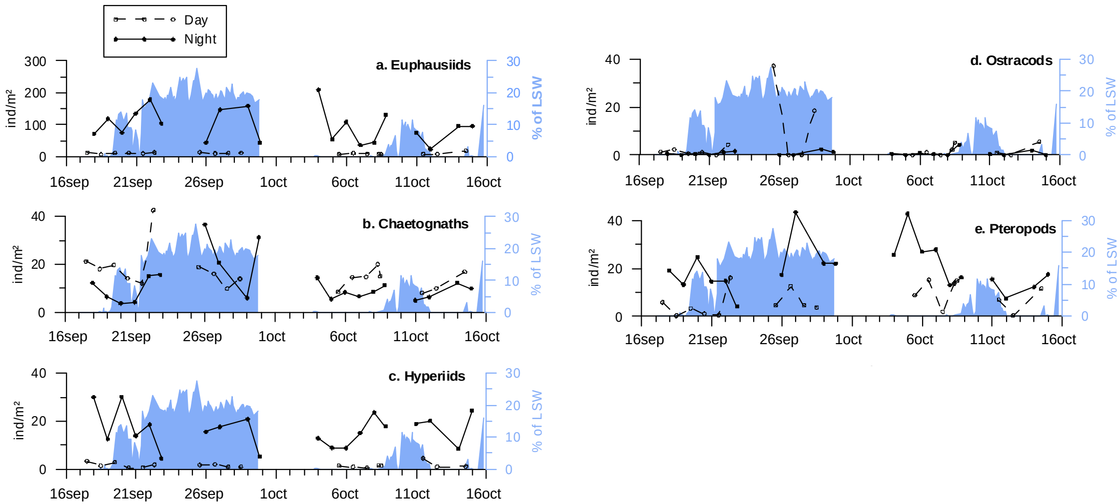

Fig. 7. Temporal variation of major non-copepods groups sampled with BIONESS net during Dynaproc 2 cruise. Dashed lines: day data; continuous lines: night data. In blue: percentage of the 0–250 m water column occupied by Low Salinity Water (LSW, <38.30).

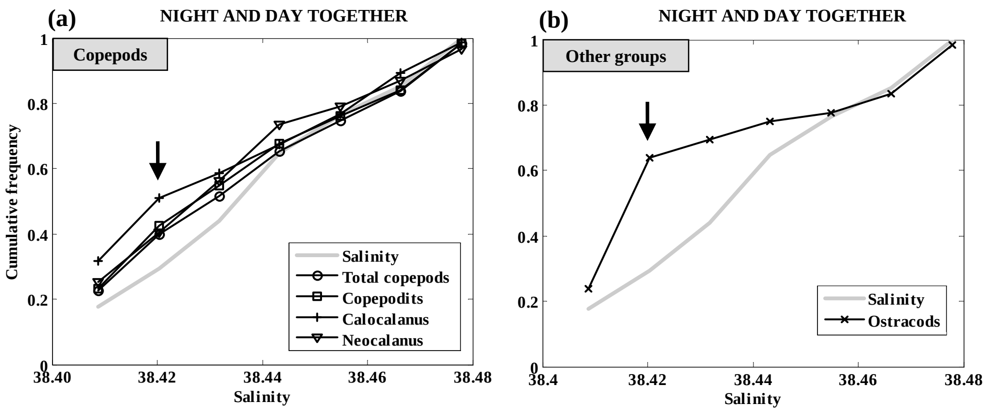

Fig. 8. Cumulative frequency distribution of different zooplankton groups sampled with WP2 net ($g(t)$, in black) in relation to salinity levels ($f(t)$, in grey). **(a)** copepods **(b)** other groups. Only taxa for which Perry's test showed a significant relationship between zooplankton abundance and salinity were plotted (Table 2). The arrow indicates the salinity class for which the greatest difference between $g(t)$ and $f(t)$ was founded. For example, in **(a)** more than 50% of *Calocalanus* spp. were sampled in the two first salinity classes.

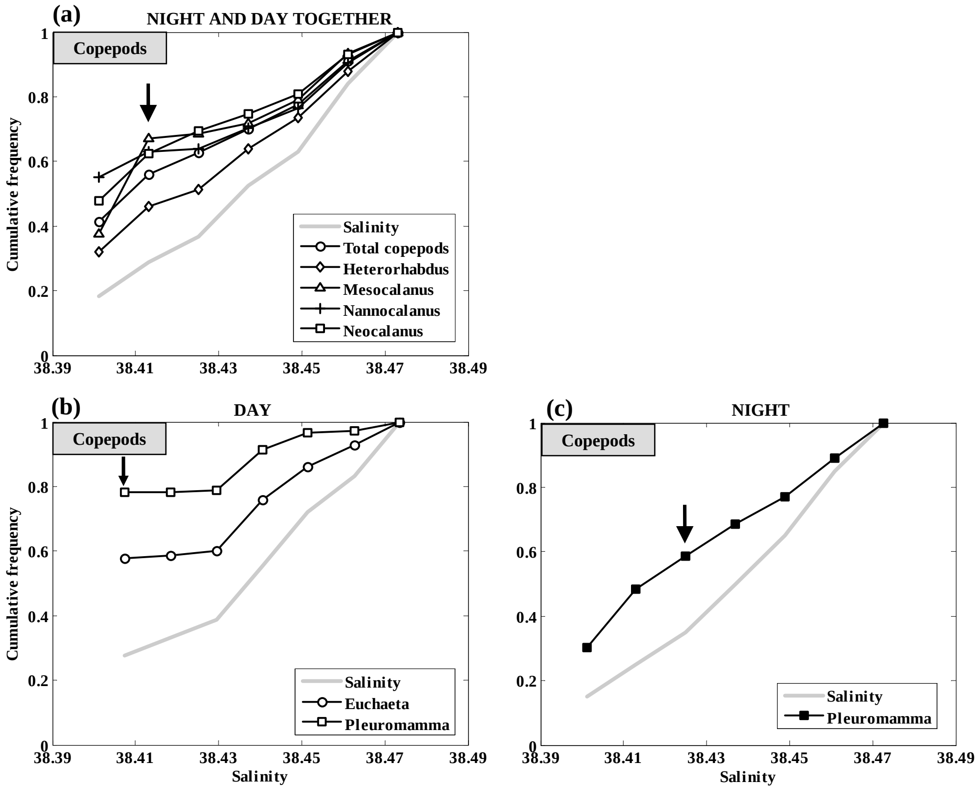

Fig. 9. Cumulative frequency distribution of copepods sampled with BIONESS net ($g(t)$, in black) in relation to salinity levels ($f(t)$, in grey). **(a)** Copepods for which day and night abundances were not significantly different (day and night data were merged). **(b–c)** Copepods for which day and night abundances were significantly different: (b) day data, (c) night data. Only taxa for which Perry's test showed a significant relationship between zooplankton abundance and salinity were plotted (Table 2). The arrow indicates the salinity class for which the greatest difference between $g(t)$ and $f(t)$ was founded.

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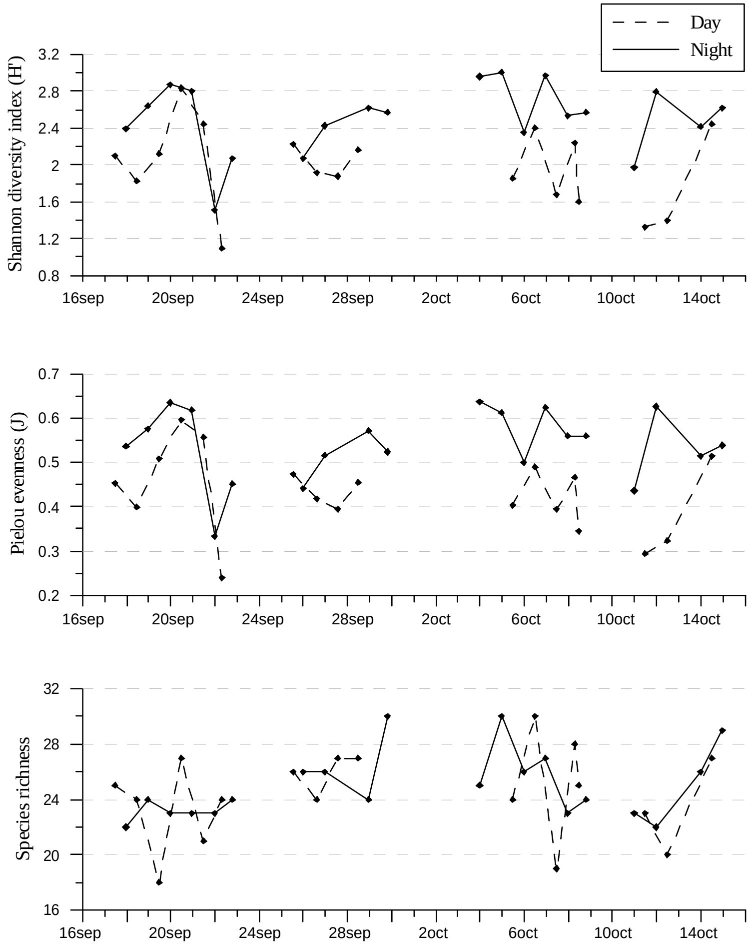

Fig. 10. Temporal variation of three diversity indices calculated on large copepods data: **(a)** Shannon index, **(b)** Pielou evenness, **(c)** Species richness.

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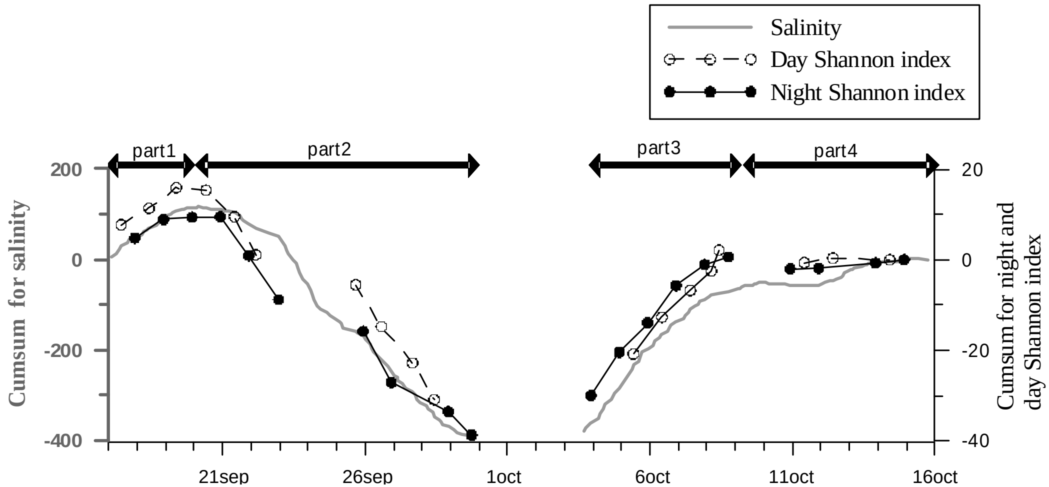

Fig. 11. Cumsum for salinity and Shannon index (night and day) calculated on large copepods (BIONESS net data) during Dynaproc 2 cruise.

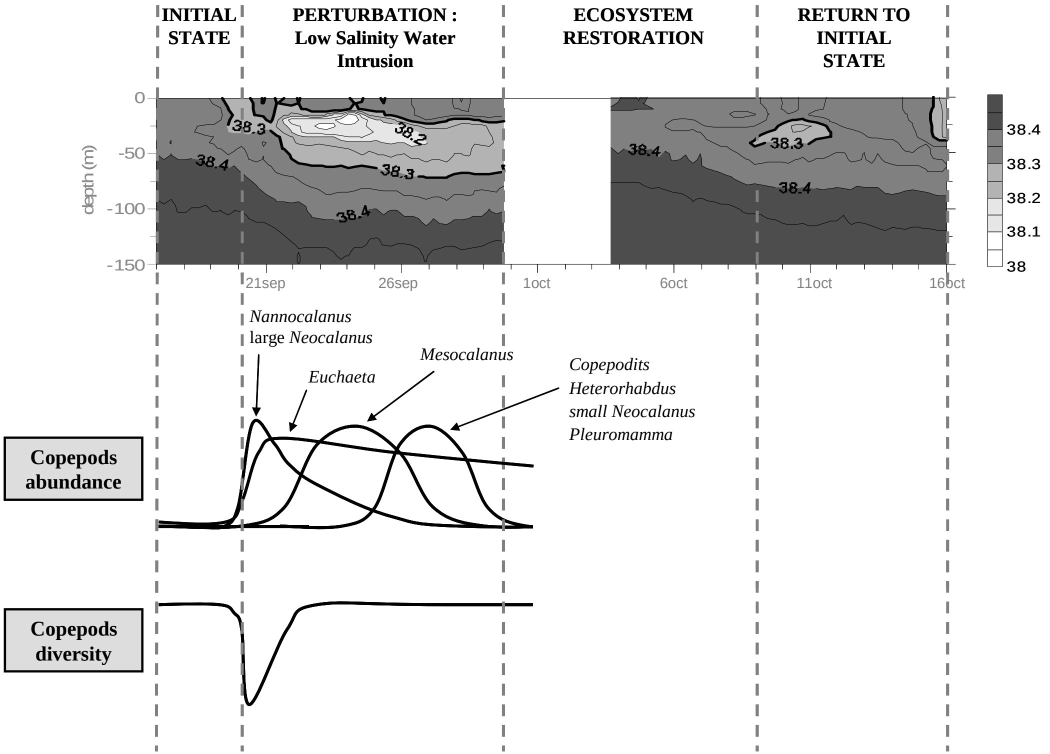

Fig. 12. Summarized scheme of the effect of LSW-1 on copepods community during Dynaproc 2 cruise.

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