



## Short-term changes in the concentration and vertical distribution of chlorophyll and in the structure of the microplankton assemblage due to a storm

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**Abstract.** Short-term changes in the concentration and vertical distribution of chlorophyll and in the structure of the microplankton assemblage due to a storm. The vertical distribution of chlorophyll-a (chl) and the composition of the microplankton assemblage were followed during a 20 d period in a shallow environment (Coliumo Bay, ca. 10 m deep) to explore their response to wind forcing. During the first 9 days fair weather and a daily S-SW wind pattern of moderate intensity dominated; on the tenth day wind changed to N direction while velocity increased (storm period) effectively mixing the water column. The microplankton assemblage was strongly dominated by diatoms during the whole period, and as expected chl stratification negatively correlated with wind speed. Before the storm chl concentration was medium to low with fairly homogeneous vertical distribution. During and after the storm a rapid increase in chl level occurred due to resuspension of sedimented matter (during storm) and active growth of a few diatom species (after storm). Chlorophyll level and its stratification peaked right after the storm (ca. 48 hs), which constituted a partly unexpected finding. Present results suggest that in shallow environments like Coliumo Bay, punctual events of severe mixing of the water column may have delayed positive effects on phytoplankton abundance and vertical distribution.

**Key words:** Phytoplankton, biomass, stratification, wind, Bahía Coliumo, Chile.

**Resúmen.** Cambios de corto plazo en la distribución vertical y concentración de clorofila y en la estructura del conjunto microplanctónico causados por una tormenta. Se monitoreó la distribución vertical y la composición taxonómica del microplancton por un período de 20 días en un ambiente somero (Bahía Coliumo, ca. 10 m de profundidad) para evaluar el efecto del viento sobre la variabilidad de la biomasa fitoplanctónica y su distribución vertical. Durante los primeros 9 días de buen tiempo el viento presentó un patrón regular diario con intensidades moderadas y dirección S-SW; durante el décimo día cambió a dirección N e incrementó su intensidad (tormenta), provocando una mezcla intensa de la columna de agua. El microplancton estuvo dominado por diatomeas durante todo el período, y como era esperable la estratificación de la clorofila se correlacionó negativamente con la velocidad del viento. Previo a la tormenta la clorofila presentó valores moderados y bajos índices de estratificación. Durante y luego de la tormenta los niveles de clorofila incrementaron rápidamente debido a procesos de resuspensión (durante la tormenta) y crecimiento de una pocas especies de diatomeas (después de la tormenta). Parcialmente contra lo esperado el máximo de clorofila y de su estratificación ocurrieron en seguida después de la tormenta (ca. 48 hs). Estos resultados sugieren que en ambientes someros como Bahía Coliumo, eventos puntuales de mezcla intensa podrían tener efectos positivos retardados en la abundancia y distribución vertical del fitoplancton.

**Palavras Chave:** Fitoplancton, biomasa, estratificación, viento, Bahía Coliumo, Chile.

### Introduction

The importance of vertical heterogeneity in the distribution of marine phytoplankton has long been recognized (Herdman 1923, Riley *et al.* 1949, Hasle

1950, Steele & Yentsch 1960, fide Cullen & Eppley 1981). The mean density of food in the surface-mixing layer is frequently below that required to meet metabolic demands for organisms like

copepods and fish larvae (Lasker 1975, Mullin & Brooks 1976, Ware *et al.* 1981, Mullin *et al.* 1985, MacKenzie *et al.* 1990, Mullin 1993). Zooplankton may escape starvation by exploiting zones of high food concentration like fronts or subsurface layers of high chlorophyll concentration (Subsurface Chlorophyll Maxima, SCM). Laboratory studies showed that a variety of zooplankters can effectively locate and utilize thin layers of elevated food concentration, leading to higher ingestion and secondary production rates (Tiselius 1992, Saiz *et al.* 1993, Ignoffo *et al.* 2005). Thus, processes affecting phytoplankton biomass levels and the formation and persistence of food-rich layers are presumed particularly important for energy transfers in pelagic food webs.

The presence of SCM can result from physical (formation of a sharp pycnocline, light penetration, nutrient diffusion across the pycnocline, vertical shear at fronts), biological (functional response to irradiance, nutrient absorption kinetics, community succession) and behavioural processes (vertical migration) (Cullen & Eppley 1981, Iriarte & Bernal 1990, Castro *et al.* 1991, Bjørnsen & Nielsen 1991, Franks 1992, Djurfeldt 1994, Franks & Walstad 1997).

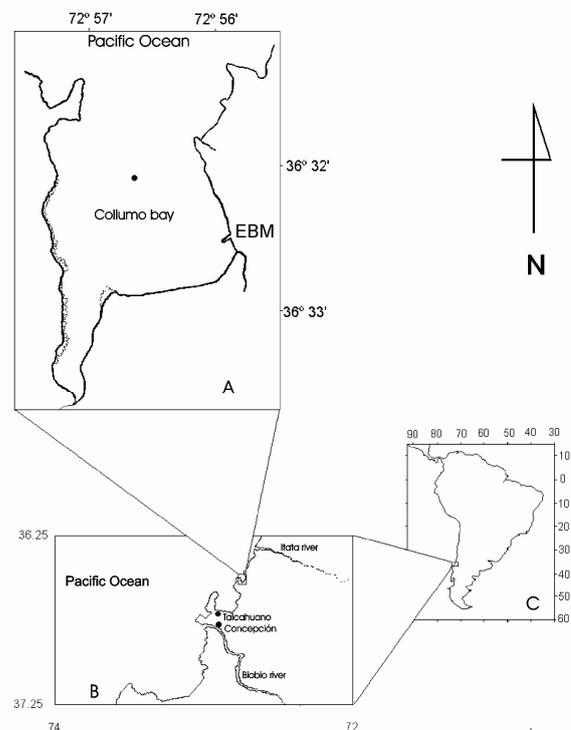
The vertical distribution of microplankton is also greatly affected by wind mixing of surface layers associated to storm events (Haury *et al.* 1990). These events may erode SCM and affect the feeding environment and survival of larval fish (Lasker 1975). However, in situ and experimental evidence also suggest that turbulent mixing may favour pelagic productivity; the alternation of vertical mixing and stratification of the water column leads to surface water fertilization and enhanced primary production (mainly by diatoms), which can be transferred up the food chain to heterotrophic consumers (Kjørboe 1993, Mann 1993, Mann & Lazier 2006).

As part of a broader study at Coliumo Bay (South-Central Chile), a field experiment was designed to assess the short-term variability in the biomass and vertical distribution of the phytoplankton in response to wind forcing. By the end of the sampling period a storm hit the study site enabling to explore the effect of extreme conditions on the microplankton assemblage (denoting here all organisms in the size range of 5 – 200  $\mu\text{m}$ , see Methods) beyond the normal wind regime. Based on observations before, during and after that storm event I here address the question of how overall phytoplankton biomass (as chlorophyll-a) and its vertical distribution, and the microplankton assemblage structure responded to a storm event at a relatively shallow coastal ecosystem.

## Material and Methods

### Study site

Coliumo Bay is a small embayment in Central-South Chile ( $36^{\circ}32' \text{ S}$ ,  $72^{\circ}57' \text{ W}$ , Fig.1) that opens to the Pacific Ocean with its main axis (ca. 3 km) oriented North-South. Coliumo River flows into the head of the bay and dilutes marine waters to some extent (Llancamil 1982). Water depth is  $< 5 \text{ m}$  along its perimeter up to 400 m from the shoreline, reaching a maximum of ca. 20 m near the mouth. The organic matter content of the sediment is positively correlated with depth and about 20% of the bottom has  $> 10\%$  organic matter (Soto 1997, Rivas 1997). Water is moderately transparent (light attenuation coefficient  $K_d$  ca. 0.339; Calliari & Antezana 2001) and between 3 and 4% of incident radiation reaches 10 m depth. Predominant winds associated to the South Pacific Anticyclonic gyre blow from S-SW during periods of fair weather (Saavedra & Foppiano 1992), but high topography adjacent to the bay (chilean coastal mountain range) largely protects it from such winds. However, strong winds from the N usually occur during wintertime associated to heavy rains (Saavedra & Foppiano op. cit.); under such conditions the bay is fully exposed to the wind and to the swell from open ocean.



**Figure 1.** Map of Coliumo Bay (A) in a regional (B) and general scale (C). In A, black dot inside the bay indicates the position of the sampling station; EBM stands for Marine Biological Station (UdeC), where the wind sensors were placed.

Diatoms dominate numerically the phytoplankton and *Skeletonema* Greville, 1865 is the most representative genus (González 1982). Phytoplankton biomass is relatively homogeneously distributed in the water column, with a tendency to higher values between 2 and 6 m depth (Augsburger 1981, Calliari & Antezana 2001). Zooplankton is represented by few copepod species like *Acartia tonsa* Dana, 1848, *Paracalanus parvus* Claus, 1863, *Centropages brachiatus*, Dana 1849, *Oithona* Baird, 1843, *Oncaea* Philippi, 1843, *Calanoides patagoniensis* Brady, 1883, and *Calanus chilensis* Brodsky, 1959 (Peterson & Bellantoni 1987, Peterson *et al.* 1988, Calliari 1999).

### Data collection

Sampling was performed near the centre of Coliumo Bay (depth ca. 10 m) daily between April 11<sup>th</sup> and 20<sup>th</sup>, 1997 (pre-storm period), and subsequently on April 22<sup>nd</sup> (during the storm), 26<sup>th</sup> and 30<sup>th</sup> (post-storm period). On each occasion samples for chlorophyll-a (chl) concentration were taken with a Niskin bottle at 1-meter depth intervals from surface to 9 m (except on April 22<sup>nd</sup> when samples only from 0 and 9 m could be taken). The concentration of chl and phaeopigments was estimated following Holm-Hansen *et al.* (1965) from duplicate 50 ml sub samples filtered on GF/F (0.7 µm). Pigments were extracted in 90% acetone at 4°C and in the dark for 24 h, and the fluorescence of the extract was measured before and after acidification in a Turner Designs 10-005 R fluorometer. Taxonomic analysis and quantification of microplankton was based on 10 or 50 ml aliquots from one formol-preserved daily sample (4 m depth) settled for 24 h (or >48 h for 50 ml chambers) in Utermöhl chambers and examined under an inverted microscope at 200-400 X (Leitz, DM-IL). Minimum individual size of organisms considered in microscopic analyses was ca. 5 µm; thus this dataset includes microplanktonic (20-200 µm) and part of the nanoplanktonic (2-20 µm) size range. Identification was performed to the lowest taxon possible using appropriate references (Rivera & Gebauer 1989, Tomas 1997); nomenclature follows Tomas (1997) and Guiry & Guiry (2006).

Wind direction and intensity was recorded at 1-minute interval with a Heath Kit 5000C weather station placed on the bay shoreline at Dichato Marine Laboratory (Universidad de Concepción). That record was interrupted on April 23<sup>rd</sup> owing to severe damages caused by the storm to the wind sensors. Wind for the period April 23<sup>rd</sup> to April 30<sup>th</sup> was estimated from data recorded at Bella Vista Meteorological Station (36°47'S, 73°07'W) using transfer functions specifically developed to estimate

the wind velocity at Coliumo Bay from wind data recorded at Bella Vista Station; such functions yield best predictions for the N-S velocity component ( $r = 0.93$ ) (Calliari & Alfaro 1997) which is the most relevant in the present case (see results, fig. 2). Ancillary temperature and salinity data for the pre-storm period were obtained from daily CTD profiles (Sensordata 202).

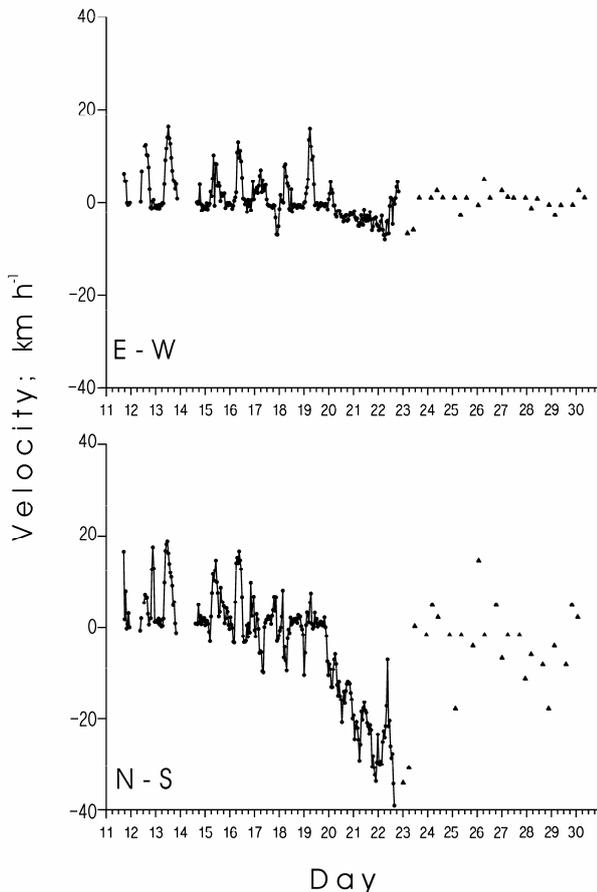
### Data analysis

A stratification index ( $S$ ,  $m^{-1}$ , equation 1, Cullen & Eppley 1981) for each daily chl profile was calculated as the maximum value of the chl gradient with respect to depth (term in the numerator in equation 1) and normalized by the average chl concentration on that day (denominator):

$$S = \frac{\text{Max}\left(\frac{\delta\text{Chl}}{\delta Z}\right)}{\frac{\sum_0^9 \text{Chl}}{n}}$$

where  $Z$  represents depth and  $n$  stands for the number of depth intervals (10).

The association between  $S$  and wind velocity was assessed by Spearman correlation analysis. The effect of the storm on chl level and microplankton cell concentration was analysed with the Mann-Whitney U test (pre-storm and post-storm conditions). The effect of the storm on the microplankton community composition was assessed by complementary non-parametric multivariate techniques. A hierarchical cluster analysis with group average linkage was employed to group successive sampling dates; this analysis was based on a Bray-Curtis similarity matrix calculated from squared root-transformed species abundance data (Clarke & Warwick 1994), and clusters were defined using a similarity threshold reference value equal to the average of the Bray-Curtis matrix (Arancibia 1988; Rodríguez-Graña & Castro 2003). Differences in the taxonomic composition and species abundance of the microplankton due to the storm were explored by Analysis of Similarity (ANOSIM), a permutation-based test between *a priori* defined groups (treatments) where generated R statistic values represent the distance scaled to the range 0 - 1 (0 indicating no difference among groups and 1 indicating that all samples are more similar within groups than to any sample from any other group, Clarke & Gorley 2001). A Similarity Percent analysis (SIMPER) was used to identify those taxa that presented largest variation between factor levels in ANOSIM. All non-parametric multivariate analyses were performed using PRIMER v5.2.



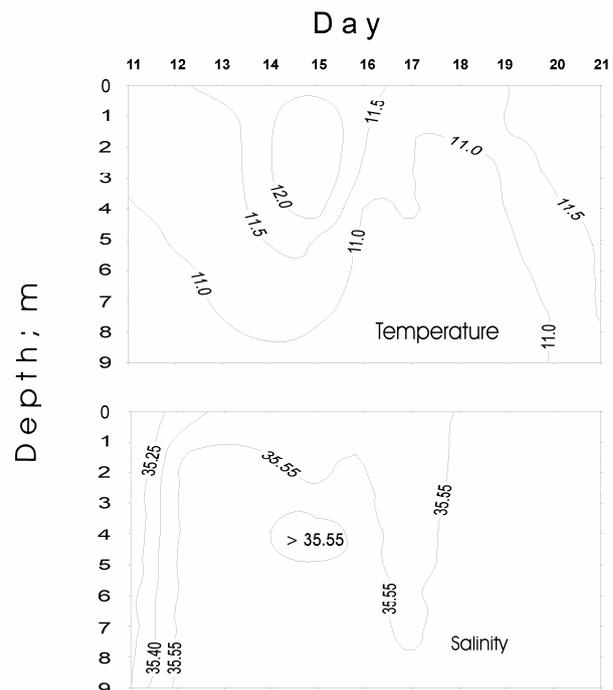
**Figure 2.** Time series of wind velocity recorded at Coliumo Bay during the study period. E-W denotes the East-West (above) and N-S indicates the North-South (below) components of the horizontal wind vector. *In situ* record ends on April 23<sup>rd</sup> (black dots) due to technical problems. From April 23<sup>rd</sup> to 30<sup>th</sup> values were estimated according to Calliari & Alfaro (1997) (triangles).

## Results

During the first 9 d wind from the S prevailed, following a daily cycle of low velocities in the morning, highest during midday and afternoon (up to ca. 19 km h<sup>-1</sup>), decreasing during evening and night to ca. 0 km h<sup>-1</sup> (Fig. 2). On April 20<sup>th</sup> that pattern changed toward N winds with sustained speeds ca 40 km h<sup>-1</sup> and gusts up to 82 km h<sup>-1</sup> (storm event). After April 24<sup>th</sup> wind pattern returned to before-storm conditions until the end of the study period. Direct observation of wave length and water colour inside the Bay during the storm indicated a thoroughly mixed water column and strong resuspension of bottom sediments. Temperature and salinity profiles evidenced a fairly mixed water column, with a weak temporary stratification between April 13<sup>th</sup> and 15<sup>th</sup> (Fig.3)

Moderate chl levels between ca. 1 (17-18<sup>th</sup> April) and 5 µg L<sup>-1</sup> (14<sup>th</sup> April) characterized the pre-storm period (Fig. 4). During the storm (22<sup>nd</sup> April) chl raised to ca. 18 µg L<sup>-1</sup>, and

reached a maximum of 23 µg L<sup>-1</sup> following the storm (26<sup>th</sup> April), remaining at an elevated concentration until the end of the study; chlorophyll levels after the storm were significantly higher compared to before storm (Mann-Whitney U = 0, n=106, p<< 0.01), and so was cell concentration (U = 0, n= 13, p< 0.05). Phaeopigment levels were low during the pre-storm period (range: <0.1 to 0.7 µg L<sup>-1</sup>) and increased by ca. one order of magnitude during the storm (5.5 µg L<sup>-1</sup>); however, on the first sampling day after the storm phaeopigments had disappeared from the water column except near the bottom at 8 and 9 m depth, and remained at very low values until the end of the study. Stratification index *S* correlated negatively with wind speed averaged over 12 h before sampling when the whole period was considered (Spearman r = -0.57, n = 13, p < 0.05, Fig. 5A), but strongly peaked immediately after the storm (on the 26<sup>th</sup> April, Fig. 5B). Chlorophyll stratification on 26<sup>th</sup> April seemed to diverge from the general correlation trend of *S* vs wind intensity; if that date is not considered the correlation becomes highly significant (Spearman r = -0.68, n = 12, p = 0.01).



**Figure 3.** Temperature (°C) and salinity (practical units) measured at Coliumo Bay during the pre-storm period.

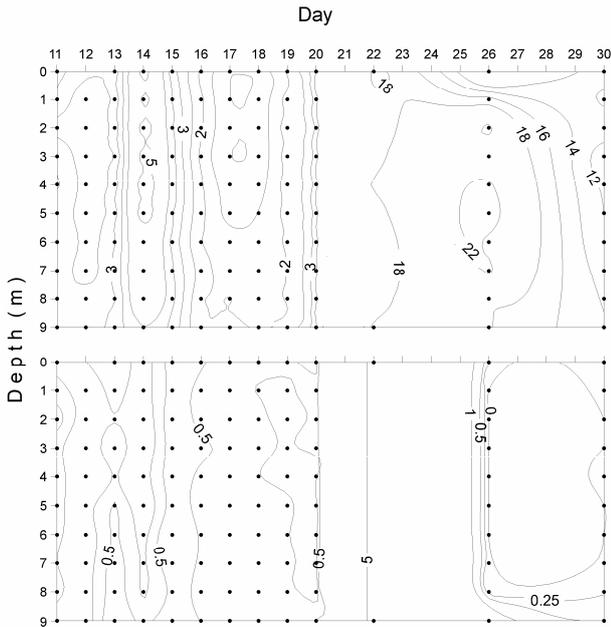
The microplankton assemblage was strongly dominated by diatoms and dinoflagellates to a lesser extent during the whole study period (Table 1). However, before storm samples on one side, and samples taken during and after the storm on the other side were much more similar within each group and formed clearly separated clusters (Fig. 6).

**Table I.** Microplankton abundance (cells L<sup>-1</sup>) in Coliumo Bay before (n=10), during (n=1) and after (n=2) the storm. Std = standard deviation. n.i. = non identified.

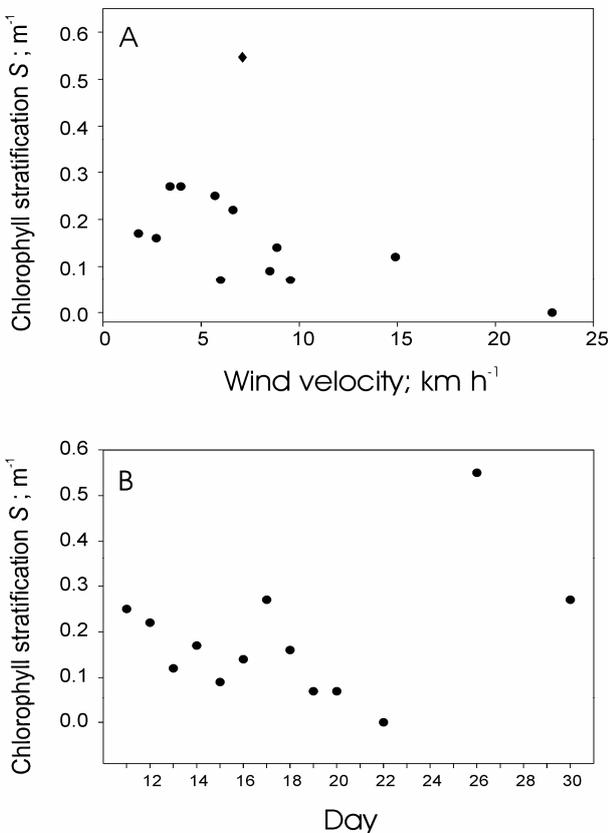
	Before	Std	During	After	Std
<b>Diatoms</b>					
<i>Thalassiosira</i> sp	2963	3195	8435	6397	3131
<i>Chaetoceros</i> sp	14404	18883	4569	5320	1609
<i>Skeletonema</i> sp	925	2789	1406	0	0
<i>Actinoptychus</i> sp	10	21	703	154	217
<i>Amphora</i> sp	0	0	1230	0	0
<i>Asterionella</i> sp	0	0	0	923	1305
<i>Biddulphia</i> sp	5	16	0	0	0
<i>Cymbella</i> sp	0	0	246	0	0
<i>Cocconeis</i> sp	0	0	351	0	0
<i>Coscinodiscus</i> sp	69	53	0	0	0
<i>Cylindrotheca</i> sp	359	915	1757	0	0
<i>Diploneis</i> sp	0	0	0	0	0
<i>Detonula schröderella</i>	2367	2714	0	0	0
<i>Eucampia</i> sp	527	725	784465	1317366	418082
<i>Grammatophora</i> sp	79	107	17925	123	174
<i>Licmophora</i> sp	5	16	351	0	0
<i>Leptocylindrus</i> sp	0	0	6326	5874	43
<i>Navicula</i> sp	69	152	4218	1046	609
<i>Paralia</i> sp	0	0	6326	0	0
<i>Pinnularia</i> sp	0	0	1054	0	0
<i>Pleurosigma</i> sp	5	16	492	369	174
<i>Pseudonitzschia</i> sp	910	1937	3163	1968	2436
<i>Rhizosolenia</i> sp	5	16	1406	154	217
<i>Thalassionema</i> sp	49	156	0	0	0
<b>Dinoflagellates</b>					
Dinoflagellate n.i.	344	429	492	1845	174
<i>Dinophysis</i> sp	5	16	0	984	696
<i>Diplopsalis</i> sp	276	436	492	1722	696
<i>Gonyaulax</i> sp	20	34	984	369	174
<i>Peridinium sympholis</i>	15	33	0	0	0
<i>Protoperdinium. aspidiotum</i>	20	34	0	123	174
<i>P. conicum</i>	20	34	0	738	1044
<i>P. grenlandicum</i>	192	301	0	738	348
<i>P. aff. leonis</i>	0	0	0	0	0
<i>P. parapyriforme</i>	10	21	0	246	0
<i>P. steinii</i>	15	24	0	0	0
<i>P. thorianum</i>	5	16	0	0	0
<i>Scrippsiella trochoidea</i>	118	237	0	0	0
<b>Ciliates</b>					
Tintinnids	202	182	2214	1845	174
	335	271	2214	2337	174

Consequently, for the ANOSIM observations were grouped into factor levels Before (on one side), and During and After storm (on the other side). ANOSIM confirmed differences in the taxonomic composition due to the storm (Global R= 0.99 on 286 possible permutations,  $p < 0.05$ ) with intragroup

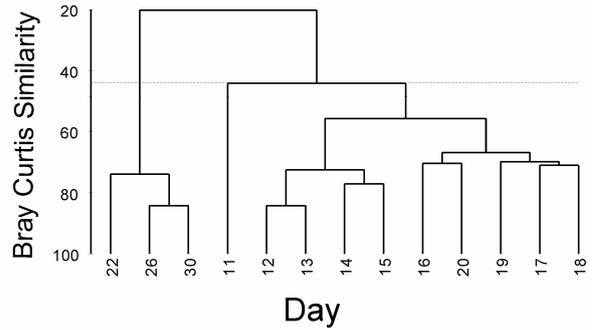
average similarities of 58 and 77% (before and after storm, respectively) and intergroup dissimilarity of 80% (SIMPER); taxa that contributed most heavily to dissimilarity between groups were *Eucampia* sp. (47.7%), *Leptocylindrus* sp. (3.6%) and *Chaetoceros* sp. (2.3%).



**Figure 4.** Chlorophyll-a (A) and phaeopigments (B) concentrations ( $\mu\text{g L}^{-1}$ ) measured at Coliumo Bay for the period 11<sup>th</sup> – 30<sup>th</sup> April 1997. Dots indicate sampling dates and depths. On April 22<sup>nd</sup> (storm) only surface and bottom samples were taken. Note that interpolation during the storm and after-storm period was kept to a minimum since no information is available on pigment change patterns on a daily scale.



**Figure 5.** A.- Plot of chlorophyll stratification index  $S$  vs. wind velocity in Bahia Coliumo for the period 11 – 30 April 1997. B - Time series of chlorophyll stratification index  $S$  for the same period.  $\blacklozenge$  =  $S$  estimated 48 hs after storm (April 26<sup>th</sup>), for details see text.



**Figure 6.** Cluster analysis of microplankton samples (dates) from Coliumo Bay between 11 and 30 April 1997 (one sample per day). Analysis was based on a Bray-Curtis similarity matrix of taxa abundance. Dotted line indicates reference value used to separate groups (average of Bray-Curtis similarity matrix).

**Discussion**

Wind intensity had detrimental direct effects on chl stratification as indicated by negative correlation between both variables. But a short period of N wind with sustained velocities up to 40 km h<sup>-1</sup> had delayed positive effects that favoured phytoplankton blooming (*sensu* Sverdrup 1957) and stratification. Strong stratification was a short lived phenomenon (< 4 d), but post-storm biomass levels roughly 10 – 20  $\mu\text{g L}^{-1}$  constitute remarkably high values for this site (Augsburger 1981, Calliari 1999) and lasted for at least twice as long (22 – 30 April). It is unlikely that the observed chl increase resulted from an intrusion of high chl waters from adjacent areas. No estimates outside Coliumo Bay are available for the same period, but chl levels outside the bay are generally much lower than those reported here for the post-storm period (Augsburger 1981, Peterson & Bellantoni 1987, Peterson *et al.* 1988).

It could be argued whether chl increase during storm and post-storm periods reflected real phytoplankton growth, or mainly resulted from turbulence-induced resuspension of sedimented, senescent cells. Phaeopigments could be of use as tracers of resuspended, partially decomposed phytoplankton-derived matter; they indeed increased sharply after April 20<sup>th</sup>, indicating strong resuspension that may also explain the quick chl increase between April 20<sup>th</sup> and 23<sup>rd</sup> (storm period). However, active growth likely contributed to the biomass peak following the storm as indicated by continued increasing trend of chl to maximum levels after the storm, while phaeopigments disappeared from the water column (presumably due to sinking). The fact that highest chl concentration and its maximum stratification occurred simultaneously further suggests that both processes were mediated by algal growth rather than by turbulent mixing.

Changes in the microplankton assemblage also support that biomass enhancement was mostly mediated by resuspension of benthic micro algae (during the storm) and by active growth (after the storm). The diatoms *Amphora* sp., *Cymbella* sp., *Cocconeis* sp., *Paralia* sp. and *Pinnularia* sp. only occurred during the storm. *Paralia* is a coastal brackish genus frequently found in the sediments and water column at shallow coastal systems (Witkowski *et al.* 2000). *Cymbella*, *Amphora* and *Pinnularia* are mostly freshwater/brackish epibenthic diatoms which may be resuspended during highly energetic conditions (Krammer 2000, 2002, Krammer & Lange-Bertalot 1988, 1991a, 1991b, Metzeltin & García-Rodríguez 2004), so their presence in the plankton strongly suggests resuspension processes contributing to bulk algal biomass in the water column during the storm. Several taxa increased their numbers after the storm, but *Eucampia* sp. showed the most remarkable shift from  $10^2$  cells  $L^{-1}$  to  $10^6$  cells  $L^{-1}$  over a 10 d period. Also, cell numbers after the storm considering all taxa were higher than before storm numbers by a factor  $> 50$ , a further indicator that algal growth was an important factor contributing to the observed biomass increase. Among the least abundant groups is noteworthy that ciliates and tintinnids, representing the heterotrophic components of the microplankton, showed an order of magnitude increase in their abundance during and after the storm compared to before storm values.

Interestingly, vertical stratification of chl also peaked ca. 48 hs after the storm along with phytoplankton biomass, a somewhat counterintuitive finding. Formation of SCM can respond to a combination of physical, physiological and behavioural mechanisms. Briefly, physical factors involve the formation of pycnocline and nutricline, and the depth distribution of light. Physiological features may include the growth response to the physical scenario, like shifting the carbon:Chl ratio (shade adaptation, Steele 1964). Behavioural responses include aggregations at preferred depth ranges mediated by vertical migration (mostly by dinoflagellates but also diatoms, Iriarte & Bernal 1990). Relative importance of each mechanism may vary from one geographic area to another (Cullen & Eppley 1981). It is beyond the scope of this paper to identify actual mechanisms leading to observed changes in chl concentration and vertical distribution. However, we hypothesize that phytoplankton growth was likely enhanced by a pulse of nutrients supplied by the strong mixing of the water column. It should also be noted the potential improvement in the light environment (i.e. mixed to photic depths ratio) experienced by

diatoms due to resuspension by increased turbulence and a subsequent stabilisation of the water column after the storm. Indeed, stabilization may have been favoured by freshwater runoff after the storm, although lack of CTD data for this period prevents to assess this matter. This interpretation is consistent with results from deeper areas: discrete wind-induced mixing events also led to nutrient enrichment that stimulated subsequent phytoplankton growth and biomass accumulation in the euphotic zone (Marra *et al.* 1990, Kiørboe & Nielsen 1990, Nielsen & Kiørboe 1991). Results of mesocosms studies that assessed combined effect of mixing and nutrient addition suggested similar patterns (Donaghay & Klos 1985, Estrada *et al.* 1988).

Possible consequences of severe wind events for higher trophic levels are not obvious, since they represent the outcome of relatively complex trophic processes. On one side, short-lived blooms may not be efficiently transferred to higher trophic levels. The fraction of energy transferred to large consumers by trophic interactions is dependent on the dominant grazer type (i.e. metazoan vs. protozoan; Kiørboe 1993), and the match between the time scale of the phytoplankton bloom and the time response of their grazers (Kiørboe & Nielsen 1990). Ephemeral pulses of enhanced production (i.e. lasting few days) may not be usable by metazoan grazers like copepods to increase population numbers (Mann & Lazier 2006). For example, small coastal copepods (i.e. genus *Acartia*, *Paracalanus* or *Centropages*) may exhibit productivity peaks associated to short-lived phytoplankton blooms, but their relatively long generation times (ca. one month) prevent population increases on a daily or weekly scale (Kiørboe & Nielsen 1990). In contrast, ciliated protozoa and parthenogenetic metazoans (rotifers) have higher growth rates and much shorter generation times (hours to days) enabling faster numerical responses to sudden changes in food availability (Nielsen & Kiørboe 1990), as observed here for heterotrophic protozoans. However, the production of such organisms may not be readily available for higher trophic levels.

On the other side, actively growing phytoplankton and protozoan microplankton (as observed in post-storm conditions) represent highly nutritious and preferred food types for crustacean grazers, and enhance trophic transfer efficiencies in planktonic webs (Jónasdóttir *et al.* 1995, Müller-Navarra *et al.* 2000, 2004, Park *et al.* 2003), boosting energy transfers to larger consumers. A thorough evaluation of the potential significance of temporal phytoplankton blooms for higher trophic

levels requires more field data and a complement of modelling approaches. Models of planktonic trophic webs explicitly considering prey quality effects (i.e. Mitra 2006) represent an interesting avenue in that regard.

In summary, results presented here suggested that strong mixing events in shallow ecosystems may impact on the assemblage structure and have delayed positive effects on phytoplankton growth, biomass levels and stratification on short time-scales (days). The extent to which such energy and matter is transferred up the food webs remains an open question that deserves further attention.

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