

Defining zooplankton habitats in the Gulf of Lion (NW Mediterranean Sea) using size structure and environmental conditions

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ABSTRACT: The size structure of zooplankton communities in the Gulf of Lion, NW Mediterranean Sea, was studied in May 2010 and January 2011. The integrated physical and biological measurements provided a 3D view with high spatial resolution of the physical and biological variables and their correlations over the whole gulf. The effects of physical processes such as freshwater input, coastal upwelling, and water column mixing by winds on phytoplankton and zooplankton distributions were analyzed using these data. During the winter, strong northerly winds mixed the water column, and the vertical distributions of biological variables were uniform over most of the gulf while there were local hot spots with high chlorophyll *a* (chl *a*) concentrations in front of the Rhône mouths and in coastal areas. During the spring, light winds and water column stratification resulted in less vertical mixing, and the Rhône River freshwater plume spread over a large part of the gulf. The nutrients delivered by the freshwater input encouraged high primary production in the surface layer. In the pycnocline, a thin layer of high particle concentration was associated with these high phytoplankton biomasses. Three habitats were distinguished based on statistical analysis performed on biological and physical variables: (1) the coastal area characterized by shallow waters, high chl *a* concentrations, and a steep slope of the normalized biomass size spectrum (NBSS); (2) the area affected by the Rhône with high stratification and flat NBSS slope; and (3) the continental shelf with a deep mixed layer, relatively low particle concentrations, and moderate NBSS slope. Defining habitat is a relevant approach to designing new zooplankton sampling strategies, validating distribution models and including the zooplankton compartment in trophodynamic studies.

KEY WORDS: Plankton dynamics · Size spectra · Freshwater plume · Stratification · Coastal ecosystems · River Rhône

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INTRODUCTION

Continental margins are generally highly productive areas compared to the open sea and provide the main spawning habitats for small pelagic fishes (Palomera et al. 2007, Planque et al. 2007, Bellido et al. 2008, Nicolle et al. 2009). Shallow waters, stronger currents, river discharges, and wind-driven upwelling cause strong variations in physical struc-

tures, resulting in a variety of hydrological patterns (Yanagi 2000). Physical processes have direct effects on the production of the first trophic levels by mixing different water masses and bringing nutrients from terrestrial runoff and coastal upwelling. To understand how these environmental conditions affect zooplankton distributions at the mesoscale, physical and biological variables must to be measured simultaneously at a sufficiently high resolution to detect fine

structures in the water column (Labat et al. 2009, Möller et al. 2012, Ohman et al. 2012). The data from high-resolution measurements can be used to determine zooplankton habitats with specific hydrological and biological features. Recent advances in *in situ* optical and acoustic sensors have made such high-resolution measurements of physical and biological variables possible (Mikkelsen & Pejrup 2001, Davis et al. 2004, Jiang et al. 2007, Picheral et al. 2010, Powell & Ohman 2012). The laser optical plankton counter (LOPC) can be used to measure the size spectrum of zooplankton communities (Herman et al. 2004) and can also be coupled with other sensors to monitor simultaneous changes in the physical and biological variables along the water column. In conjunction with net tows to establish ground truth, this size structure approach provides important information on the functioning of marine ecosystems. The characteristics of the size spectrum have been successfully used in several studies as an indicator for the dynamics of plankton communities (Matsuno et al. 2012, Tarling et al. 2012, Schultes et al. 2013, Basedow et al. 2014). Size-based mathematical models have been developed and can be used to determine the characteristics of plankton communities and to quantify the efficiency of energy transfer between trophic levels (Zhou 2006, Andersen et al. 2009). Sizes of zooplankton organisms also play an important role in predator–prey interactions, espe-

cially in the survival of fish larvae (Plounevez & Champalbert 2000, Costalago et al. 2012, Nikolioudakis et al. 2012). Although the concept of habitat is widely used and well defined for the study of fish (Bellido et al. 2008, Giannoulaki et al. 2011, Tugores et al. 2011, Salas-Berrios et al. 2013), only a few studies have used this concept for zooplankton. The species-based approach used to study fish is difficult to transpose to the zooplankton compartment, especially in tropical and temperate regions with high biodiversity. Zooplankton habitats are therefore generally defined as function of the environmental conditions that create a specific assemblage of species characterized by taxonomic composition (Schulz et al. 2012, Sano et al. 2013) or size structure features (Matsuno et al. 2012). In this study, we characterized zooplankton communities by their abundances and size structures rather than by taxonomic composition. The term ‘habitat’ is used to refer to geographical areas where there are statistically meaningful relationships between the environmental conditions and zooplankton community variables.

The Gulf of Lion in the northwestern (NW) Mediterranean Sea has a large continental shelf up to 80 km wide (Fig. 1). Several rivers, in particular the Rhône River, flow into the Gulf of Lion carrying freshwater, terrestrial particles, and nutrients. The Northern Current (NC) flows southwestwards along the continental slope and sometimes intrudes onto

the shelf, bringing oligotrophic waters into the gulf. Strong winds such as the Mistral and Tramontane occur frequently, creating coastal upwellings and driving the dispersion and dilution of the Rhône River plume. The hydrography of the Gulf of Lion is well documented (Millot 1990, Broche et al. 1998, Petrenko et al. 2005) and simulated by several physical models (Estournel et al. 2003, André et al. 2005, Rubio et al. 2009). The MARS-3D hydrodynamic model simulates circulation in the NW Mediterranean and resolves the coastal dynamics. The effects of the Rhône River plume on biological processes have been described in many studies dealing with nutrient inputs, phytoplankton growth, and zooplankton grazing and behavior (Gaudy et al. 1990, Pagano et al. 1993, Pujo-Pay et al. 2006, Diaz et al. 2008). However, very few studies have been undertaken for the area

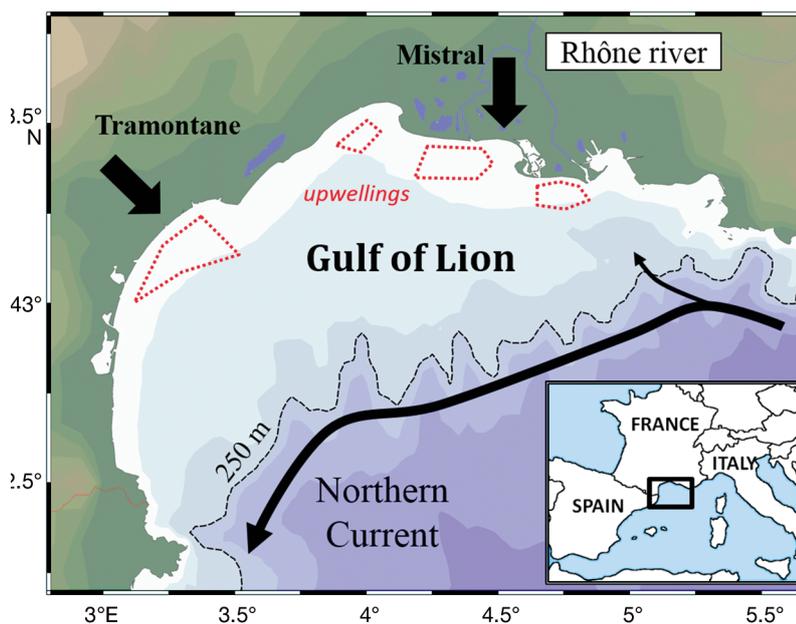


Fig. 1. Schematic representation of the main hydroclimatic phenomena that interact with the physical features in the Gulf of Lion. Tramontane and Mistral are frequently occurring strong winds that create coastal upwellings and drive the dispersion and dilution of the Rhône River plume

spanning coastal runoff to the NC in the past 25 yr (Kouwenberg 1994, Gaudy et al. 2003), and these do not provide an overall view of the distributions. Furthermore, only 1 study focused on the size structure of zooplankton communities (Riandey 2005). Considerable efforts have been made to study trophic dynamics and effects of physical processes at different scales in the Gulf of Lion (Raimbault & Durrieu de Madron 2003, Bănaru et al. 2013), but, despite the key position of the zooplankton compartment in the food web, no studies have used a specific sampling strategy to determine zooplankton dynamics.

Two surveys were conducted in May 2010 and January 2011 over the entire Gulf of Lion to produce 3D maps of zooplankton distributions and environmental conditions simultaneously at a synoptic scale. The aims of this study were (1) to define spatial zooplankton habitats in relation to environmental conditions, (2) to identify the main processes shaping the habitats, and (3) to suggest a method suitable for coastal marine ecosystem monitoring and management in the future.

MATERIALS AND METHODS

Data collection and sampling

Two surveys were conducted on board the RV ‘Téthys II’: from 25 April to 2 May 2010 (COSTEAU 4) and from 23 to 27 January 2011 (COSTEAU 6). Six transects from the coast to the open sea were surveyed with up to 15 sampling stations at regular intervals of 2.5 nautical miles (Table 1). All sampling operations were carried out during the day from the bottom, or a maximum depth of 200 m for offshore stations, to the surface using a Seabird 911 CTD

Table 1. Dates and numbers of stations for each transect during 2 sampling campaigns in the NW Mediterranean Sea: COSTEAU 4 (2010) and COSTEAU 6 (2011); ‘trans.’ stations were between 2 transects. Positions of the stations are shown in Fig. 3a

Transect	— COSTEAU 4 —		— COSTEAU 6 —	
	Date (dd/mm)	No. of stations	Date (dd/mm)	No. of stations
A	27/04	11 (+ 2 trans.)	23/01	13 (+ 1 trans.)
B	28/04	14	24/01	7
C	29/04	12	25/01	15 (+ 2 trans.)
D	30/04	14 (+ 1 trans.)	26/01	14 (+ 1 trans.)
E	01/05	6	27/01	15
F	02/05	6		

(Sea-Bird Electronics), an Aqua Tracka 3 fluorometer (Chelsea Technologies Group), and a LOPC (Herman et al. 2004) mounted on a 12-bottle Rosette water sampler. Water samples were collected at a range of depths and immediately filtered using GF/F filters. In the laboratory, chlorophyll *a* (chl *a*) was extracted in an acetone solution as described by Aminot & K erouel (2004). The regression between *in situ*-measured fluorescence (fluo) and laboratory-measured chl *a* were determined as chl *a* = 1.64 × fluo ($R^2 = 0.77$, $n = 202$) for COSTEAU 4 and chl *a* = 5.43 × fluo ($R^2 = 0.83$, $n = 201$) for COSTEAU 6. Wind data were obtained from the maritime meteorological station and weather forecast model Aladin from M et eo-France.

The recently developed LOPC has already been used in several studies (Finlay et al. 2007, Checkley et al. 2008, Gaardsted et al. 2010, Ohman et al. 2012, Basedow et al. 2013). The high acquisition rate of the LOPC, and the simultaneous measurements of other variables, provides the fine spatial resolution mapping necessary for understanding the interactions between environmental conditions and zooplankton communities. The LOPC was coupled to a data logger and a micro-CTD to measure the vertical distribution of the size spectrum and abundance of particles (zooplankton and suspended particulate matter) from 100 µm to 1 cm equivalent spherical diameter (ESD; Herman et al. 2004). The LOPC has a flow-through tunnel with an open area of 7 × 7 cm and measures the attenuation of the light intensity caused by particles passing through the tunnel and crossing at the laser beam. The digital size of the particles is inferred from the changes in intensity and is converted to the ESD. The data were processed using a program developed on MATLAB software (Mathworks). Like other laser-based sensors, the LOPC does not distinguish between organisms and suspended particulate matter (SPM). However, recent studies have described the development of new theoretical ways for separating living and non-living particles, based on the lognormal distribution expected for particle spectra (Petrik et al. 2013), and using an opacity index to separate zooplankton organisms from SPM for particles over 1.5 mm ESD (Checkley et al. 2008). Unfortunately, these methods were not suitable for this study owing to the low concentrations of organisms over 2 mm ESD in the Mediterranean Sea and the small volume of water analyzed at each cast.

Spatial and transect maps were generated using Ocean Data View (Schlitzer 2014) with the embedded gridding software DIVA (Troupin et al. 2012). Data from a hull-mounted acoustic Doppler current profiler (ADCP, 150 kHz, RD Instruments) and simu-

lations from the MARS-3D hydrographic model (André et al. 2005) were used to assess the stability of the physical structures during the surveys.

Habitat mapping

The methodology used to define habitats followed a sequence of operations: (1) selection of a limited number of measured or calculated variables; (2) principal component analysis (PCA) of these variables; (3) cluster analysis of the stations characterized by their coordinates on the principal components (PCs); (4) definition of the number of clusters using an objective measure of partitioning efficiency.

The first step characterized each station using a limited set of variables representing hydrological and biological features and including vertical information (Table 2). Several sets of variables were tested with the objective of balancing them between physical and biological variables. Physical variables were selected to be representative of all the physical processes occurring in the gulf. Five variables were selected: sea surface temperature and salinity, mixed layer depth, stratification index, and potential density at the bottom. The stratification index was calculated using the Brunt-Väisälä frequency (N). Each station where at some depths N^2 was higher than 10^{-3} s^{-2} was considered to have a pronounced pycnocline. To calculate the intensity of the pycnocline, a density profile model (ρ_{mod}) was defined using the following function:

$$\rho_{\text{mod}} = \rho_{h0} + \frac{\Delta\rho_h}{2} [1 + \tanh \alpha(z - z_0)] \quad (1)$$

where ρ_{h0} (density at top of section), $\Delta\rho_h$ (density change over the section), and z_0 (absolute depth at inflexion point) were evaluated directly on a profile section centered on the pycnocline. Parameter α was estimated using least-squares minimization of the difference between the modeled density profile and the observed profile. Differentiating this equation related to dz gives:

$$\frac{d\rho_{\text{mod}}}{dz} = \frac{\Delta\rho_h}{2} \alpha [1 - \tanh^2 \alpha(z - z_0)] \quad (2)$$

The stratification index $d\rho_{\text{mod}}/dz$ is the value of the slope at the inflexion point, where $z = z_0$:

$$\frac{d\rho_{\text{mod}}}{dz} = \frac{\Delta\rho_h}{2} \alpha \quad (3)$$

The depth at which N^2 was greater than $0.2 \times 10^{-3} \text{ s}^{-2}$ was taken to define the mixed layer depth. In

Table 2. Physical and biological variables and indices. SST: sea surface temperature; SSS: sea surface salinity; NBSS: normalized biomass size spectrum

Variable	Notation	Unit
Physical conditions		
SST	Temp_0	°C
SSS	Sal_0	
Bottom potential density	Rho_b	kg m ⁻³
Mixed layer depth	Z_ML	m
Stratification index	Rho_grad	
Biological conditions		
Integrated chlorophyll a concentration	Chla_int	mg m ⁻³
Integrated particle abundance		no. m ⁻³
0.1–0.3 mm	$X_{0.1-0.3\text{mm}}$	
0.3–0.5 mm	$X_{0.3-0.5\text{mm}}$	
>0.5 mm	$X_{0.5\text{mm}}$	
Slope of NBSS		

addition to the chl *a* concentration, biological variables were selected to characterize zooplankton communities. The selection was based on the type of data obtained by the optical sensors used. The variables selected were the abundance of 3 particle size classes integrated along the water column and the slope of the normalized biomass size spectrum (NBSS).

The next step was to perform a PCA on the data set constructed from all of these variables. This step identified any significant correlation between the variables, showed which variables influenced the variability between stations, and reduced the number of variables to the 3 principal components. Outliers were defined arbitrarily by calculating the Mahalanobis distance (MD) for the distributions of stations, and setting a threshold of $MD^2 = 50$, which resulted in 2 outliers (out of 165 stations). Although outliers were excluded from the data set used for the calculation, their coordinates on the PC axes were calculated. The PCA was performed separately on the data sets for each survey in order to avoid the cluster definition being biased by the variability in the variables between the 2 surveys.

A cluster analysis was then performed on the stations characterized by the PCs. The Davies-Bouldin (DB) index, which is an objective measure of partitioning efficiency, provided the optimal number of groups defined by clustering (Davies & Bouldin 1979). The number 3 was selected since it gave one of the lowest DB index values for both the COSTEAU 4 and the COSTEAU 6 surveys (Fig. 2), making it possible to compare the distribution of the habitats between the 2 periods. Furthermore, although the DB index was relatively low for 7 clusters for the May

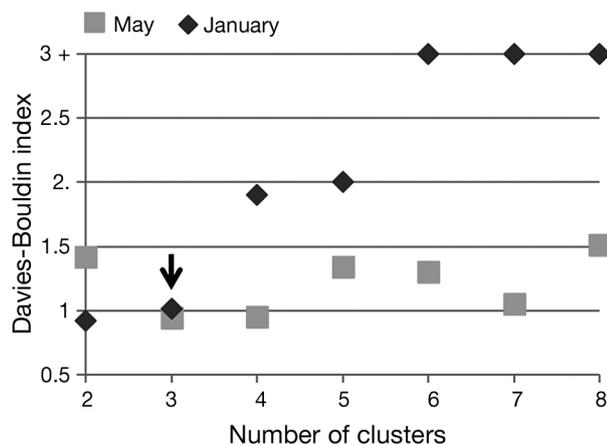


Fig. 2. Davies-Bouldin index of partitioning efficiency as a function of number of clusters. Lower index values indicate better partitioning. The black arrow shows the number of clusters selected

data, it was preferable to have a limited number of habitats for summarizing the information and be able to explain the differences between each region. All statistical tests were carried out using the `dudi.pca`, `kmeans`, and `index.DB` functions of the 'R' free statistical software (R Development Core Team 2014).

Size spectrum

Normalized biomass size spectra (NBSS) were calculated as described by Herman & Harvey (2006). Using logarithmic bins provided high resolution for small sizes and avoided empty classes for large sizes. The biomass within each size class was divided by the class width to normalize the biomass size spectrum. Finally, each NBSS was divided by the corresponding volume of filtered water. A linear regression performed on the NBSS provided the slope and the y-intercept of the NBSS. NBSS slopes were calculated from the third class (120 μm ESD) to the first empty class in the spectrum. The NBSS slope is linked to the community assimilation efficiency across the size spectrum and the number of trophic levels (Gaedke 1993, Gilabert 2001, Zhou 2006).

RESULTS

Weather conditions and river discharges

During the January survey, strong northerly winds blew regularly and played an important role in homogenizing and cooling the water column. The Rhône River discharge was up to 3410 $\text{m}^3 \text{s}^{-1}$ 2 wk

before the survey, well above the annual average (1721 $\text{m}^3 \text{s}^{-1}$; Ludwig et al. 2009) but below extreme flash flood events ($>5000 \text{m}^3 \text{s}^{-1}$). In May, the winds were light with frequent changes in direction, and the Rhône River discharge was slightly below the annual average, down to 1343 $\text{m}^3 \text{s}^{-1}$ during the 2 wk preceding the survey.

Stability of the physical structures

The stability of the physical structures during the survey (6 d for COSTEAU 4 and 5 d for COSTEAU 6) was investigated using ADCP data (not included in this paper) and simulations from the hydrodynamic circulation model MARS-3D. The predictions from the MARS-3D model gave a better, more detailed insight of spatial and temporal scales of variability. The wind conditions and river flows, which are the main factors of non-stationarity over short time scales in the Gulf of Lion, were constant during both surveys, resulting in the model predicting nearly stable physical structures. This was in agreement with the low values of currents inferred from ADCP data. We therefore assumed that the spatial distributions were quasi-stationary and good representatives of their mean values over the time scales of the surveys.

Hydrological structures

In January 2011, the effect of the Rhône was limited to the area near the coast, easily identifiable with colder, low salinity surface waters compared to the marine waters (temperature, $T < 12^\circ\text{C}$ and salinity, $S < 35$; Fig. 3a). The Rhône divides into 2 branches 50 km upstream of the coast, which explains the presence of 2 plumes: 1 to the east associated with the Great Rhône and 1 to the west associated with the Little Rhône. Along the continental slope, $S > 38$ and high temperature ($>13^\circ\text{C}$) revealed the presence of the NC. Cooling processes take place in the western part of the Gulf of Lion in the shallowest waters ($<11.5^\circ\text{C}$). The slight decrease in salinity was associated with the mouths of several small rivers. Cooling processes were found along Transect D with a tongue of cold water ($<11.5^\circ\text{C}$) in the bottom layer (Fig. 3b). A front separating the continental shelf waters from the NC waters was also clearly identifiable ($S > 38$ and $T > 13^\circ\text{C}$), 50 km away from the coast. The Rhône River plume was a very thin surface layer near the coast (less than 3 m thick) and diluted vertically towards the open sea.

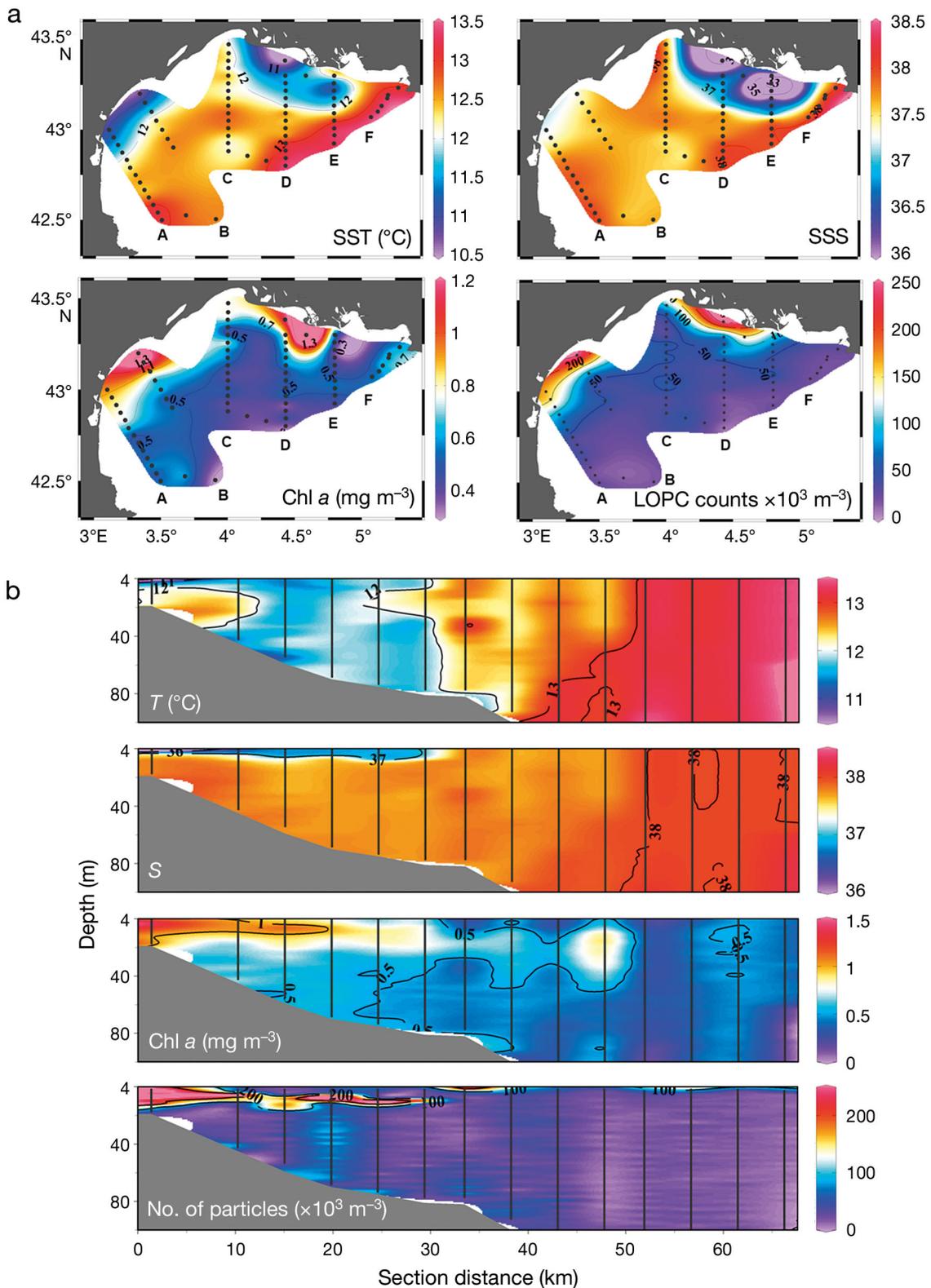


Fig. 3. COSTEAU 6 (23 to 27 January 2011): (a) Spatial distributions of sea surface temperature (SST), sea surface salinity (SSS), chlorophyll *a* (chl *a*) concentration, and particle concentration (laser optical particle counter [LOPC] counts, 0.1–35 mm equivalent spherical diameter [ESD]). Stations are represented by the black dots and Transects A–F are indicated. (b) Vertical distributions of sea temperature (*T*), sea salinity (*S*), chl *a* concentration, and particle concentration along Transect D. Black vertical lines represent the fluorometer-CTD-LOPC casts

In May 2010, the Rhône outflow affected a large part of the Gulf of Lion, far out to the west to the coast and to the south up to the continental slope ($S < 37$ and $T > 16^{\circ}\text{C}$; Fig. 4a). The tip of the plume curved slightly westward. At the surface, continental shelf waters were only visible in the eastern part of the gulf ($S > 38$). Transect D in front of the mouth of the Little Rhône crossed the tip of the Great Rhône plume. The spring warming of the surface waters stratifies the water column along the whole transect. In the vicinity of the Rhône River plume, mixing of warmer waters with the fresh water of the plume created a strong potential density gradient between the surface and bottom layers. The pycnocline was at a depth of around 12 m (Fig. 4b).

Chlorophyll *a* and zooplankton distributions

During the winter survey (23 to 27 January 2011), the integrated chl *a* concentrations were highest in coastal waters, in front of the Rhône estuaries and in the coldest waters in the western part of the gulf (Fig. 3a). However, concentrations on the continental shelf were fairly high, generally over 0.5 mg m^{-3} . In the center of the gulf, the vertical distributions showed 3 identifiable patterns (Fig. 3b): the highest concentrations were situated near the coast in the subsurface water layer affected by freshwater inputs, intermediate concentrations were found in continental shelf waters, and the lowest concentrations were in the oligotrophic waters of the NC.

The distributions of particle concentrations were correlated with chl *a* distributions: the highest concentrations were found near the coast in the western part of the gulf and in front of the estuaries, especially that of the Little Rhône (Fig. 3a). On the continental shelf, the particle concentrations were lower but uniform. In the water column, high particle concentrations were concentrated in a thin layer centered on the pycnocline (Fig. 3b). Farther offshore, some smaller patches appeared near the surface.

During the spring survey (27 April to 2 May 2010), vertically integrated chl *a* concentrations were not uniformly distributed and, although there were a few hot spots in the coastal area, concentrations were lower than in January (Fig. 4a). Mean concentrations on the continental shelf were also quite low compared to January ($< 0.3\text{ mg m}^{-3}$). Along transect D, chl *a* vertical distributions were very patchy (Fig. 4b). The highest concentrations were found in the freshest waters at the tip of the Rhône River plume

($> 1.5\text{ mg m}^{-3}$). Deeper, about 40 m, concentrations occasionally reached 0.5 mg m^{-3} .

The highest particle concentrations were in the coastal area, in both the western and eastern parts of the gulf ($> 150 \times 10^3\text{ counts m}^{-3}$; Fig. 4a). High particle concentrations, correlated with the spatial distribution of the Rhône River plume, were also present far from the coast on the shelf. Vertical particle distributions show several patches distributed in the subsurface layer at the interface between the warm surface waters and the colder continental shelf waters (Fig. 4b). The highest concentrations were found in the Rhône River plume ($> 400 \times 10^3\text{ counts m}^{-3}$). Concentrations under the pycnocline were quite low ($> 30 \times 10^3\text{ counts m}^{-3}$), although several hot spots appeared near the bottom on the shelf up to the continental slope.

Analytical results

Statistical tests were performed separately for each data set. In January, the first PC calculated by the PCA had positive coordinates for mixed layer depth and sea surface temperature and negative coordinates for small- and medium-sized particles (Table 3). The second component was defined by the stratification index and the NBSS slope on the positive side and sea surface salinity on the negative. The correlation circle formed by PCs 1 and 2 (Fig. 5a) shows a positive correlation between the abundance of small particles and chl *a* concentration, and between the stratification index and the abundance of large particles.

In May, the main pattern from the variable coordinates was a positive correlation between water column stratification (Rho_grad, Temp_0, and Sal_0) and the abundance of large particles (Table 3). The second component showed that the NBSS slopes were negatively correlated with chl *a* concentrations and the abundance of small particles. Some of the patterns highlighted by the correlation circle (Fig. 5b) were similar to those found for the January data (Fig. 5a), with similar correlations between the water column stratification and the abundance of large particles and between chl *a* concentrations and the abundance of small particles.

Stations D1 and E1 were considered as outliers for COSTEAU 6 (January) and COSTEAU 4 (May), respectively. These stations gave extreme values which were clearly different from the other stations (Fig. 6). Station D1 was the shallowest station (15 m depth) with extreme values for chl *a* and particle concentrations. Station E1, in front of the Rhône River

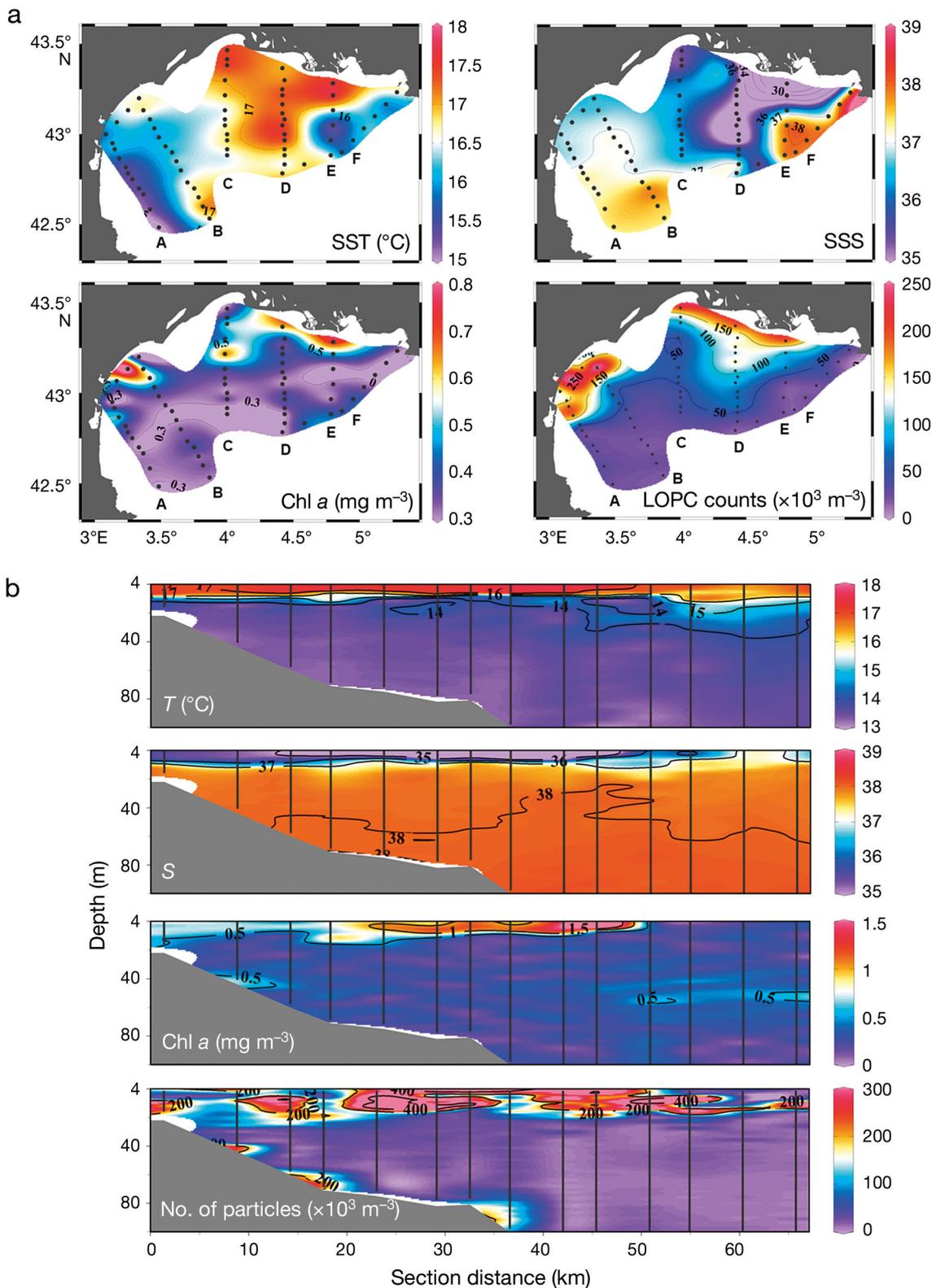


Fig. 4. COSTEAU 4 (27 April to 2 May 2010): (a) Spatial distributions of sea surface temperature (SST), sea surface salinity (SSS), chlorophyll *a* (chl *a*) concentration, and particle concentration (laser optical particle counter [LOPC] counts, 0.1–35 mm equivalent spherical diameter [ESD]). Stations are represented by the black dots and Transects A–F are indicated. (b) Vertical distributions of sea temperature (*T*), sea salinity (*S*), chl *a* concentration, and particle concentration along Transect D. Black vertical lines represent the F-CTD-LOPC casts

Table 3. Correlation coefficients of the parameters (with percentages of the total variance in parentheses) for the 3 first principal components for COSTEAU 6 (January) and COSTEAU 4 (May). Significant coefficients of each component are shown in **bold**. Parameter abbreviations are defined in Table 2; NBSS: normalized biomass size spectrum

Parameter	COSTEAU 6			COSTEAU 4		
	PC1 (-44.50%)	PC2 (-24.70%)	PC3 (-13.50%)	PC1 (-43.90%)	PC2 (-19.90%)	PC3 (-11.60%)
Z_ML	0.79	-0.16	-0.39	0.5	0.24	0.54
Rho_grad	-0.51	0.76	0.06	-0.75	0.45	-0.29
Temp_0	0.89	0.03	-0.16	-0.78	0.3	-0.22
Sal_0	0.66	-0.65	-0.16	0.82	-0.37	0.28
Rho_b	0.13	0.38	0.72	0.44	0	-0.57
Chla_int	-0.67	-0.55	-0.12	-0.39	-0.56	-0.02
X _{0.1-0.3mm}	-0.84	-0.47	-0.09	-0.7	-0.62	0.06
X _{0.3-0.5mm}	-0.89	-0.03	-0.32	-0.86	-0.26	0.29
X _{0.5mm}	-0.4	0.59	-0.59	-0.8	0.12	0.43
NBSS slope	0.46	0.65	-0.39	-0.03	0.85	0.25

mouth, was characterized by the freshest surface waters (Sal₀ < 25) and therefore a very stratified water column (Rho_grad very high).

Habitat mapping

The plot of the 3 groups of stations defined by the cluster analysis produced a consistent spatial representation for the 2 surveys (Fig. 7). In January, Habitat 2 contained only 3 stations directly in front of the Rhône River mouth, whereas in May this habitat covered a large area in front of the Rhône River mouth and along the coast to the west. Habitat 1 cov-

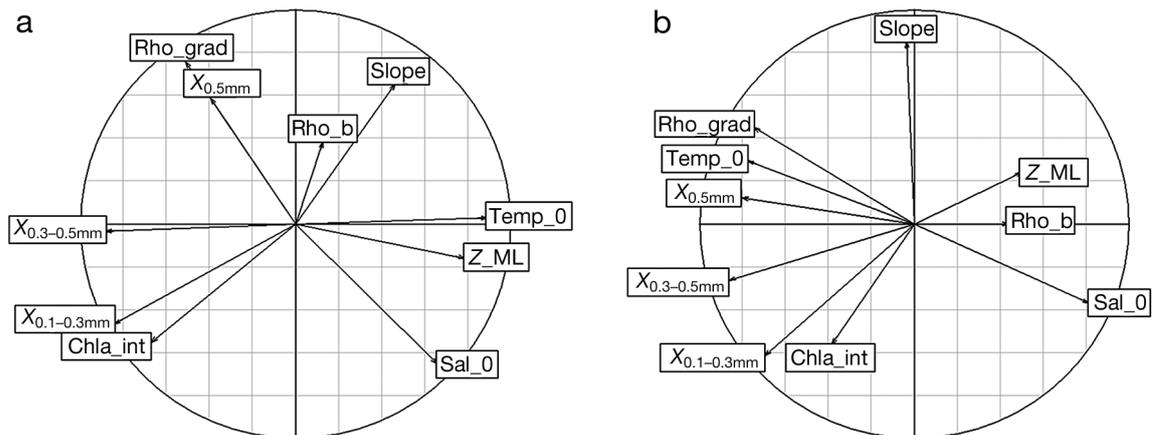


Fig. 5. Principal component analysis correlation circle on axes 1 and 2 for (a) COSTEAU 6 (January) and (b) COSTEAU 4 (May). Abbreviations are given in Table 2

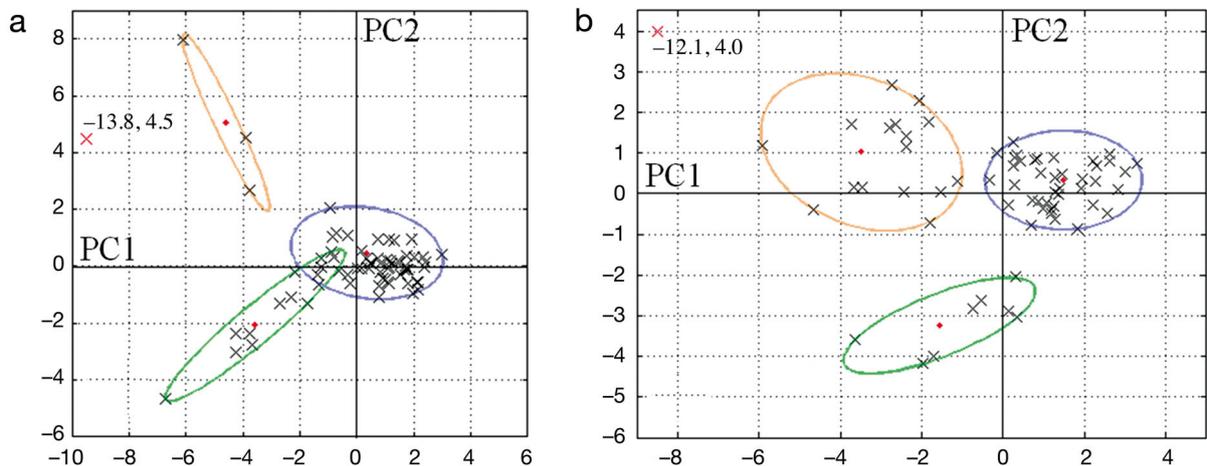


Fig. 6. Positions of the stations (gray crosses) in the plane formed by the first 2 principal components for (a) COSTEAU 6 (January) and (b) COSTEAU 4 (May). The results of cluster analysis are represented using the minimum volume enclosing ellipsoid function. Red crosses represent (a) Station D1 and (b) Station E1, which are considered to be outliers. Red diamonds represent the centers of the ellipses

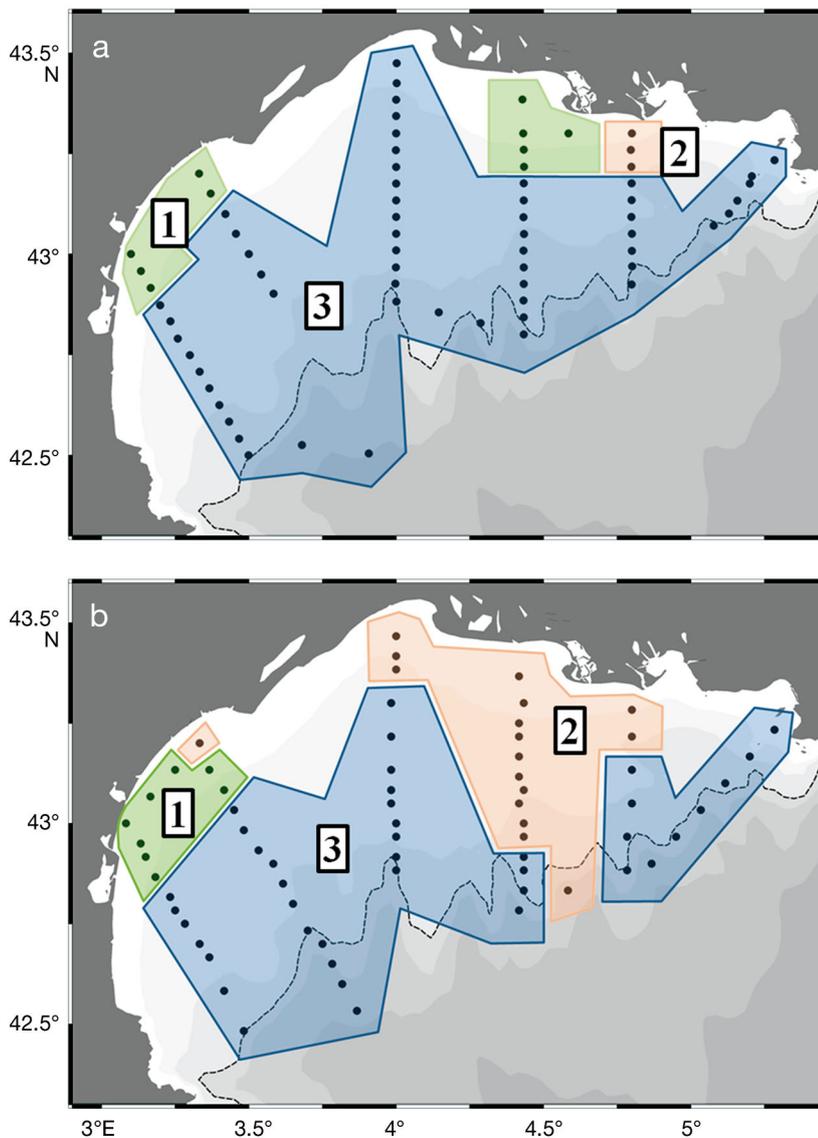


Fig. 7. Spatial distribution of the 3 habitats defined by the cluster analysis for (a) COSTEAU 6 (January) and (b) COSTEAU 4 (May). Habitat 1 (green) corresponds to 'coastal area,' Habitat 2 (red) to 'area affected by the Rhône,' and Habitat 3 (blue) to 'continental shelf.' Black dots represent the stations

ered only the west part of the coast in May, but in January it included an additional area in the center. Habitat 3 was the most extensive of the 3 habitats, containing all stations situated along the slope and in the eastern part of the gulf to the Bay of Marseilles. There were similarities between the distribution and the characteristics of the 3 habitats even though statistical tests were performed independently on the 2 data sets. The means of the variables defining the 3 habitats showed the following features (Table 4):

- Habitat 1, coastal area: shallow waters, steep NBSS slope, high chl a concentration
- Habitat 2, area affected by the Rhône: marked stratification, flat NBSS slope
- Habitat 3, continental shelf: deep mixed layer, low density gradient, low particle concentrations

Habitat characteristics

To confirm the definition of the habitats, the size spectra of living and non-living particles from 100 μm to 5 mm ESD were investigated using NBSS (Fig. 8). NBSS showed different patterns between the 2 surveys in each of the 3 habitats. In general, NBSS shapes were linear in January whereas a break point appeared around 1.5 $\log(\mu\text{g})$ for May stations, and the mean NBSS slopes were steeper in January than in May. Within each survey, the NBSS slopes were steepest in Habitat 1, ow-

Table 4. Mean values of the parameters within the 3 habitats for the 2 campaigns. Parameter abbreviations are defined in Table 2; NBSS: normalized biomass size spectrum

	Z_ML	Rho_grad	Temp_0	Sal_0	Rho_b	Chla_int	X _{0.1–0.3mm}	X _{0.3–0.5mm}	X _{0.5mm}	NBSS slope
January										
Habitat 1	18	0.07	11.35	37.08	28.69	0.93	127910	6119	890	–1.15
Habitat 2	1	1.46	11.57	33.88	28.71	0.47	63480	7610	2730	–0.79
Habitat 3	74	0.02	12.58	37.70	28.70	0.53	35620	2932	1207	–0.85
May										
Habitat 1	1.8	0.13	16.16	36.78	28.72	0.50	165491	14800	3075	–1.03
Habitat 2	2.6	0.59	17.26	34.95	28.64	0.38	89478	15480	6389	–0.74
Habitat 3	5.3	0.13	16.19	37.07	28.73	0.32	31656	4698	1632	–0.80

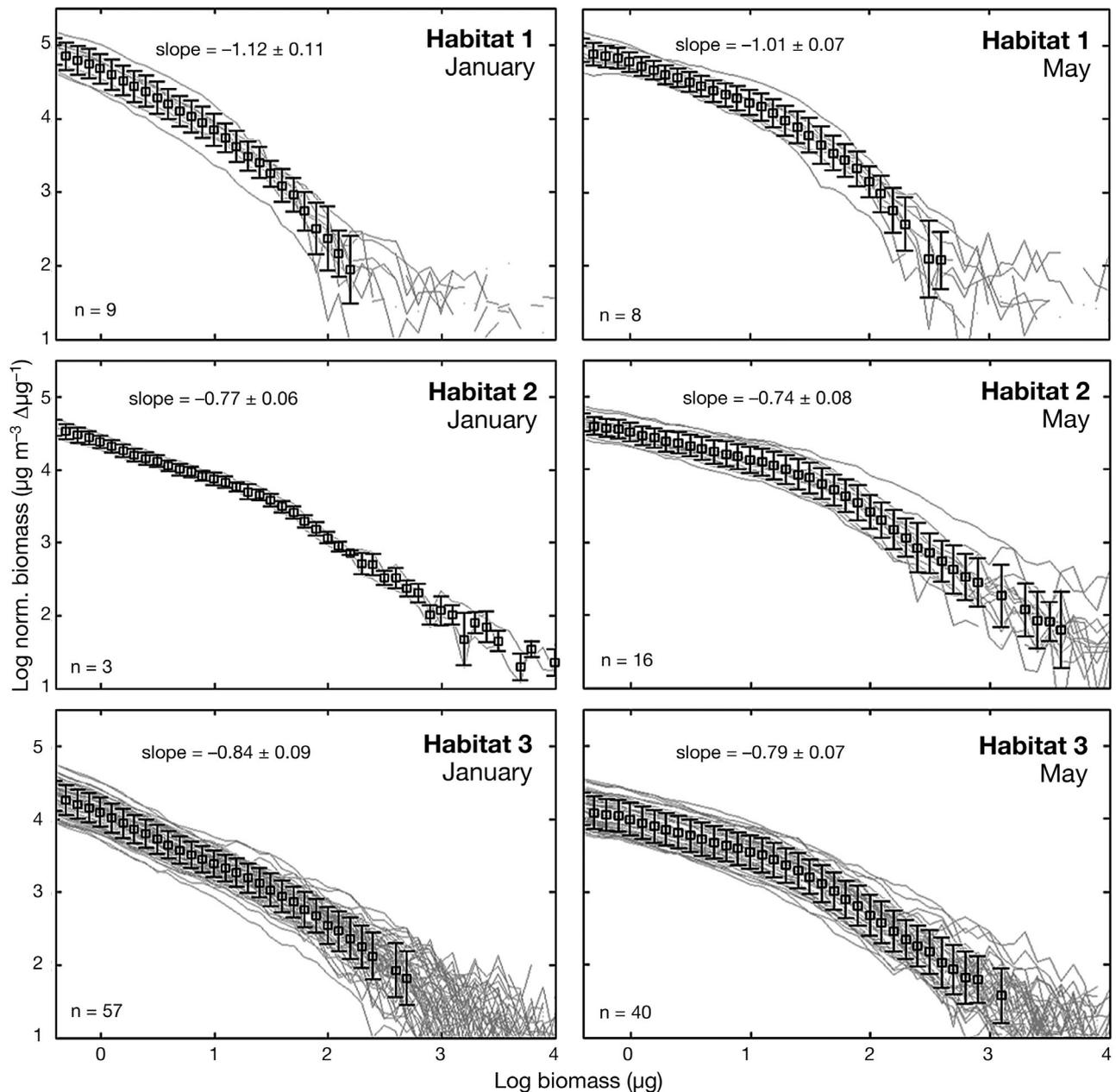


Fig. 8. Normalized biomass size spectrum (NBSS) of the stations (light grey lines) included in the 3 habitats (see Fig. 7) for the 2 campaigns. The mean NBSS and standard deviation for each habitat is represented by the squares and the error bars. Mean NBSS slopes (\pm SD) and number of stations (n) are shown

ing to the high abundances of small particles (<0.9 $\log(\mu\text{g})$; 0.3 mm ESD) and flattest in Habitat 2, owing to the high abundances of large particles (>1.6 $\log(\mu\text{g})$; 0.5 mm ESD). In Habitat 3, NBSS slopes had intermediate values and a lower y -intercept.

Based on the spatial proportion, i.e. the ratio between the number of stations included in the habitat and the total number of stations, and the mean particle concentrations in each habitat (Table 4), the indi-

cators of the contributions to the global zooplankton stock were calculated for 3 size classes in January and May (Table 5). In January, most of the medium to large organisms were concentrated in the continental shelf habitat, while the small organisms used both the continental shelf and the coastal area. In May, most of the large organisms were in the area affected by the Rhône, while small organisms were equally distributed across the 3 habitats.

Table 5. Indicators of zooplankton stock for each habitat estimated from the spatial proportion and the mean particle concentrations (VS: very small; S: small; M: medium; L: large, VL: very large) within 3 size classes during January and May surveys. Spatial distribution of the habitats is shown in Fig. 7 and mean particle concentrations in Table 4

	January			May		
	$X_{0.1-0.3mm}$	$X_{0.3-0.5mm}$	$X_{0.5mm}$	$X_{0.1-0.3mm}$	$X_{0.3-0.5mm}$	$X_{0.5mm}$
Habitat 1	L	M	S	M	S	S
Habitat 2	VS	S	S	M	L	VL
Habitat 3	L	VL	VL	M	M	L

DISCUSSION

LOPC data

The use of *in situ* optical counters in coastal regions and stratified waters could be tricky owing to high particle concentration peaks caused by resuspension and aggregation processes. For the LOPC, coincidence issues could result in incoherent multi-element plankton (MEP) sequences and an overestimation of large-particle abundances. Schultes & Lopes (2009) suggested the ratio of Total Count (TC):MEP Count as an indicator to show whether a profile is coherent. If this ratio drops below 20, the system has been probably overloaded by MEP counts during counting. In the present study, incoherent MEP sequences appeared in stratified waters (9 out of 135 stations) and did not always correspond to a TC:MEP ratio below 20 (2 out of 135 stations). This is probably because the ratio was integrated along the water column and its mean value will depend on the height of the water column under the pycnocline, where the ratio is generally very low owing to high transparent aggregate concentrations. Basedow et al. (2014) showed that in polar regions, a low TC:MEP ratio can also be the result of a high concentration of large organisms. In all cases, the number of profiles concerned in this study is low and we consider that the conditions were suitable for LOPC during the surveys.

Physical processes

The regions of freshwater influence (Simpson 1997) for the Rhône River were different for the 2 surveys. The plume position, movement, and dilution were closely associated with wind conditions. During the January survey, strong northerly winds mixed the water column and diluted the Rhône River plume, leaving only a small area affected by the freshwater

input. In May, a lens of freshwater was separated from the rest of the plume (Fig. 4a). Light winds pushed the plume southwards. At the same time, the Coriolis force caused the tip of the plume to drift to the west (Ekman transport). The creation of freshwater lenses and, more generally, the stratification of the water column at this time imply that a large part of the gulf was affected by the Rhône River discharge during the May survey.

The NC separates the continental shelf from the open sea. Intrusions were recorded along Transect D in the east of the gulf in January (Fig. 3b). At this time, the NC was narrow, strong, and close to the slope with frequent intrusions onto the shelf (Estournel et al. 2003, Petrenko 2003). Saltier and ultra-oligotrophic waters carried by the NC intrude onto the shelf and create a front with the continental shelf waters. In the coastal western part of the gulf, the cold, strong northerly winds cool the shallowest waters and mix them with freshwaters coming from the Rhône River and other sources (Broche et al. 1998, Petrenko 2003).

Environmental conditions

Hydrodynamic conditions in the coastal area have a significant influence on the distribution and availability of nutrients and therefore drive the distribution and the population dynamics of primary producers. In the Gulf of Lion, the winds and the fluvial inputs are the 2 main factors affecting the physical structures. The combination of these 2 factors creates 2 main highly productive areas, viz. the nearshore area and the area where the Rhône river plume is diluted (Champalbert 1996, Lefevre et al. 1997, Gaudy et al. 2003), corresponding to 2 of the 3 habitats identified by statistical analysis in this study.

The habitat in the nearshore area is characterized by shallow mixed waters and high chl *a* concentrations. In this area (<50 m depth), biological production was increased by nutrient-rich freshwater discharges and wind-driven resuspension, especially in the western part, where there are many river mouths and the Tramontane is frequent and strong.

The habitat in the area affected by the Rhône waters is characterized by stratified waters caused by the freshwater runoff in a thin surface layer. The Rhône River plume has food webs that are time dependent and can be divided into several steps from microbial loop dominance at the mouth, to large size

phytoplankton production a few days later (Diaz et al. 2008). The combination of high chl *a* concentration in the surface waters with a stratified water column results in an increase in biomass at the interface of the water masses which is caused by a slowing down of the sinking biomass and aggregation processes at the pycnocline (Alldredge et al. 2002, Checkley et al. 2008, Jackson & Checkley 2011). This represents an important source of food for zooplankton which come to feed at the front between the water masses (Gaudy et al. 1990, 1996, Pagano et al. 1993). The spread of this habitat is closely linked to the hydroclimatic conditions, especially thermal stratification and wind.

The third habitat was characterized by the mean conditions on the continental shelf and was less affected by coastal dynamic variability. The biological production was lower in this area than in the other 2 habitats, owing to the oligotrophic influence of the NC and to the lack of nutrient inputs.

Zooplankton habitats

Based on the zooplankton size structure and the environmental conditions, 3 zooplankton habitats were defined (Table 4, Fig. 7). In this study, vertical information was integrated to produce 2D habitat maps that are easier to use and visualize. Defining habitats is a statistical way of analyzing the distribution of zooplankton communities as a function of environmental conditions (Zarauz et al. 2007, Schulz et al. 2012). This approach is particularly useful for continental shelves and, more generally, coastal areas where changing physical structures have a significant effect on the marine ecosystems by creating different environmental patterns. Given the variability of the physical structures, habitats can only be identified by mapping the study area at high spatial resolution and checking that the physical structures are stable during the surveys. Using *in situ* optical captors was less time-consuming than traditional sampling and provides characteristics of size spectra as indicators of zooplankton communities. The processes which shape the habitats lead to different zooplankton size structure characterized by changes in NBSS slopes (Fig. 8).

Mixed-water ecosystems are known to promote small mesozooplankton production (Jackson et al. 1997, Checkley et al. 2008), which is in agreement with the steep NBSS measured in the nearshore habitat. It is likely that the highly variable hydrological conditions in the shallowest waters are not

favorable to the development of large-sized species. The steepness of the slope indicates a short food web adapted to episodic phytoplankton bloom driven by winds. This habitat is the most productive during the winter and supports biological production within the Gulf of Lion when production on the shelf is low (Kouwenberg 1994, Gaudy et al. 2003). Moreover, despite the small area covered by this habitat, there was a large stock of small-sized species in January (Table 5).

Stratified ecosystems encourage the development of large copepods (Williams et al. 1994, Poulet et al. 1996, Sourisseau & Carlotti 2006), which is confirmed by the flat NBSS found in the habitat closely associated with the spreading of the Rhône waters. The diversity of food sources prevented food limitation for zooplankton and encouraged the biodiversity of species resulting in the ecosystem being efficient at transferring the biomass from the small to large organisms, illustrated by the flattening of the slopes (Zhou et al. 2009, Basedow et al. 2010). When the water is stratified and the Rhône waters are spread widely, as during the May survey, this habitat is a refuge for large zooplankton species (Table 5).

A coastal to offshore gradient in particle concentrations was observed during this study which agrees with previous surveys conducted in the Gulf of Lion (Kouwenberg 1994, Gaudy et al. 2003). The third habitat was the main part of the continental shelf, the continental slope, and the eastern end of the gulf and had lower particle concentrations than the other habitats. The oligotrophic influence of the NC was clear, especially in the eastern part of the shelf. However, this habitat is larger than the other 2 and is an important reserve for large species during the winter (Table 5).

The differences between the NBSSs for the habitats confirm that the size structures and, therefore, zooplankton communities were not the same, showing that they were distinct zooplankton habitats, or 'guilds,' according to the classification proposed by Costello (2009).

Use and future of habitat definition

Based on data from field samples over 2 periods, our study shows a significant correlation between physical and biological features (Fig. 5, Table 3). Although statistical analysis was performed separately on the data sets for each survey, the characteristics of the habitats are similar. This is due to the permanent presence of certain processes, such as the

Rhône water runoff and the wind-driven mixing of coastal waters, which drive the distribution of the habitats. Therefore, changes in the distribution of habitats can be determined by identifying the variables which characterize these processes and by estimating the values of these variables at high spatio-temporal resolution using simulations from hydrological models (Planque et al. 2004, Zarauz et al. 2007). Remote sensing data also provide certain variables that are characteristic of the surface layer. These types of data can be used to determine spatial distribution of the habitats during the year.

Defining habitats provides a firm basis for developing efficient sampling strategies for studying zooplankton dynamics by defining a limited number of stations that are representative of specific conditions. By mapping large, consistent habitats to collate the information on zooplankton distribution and characteristics, defining habitats is the best way of including zooplankton communities in trophodynamic studies, especially in the Gulf of Lion which is considered to be one of the main reproduction areas for small pelagic species (Plounevez & Champalbert 2000, Palomera et al. 2007). Furthermore, determining habitats with distinct zooplankton size structures provides important information given that recent studies have highlighted the role of prey size in the recruitment success of fish larvae (Irigoién et al. 2009, Costalago et al. 2011). Defining habitats would also be useful for validating zooplankton distribution models and estimating indicators of zooplankton stocks in different parts of and over the whole gulf, as shown in Table 5. This type of information is suitable for coastal management programs, such as coastal ecosystem observatory networks, in order to determine the best means for protecting and preserving coastal marine ecosystems.

Acknowledgements. We acknowledge the Captain and crews of the RV 'Téthys II' for their assistance during the cruise. We thank A. Desnues for the laboratory assessment of chl *a* concentrations. This study was supported by the Agence Nationale de la Recherche (ANR): ANR COSTAS funded the research cruises and laboratory analysis, whereas the ANR FOCEA funded the optical sensors implemented and used during the cruises and the data analysis from these captors. The manuscript was improved by comments from 3 anonymous reviewers.

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Editorial responsibility: Antonio Bode,
A Coruña, Spain

Submitted: October 25, 2013; Accepted: March 27, 2014
Proofs received from author(s): June 3, 2014