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Dynamics of microphytoplankton abundance and diversity in NW Mediterranean Sea during late summer condition (DYNAPROC 2 cruise; September–October 2004)

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Abstract

Changes in marine phytoplankton communities over short-time scales have rarely been examined. We sampled nearly daily, and determined taxonomic composition and abundance of the main microplanktonic groups from both net and bottle sampling during the DYNAPROC 2 cruise (September–October 2004), in the NW Mediterranean Sea. Hydrological conditions were characterised by the existence of a highly-stratified water column and nutrient-depleted conditions. In this almost steady state situation, we found a decrease in regularity, which we attribute to competitive exclusion, leading to the dominance of species with the best fitness. While overall diversity appeared to be quite invariant, important variations occurred among specific taxonomic groups. For example, within the genus *Ceratium*, the dominance index tended to increase throughout the study from 44% to a maximum of 73% at the end of the cruise. We also discuss the value of taxonomic studies, especially in the context of global change, as able to provide valuable information on biogeochemically-important groups of species, as well as those indicative of water masses or warming, and trophic aspects of the community that are ignored or largely underestimated with other kind of phytoplankton studies, such as pigment analysis.

1 Introduction

Marine phytoplankton constitute the base of the pelagic food-web and are responsible for about half of the net annual primary production on Earth (Field et al., 1998; Falkowski et al., 2004). Current studies on monitoring marine phytoplankton responses to climate alterations are mainly based on satellite-derived values from remote sensing (Kyewalyangaa et al., 2007) or deal with the pigment diversity (Marty et al., 2002), rather than examining changes in diversity or species compositions. This is surprising since it is generally believed that ecosystems functioning, stability and efficiency are in some manner linked to diversity (e.g. Loreau et al., 2001). Moreover, the few

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existing studies on marine phytoplankton communities assessed seasonal to plurian-
nual periods (Venrick et al., 1997; Caroppo et al., 1999; Gómez and Gorsky, 2003).
Short-time scale studies of the microphytoplankton diversity dynamics (i.e. day to day)
have concerned lakes (Padisák et al., 1988; Padisák, 1993; Pinckney et al., 1998) or
5 were based on pigment analyses of seawater samples (Bidigare and Ondrusek, 1996).
Studies dealing with daily changes in microphytoplankton abundance and diversity are
needed to provide minimum estimates of variability, a necessary first step before con-
sidering the possible effects of global change on marine ecosystems and the effects
of changes on the efficiency of “ecosystem goods and services” (e.g. Naeem, 1998;
10 Walker et al., 1999).

Within theoretical ecology, the Intermediate Disturbance Hypothesis (IDH), originally
proposed to explain incomplete dominance of Pacific rocky intertidal communities (i.e.
Paine and Vadas 1969; Connell 1978) has been generally extended and applied to
planktonic communities (e.g. Reynolds et al., 1993). The hypothesis describes diver-
15 sity as a variable dependant upon disturbance frequency and intensity. Very high or
very low disturbances intensities and/or frequencies result in keystone species per-
sistence and a loss of diversity, while intermediate intensity and periodicity prevent
competitive exclusion resulting in high diversity. In planktonic systems, disturbances is
mainly considered as wind events and the increasing in the frequency and intensity of
20 storms is one of the many aspects of the global changes forecasted for the decades to
come (Knutson et al., 1998; Emanuel, 2005). Studies related to IDH have been con-
ducted in lakes or fresh water ecosystems (Lindenschmidt and Chorus, 1998; Flöder
and Sommer, 1999; Weithoff et al., 2001) but few studies report investigations in the
marine ecosystem. The outcomes of these disturbances on biodiversity cannot only be
25 assessed with dominant species studies (Paine, 1966). Dominant species are easily
observable from their obviousness and constitute a pillar of community architecture (Pi-
raino et al., 2002). However it is necessary to take into account rare species that play
supporting roles and, in spite of their relatively low abundance, may increase rapidly in
response to environmental disturbances (Mills et al., 1993).

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In order to study the short-term dynamics and the impact of disturbances on marine microphytoplankton abundance and diversity, we studied samples taken during four periods of five days from a cruise in the NW Mediterranean from September to November 2004. This expected transition period from summertime oligotrophic stratified system to autumnal system was considered favourable and pertinent because of higher frequencies of wind events.

Two complementary sampling methods (net and hydrological bottles) were used to sample microphytoplankton groups, in order to obtain the most exhaustive description of the community possible. Many other parameters are available since the whole project, named DYNAPROC 2, consisted in evaluating the DYNamic of rapid PROCesses in water column that control vertical flux of matter. Furthermore, some comparative data is available from the DYNAPROC 1 cruise which took place in May 1995 in order to document the effects of episodic wind events on the dynamics of the ecosystem during a post-bloom period, characterised by the transition from a mesotrophic to an oligotrophic system (Andersen and Prieur, 2000).

2 Material and method

2.1 Cruise track

The DYNAPROC 2 cruise was conducted in 2004 from 17 September to 17 October (Julian days 261 to 291) on board R/V *Thalassa*, at the vicinity of the NW Mediterranean French JGOFS Station DYFAMED (43°25′ N, 7°52′ E), approximately 45 km South of Cape Ferrat, France, where maximal depth is 2350 m. It was divided into two legs (here after leg 1 and leg 2) that consisted of two cycles of five days each (cycles 1 to 4). In order to describe the hydrological environment, a grid of 16 stations, centred on a fixed station (“central point”), was occupied at least four times during the cruise. The main observations were done near this fixed station. More explanations on cruise development and hydrological/meteorological evolutions can be found in Andersen et

al. (2008).

2.2 Field sampling

In order to obtain the most accurate description and characterisation of the microphytoplankton, two sampling methods were used. Hydrological bottle sampling allowed collection of small-sized and abundant microphytoplanktonic species. This method was also appropriate to preserve delicate or colonial organisms. Net sampling was employed to collect less abundant species (which were often the biggest) since the net filtered a great volume of seawater.

2.2.1 Hydrological bottle sampling

Samples were collected every 10 m from 90 m to the surface with hydrological NISKIN bottles coupled with a Seabird CTD (Conductivity-Temperature-Depth) instrument that recorded continuously hydrological parameters (temperature, salinity, density and in situ fluorescence). Aliquots of 250 ml of seawater from each depth, fixed with acid lugol's solution (final concentration, 2% v/v; Thronsen, 1978) were stored in dark cold room (4°C) until microscopic analysis. Samples were collected every day of each cycle (~12:00 a.m., ITU), yielding a total of 200 samples. Aliquots were analysed using the Utermöhl method with sedimentation of 100 ml seawater in settling chambers. Counts and observations were done with an inverted light microscope (Zeiss© Axiovert 35), at 200× and 400× magnification. For each sample, a minimum of 250 cells were counted. Instead of analysing strictly microphytoplankton species, which are formally defined as ranging from 20 to 200 μm, we preferred counting every species of the 3 groups typical of the microphytoplankton: diatoms, dinoflagellates and silicoflagellates. For instance, some small species of the genus *Gymnodinium*, with a mean size lower than 10 μm, were counted. Coccolithophorids were not counted, since acid lugol's solution alters calcified structures. Enumeration of microzooplanktonic groups (tintinnids and naked ciliates) was also carried out. Naked ciliates were separated in 3 size classes

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(equivalent diameter $<30\ \mu\text{m}$, between 30 and $50\ \mu\text{m}$, $>50\ \mu\text{m}$).

2.2.2 Net sampling

In addition to the hydrological bottle sampling, we also used net sampling daily during each cycle using a phytoplankton net ($53\ \mu\text{m}$ mesh size, $54\ \text{cm}$ diameter and $280\ \text{cm}$ length). A vertical haul was performed from $90\ \text{m}$ depth to the surface at the same time of the day ($\sim 10:00\ \text{a.m.}$, ITU) to collect large microplankton. The volume filtered by the net was calculated as equivalent to the surface at the opening of the net multiplied by the height of sampled water column. Due to bad weather, there were no net samples for julian days 285 (11 October) and 289 (15 October). The samples were split once or twice using a Motoda splitter (Motoda, 1959) and preserved with acid lugol's solution (Thronsen, 1978) to 2% final concentration. The cells were enumerated in $1\ \text{mL}$ calibrated slides using a light microscope (Alphaphot 2-YS2, Nikon Instruments, Badhoevedorp, Netherlands). More than 250 cells were counted per samples. Dinoflagellates were identified at least to the genus level. We focused more particularly on genus *Ceratium* Schrank since it is specious in the Mediterranean and often dominates among large armoured dinoflagellates, thus constituting a good model for biodiversity studies (Tunin-Ley et al., 2007). Determination of taxa belonging to genus *Ceratium* was carried out at infraspecific level. Although they do not belong to phytoplankton, the total radiolarians were also enumerated in net samples, without detailed taxonomic identification, because they exhibited significant abundances.

2.3 Estimation of taxonomic diversity

2.3.1 Taxonomic identification

The species identification of cells within the 3 selected groups was based on the following references: Trégouboff and Rose (1957a, b), Dodge (1982), Sournia (1986), Balech (1988), Hasle and Syversten (1996), Steidinger and Tangen (1997). In net

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samples, *Ceratium* cells were identified at the infraspecific level, using the monograph and the parasystematic nomenclature published by Sournia (1967). Because of the frequent changes of the nomenclature of certain species, the Irish database Algaebase (<http://www.algaebase.org>) was used as reference for the name and the authorities of the species observed (see authorities in Tables 1 and 2).

Some limits with regard to identification constrained our results. Thus, for small-sized cells, resolution of light microscopy and fixation with acid lugol made some determinations difficult. For instance, in *Coscinodiscus* and *Thalassiosira* (diatoms) and some Gymnodiniales (dinoflagellates) determination was to genus level. However, different species were distinguished via size, form and ornamentation. In the same way, species name were not ascribed to some *Pseudo-Nitzschia*, which were discriminated as several species belonging to *Pseudo-nitzschia delicatissima complex* or *Pseudo-nitzschia seriata complex* (Hasle and Syversten, 1996).

2.3.2 Diversity indices

Biodiversity parameters were calculated for the main planktonic groups in bottle samples on one hand, and in net samples on the other hand. The taxonomic richness S corresponds to the number of taxa in each group. The diversity was calculated using Shannon's index $H' = -\sum p_i \log_2 p_i$, where $p_i = n_i/N$, n_i = number of individuals of one taxon and N = total number of individuals. Regularity was estimated as Pielou's index $J' = H'/\log_2 S$. The net samples were divided into three replicates before counting. This allowed application of the nonparametric jackknife 1 method (Manly, 1991), which gives estimations of the biodiversity parameters after correcting the bias induced by the sampling effort and the sampling size (Carpentier and Lepêtre, 1999). For richness, jackknife 1 = $SO + (r_1(n-1)/n)$, where SO is the observed taxonomic richness, n the number of replicates and r_1 the number of taxa occurring in one single replicate. For diversity and regularity, jackknife 1 = $\sum \Phi_i / n$, with $\Phi_i = nSt - (n-1)St_{i-1}$, where St is the estimation of the indicator for the n replicates and St_{i-1} the estimation of the indicator for the $n-1$ replicates. These estimations were calculated on a minimal basis

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of 100 counted cells per replicate, which represents a minimal total of 300 cells per sample. For diversity calculations, Magurran (2004) recommended use of abundances ranging from 200 to 500 cells per samples. The jackknife 1 method was not applied on bottle samples, for which no replicates were available. In order to identify the important 5 genus or taxa within dinoflagellates and within genus *Ceratium* from net samples, a dominance index was also calculated as $\delta=100(n_1+n_2)/N$, where n_1 and n_2 are the abundances of the two most important taxa and N the total cell concentration (Hulburt, 1963).

2.4 Data analysis

10 The variability of the main planktonic groups was analysed using a multivariate analysis producing a synthesis of co-occurring factors. The Correspondence Analysis (CA) aims to describe the total inertia of a multidimensional set of data in a sample of fewer dimensions (or axes) that is the best summary of the information contained in the data (Benzecri, 1973). The CA is applied to contingency tables and uses a Chi square metric. The different calculations of this method are detailed in Legendre and Legendre 15 (2000). This ordination method was applied to our matrix describing the planktonic groups in bottle samples (samples in rows and planktonic groups in columns), in order to underline the kinetics of plankton composition over time. The composite mean depths' and the composite mean day's coordinates, calculated as the average of the 20 samples of the same depth, or the average of the samples of the same day, were used as illustrative qualitative variables.

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3 Results

3.1 Physical environment

3.1.1 Meteorological data

Wind regime was characterised by the alternation of strong wind events and calm periods. The leg 1 was characterised by two significant wind events, one at the beginning of the leg, which lasted 48 h, and a later one with a highest intensity yet shorter in time. Both corresponded to NE winds, whereas winds are usually blowing from W or SW in the area at this period (Raybaud et al., 2008). By contrast, the end of leg 2 was dominated by persistent and strong NE and SW winds. In addition, an episode with significant precipitations occurred just before the campaign started.

3.1.2 Hydrological and biological parameters (CTD acquisition)

The hydrological structure along the cruise revealed a typical late summer situation with a stratified water column, whereas a transition from summer period to fall structure was expected (i.e. destratification). Thus, the thermocline ranged from 20 to 40 m depth, with surface temperatures above 20°C. Salinity dynamics were characterised by the intrusion of Low Salinity Water (LSW) with likely coastal characteristics (<38.3 PSU) during leg 1 (day 265 to day 274 = 21 September to 30 September) just under the thermocline. This phenomenon, detailed by Andersen et al. (2008) and Raybaud et al. (2008), was also observed to a lesser degree during leg 2 (day 283 to day 286 = 9 October to 12 October). Each time, this resulted in a light shallowing of the thermocline, as a consequence of the expansion of the less dense water mass. The destratification seemed to be initiated at the end of the cruise, with a deepening of the temperature and the salinity isoclines, in response to the regime of persistent and strong wind at this time. At the beginning of leg 1, fluorescence measurements displayed a chlorophyll-a peak about 80 m depth, followed by another distinctive one about 50 m depth. Through-

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out the second part of the cruise, the Deep Chlorophyll Maximum (DCM) was located just under the thermocline, following its shift to a deeper depth.

3.2 Diversity and abundance of microplankton

3.2.1 Hydrological bottle sampling

5 Summing over the whole cruise, 151 species of microphytoplankton were found in hydrological bottle samples. Dinoflagellates were the most diverse group with 94 species (33 armoured and 61 unarmoured), followed by 55 species of diatoms (30 centrics and 25 pennates). We found only 2 species of silicoflagellates. Additionally we encountered empty *Leptocylindrus mediterraneus* cells (centric diatom), but they were
10 integrated neither in abundance nor in diversity calculation since they were not alive. Near 58% of taxa were determined to the species level, 98% to genus level; the rest were composed of indeterminate armoured dinoflagellates. The maximum abundance of total microphytoplankton was often just under the thermocline and reached more than 40 000 ind l⁻¹ at the beginning of leg 2, cycle 4 (Fig. 1a). Throughout the study
15 diatoms were mostly in the lower depths (Fig. 1b), with abundance ranging from 200 to 800 cell l⁻¹ in surface and from 1000 up to 5000 cell l⁻¹ below the thermocline. Temporally, two distinct peaks of abundance were observed. The first one (from 4000 to 5000 cell l⁻¹) occurred at 80 m depth at the beginning of the first cycle (Julian day 262 = 18 September) and was mainly composed by the centric species *Corethron criophilum* probably in senescent phase as half-empty cells were found. The second peak
20 occurred during cycle 3 (Julian day 278 = 4 October) and was mainly composed of pennate species represented by the complexes *Pseudo-nitzschia delicatissima* spp. and *Pseudo-nitzschia seriata* spp. In leg 1 samples, we also found the centric species *Leptocylindrus mediterraneus* and its epiphyte (Fig. 2a), the heterotrophic flagellate *Rhizomonas setigera*.
25

In contrast to the diatoms, dinoflagellates were found largely in the upper layers during the whole cruise (Fig. 1c). The group of naked dinoflagellates, mainly repre-

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sented by small-sized species *Gyrodinium* spp. and *Gymnodinium* spp., dominated in both legs. Abundance increased from 5000 to 20 000 ind l⁻¹ during leg 1 to 10 000 to 35 000 ind l⁻¹ during leg 2. The armoured species *Scrippsiella* sp. was found subsequent to the intrusions of less saline water (Fig. 2b).

5 Silicoflagellates (Dictyochophyceae) abundance was lowest in comparison with the two other groups (Fig. 1d). Two species were found, *Dictyocha fibula* and *Dictyocha speculum*, the first one being the most abundant. Silicoflagellates showed marked spatio-temporal variations. Abundance varied from less than 50 cell l⁻¹ to more than 600 cell l⁻¹. During first leg, two maxima of abundance were identifiable (days 264–
10 265 and 270 (20–21 September and 26 September) with a range from 400 cell l⁻¹ up to 600 cell l⁻¹). The end of leg 1 marked the decrease in abundance with low concentrations found during the second leg. Finally, the trends of naked ciliate abundances (Fig. 2c) showed a slight increase from 500 to 1250 cell l⁻¹ during the first leg leading to maximal value of 2000 cell l⁻¹ in the second leg. In each sample, the great majority
15 (more than 90%) of ciliates were of small size (less than 30 μm).

The total richness of the microphytoplankton varied from 47 to 100 species (Fig. 3a). The total richness slightly increased during the first leg, reached a maximum during the cycle 3 and then decreased during cycle 4 although values stayed superior to the richness observed in leg 1. Diatoms and dinoflagellates species richness followed the
20 same pattern as total microphytoplankton, but the increase was more marked for dinoflagellates richness. Number of diatoms species ranged from 17 to 39, with nearly equal portions of pennates (10 to 21 species) and centrics (7 to 18 species) (Fig. 3b). Dinoflagellate species richness ranged from 28 to 63 species, with a similar contribution of armoured species (14 to 32 species) and naked species (12 to 31 species).
25 The diversity of microphytoplankton was about 3–4 bit ind⁻¹ and was globally constant (Fig. 3c). Diversity indices for total dinoflagellates and total diatoms showed the same feature. Yet, there was a trend of decreasing diversity of armoured species within dinoflagellates and of the diversity of centric species within diatoms (Fig. 3d). Actually, the few variations in diversity resulted from an opposite trends in richness and regu-

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5 larity indices. Indeed, the index of regularity decreased for total microphytoplankton (Fig. 3e), and was mainly driven by a pattern of decreasing dinoflagellates regularity, both displayed by armoured species and by naked species to a lesser extent. In contrast, the regularity of total diatoms remained at a high level without any clear trend of variation. Regularity of pennate diatoms was constant whereas it slowly decreased for centric species (Fig. 3f). Thus, while overall diversity appeared to be quite invariant, important variations occurred among specific taxonomic groups.

3.2.2 Net sampling

10 Microplankton abundance in net samples, corresponding to radiolarians and large armoured dinoflagellates, decreased throughout the study, from over 8000 cells per m³ at the beginning to about 3000 cells per m³ at the end of the cruise (Fig. 4a). Overall, radiolarians were the dominant group (from 828 to 5344 cell m⁻³), while *Ceratium* spp. represented about 50% (from 834 to 3734 cell m⁻³) of the total dinoflagellates. *Ceratium* became largely dominant within dinoflagellates at the end of the cruise, while the total microplankton abundance decreased. This trend was reflected in the evolution of dinoflagellates biodiversity parameters. While a total of 27 dinoflagellates genera was described (Table 2), the generic richness in dinoflagellates was about 20 genera along the study (Fig. 4b). In the same time, the diversity of dinoflagellates genera was quite constant until day 265 (21 September), and then varied more until an important decrease at the end of the cruise (Fig. 4c). This pattern is partly related to regularity, which varied little during the cycles 1 and 2 both for dinoflagellates. Regularity became more variable during the leg 2 with a final decrease that followed a trend to increase.

15 Within the genus *Ceratium*, the number of infraspecific taxa increased from 43 to 56 taxa during the cycle 1 and then decreased after day 269 (25 September) to reach a value of 28 taxa. Conversely, infraspecific diversity in *Ceratium* slowly decreased and then increased at the end of the cruise, whereas regularity strongly increased during the cycle 2 and then decreased as for dinoflagellates genera at the very end of the last cycle (Fig. 4d).

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In term of dominance, the genus *Ceratium* was prominent throughout the cruise within the dinoflagellates, and followed by the genus *Goniodoma* during the first leg, then the genera *Goniodoma*, *Gonyaulax* and *Podolampas* (Fig. 5a). The association *Ceratium/Podolampas* at the middle of cycle 3 corresponded to a minimum of the dominance index (about 50%) whereas during the last cycle, the dominance of the association *Ceratium/Gonyaulax* exceeded 90%.

Within the genus *Ceratium*, the dominance index tended to increase throughout the study from 44% to a maximum of 73% at the end, and was globally higher during the leg 2 (Fig. 5b). One single taxon, *C. pentagonum* var. *tenerum*, corresponding to the thermophilic variety of the species *C. pentagonum*, was also common throughout the cruise. Other abundant taxa included *C. pentagonum* “*robustum-tenerum*”, *C. horridum* var. *buceros*, *C. symmetricum* var. *orthoceras*, *C. limulus* and *C. concilians* during the leg 1, and to *C. declinatum* f. *brachiatum*, *C. declinatum* f. *normale*, *C. concilians*, *C. horridum* var. *buceros*, *C. platycorne* “*platycorne-compressum*” and *C. pentagonum* “*robustum>tenerum*” during the leg 2. These 10 prominent taxa represented a small fraction of the 64 infraspecific taxa which were encountered in the genus *Ceratium* (Table 2).

3.3 Spatio-temporal dynamics of microplankton

The Correspondences Analysis, applied to the abundances of the main planktonic groups, yielded an interesting synthesis of the spatio-temporal patterns of the microplankton (Fig. 6). The planktonic groups were discriminated by their different coordinates on the 2 first factors, explaining respectively 54.8% and 24.3% of the total inertia. Thus, siliceous organisms, corresponding to centric and pennate diatoms and silicoflagellates, had negative coordinates on axis 1, while armoured dinoflagellates and the heterotrophic possibly mixotrophic, and autotrophic ciliates and naked dinoflagellates, had coordinates close to 0 on this axis. The axis 2 discriminated centric diatoms, Dictyochophyceae and armoured dinoflagellates (negative coordinates) from pennate diatoms and the mainly heterotrophic group (positive coordinates). Pro-

jection of sampling days and sampling depths as illustrative variables indicated that the planktonic groups had particular vertical distributions: the group with ciliates and naked dinoflagellates was located above the thermocline in the surface layer; the armoured dinoflagellates were associated with depths close to 50 m, i.e. close to the mean depth of the thermocline and the chlorophyll maximum; Dictyochophyceae and more particularly diatoms were characteristic of the deepest layers. In addition, there was an opposition on axis 2 between the days of the leg 1, associated with diatoms, Dictyochophyceae and armoured dinoflagellates, and the days of the leg 2 associated with ciliates, naked dinoflagellates and pennate diatoms.

4 Discussion

4.1 Dynamics and trophic importance of microplankton

In the NW Mediterranean Sea, the summer period usually starts in May–June with the development of the thermocline at this time. This thermocline persists until mid-September or late October, when storms frequency is high. The mixing effect of the storms and wind events allows the reinjection of nutrients from depth towards the upper layer. In addition to the enrichment of waters, the development of a high pressure system following the storm period leads to calm and sunny weather conditions, known as St Martin's summer, which triggers the autumnal phytoplankton bloom in the NW Mediterranean (Duarte et al., 1999). Despite the specific choice in timing for the DYNAPROC 2 cruise, the conditions that we encountered were characteristic of late summer stratification, with a well-established thermocline and a situation of nutrient depletion in the surface layer. The destratification began only at the end of the campaign in response to the action of persistent wind during the cycle 4. The microplankton also corresponded to a typical summer situation, with the general dominance of small-sized species. Indeed, ciliates, radiolarians and mixotrophic and heterotrophic dinoflagellates formed the largest proportion of the microplankton community abun-

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dance. Dinoflagellates usually dominate the microphytoplankton during the stratified period in the NW Mediterranean (Gómez, 2003; Gómez and Gorsky, 2003), since they do prefer conditions of low turbulence and warm temperatures, while low nutrients concentrations in the surface layer and stratification limit the development of diatoms and silicoflagellates. The significant contribution of naked dinoflagellates, mainly of the genera *Gyrodinium* and *Gymnodinium*, could be attributed to the oligotrophic environment, since several species are known to have phagotrophic activity (Steidinger and Tangen, 1997; Stoecker, 1999). Within less abundant armoured dinoflagellates, the prominence of *Ceratium* species, which characterised the net samples, has been already reported in the Ligurian Sea (Halim, 1960; Gómez and Gorsky, 2003). We found abundances are of the same magnitude, even slightly lower, than those observed in the coastal waters of Villefranche bay at the same time (Tunin-Ley et al., 2007). Although the majority of *Ceratium* species possesses chloroplasts, the cells can contain vacuoles, which could result from phagotrophic behaviour (Chang and Carpenter, 1994). Radiolarians are known to be common in late summer and fall (Lange et al., 1997). Within radiolarians, the polycystines occur in the upper strata of the water column as they may bear algal symbionts, with maximal abundances ranging from 25 to 50 m depth in extrapolar areas (Anderson et al., 2000). Thus, the radiolarians described in the present study were likely dominated by polycystines. Observed densities were remarkably higher than those usually observed, with an order of magnitude of tens to hundreds individuals per cubic meter. During the first DYNAPROC cruise (May 1995), abundances of radiolarians ranged from 200 to more than 1000 ind m⁻³ with maximal abundances comprised between 50 and 70 m (Andersen et al., 2000). That represents slightly lower abundances than those reported for the present cruise. Radiolarians may have significantly contributed to primary production since it has been established its association with photosynthetic symbionts (Foster et al., 2006). The naked ciliates represented an important part of the total microplankton, especially during the leg 2 (2 to 17 October) and their abundances were consistent with values described in the Villefranche bay at the same period (Gómez and Gorsky, 2003). In contrast, during the

first DYNAPROC cruise, much higher ciliate abundances (avg of 3000 cells l⁻¹) were recorded (Perez et al., 2000).

In addition to the overall dominance of small-sized dinoflagellates during the study in term of total abundances, there was also a temporal shift in microplankton composition from a system characterised by the presence of autotrophic organisms and by the significant contribution of siliceous species during leg 1 (14 to 29 September) to a regeneration-dominated system with mainly mixotrophic or heterotrophic organisms during leg 2 (Julian day 276 to 291 = 2 October to 17 October). A slight decrease in silicate concentration was found (Marty et al., 2008) that may partly explain the decline of siliceous organisms during leg 2. The rapid development of diatoms species in the deep layer was clearly associated with increases in silicate concentrations (Marty et al., 2008). Indeed, diatoms species are able to respond very fast to nutrient pulses (Cloern and Dufford, 2005). The disappearance of the silicoflagellates could result then from the competition with diatoms. As the first observed population of diatoms dominated by *Corethron criophilum* was senescent, the competition for silica was weak, likely allowing the development of the silicoflagellates, whereas the competition for silica may have increased towards the middle of the campaign with the significant development of mainly pennate diatoms.

Predation pressure also differed along the study, with a change in zooplankton species composition (Raybaud et al., 2008). Both diatoms, which were represented by several large-sized species, and silicoflagellates, are potentially protected from herbivorous copepod predation, were well represented during leg 1 (Julian day 261 to 274 = 17 September to 30 September) whereas their contribution decreased during leg 2, corresponding with presence of other predator species with more generalist and non-selective diets like Pteropods (Raybaud et al., 2008).

The trophic importance of microzooplankton is well recognized; nevertheless, this group is often exclusively composed of a ciliate “box” in food web studies and models. We assumed that the contribution of hetero- and mixotrophic dinoflagellates is largely underestimated. Since Lessard and Swift (1985, 1986), we know that about half of

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dinoflagellates species in marine plankton do not possess chloroplasts and likely consume other plankton cells. A recent review of Sherr and Sherr (2007) showed that dinoflagellate biomass could sometimes be higher than ciliate biomass while small naked dinoflagellates may account for a large fraction (up to 90%) of the total heterotrophic dinoflagellates biomass. This last point was confirmed in Pacific Ocean by Masquelier and Vaulot (2008) who found, using epifluorescence microscopy, that about 80% of heterotrophic dinoflagellates were cells smaller than 20 μm and noted that typical Utermöhl method largely underestimated small dinoflagellates abundances. A large number of dinoflagellates species recorded during our study were mixotrophic or heterotrophic. For instance, all *Protooperidinium* species are known to lack photosynthetic pigments. Numerous cells of the order Gymnodiniales were observed, but our preserving and counting methods probably largely underestimated their abundance (Masquelier and Vaulot, 2008). Given the abundance and variety of ciliate and heterotrophic dinoflagellates, the ecosystem of our study had a heterotrophic microplankton pool that fed on a wide range of prey, from bacteria to centric diatoms (Sherr and Sherr, 2007). The heterotrophic microplankton likely had another important role, that of a significant food resource for mesozooplankton (Perez et al., 1997; Susuki et al., 1999; Liu et al., 2005). This has to be taken into consideration when studying the functioning of the whole ecosystem.

4.2 Advantages of species determination

The dynamics of marine phytoplankton have been assessed over short scales using pigment analysis (Vidussi et al., 2000). HPLC technique based on the pigment signature of major phytoplankton groups constitutes an efficient tool yielding an overview of relative contributions and major shifts. Additionally, converting pigments to carbon equivalent is convenient for linking the overall distribution of phytoplankton to the dynamic of organic matter. HPLC technique has been used successfully during DYNAPROC 2 (Marty et al., 2008). Yet, with this approach, groups of species that have no specific pigment signature are not identified, as well as groups without any photo-

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synthetic pigments (i.e. heterotrophic dinoflagellates). Furthermore, species composition cannot be considered. Compared to pigment diversity analysis our direct microscopic observations supply complementary information of biogeochemical and ecological interests. Thus, silicoflagellates characterised by a complex pigment-content composed of acylfucoxanthines (19'-BF et 19'-HF), fuco-, diadino-, diato-xanthine and also chlorophylle-*a*, *c*, and *c3* (Daugbjerg and Henriksen, 2001) can not be monitored using a single pigment determination method but are easily distinguished microscopically. During DYNAPROC 2, the dynamics of silicate compounds does not only concern diatoms; the siliceous silicoflagellates, even though less abundance, participated in both silicate and carbon fluxes. The abundance of *Dictyocha* spp. encountered during the first period of the cruise, argues for a non-negligible contribution in the silicate cycle. While less abundant than diatoms, they may have competed with diatoms for the nutrient resources, especially silicate. This aspect is highlighted during the first low salinity event, while we observed a decrease in diatoms, previously abundant. The shift in salinity may have constituted a physiological stress with a stronger impact on diatoms. Meanwhile silicate was available; it precisely corresponded with the highest abundances of silicoflagellates. Assuming that turbulences increased the velocity of the phytoplankton cell sinking (Ruiz et al., 2004) and that this velocity also depends on the cell shape, the specific modification that occurred within the community probably influenced geochemical processes.

In addition to silicate fluxes, our study also provides information on the nitrogen cycle. The peculiar consortium constituted by frustule of *Leptocylindrus mediterraneus* and the protozoan *Rhizomonas setigera* (Pavillard) Patterson, is involved in nitrogen fixation. As the individuals observed in oligotrophic Pacific Ocean (Gómez, 2007), *R. setigera* was always found restricted to the central section of the frustule. Indeed, this aplastial protist is characterised by a symbiosis with a nitrogen-fixing cyanobacterium (Buck and Bentham, 1998). The dynamics of *L. mediterraneus* may be important with regard to nitrogen budgets. Its increase in abundance noted during the second part of cruise may have helped to sustain the primary production.

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Species-specific analysis also permits special attention to indicator species. The dinoflagellate *Scrippsiella* sp. is associated with the less saline water incoming during the first and the second leg of the cruise. As the species belonging to this genus are considered as neritic (Hasle and Syvertsen, 1996), we thus provide evidence for the coastal origin of the water with this biological marker. The species of this genus was not determined, even if it was morphologically close to *Scrippsiella trochoidea*, since Montresor et al. (2003) have suggested the existence of cryptic species in the Mediterranean Sea.

Moreover, several cells of the naked dinoflagellate *Asterodinium gracile*, with five radiating elongated extensions as presented in Fig. 2a in Gómez and Claustre (2003), were sampled in our study (one cell at 50 m and the other at 60 m depth, Julian day 286 = 12 October). This species was initially reported in Indian Ocean (Sournia, 1986) and later in the eastern Mediterranean Sea (Abboud-Abi Saab, 1989). Concerning the western Mediterranean Sea, Gómez and Claustre (2003) found this species in the Tyrrhenian basin and considered it as a possible biological indicator of warming. To our knowledge, it is the first time that *A. gracile* was found in the Ligurian Sea and this may indicate an extension of the spatial distribution of this species. Nevertheless, recent publications suggest that the genus *Asterodinium* may correspond to life stages of a highly versatile single species regrouping taxa of the genera *Brachydinium*, *Karenia* and *Microceratium* (Gómez et al., 2005; Gómez, 2006).

Despite their large size, some dinoflagellate species characterized by non-typical or much modified morphologies are often underestimated or absent from most of microphytoplankton analysis. According to Gómez and Furuya (2004), this could be explained by a specific and not easily accessible literature and difficulty in the identification, due to folding in fixed cells. Careful analysis of our samples revealed several modified dinoflagellates. They mainly belonged to the family Leptodiscaceae Taylor (order Noctilucales Heackel). The species are strongly antero-posteriorly flattened and display a wing-like extension, called the velum. Two specimens of *Scaphodinium mirabile* were found in sub-surface (10 m depth, Julian day 280 and 2 m depth, Julian day 285

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= 11 October). This species, considered as thermophilic (Stoyanova 1999; Gómez and Furaya, 2004), was been found in NW Mediterranean Sea (Margalef, 1963; Léger, 1971; Gómez and Gorsky, 2003). We encountered 18 specimens of *Petalodinium porceli*, between 10 and 90 m depth (Julian days 279 to 289 = 5 to 15 October). It is the first time that this species has been recorded in Mediterranean Sea since its description in 1969 (Cachon and Cachon, 1969). The two other cells of *P. porcelio* were reported by Stoyanova (1999) in the Black Sea and by Gómez and Furuya (2005) in the Pacific Ocean. The most relative abundant morphologically-modified dinoflagellate was *Kofoidinium velelloides*, which belongs to the family Kofoidiaceae Taylor (Sournia, 1986). Seventy-five specimens were found, from surface to 90 m depth, throughout the study period. This species has a complex life cycle and we assumed that specimens of immature stage resembling *Gymnodinium* belong to this species, due to the morphology of the large velum at mature sampled stages. The species of the genus are not easy to identify because of the high morphological variability during the life cycle and difficulties in distinguishing species from preserved specimens (Gómez and Furaya, 2007). As for genus *Asterodinium* (see above), genetic analysis will be of great utility to clarify generic, specific and sub-specific morphological limits in Leptodiscaceae and Kofoidiaceae.

4.3 Theoretical ecology

The changes described in the microphytoplankton community should be relatable to the changes observed in the environment. This potentially raises two questions. First, did the physical changes that occurred (i.e. wind stress and an intrusion of low salinity water) affect the biodiversity of microphytoplankton? Second, do our data support the Intermediate Disturbance Hypothesis (IDH)? Indeed, according to Connell (1978), an intermediate level of disturbance leads to a peak of diversity. In the absence of disturbance, the competitive exclusion principle (Hardin, 1960) would apply, the less-fit species being eliminated, resulting in low diversity. In contrast, highly intense or frequent disturbance can restrict the community to a few pioneer species, yielding low

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diversity. This hypothesis, firstly developed for terrestrial plants, has been examined with regard to phytoplankton, in part as an attempt to solve the “paradox of the plankton” (Hutchinson, 1961), that points out the incoherence between the remarkable high richness observed in phytoplankton and the few resources which theoretically prevents the coexistence of numerous species, because of the principle of competitive exclusion. Laboratory and field studies, mainly focussing on freshwater ecosystems, have supported the application of the IDH to phytoplankton (Padisák, 1994; Sommer, 1995; Flöder and Sommer, 1999; Hambright and Zohary, 2000; Elliott et al., 2001; Weithoff et al., 2001; Shea et al., 2004). But the weakness of this hypothesis is that it considers the response to an unmeasured event (Reynolds, 1997). It is effectively really difficult to clearly define what a disturbance is and how intense it is. It has been proposed to define a disturbance as an event that alters the niche opportunities available to the species in a system (Shea et al., 2004). In our case, the intrusion of low salinity water and the wind regime may have been a disturbance. However, a cause and effect relationship was not obvious. During the first leg, the diversity of the total microphytoplankton from bottle samples was quite constant, despite the intrusion of less saline water. In fact, it corresponded to a simultaneous increase in richness and decrease in regularity. We can indeed postulate that the less saline water mass has brought new species, as illustrating by the development of the coastal *Scrippsiella* sp., or additional individuals of some already present species, thus modifying the relative abundances of the species, and consequently diversity. However, these trends in richness and regularity persisted during the second leg, until a decrease in the number of species at the end of the campaign, when the destratification was initiated. In net samples, the biodiversity followed the same trends, with a remarkable increase in *Ceratium* species dominance within dinoflagellates. Even within the genus *Ceratium*, which is known to be an interesting model for biodiversity studies (Tunin-Ley et al., 2007), the regularity decreased reflecting an increase in the dominance of a couple of taxa. Probably, the wind stress by itself did not represent a disturbance for phytoplankton, since it had no apparent effect in terms of vertical mixing. Thus, if we assume that the input of the less

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saline water mass, which only resulted in a light decrease in salinity but did not modify the other hydrological parameters, had a minor impact on the phytoplankton in term of stress, we can consider that the system was not temporally disturbed and tended to be close to a steady state. In these conditions, the principle of species exclusion must theoretically become preponderant, leading to the decrease in regularity that we observed. Interestingly, with regard to the particular stratified conditions characteristic from the ending summer, the species that have the best fitness at that time are the dinoflagellates, able to support nutrient-depleted waters.

It is also necessary to consider scale effect. The sampling interval of one day was supposed to allow the identification of any potential response to modifications of the environment. Indeed, the universe in which phytoplankton live exists at a very small scale. In phytoplankton, growth and death occur much faster by comparison with other vegetal organisms. Species succession is measured in days and months (Hambricht and Zohary, 2000). Hence, it has been estimated that the number of arboreal generations over the last 10 000 years was equivalent to the number of phytoplankton generations through a single annual cycle (Reynolds, 1995). Generation times in phytoplankton are then of a great importance in species succession. In conditions of steady state, planktonic successions may need only 12 to 16 generations to reach competitive exclusion, representing from 35 to 60 days (Reynolds, 1988). It means that theoretically, the scale within the disturbance occurs should be also small. However, it is possible that the response of an organism to disturbances can be delayed. As an example, the *Ceratium* species have relatively low growth rates, with doubling time ranging from two days to two months (Weiler, 1980). In this case, the response of the cells to environmental perturbations may not be immediate. In addition, although the relationship between diversity and disturbance is most of the time represented by a continuous, humpback shaped curve, a modelling approach has revealed that that this relationship may be discontinuous, exhibiting a cliff-shaped curve (Elliott et al., 2001). Indeed, a progressive increase in forcing frequency of the disturbance can trigger an abrupt decrease in diversity at a threshold frequency, while a low fluctuating state can precede

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the breakpoint (Elliott et al., 2001). As it is really arduous to integrate the disturbing events (i.e. the wind stress and the upcoming of less saline water) in a relevant scale defining frequency and intensity, it is impossible to obviously situate our case of study on a theoretical curve; it is possible that it corresponded to the low fluctuating state before the breakpoint. Clearly, it is very difficult to assess the effect of disturbance on the phytoplankton community in field studies, where disturbing events are not under control and thus escape accurate scaling. A relevant approach to test the IDH would implicate a medium-term or long-term study to allow the identification of patterns.

5 Conclusion

This is one of the first detailed studies dealing with daily variations of microphytoplankton abundance and diversity, done with two complementary sampling methods (i.e. hydrological bottles and plankton net). As DYNAPROC 2 is a multidisciplinary program, our results could easily be analysed in the view of physico-chemical and biological parameters, including zooplankton diversity and abundance as well as microbial community structure and activities.

Our results highlighted the value of such data to complete and complement pigment analysis. Moreover the theoretical ecology feature, the knowledge of microphytoplankton short term abundance and diversity evolution supplied complementary information of biogeochemical, biological and ecological interests. It allowed a better understanding of the interactions between autotrophs and nutrients as well as trophic relations with zooplankton. Species indicators confirmed the arrival of coastal water and the possible long term warming of NW Mediterranean. We also found some very rare dinoflagellates species, which need genetic analysis to clarify their phylogeny.

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Table 1. List of microphytoplanktonic species encountered in hydrological bottle samples during DYNAPROC 2 cruise.

Species	Authorities
<i>Bacillariophyceae</i>	
<i>Achnanthes</i> sp. a	Bory
<i>Bacteriastrium delicatulum</i>	Cleve
<i>Bacteriastrium furcatum</i>	Shadbolt
<i>Cerataulina dentata</i>	Hasle in Hasle and Syvertsen
<i>Cerataulina pelagica</i>	(Cleve) Hendey
<i>Chaetoceros affinis</i>	Lauder
<i>Chaetoceros decipiens</i>	Cleve
<i>Chaetoceros dydimus</i>	Ehrenberg
<i>Chaetoceros laciniatus</i>	Shütt
<i>Chaetoceros peruvianus</i>	Brightwell
<i>Chaetoceros</i> sp. a	Ehrenberg
<i>Chaetoceros</i> sp. b	Ehrenberg
<i>Climacosphenia</i> sp. a	Ehrenberg
<i>Corethron criophilum</i>	Castracane
<i>Coscinodiscus</i> sp. a	Ehrenberg
<i>Coscinodiscus</i> sp. b	Ehrenberg
<i>Cylindrotheca closterium</i>	(Ehrenberg) Lewin and Reimann
<i>Dactyliosolen phuketensis</i>	(Sundström) Hasle
<i>Entomoneis</i> sp. a	Ehrenberg
<i>Gosslerella tropica</i>	Shütt
<i>Guinardia striata</i>	(Stolterfoth) Hasle
<i>Haslea wawrikae</i>	(Hustedt) Simonsen
<i>Hemiaulus hauckii</i>	Grunow
<i>Hemidiscus cuneiformis</i>	Wallich
<i>Lauderia annulata</i>	Cleve
<i>Leptocylindrus danicus</i>	Cleve
<i>Leptocylindrus minimus</i>	Gran
<i>Lyrella</i> sp. a	(Ehrenberg) Karajeva
<i>Navicula</i> sp. a	Bory
<i>Navicula</i> sp. b	Bory
<i>Navicula</i> sp. c	Bory
<i>Navicula</i> sp. d	Bory
<i>Nitzschia bicapitata</i>	Cleve
<i>Planktonielle sol</i>	(Wallich) Schütt
<i>Pleurosigma</i> sp. a	Smith
<i>Proboscia alata</i>	(Brightwell) Sundström
<i>Pseudo-nitzschia</i> sp. a (<i>Nitzschia delicatissima</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. b (<i>Nitzschia delicatissima</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. c (<i>Nitzschia seriata</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. d (<i>Nitzschia seriata</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. e (<i>Nitzschia seriata</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. f (<i>Nitzschia seriata</i> complex)	Peragallo
<i>Pseudo-nitzschia</i> sp. g (<i>Nitzschia seriata</i> complex)	Peragallo
<i>Rhizosolenia decipiens</i>	Sundström
<i>Rhizosolenia hebetata</i> f. <i>semispina</i>	(Hensen) Gran
<i>Synedra pulchella</i>	Kützing
<i>Synedra</i> sp. a	Ehrenberg
<i>Thalassionema frauenfeldii</i>	(Grunow) Hallegraef
<i>Thalassionema nitzschioides</i>	(Grunow) Mereschkowsky
<i>Thalassionema</i> sp. a	Grunow ex Mereschkowsky
<i>Thalassiosira</i> sp. a	Cleve
<i>Thalassiosira</i> sp. b	Cleve
<i>Thalassiosira</i> sp. c	Cleve
<i>Thalassiosira</i> sp. d	Cleve
<i>Toxarium undulatum</i>	Bailey

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Table 1. Continued.

Species	Authorities
<i>Dinophyceae</i>	
Armoured species	
<i>Alexandrium</i> sp. a	Halim
<i>Alexandrium</i> sp. b	Halim
<i>Amylax triachanta</i>	(Jørgensen) Sournia
<i>Ceratium declinatum</i>	(Karsten) Jørgensen
<i>Ceratium furca</i>	(Ehrenberg) Claparède and Lachmann
<i>Ceratium fuscum</i>	(Ehrenberg) Dujardin
<i>Ceratium hexacanthum</i>	Gourret
<i>Ceratium horridum</i>	(Cleve) Gran
<i>Ceratium limulus</i>	Gourret
<i>Ceratium lineatum</i>	(Ehrenberg) Cleve
<i>Ceratium pentagonum</i>	Gourret
<i>Ceratium platycorne</i>	Daday
<i>Ceratocoris</i> sp. a	Stein
<i>Dinophysis acuminata</i>	Claparède and Lachmann
<i>Dinophysis acuta</i>	Ehrenberg
<i>Dinophysis dens</i>	Pavillard
<i>Dinophysis hastata</i>	Stein
<i>Dinophysis pulchella</i>	(Lebour) Balech
<i>Dinophysis punctata</i>	Jørgensen
<i>Dinophysis sphaerica</i>	Stein
<i>Diplopsalis</i> sp. a	Bergh
<i>Goniaulax digilale</i>	(Fouchet) Kofoid
<i>Goniaulax polygramma</i>	Stein
<i>Goniaulax</i> sp. a	Diesing
<i>Goniaulax spinifera</i>	(Claparède and Lachmann) Diesing
<i>Heterocapsa rotundata</i>	(Lohmann) Hansen
<i>Heterodinium leiorhynchum</i>	(Murray and Whitting) Kofoid
<i>Heterodinium</i> sp. a	Kofoid
<i>Heterodinium</i> sp. b	Kofoid
<i>Heterodinium</i> sp. b	Kofoid
<i>Katodinium glaucum</i>	(Lebour) Loeblich III
<i>Lingulodinium polyedrum</i>	(Stein) Dodge
<i>Oblea</i> sp. a	Balech ex Loeblich and Loeblich
<i>Oxytoxum constrictum</i>	(Stein) Biltschli
<i>Oxytoxum laticeps</i>	Schiller
<i>Oxytoxum longiceps</i>	Schiller
<i>Oxytoxum milneri</i>	Murray and Whitting
<i>Oxytoxum reticulatum</i>	(Stein) Schütt
<i>Oxytoxum scolopax</i>	Stein
<i>Oxytoxum tessellatum</i>	Stein
<i>Pavillardinium</i> sp. a	Pavillard
<i>Phalacroma rapa</i>	Jørgensen
<i>Phalacroma rotundatum</i>	(Claparède and Lachmann) Kofoid and Michener
<i>Phalacroma</i> sp. a	Stein
<i>Podolampas palmipes</i>	Stein
<i>Podolampas spinifera</i>	Okamura
<i>Prorocentrum compressum</i>	(Bailey) Abé ex Dodge
<i>Prorocentrum gracile</i>	Schutt
<i>Prorocentrum scutelum</i>	Schroder
<i>Prorocentrum triestum</i>	Schiller
<i>Protoperidinium cassum</i>	Balech
<i>Protoperidinium divergens</i>	(Ehrenberg) Balech
<i>Protoperidinium ovatum</i>	Pouchet
<i>Protoperidinium pyriforme</i>	(Paulsen) Balech

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<i>Protoperidinium</i> sp. a	Bergh
<i>Schuetziella mitra</i>	(Schütt) Balech
<i>Scrippsiella cf. trochoidea</i>	(Stein) Loeblich III
<i>Spiraulax kofoidii</i>	Graham
Undetermined armoured <i>Dinoflagellate</i> sp. a	
Undetermined armoured <i>Dinoflagellate</i> sp. b	
Undetermined armoured <i>Dinoflagellate</i> sp. c	
Naked species	
<i>Amphidinium</i> sp. a	Claparède and Lachmann
<i>Amphidinium</i> sp. b	Claparède and Lachmann
<i>Asterodinium gracile</i>	Sournia
<i>Cochlodinium</i> sp. a	Schütt
<i>Dissodinium pseudolunula</i>	Swift
<i>Gymnodinium</i> sp. a	Stein
<i>Gymnodinium</i> sp. b	Stein
<i>Gymnodinium</i> sp. c	Stein
<i>Gymnodinium</i> sp. d	Stein
<i>Gymnodinium</i> sp. e	Stein
<i>Gymnodinium</i> sp. f	Stein
<i>Gymnodinium</i> sp. g	Stein
<i>Gymnodinium</i> sp. h	Stein
<i>Gymnodinium</i> sp. i	Stein
<i>Gymnodinium</i> sp. j	Stein
<i>Gymnodinium</i> sp. k	Stein
<i>Gymnodinium</i> sp. l	Stein
<i>Gyrodinium falcatum</i>	Kofoid and Swezy
<i>Gyrodinium</i> sp. a	Kofoid and Swezy
<i>Gyrodinium</i> sp. b	Kofoid and Swezy
<i>Gyrodinium</i> sp. c	Kofoid and Swezy
<i>Gyrodinium</i> sp. d	Kofoid and Swezy
<i>Gyrodinium</i> sp. e	Kofoid and Swezy
<i>Gyrodinium</i> sp. f	Kofoid and Swezy
<i>Gyrodinium</i> sp. g	Kofoid and Swezy
<i>Gyrodinium</i> sp. h	Kofoid and Swezy
<i>Gyrodinium</i> sp. i	Kofoid and Swezy
<i>Kofoidinium velelloides</i>	Pavillard
<i>Petalodinium porcelio</i>	Cachon and Cachon
<i>Polykrikos kofoidii</i>	Chatton
<i>Pronoctiluca pelagica</i>	Fabre-Domergue
<i>Scaphodinium mirabile</i>	Margalef
<i>Torodinium teredo</i>	(Pouchet) Kofoid and Swezy
<i>Dictyochophyceae</i>	
<i>Dictyocha fibula</i>	Ehrenberg
<i>Dictyocha speculum</i>	Ehrenberg

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Table 2. List of dinoflagellates genera and *Ceratium* taxa encountered in net samples during DYNAPROC 2 cruise.

Dinoflagellates	Genus <i>Ceratium</i>
<i>Acanthogonyaulax</i> (Kofoid) Graham	<i>C. arietinum</i> Cleve var. <i>arietinum</i>
<i>Amphidiniopsis</i> Woloszynska	<i>C. arietinum</i> var. <i>gracilentum</i> (Jørgensen) Sournia
<i>Amphisolenia</i> Stein	<i>C. arietinum</i> Cleve "arietinum-gracilentum"
<i>Centrodinium</i> Kofoid	<i>C. azoricum</i> Cleve
<i>Ceratium</i> Schrank	<i>C. candelabrum</i> (Ehrenberg) Stein var. <i>candelabrum</i>
<i>Ceratocorys</i> Stein	<i>C. candelabrum</i> var. <i>depressum</i> (Pouchet) Jørgensen
<i>Corythodinium</i> Loeblich Jr. and Loeblich III	<i>C. candelabrum</i> (Ehrenberg) Stein "candelabrum-depressum"
<i>Dinophysis</i> Ehrenberg	<i>C. candelabrum</i> (Ehrenberg) Stein "candelabrum-depressum"
<i>Dissodinium</i> Klebs in Pascher	<i>C. candelabrum</i> (Ehrenberg) Stein "depressum>candelabrum"
<i>Goniodoma</i> Stein	<i>C. carriense</i> Gourret var. <i>carriense</i>
<i>Gonyaulax</i> Diesing	<i>C. carriense</i> var. <i>volans</i> (Cleve) Jørgensen
<i>Heterocapsa</i> Stein	<i>C. carriense</i> Gourret "carriense-volans"
<i>Heterodinium</i> Kofoid	<i>C. concilians</i> Jørgensen
<i>Kofoidinium</i> Pavillard	<i>C. contrarium</i> (Gourret) Pavillard
<i>Micracanthodinium</i> Deflandre	<i>C. declinatum</i> f. <i>brachiatum</i> Jørgensen
<i>Noctiluca</i> Surryay	<i>C. declinatum</i> f. <i>normale</i> Jørgensen
<i>Ornithocercus</i> Stein	<i>C. declinatum</i> var. <i>majus</i> Jørgensen
<i>Oxytoxum</i> Stein	<i>C. eucarvatum</i> Jørgensen
<i>Palaeophalacroma</i> Schiller	<i>C. extensum</i> (Gourret) Cleve
<i>Phalacroma</i> Stein	<i>C. falcatiforme</i> Jørgensen
<i>Podolampas</i> Stein	<i>C. falcatum</i> (Kofoid) Jørgensen
<i>Porocentrum</i> Ehrenberg	<i>C. furca</i> var. <i>eugrannum</i> (Ehrenberg) Schiller
<i>Protoperidinium</i> Bergh	<i>C. furca</i> (Ehrenberg) Clarapède and Lachmann "furca-eugrannum"
<i>Pyrophacus</i> Stein	<i>C. furca</i> (Ehrenberg) Clarapède and Lachmann "furca-eugrannum"
<i>Pyrocystis</i> Murray ex Haeckel	<i>C. furca</i> (Ehrenberg) Clarapède and Lachmann "eugrannum-furca"
<i>Spatulodinium</i> Cachon and Cachon	<i>C. fusus</i> (Ehrenberg) Dujardin
<i>Spiraulax</i> Kofoid	<i>C. gibberum</i> var. <i>dispar</i> (Pouchet) Sournia
No genera: 27	<i>C. gravidum</i> Gourret
	<i>C. hexacanthum</i> f. <i>hiemale</i> Pavillard
	<i>C. hexacanthum</i> Gourret var. <i>hexacanthum</i>
	<i>C. horridum</i> var. <i>buceros</i> (Zacharias) Sournia
	<i>C. horridum</i> (Cleve) Gran "horridum-buceros"
	<i>C. horridum</i> (Cleve) Gran "buceros-horridum"
	<i>C. inflatum</i> (Kofoid) Jørgensen
	<i>C. limulus</i> (Gourret ex Pouchet) Gourret
	<i>C. longirostrum</i> Gourret
	<i>C. longissimum</i> (Schröder) Kofoid
	<i>C. macroceros</i> (Ehrenberg) Vanhöffen var. <i>macroceros</i>
	<i>C. macroceros</i> (Ehrenberg) Vanhöffen "macroceros-gallicum"
	<i>C. massiliense</i> f. <i>armatum</i> (Karsten) Jørgensen
	<i>C. massiliense</i> (Gourret) Jørgensen var. <i>massiliense</i>
	<i>C. massiliense</i> var. <i>protuberans</i> (Karsten) Jørgensen
	<i>C. minutum</i> Jørgensen
	<i>C. paradoxides</i> Cleve
	<i>C. pavillardii</i> Jørgensen
	<i>C. pentagonum</i> f. <i>turgidum</i> (Jørgensen) Jørgensen
	<i>C. pentagonum</i> var. <i>tenerum</i> Jørgensen
	<i>C. pentagonum</i> Gourret "robustum-tenerum"
	<i>C. pentagonum</i> Gourret "robustum-tenerum"
	<i>C. platycorne</i> Daday var. <i>platycorne</i>
	<i>C. platycorne</i> var. <i>compressum</i> (Gran) Jørgensen
	<i>C. platycorne</i> Daday "platycorne-compressum"
	<i>C. platycorne</i> Daday "compressum>platycorne"
	<i>C. ranipes</i> Cleve
	<i>C. schroeteri</i> Schröder
	<i>C. setaceum</i> Jørgensen
	<i>C. symmetricum</i> Pavillard var. <i>symmetricum</i>
	<i>C. symmetricum</i> var. <i>coarctatum</i> (Pavillard) Graham and Bronikovsky
	<i>C. symmetricum</i> var. <i>orthoceras</i> (Jørgensen) Graham and Bronikovsky
	<i>C. trichoceros</i> (Ehrenberg) Kofoid
	<i>C. tripos</i> var. <i>atlanticum</i> (Ostenfeld) Paulsen
	<i>C. tripos</i> var. <i>pulchellum</i> (Schröder) Lopez
	<i>C. tripos</i> (Müller) Nitzsch "atlanticum-pulchellum"
	<i>C. tripos</i> (Müller) Nitzsch "atlanticum-pulchellum"
	No species: 34
	No infraspecific taxa: 64

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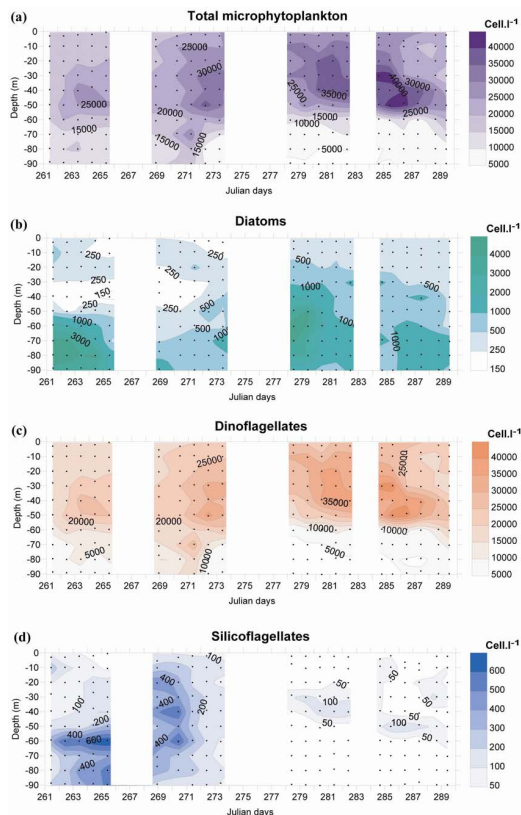


Fig. 1. Abundance of microphytoplankton during DYNAPROC 2 cruise, from hydrological bottle sampling **(a)** Total microphytoplankton, **(b)** Bacillariophyceae, **(c)** Dinophyceae, **(d)** Dityochophyceae. Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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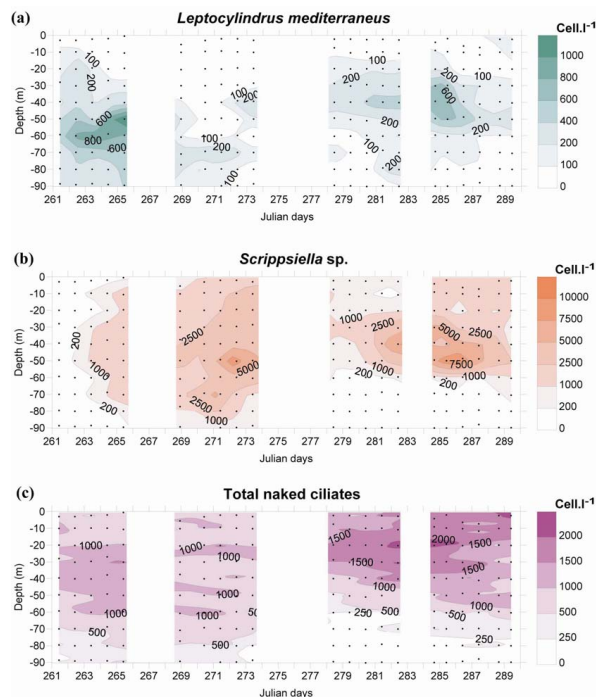


Fig. 2. Abundance of ecologically important planktonic organisms during DYNAPROC 2 cruise, from hydrological bottle sampling **(a)** The diatom *Leptocylindrus mediterraneus*, **(b)** The dinoflagellate *Scrippsiella* sp., **(c)** Naked ciliates. Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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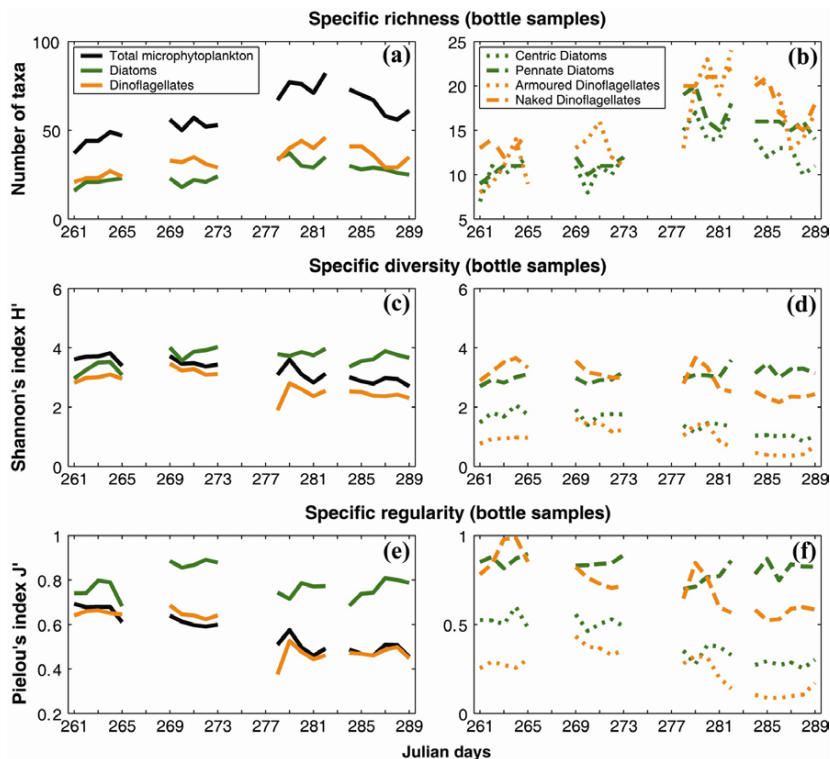


Fig. 3. Biodiversity of microphytoplankton during DYNAPROC 2 cruise, from hydrological bottle sampling. **(a)** Species richness of total microphytoplankton, **(b)** Species richness of pennates/centric diatoms and armoured/naked dinoflagellates, **(c)** Species diversity of total microphytoplankton, **(d)** Species diversity of pennates/centric diatoms and armoured/naked dinoflagellates, **(e)** Species regularity of total microphytoplankton, **(f)** Species regularity of pennates/centric diatoms and armoured/naked dinoflagellates. Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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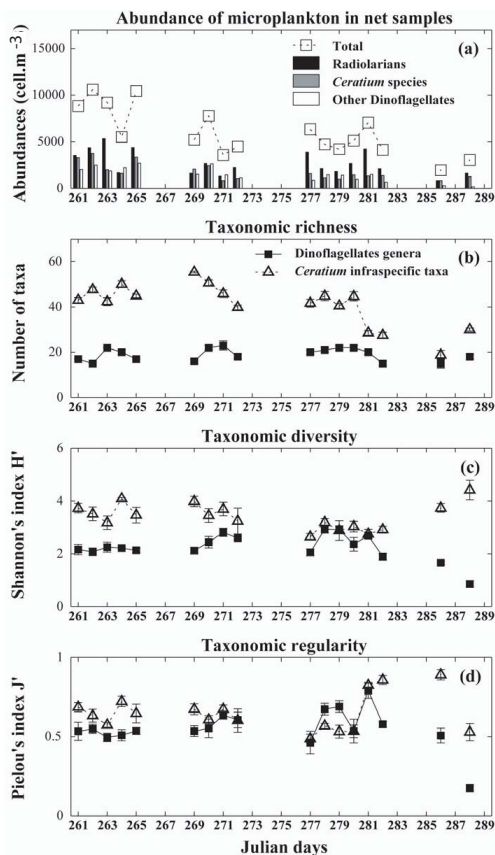


Fig. 4. Evolution of dinoflagellates genera and *Ceratium* taxa during DYNAPROC 2 cruise, from net sampling **(a)** Abundances, **(b)** Taxonomic richness, **(c)** Taxonomic diversity, **(d)** Taxonomic regularity. Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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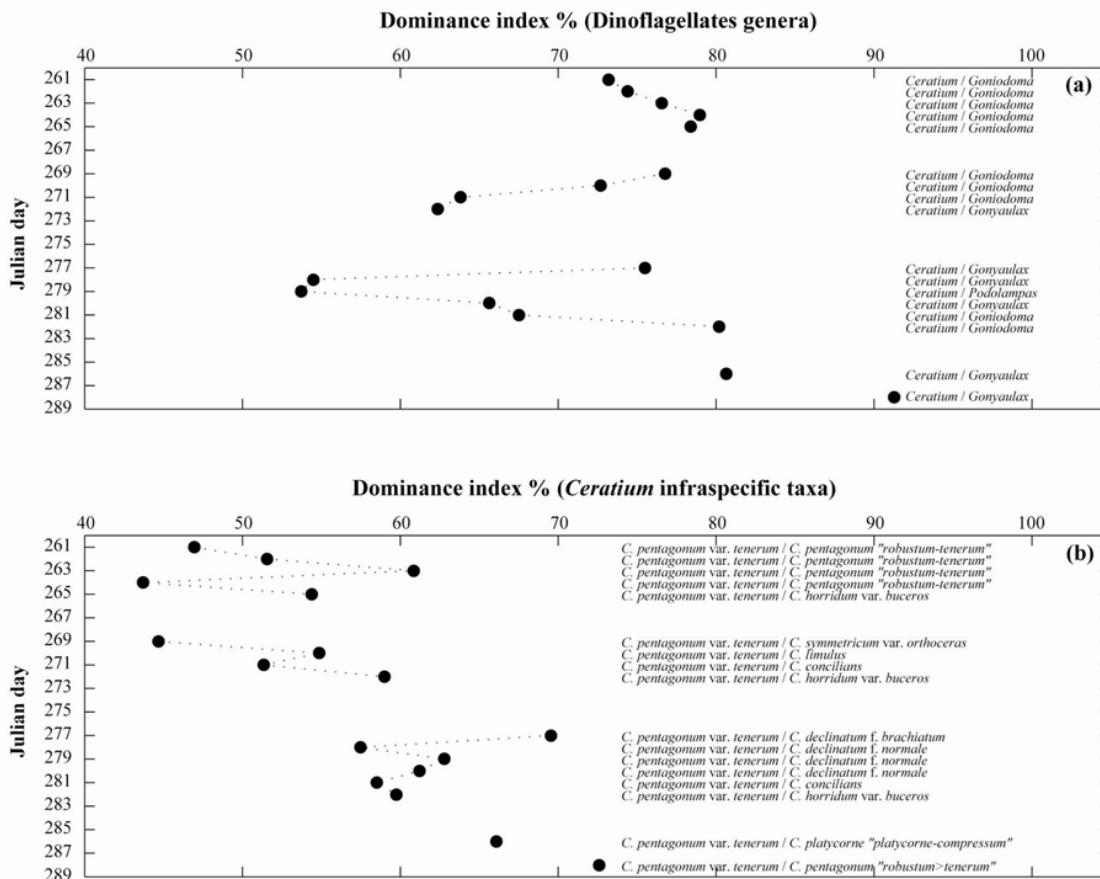


Fig. 5. Evolution of the dominance index in net samples. **(a)** Dinoflagellates genera dominance index, **(b)** *Ceratium* taxa dominance index. Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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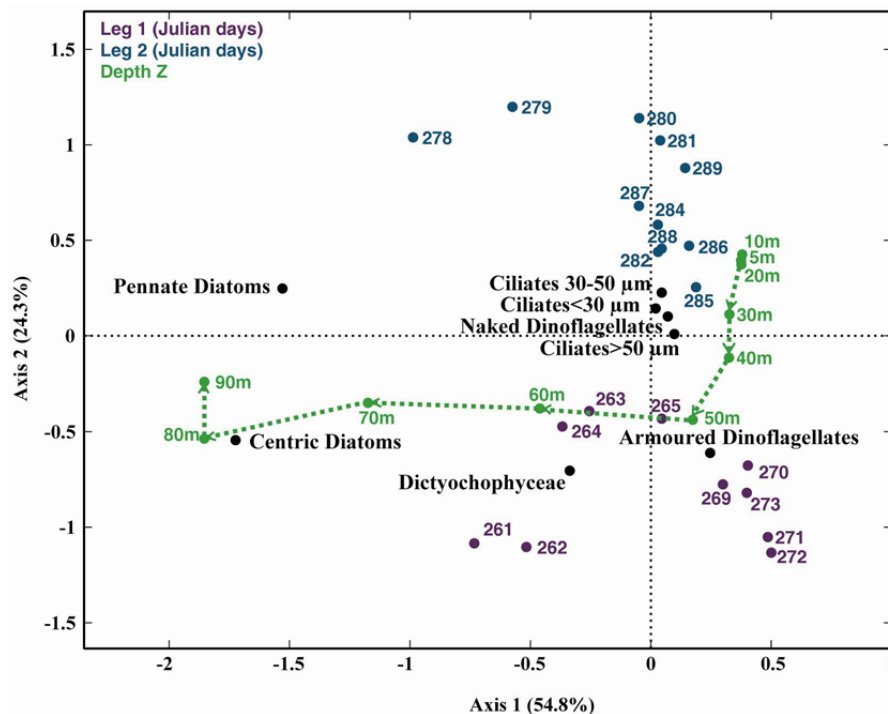


Fig. 6. Spatial and temporal dynamics of the microplankton from hydrological bottle sampling during DYNAPROC 2 cruise. The Correspondence Analysis was applied on the main microplanktonic groups. Sampling depths and Julian days were added as illustrative variables (the coordinates were calculated as the average of samples of the same days or of the same depth). Agreement with Julian Days is 17 September = JD 261; 25 September = JD 269; 3 October = JD 277 and 11 October = JD 285.

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