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Short-scale temporal variability of physical, biological and biogeochemical processes in the NW Mediterranean Sea: an introduction

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Abstract

In the framework of the PROOF-PECHE project (http://www.obs-vlfr.fr/proof/vt/op/ec/peche/pec.htm) a multi-disciplinary team performed experiments and collected samples during the DYNAPROC2 cruise aboard the RV Thalassa from September to October in 2004. The cruise provided data on the functioning of the pelagic food web by sampling over a month long period in the NW Mediterranean Sea at a fixed station subject to weak horizontal advection currents during a period of hydrological stability. This paper describes the background of the cruise and provides an overview of the results derived from the campaign which constitute the special section. The major objective of the cruise was to assess the relative importance and variability of the pathways of carbon in the open ocean. Intensive sampling through 4 periods of 5 days each was accomplished a site near the DYFAMED time-series site. The site was near stable in terms of hydrodynamics as there was some evidence of an intrusion of low-salinity coastal water. One major product of the cruise was a comprehensive data set data set acquired by sampling at high frequencies (ranging from every 3, 6, 12 and/or 24 h) and over a vertical spatial dimension so far never explored (0–1000 m) in the North Western Mediterranean Sea. Parameters investigated included the biochemical composition of DOM (lipids), and the structure of bacterial communities, phytoplankton and zooplankton community compositions and abundances, as well as zooplankton metabolism, and particulate organic carbon fluxes. Nearly all the parameters described in this section, as well as reports appearing elsewhere, showed time-course variabilities of similar magnitude to those known from a previous study of the spring-summer seasonal transition, a period of marked hydrological change, at the same study site.

1 Background

Research efforts in biological oceanography have been concentrated in recent years around two major themes: 1) the responses of biological systems to shifts in forcing factors, especially climatic changes and 2) the interactions between biogeochemical cycles and the structure and function of ecosystems. Advancing within either theme requires knowledge of the variability of the structure and function of pelagic ecosystems. The project PECHE (Production and Export of Carbon: control by HEterotrophic organisms at short temporal scale) and its main operation, the oceanographic campaign DYNAPROC 2, was designed with the specific goal of assessing variability in the pelagic food web and its effect on biogeochemistry, targeting an oligotrophic system, the NW Mediterranean Sea at the end of the summer.

Satellite images clearly show the fact that ocean physics pay an essential role in governing the spatial and temporal distribution of phytoplankton. Thus, productive areas correspond with those in which the euphotic zone is nutrient-rich, for example, from deep water inputs. For phytoplankton, the role of resources (i.e., nutrients) has long been considered as more important than that of predation or grazers. Nonetheless, the possibility that consumers of phytoplankton could play a large role, in especially in open ocean systems has been suggested repeatedly (e.g. Banse, 1994, 1995; Verity and Smetacek, 1996). Furthermore, the activity of grazers can affect, directly or indirectly, other components of the plankton food web, for example, bacteria and bacterivores (Christaki and Van Wambeke, 1995; Christaki et al. 1996, 1998; Van Wambeke et al. 1996). Likewise, activities of the terminal trophic levels in food web models often affect components throughout the food web. For example, Steele and Henderson (1992) underlined the importance of the top predators and Frost and Franzen (1992) showed that their model correctly reproduced phytoplankton dynamics only when it included 2 trophic levels of carnivores. Obviously, the functioning of pelagic food webs depends on some equilibrium between resources and predation. While the relative importance of the two remains a subject of debate (e.g., Longhurst, 1991; Banse, 1995; Franks, 2001; Marine Zooplankton Colloquium 2, 2001), there is, regardless, a need to quantify the variability in the activity of grazers on a variety of temporal and spatial scales for a correct portrayal of pelagic food web dynamics.

Further complicating the situation with regard to pelagic food webs is the fact that there are, schematically, two principle carbon flux pathways: "microbial" and "herbivorous". The microbial pathway is mediated by the activities of heterotrophic and autotrophic procaryotes, viruses, pico and nano-eucaryotes both autotrophic and heterotrophic, ciliates and other heterotrophic protists. The herbivorous pathway traces fluxes through large phytoplankton (typically diatoms and dinoflagellates) and metazoan zooplankton such as copepods, salps, etc. The distinct manners in which the two pathways contribute to the biological CO_2 pump can be illustrated by recalling Longhurst's (1991) classification of biological pumps (Fig. 1): 1) Rotary Pump, corresponding to the retention and circulation of matter within the euphotic zone inside microbial loops, 2) Archimedean Pump, representing the vertical flux of particulate matter in the form of fecal pellets, marine snow, carcasses, etc. produced by metazoan plankton and phytoplankton in the herbivorous pathway, and finally, 3) Reciprocating Pump reflecting the activities of organisms which migrate vertically in the water column from the deep layers to the surface waters. It is worthwhile reviewing mechanisms and organisms involved in each "pump" to situate the various foci of the multidisciplinary study DYNAPROC 2.

The Rotary Pump rotates around heterotrophic bacteria. They play an essential role assimilating and re-mineralizing particulate and dissolved organic matter. They are unique in their capacity to concentrate and re-package dissolved organic matter and thus release back into solution nutrients essential for primary production. Paradoxically, despite the clear importance of bacterial activities, the precise nature of the relationships between organic matter (concentrations, characteristics) and the composition or activity of bacterioplankton are poorly known and were thus one of the foci of the Dynaproc 2 study.

The Archimedean Pump (downward flux of particulate organic matter) represents the net activity of a very diverse set of metazoan organisms in terms not only of taxonomy but also ecology. For example, different organisms have very distinct relationships of prey to consumer size comparing copepods which feed on diatoms to appendicularians feeding on bacteria (Longhurst, 1991; Fortier et al., 1994). Different taxa produce particulate matter with distinct characteristics. Knowledge of the community composition of the metazoan zooplankton and its variability in feeding activity is needed to assess the effects of their activities and represented another focus of the DYNAPROC 2 cruise campaign. Another source of particulate organic matter can be phytoplankton, either whole senescent cells, or coagulated matter of phytoplanktonic origin. Little is know concerning its temporal variability.

Part of the organic matter produced in the surface layer is transferred to depth not through the sedimentation of non-living matter but rather through active transport by organisms which migrate through the water column. The Reciprocating Pump is the result of the activities of diel migrators. The possible importance of migrators both in terms of carbon flux to deep layers in the ocean, as well as a structuring element in surface layer food webs, while recognized, has been neglected (e.g. Angel, 1989; Longhurst, 1991; Banse, 1995; Marine Zooplankton Colloquium 2, 2001). Assessment of vertical migrators was an important focus for the DYNAPROC 2 study.

High-frequency observations were made during the DYNAPROC 2 study which was hydrologicaly relatively stable. This permitted some interesting comparisons to be made between the variability encountered and that recorded during a previous multi-disciplinary study carried out during the spring to summer transition in 1995 (detailed in Andersen and Prieur, 2000; Copin-Montégut, 2000; Goutx et al., 2000; Pérez et al., 2000; Stemmann et al., 2000; Vidussi et al., 2000; Andersen et al., 2001a, b; Van Wambeke et al., 2001). Below we will first very briefly review the cruise plan then briefly recapitulate some of the findings described in detail in the individual papers of this special section. In the framework of the PECHE project, two additional short-cruises were conducted at the DYFAMED site in March and June 2003 (Garcia et al., 2006; Ghiglione et al., 2007; Bourguet et al., 2008) whose results are used as spring and early summer reference in several individual papers of this special issue.

2 Cruise summary

The DYNAPROC 2 cruise campaign (Dynamique des Processus Rapide dans le Colonne d'Eau) began 14 September and ended 17 October aboard the research vessel N/O Thalassa. The principle observations were made at a Time Series Station (TSS) located at 43°25 N, 8° E between Nice and the island of Corsica near the Dyfamed Time Series Station (reviewed in Marty, 2002) (Fig. 2a). A grid of 16 satellite stations was also sampled 3 times to verify horizontal gradients surrounding the TSS central point as weak (Fig. 2b). Intensive sampling was conducted through 4 cycles of 5 day duration. The cruise was composed of two legs, with sampling at the TSS beginning on 17 September to 30 September and resuming on 2 October, continuing until 14 October.

Throughout the sampling periods, the TSS was located beyond the Liguro-Provence front and the Ligurian coastal current. This conclusion was based on: 1) monitoring the temperature and salinity of the mixed layer and the dynamic height calculated for each of 10 CTD casts per day, 2) drift of the sediment trap line, and 3) preliminary analysis of the ADCP current data. The system remained stratified throughout the cruise except at the end, when the second wind event induced the mixing of the surface layer (Fig. 3a and b). However, two incidents of an intrusion of low-salinity (<38.3) water, presumably of coastal origin, were noted. The first one occurred between 21–30 September with low salinity waters found from 15 to 75 m depth, and the second one from 9–12 October found from 20 to 40 m depth (see Fig. 3c). The sampling site was characterized by a strong, persistent, thermocline found at about 25 except at the end of the sampling period (11–16 October) when the thermocline was located at 40 m depth.

3 Phytoplankton

Organic carbon circulating in the biological pump (either Rotary, the Archimedean or the Reciprocating Pumps) originates for the most part as primary production by phyto-

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plankton. Assessing the concentrations, composition and rates of primary production, and variabilities over short time scales, was a major goal of DYNAPROC 2. Phytoplankton were investigated in terms of pigment composition and concentrations, carbon fixation (Marty et al., 2008) as well subjected to microscopic examination (Lasternas et al., 2008).

Pigment analysis was based on high frequency sampling, every 3 to 6 h during the 4 cycles of 5 days each. A distinct chlorophyll maximum was present at about 50 m depth through the sampling (Fig. 3d). Integrating through the first 100 m of the water column, which encompassed all detectable pigment concentrations and carbon-fixation rates, total chlorophyll ranged widely, from 45 to 17 mg m^2, with high values at the beginning of the cruise. Similarly, primary production ranged from roughly 500 to 200 mg C d^{-1} m^2. Interestingly, there was a quite variable assimilation rate, carbon fixation per unit chlorophyll, similar to that found during the 1995 study of the seasonal transition (Vidussi et al., 2000). Gradients in chlorophyll concentrations and shifts in community composition of the phytoplankton based on pigment-based agreed with microscope-based observations. For example, both pigment data and microscopic examinations showed two distinct occurrences of diatoms, below the chlorophyll maximum depth, first in mid-September, then again in early October (Marty et al., 2008; Lasternas et al., 2008).

The average values of chlorophyll concentration and primary production estimated during DYNAPROC 2 were similar to those estimated for DYNAPROC in 1995 which targeted a seasonal transition. Considering the total ranges found throughout the present study, the variabilities of factors of 2–3 encountered in bulk concentrations and rates (e.g. total chlorophyll-*a* and primary production) exceeded those found in the earlier study which encompassed the transition from spring to summer (Vidussi et al., 2000). Nonetheless some parameters were relatively stable. The number of taxa, for both diatoms alone and dinoflagellates alone varied within a relatively narrow range (±15%) while the identity of the taxa shifted considerably, for instance, from centric to pennate diatoms (Lasternas et al., 2008).

4 Ciliate microzooplankton

Ciliate microzooplankton consume primary production in the smaller size-fractions, from 2–20 microns. Carbon consumed by ciliates is largely respired in the surface layer; their activity then is part of the Rotary Pump of the microbial loop. Small phytoplankton taxa, based on pigment signatures, overwhelmingly dominated the phytoplankton (>80% of the biomass) during DYNAPROC 2 (Marty et al., 2008) suggesting ciliate grazing to be an important carbon pathway.

Ciliates were found in concentrations ranging narrowly, between water column averages of 750–1250 l^{-1} in the top 90 m of the water column (Lasternas et al., 2008). As most of the ciliate cells were less than 30 µm, it is likely that their major role was that of "microbial grazers". Compared to the 1995 study of the spring to summer transition (Perez et al., 2000) with average surface layer concentrations of 3000 ciliates l^{-1}, ciliate concentrations were low. Recalling that chlorophyll concentrations and primary production were similar in the 1995 study, a larger portion of the primary production may have been available to the larger metazoan grazers. The community composition of the ciliate component of the food web was assessed in part through an examination of the tintinnid ciliate assemblage. Recalling the patterns found among diatoms and dinoflagellates (Lasternas et al., 2008), the number of species found on each sampling date varied within a narrow range while the identity of the taxa changed (Dolan et al. 2008; Raybaud et al., 2008b).

5 Bacteria

Bacteria represent the center of the "Rotary" carbon pump, consuming pre-formed organic matter, both dissolved and particulate. Bacteriovores and viruses are the consumers of bacterial production most of which is respired in the surface layer and thus not exported to depth. However, bacteria attached to particles of a size sufficient to sediment represent an exception and would be part of the "Archimedean Pump". In

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the DYNAPROC 2 program bacterial abundance and production was estimated for both "free-living" and particle-attached cells over the 5 week sampling period (Mével et al., 2008). Community composition of the free-living component was examined 4 times, each time sampling communities at 10 depths between the surface and 1000 m depth. Comparison of the communities revealed the existence of distinct communities (Ghiglione et al., 2008). Molecular fingerprinting showed a vertical zonation of bacterial assemblages in three layers, above, in or just below the chlorophyll maximum and deeper, that remained stable during the entire sampling period. Direct gradient multivariate ordination analyses revealed that a complex array of biogeochemical parameters was the driving force behinds bacterial community structure shifts in the water column.

Bacterial biomass was equivalent to about 50% of that of phytoplankton, based on a chlorophyll-based estimate of phytoplankton carbon. Bacterial carbon averaged about 700 mg m^{-3} C integrating through the top 150 m of the water column (Mével et al., 2008) compared to a rough estimate of phytoplankton biomass as about 1 500 mg derived from an average of 30 mg chlorophyll m^{-3} (Marty et al., 2008) and a chlorophyll to carbon ratio of 50.

Abundance of bacteria was lower than that found in bloom and post-bloom conditions in this area (Mével et al., 2008; Van Wambeke et al., 2001). Bacterial production, in carbon units averaged about 29 mg C m^{-2} d^{-1}, suggesting that bacterial production was low relative to both total bacterial biomass and phytoplankton production. In contrast, periodically, a large portion (up to about 50%) of bacterial activity was associated with particle-attached bacteria, as previously observed at the same sampling site under spring conditions (Ghiglione et al., 2007). Thus while the Rotary Pump appeared to be a minor pathway of carbon in the surface layers, microbial biomass as particle-attached carbon, may have been significant inputs to deep layers periodically, via the Archimedean Pump.

6 Zooplankton

The zooplankton community is at the center of both the Archimedean pump, as producers of particulate organic matter, and the reciprocating pump in the form of vertically migrating taxa. Species composition, abundances and diversity are detailed in Raybaud et al. (2008a) and Mousseau et al. (2008). Zooplankton biomass was found to vary greatly, between 0.25 $g\,m^{-2}$ and 3.8 $g\,m^{-2}$ over the top 200 m of the water column. The importance of vertical migrators was evident with nighttime biomass values as much as 5 times that of daytime concentrations. The zooplankton community during the night was not only more abundant but also more diverse in terms of species of large copepods (Raybaud et al., 2008). Compared to the previous studies conducted during the spring to summer transition in 1995 (Anderson et al., 2001a, b) a similar range of concentrations of large copepods was found but the species compositions differed.

7 Lipids – dissolved organic matter

The activity of the carbon pumps can be gauged in qualitative terms by examining the composition and concentrations of dissolved lipid classes. Goutx et al. (2008) found evidence of dissolved organic matter originating from grazing on the smallest class of phytoplankton. Furthermore, they documented the appearance of zooplankton wax esters first in the surface layer and later in deep waters. They related phospholipids in the 400–1000 m depth layer to bacteria growing on DOM released from sinking agregates.

8 Export fluxes

POC fluxes varied by an order of magnitude, in the range 0.03–0.29 $mg\,C\,m^{-2}\,h^{-1}$ over the month (Marty et al., 2008). The mean export ratio for the cruise was of the order of 2% of the primary production, which agreed well with export ratios measured at the end of the DYNAPROC 1 cruise in oligotrophic conditions (1–2%) (Goutx et al.,

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2000). The most striking evidence in the data was the rapid change in fluxes of the various measured parameters. A day night periodicity was apparent in fluxes, POC fluxes being higher during night time probably linked to diel fluctuation of zooplankton grazing. Unlike during DYNAPROC 1 when the wind increased vertical particle flux, in the situation encountered here, the effect of wind events was a decrease of fluxes probably through reduction of zooplankton grazing. But fluxes increased as soon as calm conditions prevailed.

9 Intrusion of low salinity water

Intrusions of low-salinity water mass (LSW)(<38.3 psu) were observed two times during the cruise, unfortunately in coincidence with wind events. Variable possible effects were noted. A microalgae of the genus *Scripsiella* sp., a form characteristic of coastal rather than open waters, was found at the TSS coinciding with LSW (Lasternas et al., 2008). Among the phytoplankton as whole, the pigment signatures were only slightly affected (Marty et al., 2008). Similarly, among the tintinnids of the ciliate microzooplankton, no effect was noted (Dolan et al., 2008). However, the zooplankton community composition may have shifted based on relative abundances of different species of large copepods (Raybaud et al., 2008a, b). LSW was associated with an increase in total bacterial abundance and production (Mevel et al., 2008). None the less, Marty et al. (2008) concluded that LSW intrustions were probably minor influence on carbon fluxes and the main variability was probably associated more closely with the effects of wind-driven mixing (Marty et al., 2008).

10 Conclusion

The studies described in this special issue of Biogeosciences each describe separately the variability encountered in a system which viewed from a distance, for example satellite images, appears invariant. Very distinct time-course changes were documented with regard to the composition of the phytoplankton (Marty et al., 2008; Lasternas et al., 2008), microzooplankton (Dolan et al., 2008), zooplankton (Raybaud et al., 2008a) and dissolved organic matter (Goutx et al., 2008). Changes in the diversity of communities of organisms from different trophic levels varied independently (Raybaud et al., 2008b). Interestingly the least variability was found among the bacterioplankton. In terms of community composition, depth rather than time distinguished bacterial assemblages (Ghiglione et al., 2008).

The wealth of data acquired was destined to be incorporated into a model of the pelagic ecosystem. Tragically, Valerie Andersen, the architect of the cruise program and ecosystem model, passed away before she could accomplish the task she had set for herself of distilling a synthetic view, evaluating the importance of the different carbon pumps. This special issue is dedicated to her memory.

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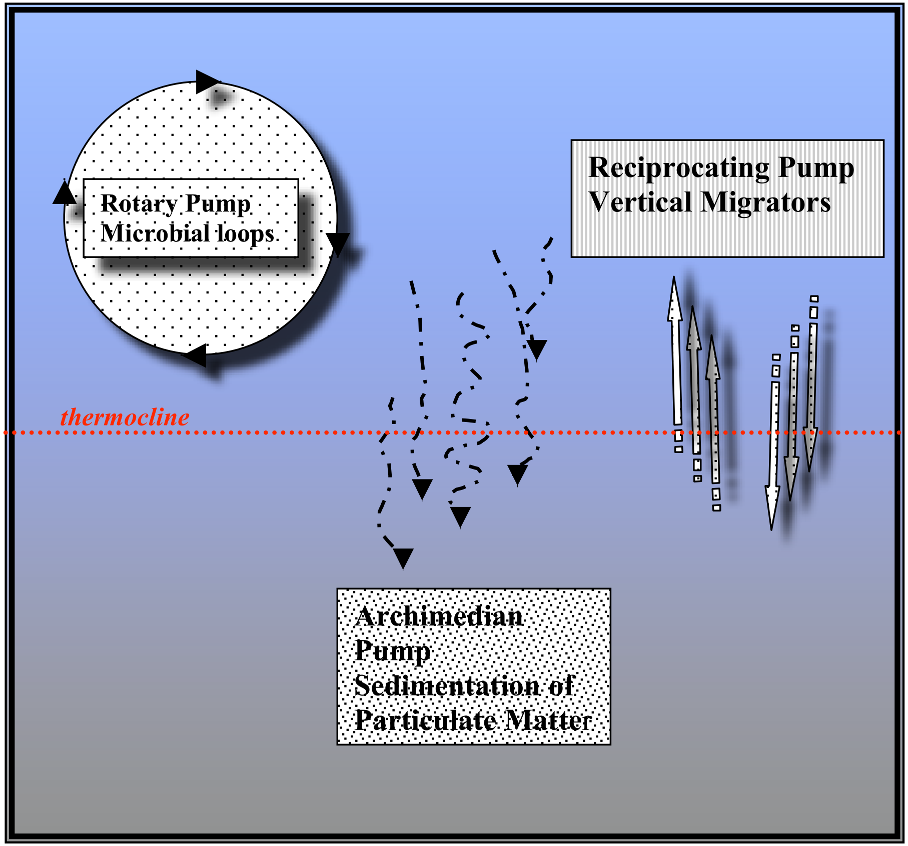

Fig. 1. Schematic representation of the carbon pumps or pathways following Longhurst (1991).

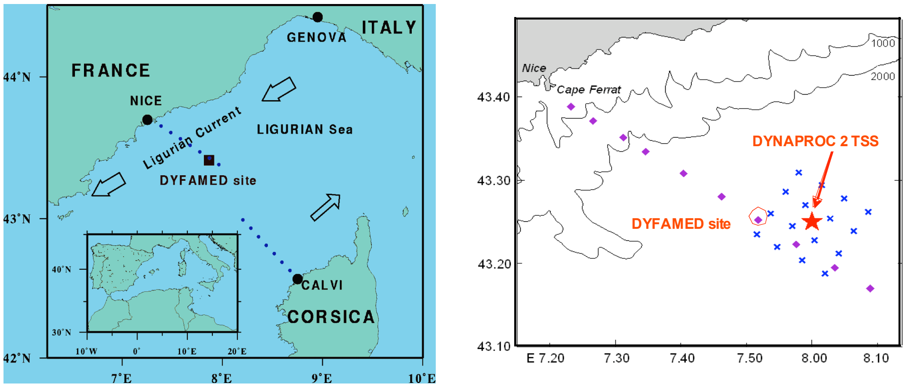

Fig. 2. Location of the time series station (TSS) occupied during the DYNAPROC 2 cruise and the grid of survey stations sampled for hydrological data.

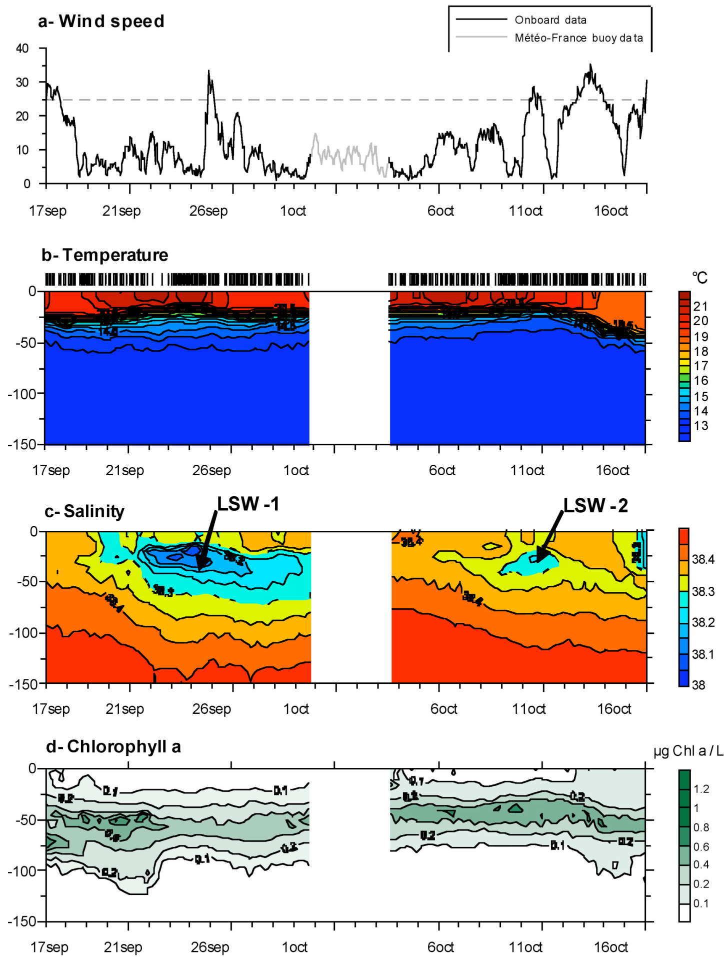

Fig. 3. Time series of meteorological and hydrological data during the DYNAPROC 2 cruise.

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