Impact of spring phytoplankton blooms on benthic copepod communities of subtidal sandbanks

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1 Introduction

The marine eutrophication in the North Sea is characterized by a shift from moderate early spring diatom growth to a non-siliceous *Phaeocystis* dominated phytoplankton community (Gieskes & Kraay, 1977; Lancelot *et al.*, 1987; Reid *et al.*, 1990; Rousseau, 2000). *Phaeocystis* has been estimated to comprise up to 96 % of the total phytoplankton biomass in the North Sea during that bloom (Zevenboom *et al.*, 1991). As the bloom progresses, nutrient depletion (Lancelot & Mathot, 1987), ciliate grazing (Moll, 1997) and virus infections (Jacobsen *et al.*, 1996) increasingly cause *Phaeocystis* mortality. Diatoms are the main constituent of the planktonic copepod's diet (Rousseau *et al.*, 2000) but a lot of controversy exists on the trophic fate of *Phaeocystis* and its predation by copepods in the water column (Weisse *et al.*, 1994). Even though *Phaeocystis* colonies were not an important food source for copepods of the zooplankton in the Southern Bight of the North Sea (Gasparini *et al.*, 2000; Rousseau *et al.*, 2000), dissolved organic carbon produced by a *Phaeocystis* bloom through excretion and lysis has been demonstrated to be a main source of carbon for the microbial foodweb in the water column, including copepods (Van Boekel *et al.*, 1992; Rousseau *et al.*, 2000). In accordance with this finding, the accumulation of *Phaeocystis* derived organic matter at the bottom may also indirectly induce changes in the community structure of the benthic fauna. Sinking of decaying *Phaeocystis* colonies and organic carbon to the bottom results in large amounts of bottom detritus (Riebesell, 1993). Osinga *et al.* (1996) also observed a continuously high sedimentation of living *Phaeocystis* cells. The natural deposition of organic matter is the primary source of food for sublittoral marine benthos (Gee *et al.*, 1985). In offshore areas it is principally derived from phytoplankton (Smetacek, 1984) and zooplankton faecal pellets and exuvia (Angel, 1984). Settling diatoms are an important food source for the benthos (Brown & Sibert, 1977; Montagna, 1984; Decho, 1988) but the role of the benthos in the remineralization pathway of deposited *Phaeocystis* derived detritus is unknown (Rousseau *et al.*, 2000).

The increased food availability due to organic enrichment often causes a significant increase in harpacticoid densities (Gee *et al.*, 1985). Changes in biodiversity patterns are less straightforward and clear. Species richness of epibenthic and endobenthic detritus feeders may increase in case the deposited organic matter (settling diatoms or *Phaeocystis* detritus) is directly consumable (Fig.II.1). If the bottom detritus is an appropriate food source for benthic microfauna which copepods feed upon, an organic enrichment may result in an increased bacterial productivity and hence an increase

in species richness and a decrease in dominance of interstitial bacteria-grazing copepods (Hockin, 1983). Diversity of diatom or detritus feeders or bacteria-grazers may follow a monotonous increasing trend if diversity continuously increases with increasing productivity, possibly reaching a maximum. Due to an enhanced primary production however diversity may decrease if it follows a unimodal relationship. This explains why harpacticoid communities were characterized by an increase in species richness in a low-dose treatment but showed an increase in dominance and a decrease in species richness with increasing organic enrichment (Gee *et al.*, 1985). Also Marcotte & Coull (1974) observed decreasing diversities of a subtidal harpacticoid community with increasing organic enrichment. The response of natural communities depends on the kind of primary production, the amount of organic mattter and the composition of the community, i.e. the proportion of bacteria-grazing and microalgae consuming species (Hockin, 1983). Consequently, eutrophication may cause an increase in biodiversity in specific areas, an impoverishment in others. To examine this hypothesis, an intensive sampling campaign was performed at two subtidal stations in the southern North Sea from the beginning of March until the beginning of July in 1999. Temporal changes in harpacticoid density, diversity and community structure in relation to the diatom and *Phaeocystis* spring bloom have been examined. Also temporal fluctuations in the vertical distribution of harpacticoids in the sediment have been studied. Special attention has been paid to the different response of epi- and endobenthic and interstitial species in order to describe the influence of organic enrichment on the functional biodiversity of harpacticoid communities. Temporal and vertical distribution patterns of the different life history stages were examined to reveal a potential interrelation between migratory behaviour and reproductive activity as a result of organic enrichment. Finally, differences are discussed between the two sandbank stations, since a decreasing trend of organic enrichment was expected with distance from the coast.

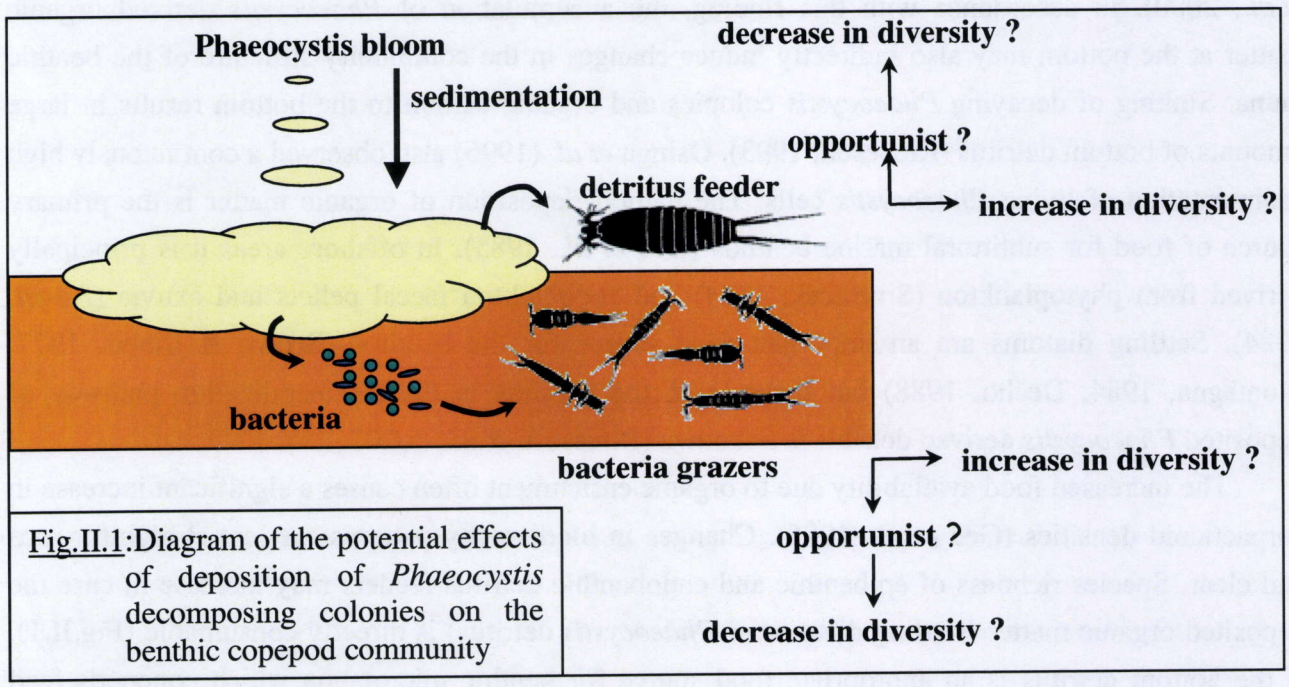

Fig.II.1:Diagram of the potential effects of deposition of *Phaeocystis* decomposing colonies on the benthic copepod community

2 Materials and methods

2.1 Description of the study area

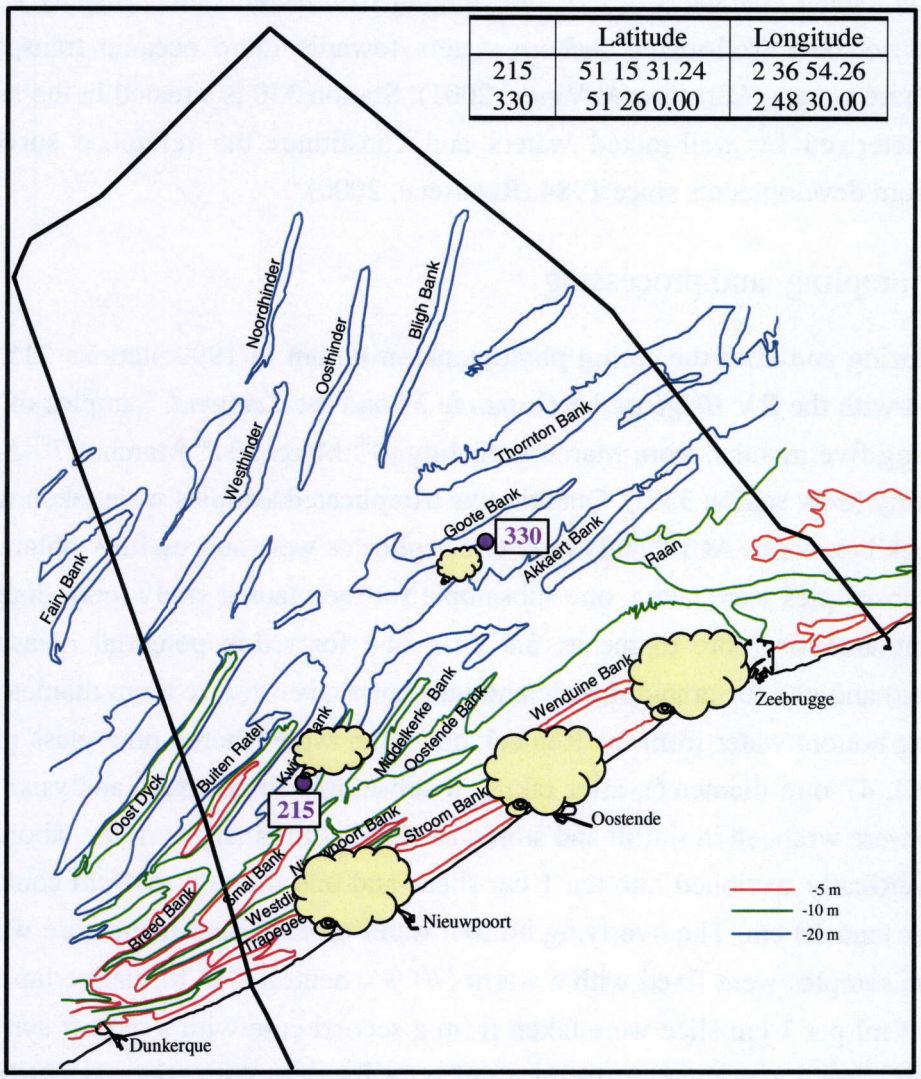

Fig.II.2: Location of the sampling stations

Two stations were sampled at the Belgian Continental Shelf (Fig.II.2). Station 215 is located at 12 m depth on the southern part of the Kwintebank, belonging to the Flemish Banks. An extensive description of the Kwintebank and the Flemish Banks area is given in chapter I. Station 330 is situated at greater depth (24 m) on the southern flank of the Gootebank. Just as the Kwintebank, the Gootebank is rectilinear at a large scale, but the direction is parallel to the coastline. The outlines of the bank are not streamlined to the same degree as the Flemish Banks. (Vlaeminck *et al.*, 1989) The Gootebank belongs to the Zeeland Ridges, a group of shelf sandbanks which are mainly located in Dutch territorial waters. The Gootebank has a length of 15 km and a maximum width of 2 km. It shows a relative elevation above the seafloor of 6 m at the ends and up to 10 m at the centre, which corresponds with a low water depth of 12 m. In comparison with the Flemish Banks, its height is less pronounced, although they occur at approximate similar water depths. (Lanckneus *et al.*, 1993) The

topography of the bank is not very explicit and rather smooth: the southwestern part of the bank is only 1 m higher than the surrounding channels (Vlaeminck *et al.*, 1989). In general, it has very mild slopes to the NW and a more steeper slope to the SE (Lanckneus *et al.*, 1993). The physical, chemical and biological characteristics of the Belgian Continental Shelf display a gradient from turbid, nutrient rich and well-mixed inshore waters towards more oceanic transparent and less productive offshore waters (Cattrijsse & Vincx, 2001). Station 330 is situated in the latter zone. This station is characterized by well-mixed waters and constitutes the reference survey station for *Phaeocystis* bloom developments since 1984 (Rousseau, 2000).

2.2 Sampling and processing

Before, during and after the spring phytoplankton bloom in 1999 stations 215 and 330 were regularly visited with the RV *Belgica*, the *Oostende XI* and the *Zeehond*. Samples of six dates were analyzed covering five months, from March until July (9th March, 31st March, 27th April, 12th May, 28th June, 12th July (only station 330)). Quantitative trireplicated samples were taken with a modified 0.017 m² Reineck box corer. At 12th July only two replicates were successfully obtained. From each replicate four subsamples were taken, one subsample for meiofaunal study (core diameter: 3.6 cm), one for pigment analysis (core diameter: 3.6 cm), one for redox potential measurements (core diameter: 3.6 cm) and one for granulometric and nutrient analysis (core 6 cm diameter). Aliquots of 0.5-1 l overlying bottom water from the Reineck box corer were filtered on a glass microfibre filter (Whatman GF/C, 47 mm diameter), after taking a subsample for nutrient analysis. The filters for HPLC analysis were wrapped in tinfoil and stored at –20°C until analysis in the laboratory. The core samples were vertically sectioned into ten 1 cm slices and one slice up to 4 cm containing the core sediment deeper than 10 cm. The overlying bottom water of each meiofauna core was preserved as well. Meiofauna samples were fixed with a warm (70 %), neutral 4 % formaline tap water solution. Subsamples of 1 ml per 1 cm slice were taken from a second core with a cut off syringe for further pigment analysis. The 1 cm slices from the third core for granulometric and nutrient study were preserved in Petri dishes in the freezer, as well as the sample units for pigment analysis. The redox potential was measured, on board, by means of a micro-platinum electrode which was connected to a pH-millivoltmeter. Seawater temperature and salinity were measured aboard with a thermosalinometer (Beckman). On each sampling event, a vertical profile of temperature, salinity, turbidity and irradiance was obtained by means of a CTD-cast.

In the lab, the same procedure was followed to elutriate the harpacticoids from the sediment as described in chapter I. A distinction was made between males, egg carrying and non egg-carrying females and copepodites. Densities are expressed as ind./10 cm², referring to the surface area of the core but actually a volume is concerned, comprising the whole core up to 10 cm of depth for total densities and a volume of 10 cm² x 1 cm for densities per depth layer to describe the vertical distribution of the copepods.

Sediment granulometry was analyzed with a Coulter LS100 Particle Size Analyzer using laser light of 750 nm. The sediment fractions are listed according to the Wenthworth scale (Buchanan, 1984). For nutrient analysis (silicate, nitrate plus nitrite and ammonia) the overlying water or the interstitial water extracted from the sediment were analyzed through an automatic chain SKALAR SAN^{plus} Segmented Flow Analyzer using a photometric method. The filters for chlorophyll *a* analysis were cut into small pieces and placed in tubes (10 ml) containing 5 ml of 90 % acetone and were sonicated for 30 seconds. Reverse-phase high-performance liquid chromatography (RP-HPLC) (Gilson) was conducted using the method recommended by Wright & Jeffrey (1997). The organic matter content was calculated by the loss on ignition method: drying at 105°C, 24 h; then combusting at 550°, 2h. (Kristensen & Anderson, 1993).

Water column samples for diatom and *Phaeocystis* colonies enumeration were processed by ULB (Rousseau). The C-biomass of diatoms in the water column was determined according to the procedure described in Rousseau *et al.* (2002). The C-biomass of *Phaeocystis* in the water column was calculated according to Rousseau *et al.* (1990).

2.3 Statistics

Total density (log (x+1) transformed) and species richness values were analyzed by 2-way fixed-factor ANOVA. The dominance structure of the harpacticoid assemblages was compared by means of k-dominance curves (Lambshead *et al.*, 1983). Temporal changes and spatially structured variation in the harpacticoid species assemblages were examined by pCCA on fourth root transformed data using dummy variables for the factors time and station (Borcard *et al.*, 1992; ter Braak & Smilauer, 1998; Hallgren *et al.*, 1999). 2-way fixed-factor ANOVA or Kruskall-Wallis ANOVA by Ranks was performed on total ecotype proportions and percentages of life history stages. Overall significant differences were pairwise compared using the planned comparison option in ANOVA for parametric data or following Conover (1971) for non-parametric data.

Density and species richness per depth layer were analyzed with ANOVA arranged in a split plot design. The trireplicated samples were nested within station*time and the variable replicate was defined as a random factor, resulting in a 4-way mixed-factor ANOVA (Fig.II.3). The variation in the dataset due to the vertical zonation of harpacticoids was defined by pCCA on fourth root transformed data. Replicate A from depth layer 0-1 cm taken on 27th April at station 215 and replicate B from the overlying water on 28th June at station 330 were outliers and excluded from this analysis. Significant effects of the variables station, time, depth and the interactions between them on the species composition were examined with Monte-Carlo permutation tests restricted for split-plot design using pCCA in CANOCO for Windows (Table II.1) (ter Braak & Smilauer, 1998). Since after transformation of the ecotype proportions and percentages of life history stages none of the assumptions for ANOVA were met, these data (arcsin(x/100) transformed) were also analyzed with Monte-Carlo permutation tests restricted for split-plot design using pRDA (Table II.2). This

technique was also applied to univariate log (x+1) data such as the densities of selected species. Forward selection using Monte-Carlo permutation tests restricted for split-plot design in pCCA and pRDA selected the variables significantly contributing to the effect of time or depth or the interactions between the factors station, time and depth. The results of the 4-way mixed-factor ANOVA on total densities and species richness were compared with the Monte-Carlo permutation tests restricted for split-plot design.

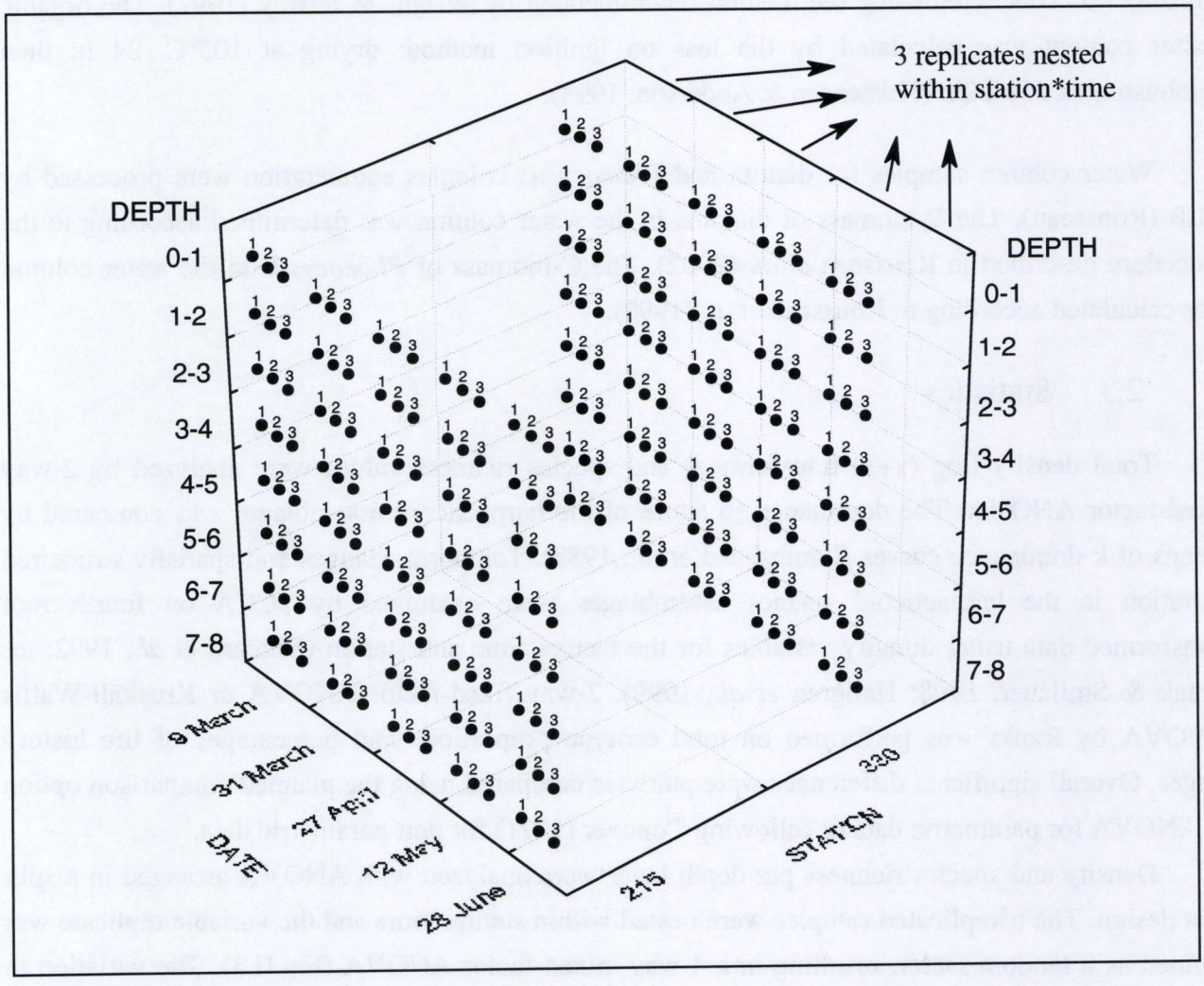

Fig.II.3: Representation of the statistical design (4-way mixed-factor ANOVA) to define significant effects of the variables station, time, depth and the interactions between these variables on density and species richness

				Monte-Carlo permutation test restricted for split-plot design			
	Analysis	Explanatory variables (as dummy variables)	Covariables (as dummy variables)	covariables as blocks	whole plots (in one block, if defined) (one sample per whole plot)	split plots in one whole plot	permuted
Total variation	CA	none	none				
Spatial + temporal + depth structured variation	CA	stations + dates + depth layers	none				
Spatially structured variation	CCA	stations	none	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-temporal spatial variation	pCCA	stations	dates	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Non-depth related spatial variation	pCCA	stations	depth layers	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-temporal and non-depth related spatial variation = effect station	pCCA	stations	dates + depth layers	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Temporally structured variation	CCA	dates	none	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-spatial temporal variation	pCCA	dates	stations	stations	samples on all dates at one station	7 depth layers of one sample	whole plots
Non-depth related temporal variation	pCCA	dates	depth layers	none	samples of both stations on all dates	7 depth layers of one sample	whole plots
Non-spatial and non-depth related temporal variation = effect time	pCCA	dates	stations + depth layers	stations	samples on all dates at one station	7 depth layers of one sample	whole plots
Depth structured variation	CCA	depth layers	none	none	samples of both stations on all dates	7 depth layers of one sample	split plots
Non-spatial depth structured variation	pCCA	depth layers	stations	stations	samples on all dates at one station	7 depth layers of one sample	split plots
Non-temporal depth structured variation	pCCA	depth layers	dates	dates	samples of both stations on one date	7 depth layers of one sample	split plots
Non-temporal and non-spatial depth variation = effect depth	pCCA	depth layers	dates + stations	stations	samples on all dates at one station	7 depth layers of one sample	split plots
Spatially temporal structured variation = effect time*station	pCCA	all possible interactions of date*station	dates + stations	dates	samples of both stations on one date	7 depth layers of one sample	whole plots
Spatially depth structured variation = effect depth*station	pCCA	all possible interactions of depth layer*station	depth layers + all possible interactions of depth layer*date	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots
Temporally depth structured variation = effect depth*time	pCCA	all possible interactions of depth layer*date	depth layers + all possible interactions of depth layer*station	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots
Spatially and temporally depth structured variation = effect station*time*depth	pCCA	all possible interactions of depth layer*date*station	all possible interactions of date*station, depth layer*station and depth layer*date	samples	samples of both stations on all dates = blocks	7 depth layers of one sample	split plots

Table II.1: Statistical design to define significant effects of the variables station, time, depth and of the interactions between these variables on species composition, the sample values are mean values of 3 replicates

				Monte-Carlo permutation test restricted for split-plot design			
	Analysis	Explanatory variables (as dummy variables)	Covariables (as dummy variables)	covariables as blocks	whole plots (in one block, if defined) (one replicate per whole plot)	split plots in one whole plot	permuted
Non-temporal and non-depth related spatial variation	pRDA	stations	dates + depth layers	dates	3 replicates of both stations on one date	8 depth layers of one sample	whole plots
Non-spatial and non-depth related temporal variation	pRDA	dates	stations + depth layers	stations	3 replicates of one station on all dates	8 depth layers of one sample	whole plots
Non-temporal and non-spatial depth variation	pRDA	depth layers	dates + stations	stations	3 replicates of one station on all dates	8 depth layers of one sample	split plots
Spatially temporal structured variation = effect time*station	pRDA	all possible interactions of date*station	dates + stations	dates	3 replicates of both stations on one date	8 depth layers of one sample	whole plots
Spatially depth structured variation = effect depth*station	pRDA	all possible interactions of depth layer*station	depth layers + all possible interactions of depth layer*date	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots
Temporally depth structured variation = effect depth*time	pRDA	all possible interactions of depth layer*date	depth layers + all possible interactions of depth layer*station	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots
Spatially and temporally depth structured variation = effect station*time*depth	pRDA	all possible interactions of depth layer*date*station	all possible interactions of date*station, depth layer*station and depth layer*date	replicates	3 replicates of both stations on all dates = blocks	8 depth layers of one sample	split plots

Table II.2: Statistical design to define significant effects of the variables station, time, depth and of the interactions between these variables on density, species richness, ecotype proportions and percentages of life history stages

3 Results

3.1 Environmental data

3.1.1 Temperature and salinity

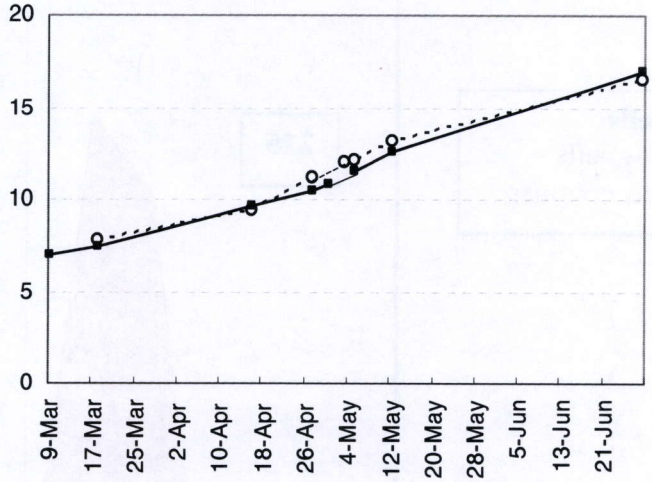

Fig.II.4: Temperature measurements at stations 215 (open circles + dotted line) and 330 (closed squares + full line) during the sampling period

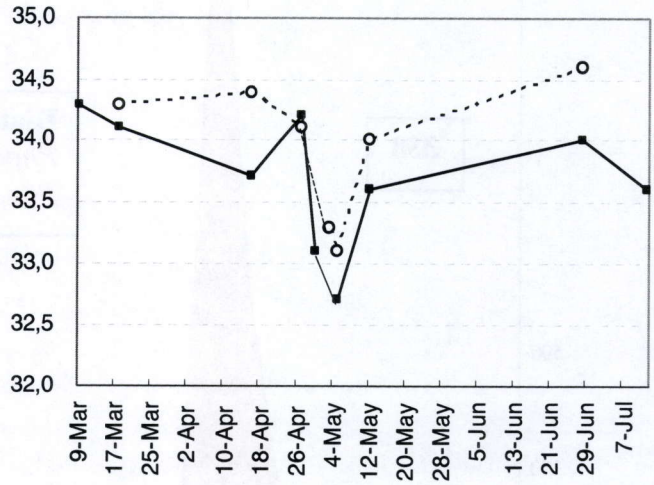

Fig.II.5: Salinity measurements at stations 215 (open circles + dotted line) and 330 (closed squares + full line) during the sampling period

Temperature linearly increased from 7°C on 9th March up to 17°C on 12th July (Fig.II.4). During approximately two weeks (27th April-12th May) temperature was almost 1°C higher at station 215 than at station 330. This period coincides with a drop in salinity at both stations (Fig.II.5). Between 27th April and 30th April salinity dropped with one unit, further decreasing toward 3rd May and increasing again afterwards. Through the whole period salinity was slightly higher at station 215 than at station 330.

3.1.2 Description of the diatom and *Phaeocystis* spring bloom

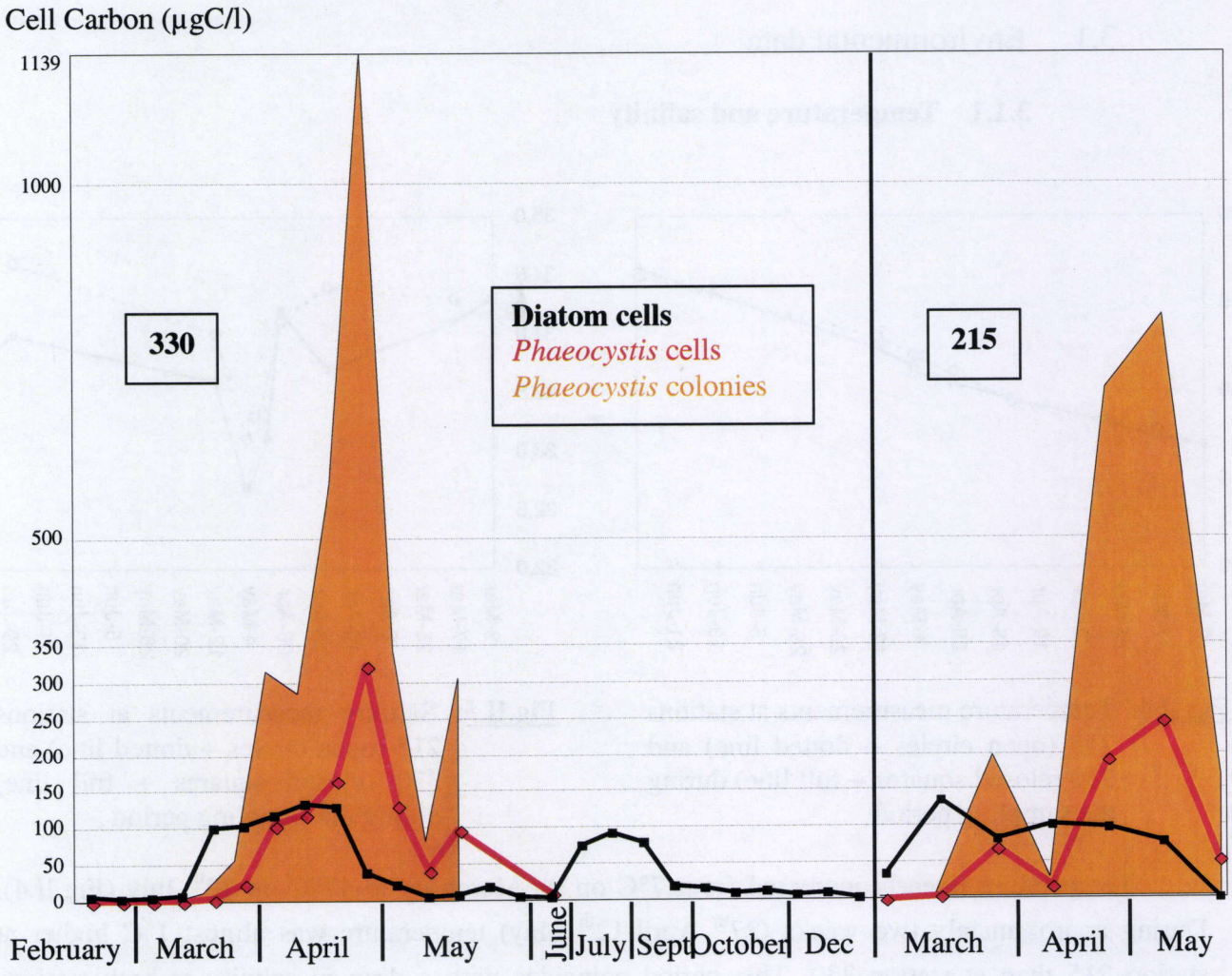

Fig.II.6: Carbon content in the water column, derived from diatom cells, *Phaeocystis* cells and *Phaeocystis* colonies (mucilage included) during the sampling period, measured at stations 330 and 215 in 1999

From 19th March (100 µg/l) until 27th April a high carbon content, derived from diatom cells, was measured in the water column at station 330, reaching a maximum of 132 µg/l on 23rd April (Fig.II.6). During this spring diatom bloom the onset of the *Phaeocystis* bloom was observed on 19th March. *Phaeocystis* derived cell carbon increased during April and peaked after the diatom bloom terminated on 29th April. *Phaeocystis* derived colonial carbon (including mucilage) amounted to 1139 µg/l at this date. During May *Phaeocystis* cell carbon content decreased to 11 µg/l on 2nd June. Diatoms showed a second moderate bloom in July. At station 215 the diatom bloom started at the same moment as at station 330 but lasted a bit longer until 3rd May. In the water column lower values were recorded for *Phaeocystis* derived carbon at station 215 than at station 330, the peak of *Phaeocystis* derived cell carbon (244 µg/l) and colonial cell carbon (782 µg/l) being less pronounced and occurring on 3rd May whereas on 29th April at station 330.

3.1.3 Chlorophyll *a* and total organic matter

3.1.3.1 Station 330

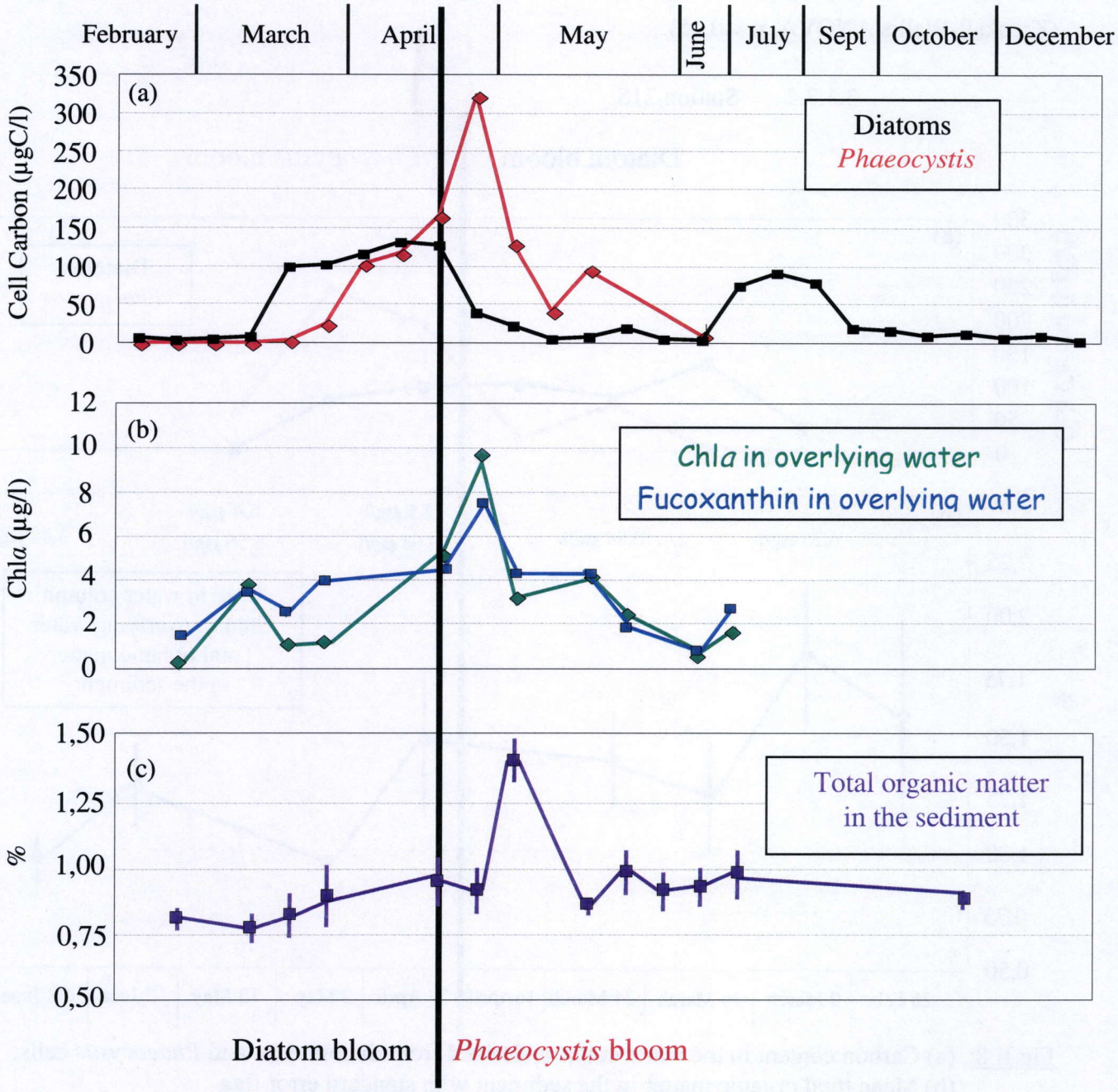

Fig.II.7: (a) Carbon content in the water column, derived from diatom cells and *Phaeocystis* cells;
(b) Chlorophyll *a* content in water column and overlying water;
(c) Mean total organic matter in the sediment with standard error
measured at station 330 in 1999

Chlorophyll *a* content in the water column and in the overlying water started to rise during the diatom bloom and peaked at the same moment as the *Phaeocystis* bloom (Fig.II.7.b). In May chlorophyll *a* content in the overlying water showed the same trend as the *Phaeocystis* bloom.

Elevated values for chlorophyll *a* were also recorded in the overlying water on 9th May whereas this increase was not recorded in the water column (Rousseau, unpubl. data). Total organic matter (Fig.II.7.c) showed a distinct peak on 3rd May, indicating that 4 days after the peak of the *Phaeocystis* bloom a significant higher amount of organic matter was present in the sediment (Kruskall-Wallis ANOVA, $p < 0.05$).

3.1.3.2 Station 215

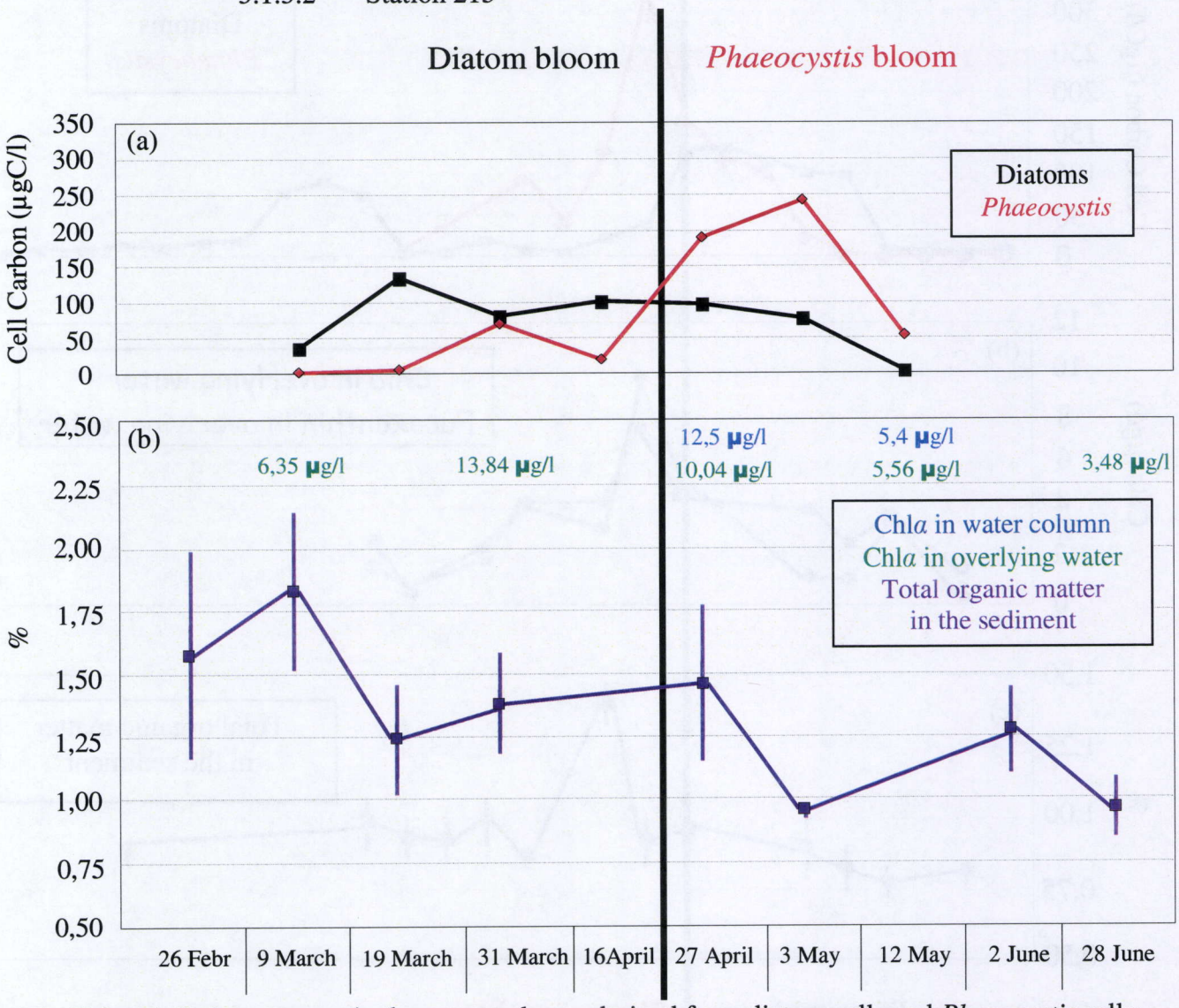

Fig.II.8: (a) Carbon content in the water column, derived from diatom cells and *Phaeocystis* cells;
(b) Mean total organic matter in the sediment with standard error flag
measured at station 215 in 1999
Measurements of chlorophyll *a* content in water column and overlying water are given in the graph of total organic matter.

At station 215 the few measurements of chlorophyll *a* indicate that the concentration of chlorophyll *a* in the water column was nearly the same as in the overlying water. The highest value for chlorophyll *a* near the bottom was measured on 31st March. This value even exceeded the measurement during the *Phaeocystis* bloom on 27th April.

On any date, the total organic matter content in the sediment was higher at station 215 than at station 330, resulting in a significant difference between both stations (Kruskall-Wallis ANOVA, $p < 0.001$). At station 215 the highest percentages of total organic matter were recorded at the end of February and the beginning of March while the lowest percentages were measured in the beginning of May and at the end of June. In contrast with station 330, a peak in total organic matter was not found on 3rd May.

3.1.4 Nutrients

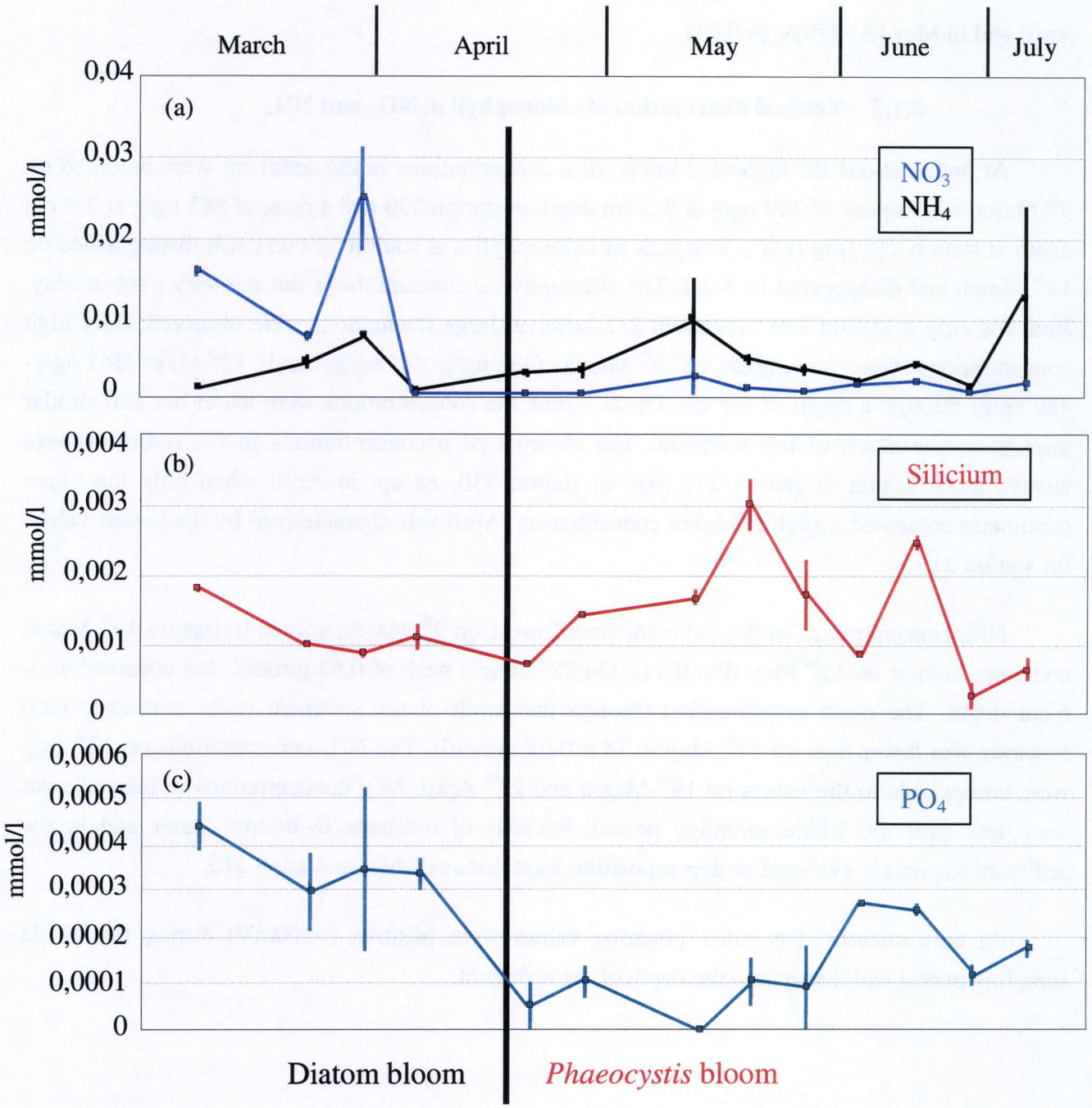

Fig.II.9: (a) NO_3 and NH_4 concentrations; (b) silicium concentrations and (c) PO_4 concentrations measured at station 330 in 1999

At station 330 the highest NO_3 concentrations (Fig.II.9.a) were measured in March with two distinct peaks on 9th March (0.016 mmol/l) and 31st March (0.026 mmol/l) (Kruskall-Wallis ANOVA, $p < 0.05$). Low values were recorded throughout the following sampling period. NH_4 concentrations showed three significant peaks at station 330 (Kruskall-Wallis ANOVA, $p < 0.05$). The first peak appeared on 31st March (0.008 mmol/l), the second on 12th May (0.010 mmol/l) and the third on 12th July (0.013 mmol/l). Silicium concentrations (Fig.II.9.b) were low in March and April and significantly higher on 20th May (0.003 mmol/l) and 16th June (0.002 mmol/l) (Kruskall-Wallis ANOVA, $p < 0.05$). PO_4 concentrations (Fig.II.9.c) were significantly lower at the end of April and in May (ANOVA, $p<0.01$).

3.1.5 Vertical distribution of chlorophyll *a*, NO_3 and NH_4

At both stations the highest chlorophyll *a* concentrations in the sediment were recorded on 9th March with a peak of 349 ng/g at 2-3 cm depth at station 330 and a peak of 881 ng/g at 3-4 cm depth at station 215 (Fig.II.10). The peak of chlorophyll *a* at station 330 was still distinguished on 19th March and disappeared in April. The chlorophyll *a* concentrations did not vary a lot in May, June and July at station 330. At station 215 however large fluctuations were observed. Very high concentrations were measured on 9th March (438 ng/g- 881 ng/g) and 12th May (347 ng/g-450 ng/g) through a depth of 4-5 cm. On 28th June the concentrations were lower but still similar throughout the depth of the sediment. The chlorophyll *a* concentrations in the sediment were always much higher at station 215 than at station 330, except in April when only the upper centimetre contained a slightly higher concentration. April was characterized by the lowest values for station 215.

NH_4 concentrations in the sediment were lowest on 9th March, started to rise on 19th March and were highest on 12th May (Fig.II.11). On 28th June a peak of 0.67 mmol/l was observed at 5-6 cm depth. The mean concentration through the depth of the sediment (0.26 mmol/l $\pm$ 0.05) however was lower than on 12th May (0.34 $\pm$ 0.02 mmol/l). The NH_4 concentrations on 12th July were comparable to the values on 19th March and 27th April. NO_3 concentrations in the sediment were low over the whole sampling period. Records of nutrients in bottom water and in the sediment to provide evidence of decomposition were not available for station 215.

At both stations, the redox potential values were positive (>100mV) during the whole sampling period and throughout the depth of the sediment.

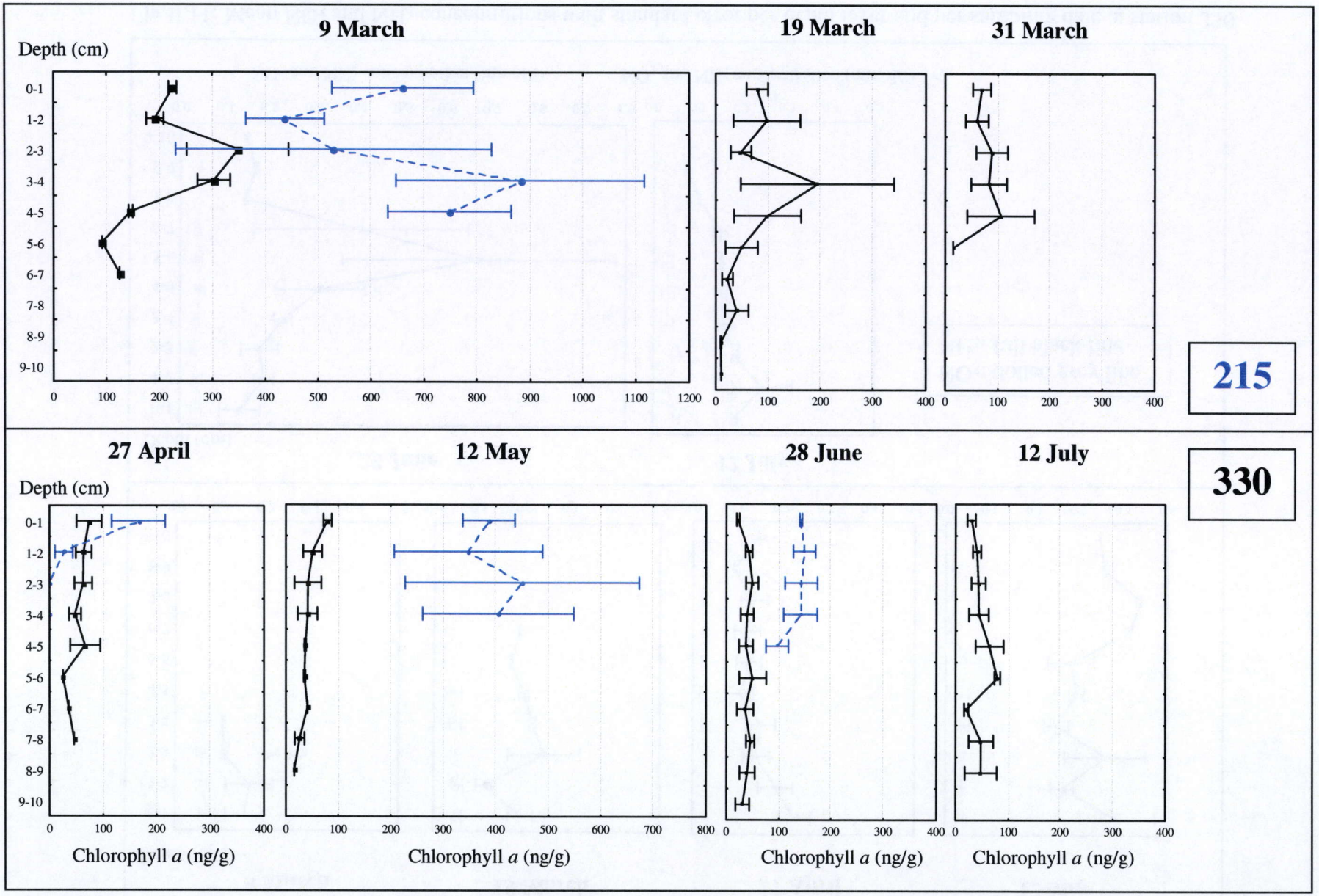

Fig.II.10: Mean chlorophyll *a* concentration with standard error per depth layer and per sampling date at station 215 and station 330, on 19th March, 31st March and 12th July chlorophyll *a* measurements were not available for station 215

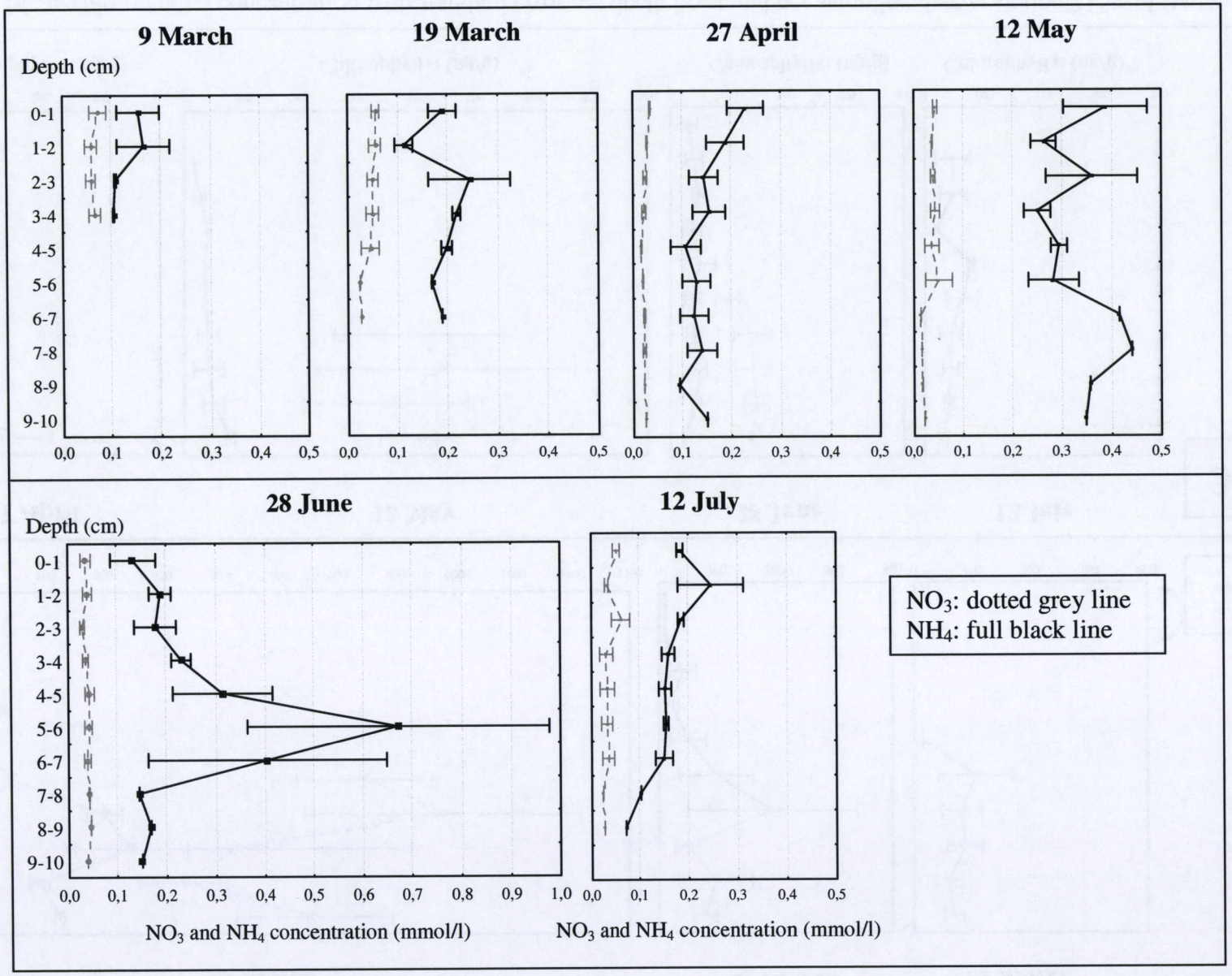

Fig.II.11: Mean NO_3 and NH_4 concentrations with standard error per depth layer and per sampling date at station 330

3.1.6 Sediment characteristics

Medium sand dominated at both stations. The mean median grain size over the whole period was 310 ± 24 µm at station 215 and amounted to 350 ± 10 µm at station 330. Sediment composition was very constant at station 330 throughout the whole period, except for a slight increase in coarse and very coarse sand on 27th April. Because of the low variance between the replicates at station 330 an increase in median grain size of 40 µm on 27th April resulted in a significant difference in comparison with the other sampling dates (ANOVA, $p < 0.01$). At station 215 the median grain size was significantly higher on 9th March in comparison with the median grain size in April and June (Kruskall-Wallis ANOVA, $p < 0.01$), due to a significant higher contribution of coarse sand on 9th March (ANOVA, $p < 0.001$). At station 330 the sediment is very well sorted and predominated by medium sand (69 % ± 1 %) (Fig.II.12), whereas at station 215 the sediment is rather poorly sorted, containing a lot of fine (35 % ± 6 %) as well as very coarse sand (11 % ± 1 %).

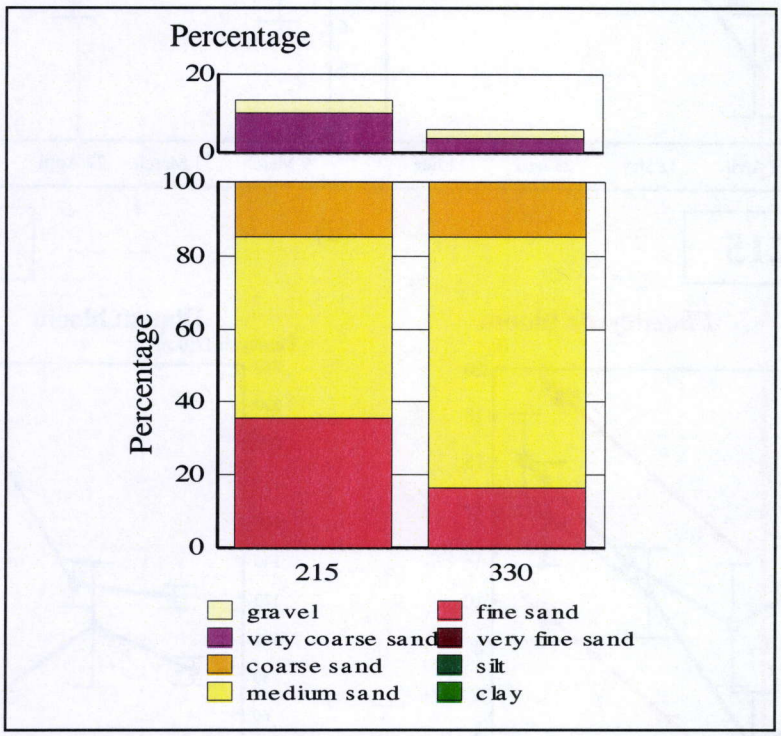

Fig.II.12: Mean sediment composition over the whole sampling period at station 215 and 330

3.2 Time series of harpacticoid data

3.2.1 Total harpacticoid density and diversity

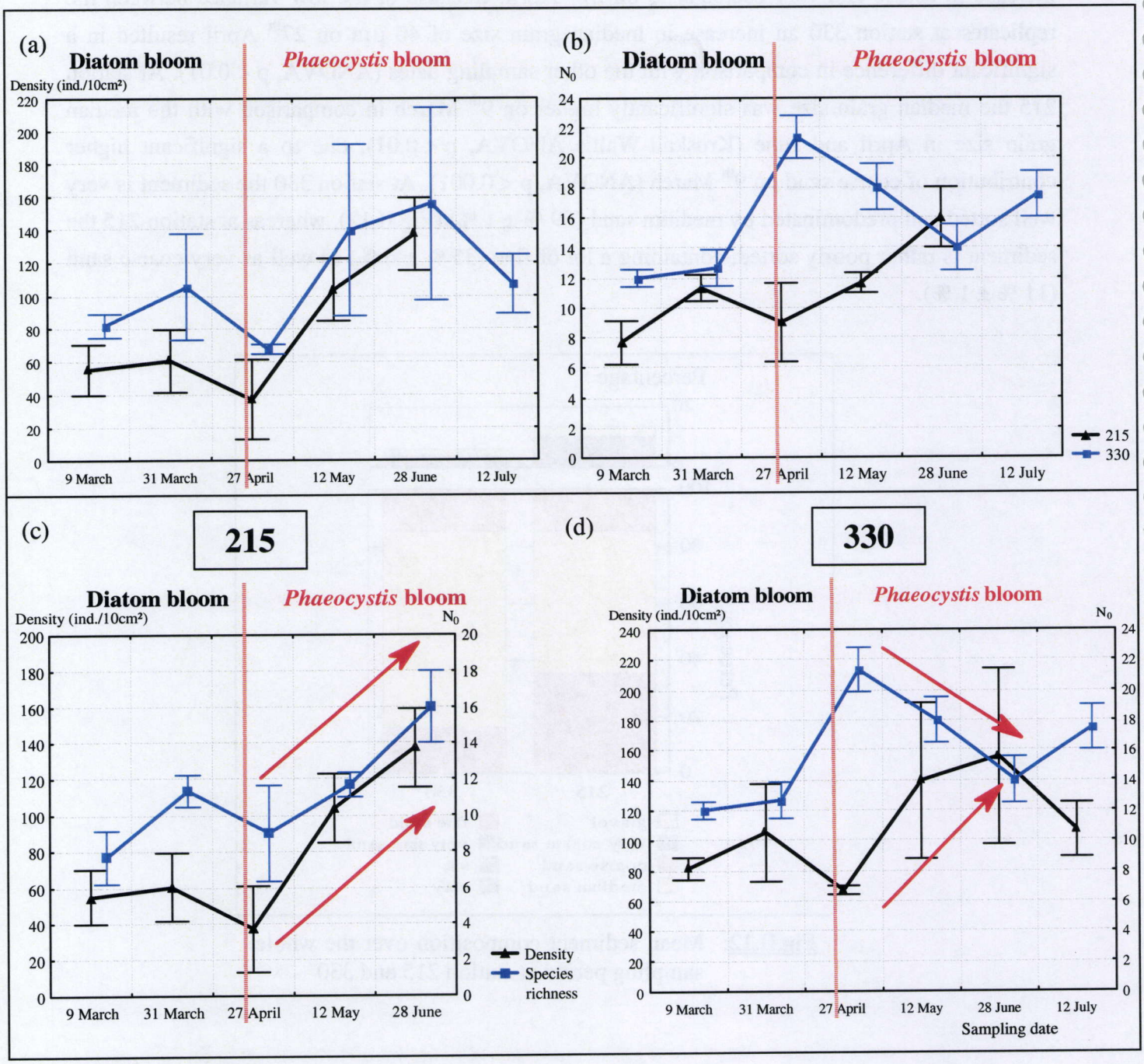

Fig.II.13:(a) Mean total densities with standard error at stations 215 and 330;
(b) Mean total number of species with standard error at stations 215 and 330;
(c) Mean total densities and number of species with standard errors at station 215;
(d) Mean total densities and number of species with standard errors at station 330

Harpacticoid total density showed a very similar trend at both stations. A slight increase from the beginning toward the end of March was followed by a decrease in April at the end of the diatom bloom (Fig.II.13.a). Total densities rose during the *Phaeocystis* bloom to a maximum in June. At station 330 total density decreased again in July. The significant temporal pattern (Table II.3) resulted from significant differences between April and May or June (twice $p < 0.01$) and between 9th March and June ($p < 0.05$).

ANOVA	df	df	Density		Species richness	
	Effect	Error	F ratio	p value	F ratio	p value
Station	1	20	4.18334	0.05421	*21.7913*	*0.00015*
Time	4	20	*3.7476*	*0.01967*	*4.89563*	*0.00645*
Station*Time	4	20	0.68955	0.60771	*6.39078*	*0.00176*

Table II.3: Results of the 2-way fixed-factor ANOVA analyzing the effect of station, time and the interaction term station*time on total densities and number of species

Species richness revealed exactly the same pattern as density at station 215, reaching maximum values in June at the end of the *Phaeocystis* bloom (Fig.II.13.c). An opposite trend of density and species richness typified station 330 (Fig.II.13.d). At station 330 a huge increase in species richness was observed between the end of March and the end of April, whereas density decreased in this period. In April density was even lowest while species richness was highest. Species richness decreased during the *Phaeocystis* bloom as long as density was rising. When density dropped in July, species richness increased again. Consequently, species richness showed an opposite course at station 215 and 330 (Fig.II.13.b), reflected in the significant effect of the interaction term station*time (Table II.3). Both stations also significantly differed in overall species richness (Table II.3), which was generally higher at station 330 than at station 215. In June however more species were encountered at station 215 than at station 330. The significant temporal pattern (Table II.3) reflected significant differences in species richness between 9th March and April or May or June (3x $p < 0.01$) and between 31st March and April ($p < 0.05$).

3.2.2 Harpacticoid community changes

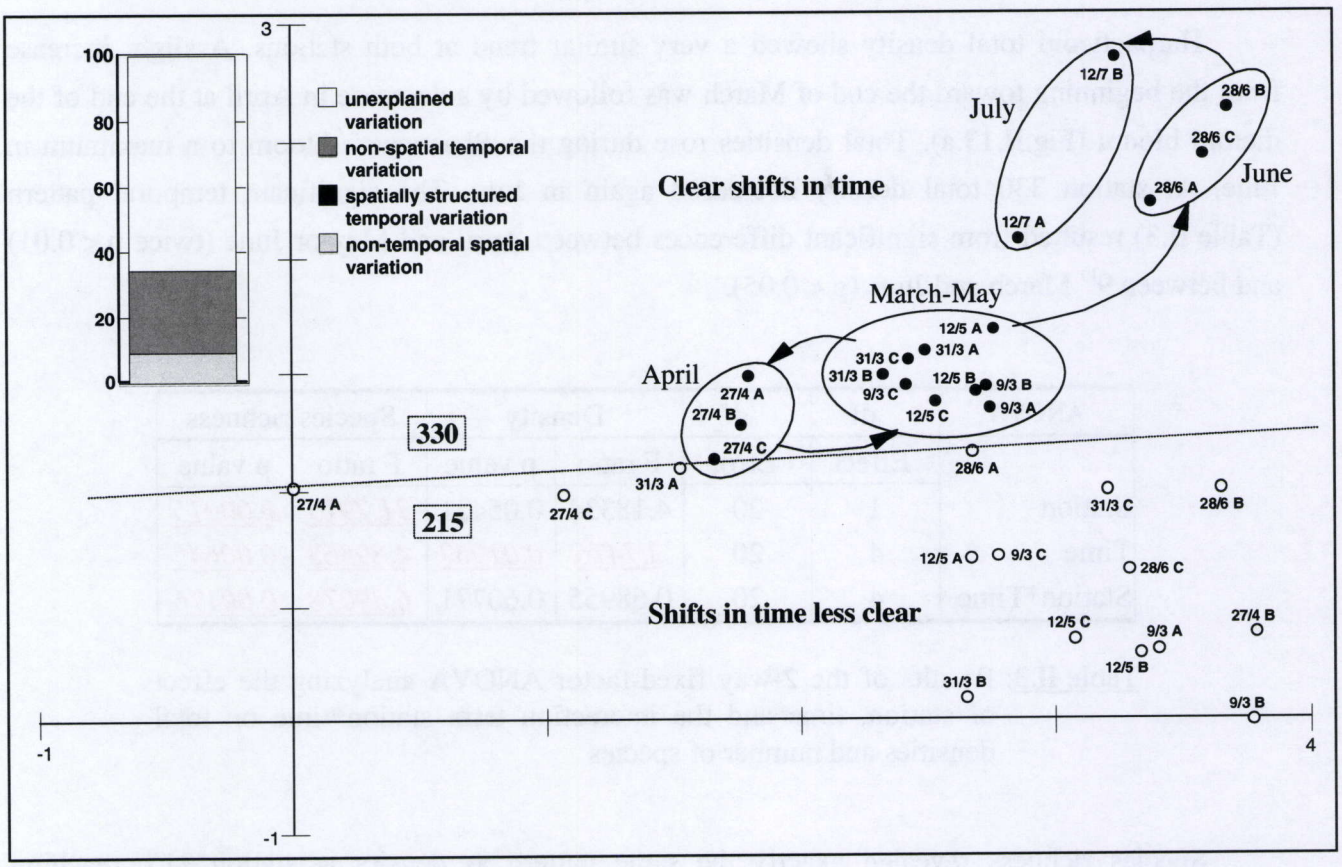

Fig.II.14: Plot of the replicates of each date for stations 215 and 330 in a DCA based on total absolute species abundances, the different proportions of variation in the pCCAs are represented in the upper left corner.

Overall analysis	Analysis	Explanatory variables (dummy variables !)	Covariables (dummy variables !)	Eigenvalue	% of total variation	p value	
Total variation	CA	none	none	4.237			1
Total explained variation	CCA	stations and dates	none	1.488	35	< 0.001	2
Spatially structured variation = effect station + station*time	CCA	stations	none	0.399	9	< 0.001	3
Temporally structured variation = effect time + station*time	CCA	dates	none	1.094	26	< 0.001	4
Non-temporal spatial variation = effect station	pCCA	stations	dates	0.394	9	< 0.001	5
Non-spatial temporal variation = effect time	pCCA	dates	stations	1.089	26	< 0.001	6
Spatially structured temporal variation = effect station*time				0.005	0		= 4 -6
Unexplained variation				2.749	65		= 2 -1

Table II.4: Results of the pCCA analyzing the effect of station, time and the interaction term station*time on total absolute species abundances

The harpacticoid fauna significantly varied by station and significantly changed through time (Table II.4, Fig.II.14). The highest proportion of variation was induced by community changes in April (9 %) and by the differences between both stations (9 %). The community composition in May was very similar to the species composition in March and evolved towards a significantly differing situation in June. The changes in June accounted for 6 % of the total variation in the dataset. The temporal trend was clearer for station 330 than for station 215. At station 215 only April contributed to the significant overall effect of time (Table II.5). The variation in species composition was not significantly related to changes in chlorophyll *a* content.

330	Analysis	Explanatory variables (as dummy variables !)	Covariables	Eigenvalue	% of total variation	p value
All variation	CA	none	none	2.396		
Temporally structured variation	CCA	all dates	none	1.252	52	< 0.05
April structured variation	CCA	april	none	0.372	16	< 0.05
June structured variation	CCA	june	none	0.41	17	< 0.05
Unexplained variation				1.144	48	
215						
All variation	CA	none	none	2.804		
Temporally structured variation	CCA	all dates	none	1.167	42	< 0.05
April structured variation	CCA	april	none	0.587	21	< 0.05
Unexplained variation				1.637	58	

Table II.5: Results of the pCCA analyzing the effect of station, time and the interaction term station*time on total absolute species abundances

At station 215 the eveness was clearly higher on 31st March and 27th April (Fig.II.15.a). The most important species contributed equally to the community on 9th March, 12th May and 28th June. On these dates, *Paraleptastacus espinulatus* and *Leptastacus laticaudatus s.str.* co-dominated (Fig.II.16.b). On 28th June a third species, *Apodopsyllus* n.spec.1 reached high abundances.

At station 330 the k-dominance curves clearly distinguished between April and the other dates (Fig.II.15.b). On 28th June the very high dominance of the most important species was attributed to the very high abundance of *Apodopsyllus* n.spec.1 (Fig.II.16.a). On any date, *Leptastacus laticaudatus s.str.* and *Kliopsyllus* n.spec. 2 reached similar densities and co-dominated on 9th March and 31st March, while *Arenosetella* n.spec.1 was the second most abundant species on 12th May.

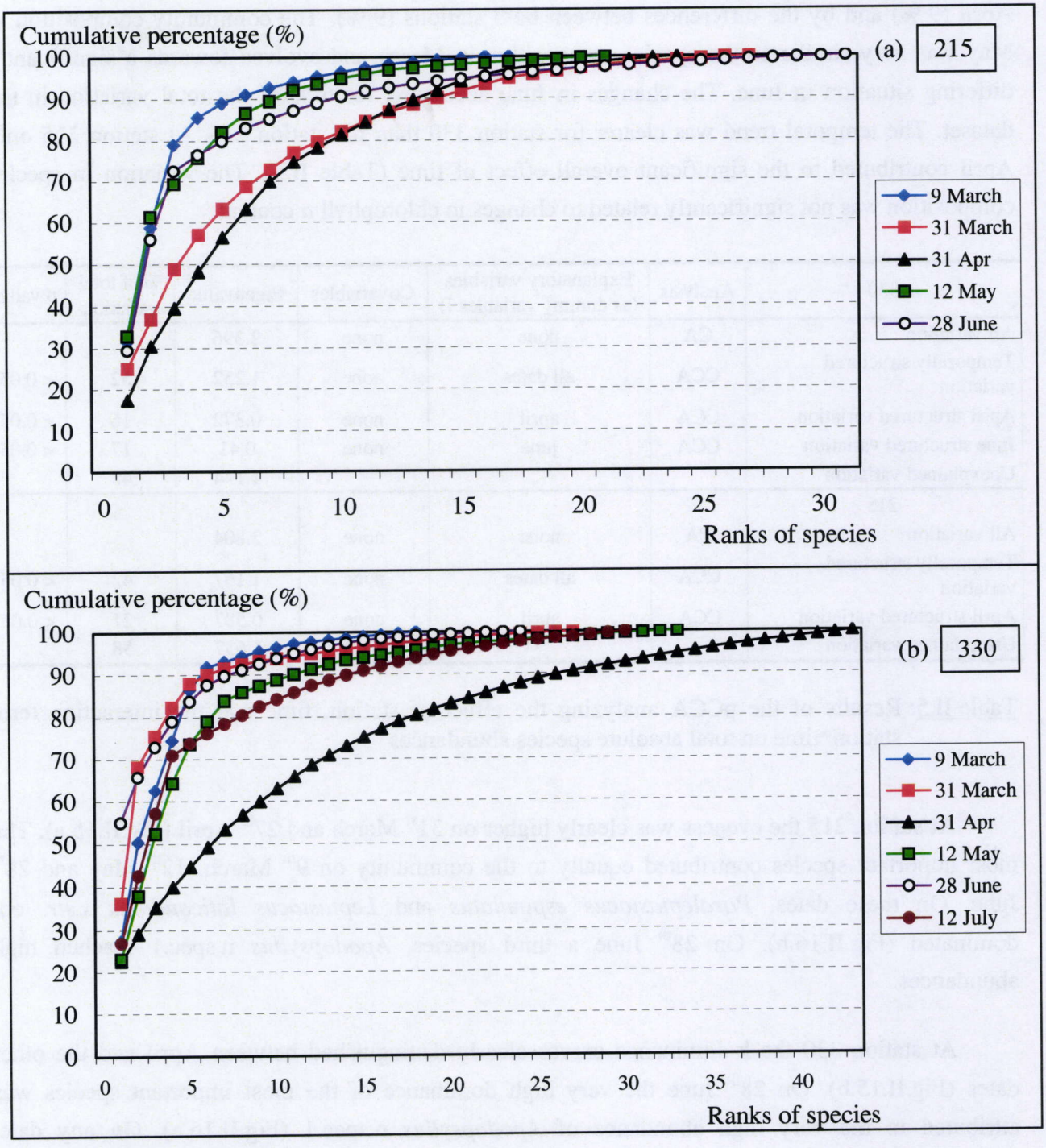

Fig II.15: k-dominance curves of each date for station 215 (a) and 330 (b)

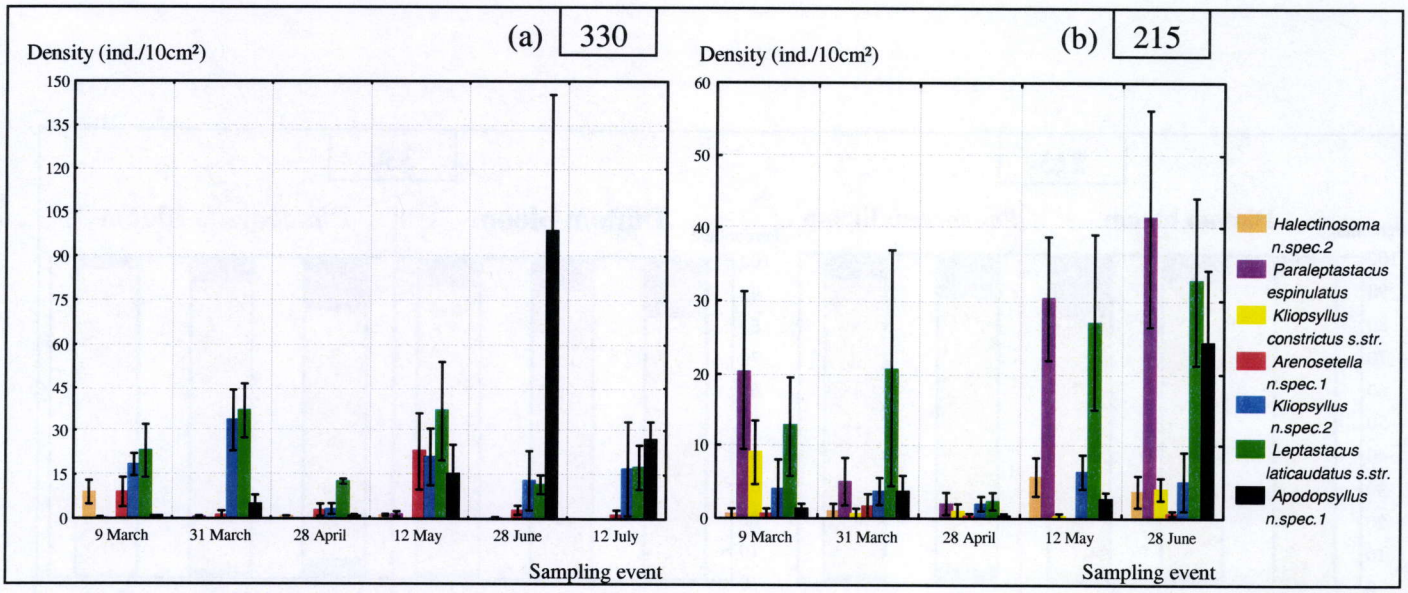

Fig II.16: Mean absolute abundances of the most important species on each date at stations 330 (a) and 215 (b)

3.2.3 Ecotype proportions

Ecotype	Analysis	Effect	df Effect	df Error	F	p value
Epibenthic species	Kruskal-Wallis ANOVA	Station	1	28		0.1399
		Time	4	25		0.4759
Endobenthic species	Kruskal-Wallis ANOVA	Station	1	28		*0.0396*
		Time	4	25		0.5311
Intersitial species	2-way ANOVA	Station	1	20	0.80262	0.3810
		Time	4	20	0.93156	0.4656
		Station*Time	4	20	1.15061	0.3618
Free-swimming species	Kruskal-Wallis ANOVA	Station	1	28		0.5949
		Time	4	25		*0.0364*

Table II.7: Results of the analyses of the effect of station, time and the interaction term station*time if possible on ecotype proportions

Ecotype proportions did not significantly change through time during the spring phytoplankton bloom (Table II.7). The significant temporal pattern for free-swimming species resulted from significant differences in May and June in relation to 9th March ($p < 0.05$), caused by the presence of *Temora longicornis* on top of the sediment in May (5 % at both stations) and other planktonic species in June (2 % at both stations). Throughout the whole period endobenthic species were more abundant at station 330 than at station 215 (Fig. II.17; Table II.7). At station 215 epi- and endobenthic species increased during the diatom bloom to a maximum at the end of April (19 % epibenthic and 11 % endobenthic species) and decreased again during the *Phaeocystis* bloom (Fig.II.17). At station 330 the highest percentages of interstitial species were found in June and July (90 % and 95 % respectively).

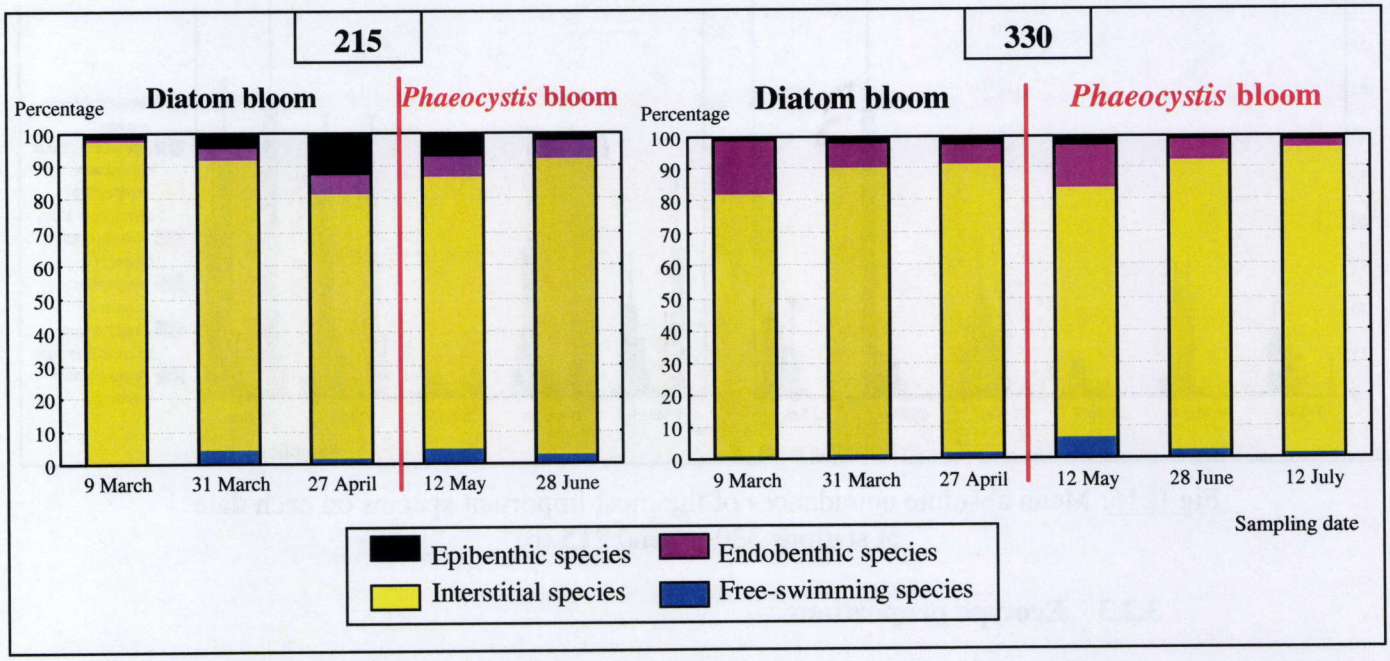

Fig.II.17: Mean relative abundances of different ecotypes at stations 215 and 330

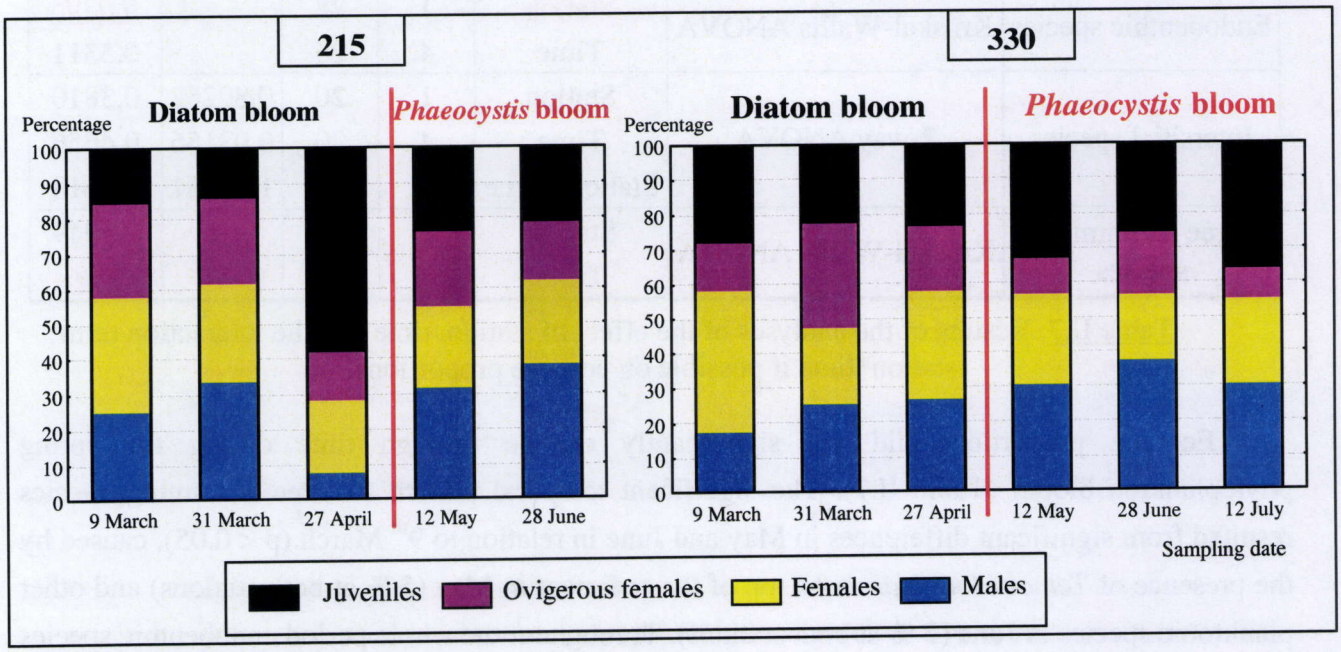

Fig.II.18: Mean relative abundances of different life history stages at stations 215 and 330

3.2.4 Life history stages

Life history stages	Analysis	Effect	df Effect	df Error	F	p-level
Males	2-way ANOVA	Station	1	20	1.18659	0.2890
		Time	4	20	*2.93588*	*0.0463*
		Station*Time	4	20	0.83805	0.5171
Females	2-way ANOVA	Station	1	20	0.43692	0.5162
		Time	4	20	*2.99884*	*0.0433*
		Station*Time	4	20	0.81345	0.5314
Ovigerous females	2-way ANOVA	Station	1	20	2.59215	0.1231
		Time	4	20	*3.17546*	*0.0358*
		Station*Time	4	20	1.68518	0.1928
Copepodites	Kruskal Wallis ANOVA	Station	1	28		*0.0294*
		Time	4	25		0.1687

Table II.8: Results of the analyses of the effect of station, time and the interaction term station*time if possible on the proportions of life history stages

Significant temporal gradients were discerned for males, females and ovigerous females (Table II.8). The contribution of females significantly decreased from 9th March in relation to all succeeding months ($p < 0.05$) whereas the relative abundance of males significantly increased between 9th March ($p < 0.01$) or 31st March ($p < 0.05$) and June. The percentage of ovigerous females dropped significantly between 31st March and May or June (twice $p < 0.01$). Fig.II.18 shows that a very high mean relative abundance of juveniles (59 %) was recorded at the end of April at station 215.

3.3 Vertical distribution of harpacticoids

3.3.1 Density

Throughout the whole period a minimum of about 60 % harpacticoids was present in the upper 5 cm of the sediment, with a mean of 75 % over the whole period. Only on 9th March at station 215 the major proportion of the population (53 %) was recorded from deeper levels. Figure II.19 illustrates that harpacticoids are more concentrated in the upper sediment layers in May and June at both stations and on 31st March at station 330 relative to 9th March and 27th April, when harpacticoids were more evenly distributed among depth layers. The temporal differences in vertical distribution were not defined as significant (effect time*depth, Table II.9). Only the effect of depth unrelated to time was judged significant at both stations (Table II.9), attributed to overall higher densities in the depth layers 0-1 cm and 1-2 cm (2x $p < 0.001$).

Station 215 + 330	ANOVA in a split-plot design					pRDA[(1)]
Effect	Error	df Effect	df Error	F ratio	p value	p value
Station	Replicate{station*time}	1	20	2.49111	0.130	0.057
Time	Replicate{station*time}	4	20	*2.99000*	*0.044*	*0.016*
Depth	Depth*replicate{station*time}	7	140	*14.71677*	*0.000*	*0.001*
Time*Station	Replicate{station*time}	4	20	2.80628	0.054	0.930
Depth*Station	Depth*replicate{station*time}	7	140	*2.48000*	*0.020*	*0.001*
Depth*Time	Depth*replicate{station*time}	28	140	1.19167	0.250	0.063
Station*Time*Depth	Depth*replicate{station*time}	28	140	1.15889	0.283	0.417
Station 215		df	df			
Effect	Error	Effect	Error	F ratio	p value	
Time	Replicate{station*time}	4	10	*4.022039*	*0.034*	
Depth	Depth*replicate{station*time}	7	70	*2.715466*	*0.015*	
Time*Depth	Depth*replicate{station*time}	28	70	0.928577	0.574	
Station 330		df	df			
Effect	Error	Effect	Error	F ratio	p value	
Time	Replicate{station*time}	4	10	1.22296	0.361	
Depth	Depth*replicate{station*time}	7	70	*18.53903*	*0.000*	
Time*Depth	Depth*replicate{station*time}	28	70	1.59214	0.060	

(1) Monte-Carlo permutation tests restricted for split-plot design

Table II.9: Results of the analyses of the effect of station, time, depth and the interactions between these factors on densities per depth layer

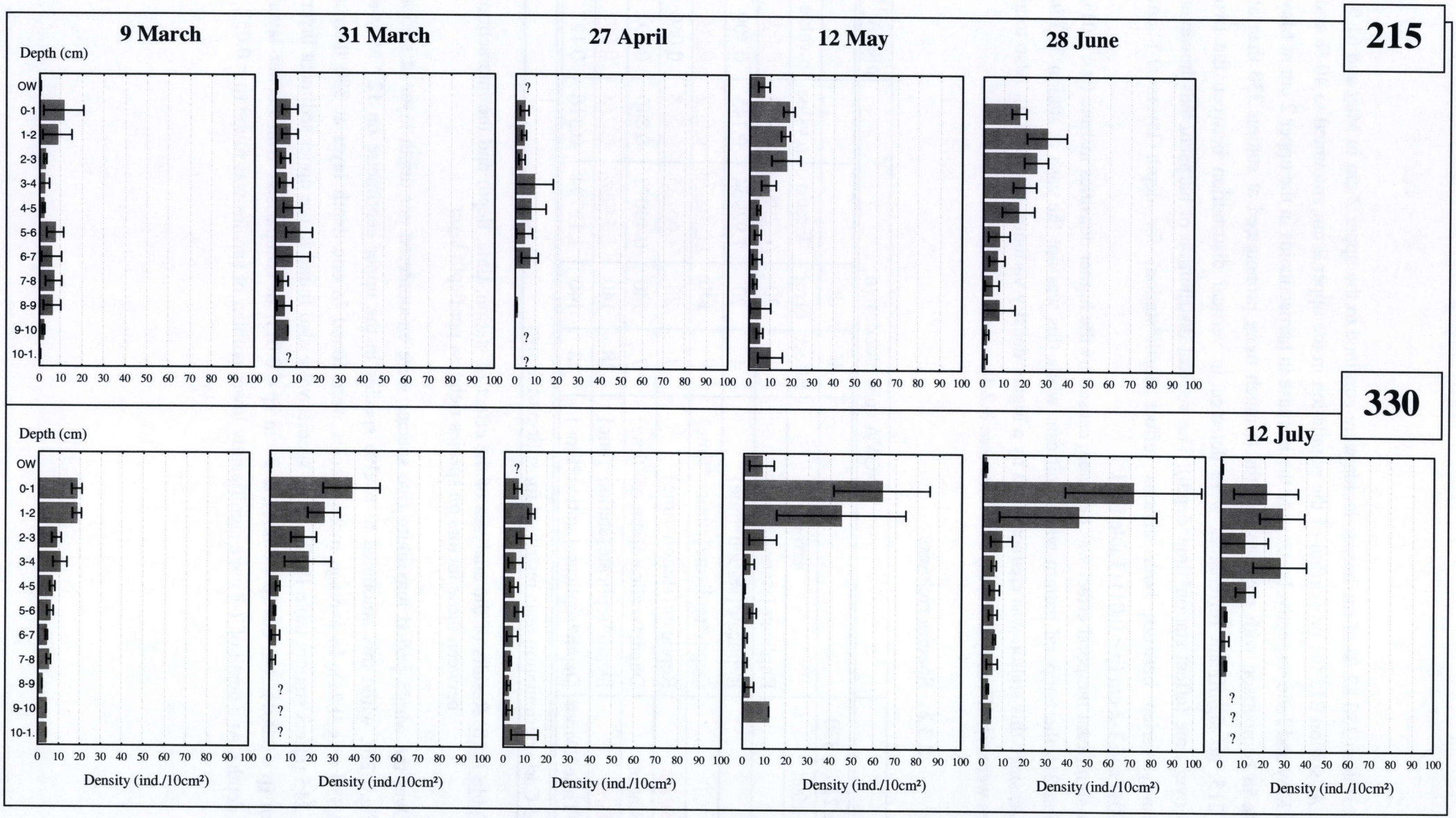

Fig.II.19: Total mean density with standard error per depth layer and per sampling date at stations 215 and 330
A question mark indicates that no data are available from that depth layer.

At station 330 82 % of the harpacticoids were confined to the upper 2 cm in May and 61 % in June. At station 215 the proportion of the population in the upper 2 cm amounted to 40 % and 26 % in May and June respectively. Despite the increase in harpacticoids in the upper 2 cm in May and June in comparison with previous months is much more pronounced at station 330 than at station 215, no significant differences were detected in vertical distribution between the two stations over time (effect station*time*depth). The vertical distribution of harpacticoids however significantly varied between both stations (effect depth*station) for depth layers 0-1 cm ($p < 0.001$) and 1-2 cm ($p < 0.01$) (Table II.9).

A significant temporal effect was detected, caused by the higher densities in June ($p < 0.01$). At station 215 the temporal pattern was significant while this was not the case at station 330 in ANOVA, since this station was characterized by a higher density variation (Table II.9). Also total densities were significantly different over time (see 3.2.1).

3.3.2 Species richness

	ANOVA split plot design					pRDA[1]
Station 215 + 330		df	df			
Effect	Error	Effect	Error	F ratio	p value	p value
Station	Replicate{station*time}	1	20	*10.29592*	*0.004*	*0.006*
Time	Replicate{station*time}	4	20	1.92964	0.145	0.409
Depth	Depth*replicate{station*time}	7	140	*11.81873*	*0.000*	*0.001*
Time*Station	Replicate{station*time}	4	20	*4.66785*	*0.008*	0.060
Depth*Station	Depth*replicate{station*time}	7	140	0.49072	0.840	0.292
Depth*Time	Depth*replicate{station*time}	28	140	*1.64090*	*0.033*	*0.002*
Station*Time*Depth	Depth*replicate{station*time}	28	140	1.12794	0.316	0.122

[1] Monte-Carlo permutation tests restricted for split-plot design

Table II.10: Results of the analyses of the effect of station, time, depth and the interactions between these factors on species richness per depth layer

Over the whole period maximum five species were encountered per depth layer at station 215 (Fig.II.20), while this amounted to twelve species in the upper centimetre on 12th May at station 330 (Fig.II.21). In average more species were found in one depth layer at 330 than at station 215 (effect station, table II.10). More species were also found in the upper sediment layers (0-1 cm ($p < 0.001$), 1-2 cm ($p < 0.001$), 2-3 cm ($p < 0.01$)) in comparison with deeper layers (effect depth). At a depth of 7-8 cm a significantly lower number of species was found ($p < 0.05$).

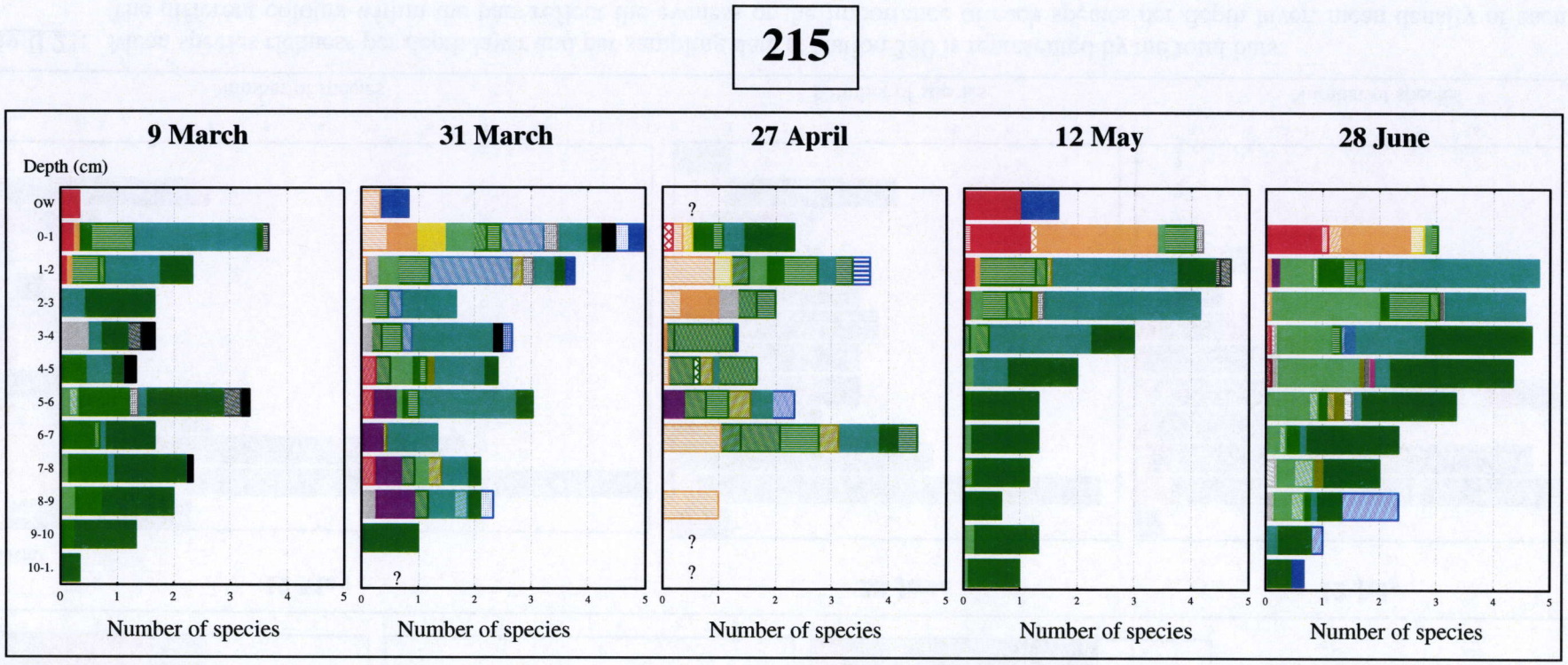

Fig.II.20: Mean species richness per depth layer and per sampling date at station 215 is represented by the total bars.
The different colours within the bars reflect the evenness or the importance of each species per depth layer, mean density of each species being represented as a proportion of the species richness. Hence it is clear how many species were present in the three replicates, contributing to the mean species richness per depth layer.
Red coloured patterns are epibenthic species, orange coloured patterns are endobenthic species, bright blue coloured patterns are phytal or free-swimming species and all other colours point to interstitial species.
A question mark indicates that no data are available from that depth layer.

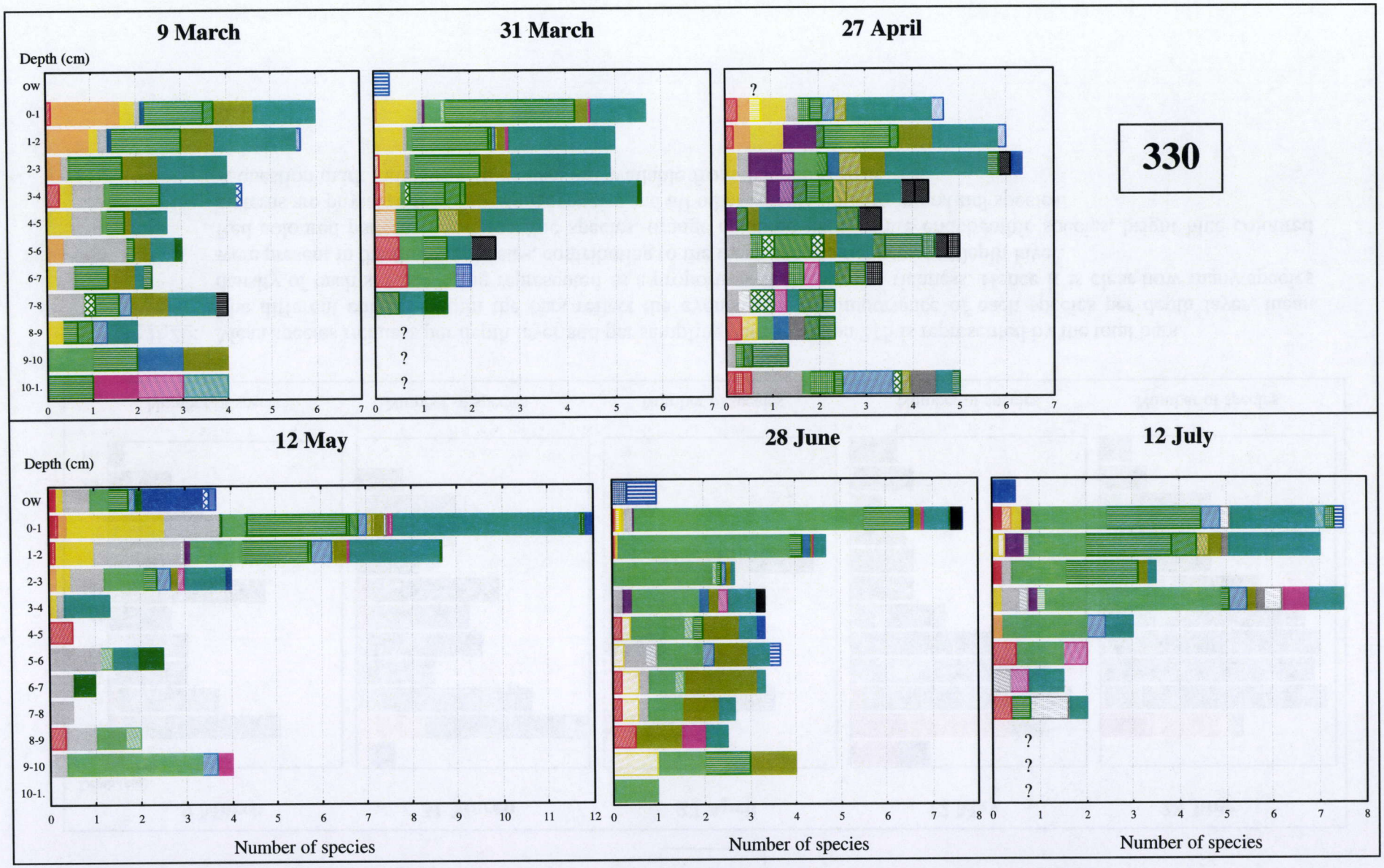

Fig.II.21: Mean species richness per depth layer and per sampling date at station 330 is represented by the total bars.
The different colours within the bars reflect the eveness or the importance of each species per depth layer, mean density of each species being represented as a proportion of the species richness. Hence it is clear how many species were present in the three replicates, contributing to the mean species richness per depth layer.
Red coloured patterns are epibenthic species, orange coloured patterns are endobenthic species, bright blue coloured patterns are phytal or free-swimming species and all other colours point to interstitial species.
A question mark indicates that no data are available from that depth layer.

A clear temporal trend in mean species number per depth layer was not observed. For specific depth layers however significant changes were recorded through time (effect depth*time). In May more species were present in the upper 3 cm of the sediment (0-1 cm ($p < 0.001$), 1-2 cm ($p < 0.01$), 2-3 cm ($p < 0.01$)). In April the upper cm yielded a lower number of species ($p < 0.05$) while more species were concentrated in the deeper layers (6-7 cm ($p < 0.05$)). More copepod species also preferred to stay deeper in the sediment on 9th March in comparison with the succeeding months (7-8 cm ($p < 0.05$). The effect time*station reflected the different trend in species richness between both stations.

3.3.3 Species composition

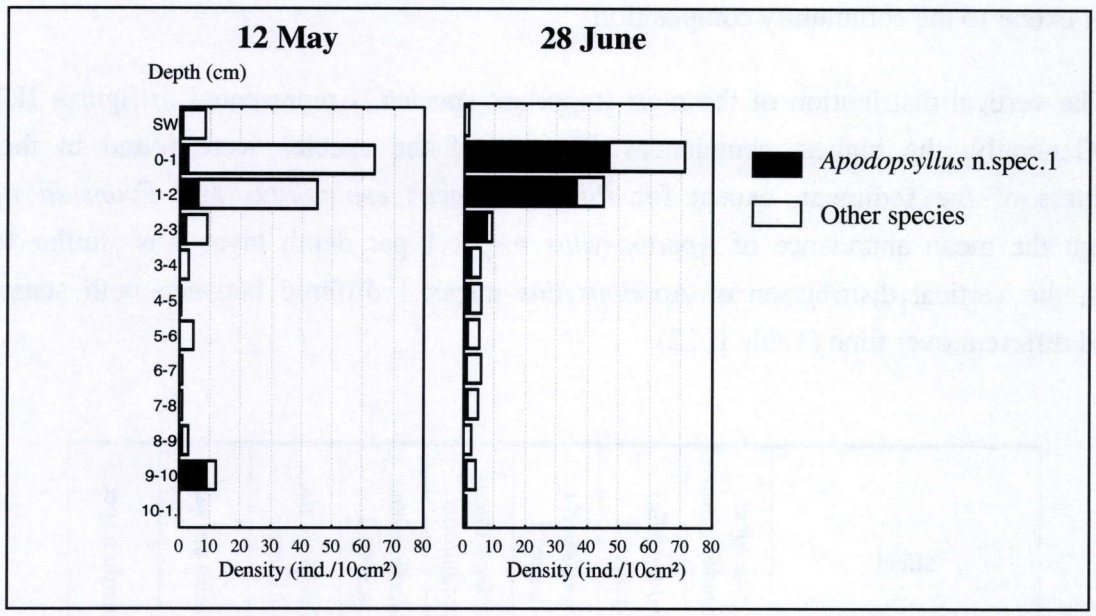

Fig.II.22: Mean absolute densities of *Apodopsyllus* n.spec.1 per depth layer in relation to the importance of other species on 12th May and 28th June at station 330

Fig.II.20 and II.21 illustrate that the species composition between both stations differed considerably and that a lot of species appeared only in April and were not encountered at any other date. April was also characterized by a higher eveness of the species, detected in all depth layers. Below 2 cm depth the variation between the replicates was much higher than at any other moment, while the mean number of species per depth layer was not higher than for the other recordings. The unique characteristics of the harpacticoid community in April applied to both stations.

At station 215 the harpacticoid community of 9th March, 12th May and 28th June was characterized by a high proportion of a few and largely the same species through the depth of the sediment. On 31st March an intermediate species assemblage between 9th March and 28th April was discerned. Especially in the surface layers of the sediment most of the species varied between the replicates. One species (*Leptastacus laticaudatus s.str.*) dominated the community through the depth of the sediment but eveness was already higher at this time.

In June *Apodopsyllus* n.spec.1 became very abundant (17 % of the total density) and preferred the upper 5 cm of the sediment. The same happened in June at station 330, *Apodopsyllus* n.spec. 1 accounting for 55 % of the total density. This species made up 67 % and 54 % in the 0-1 cm and 1-2 cm depth layer respectively (Fig.II.22).

At station 330 the species assemblage on 31st March was very similar to the situation on 9th March, in contrast with station 215. At station 330 the species assemblage in May and June also deviated from that on 9th March. On 12th May a lot of species occur in the upper 3 cm while the deeper layers were impoverished. In June a lot of the species had withdrawn to deeper levels while *Apodopsyllus* n.spec. 1 dominated the upper centimetres. In July more species contributed again in a higher extent to the community composition.

The vertical distribution of the most important species is represented in figures II.23 upto II.30. Generally, the highest abundances of most of the species were found in the upper centimetres of the sediment, except for *Paraleptastacus espinulatus* and *Evansula* n.spec.1. Although the mean abundance of *Apodopsyllus* n.spec.1 per depth layer was similar for both stations, the vertical distribution of *Apodopsyllus* n.spec.1 differed between both stations and behaved different over time (Table II.12).

effect	*Leptastacus laticaudatus s.str.*	*Apodopsyllus* n.spec.1	*Arenosetella* n.spec.1	*Paraleptastacus espinulatus*	*Halectinosoma* n.spec.2	*Thompsonula hyaenae*	*Ameira parvula*	*Evansula* n.spec.3
station	n.s.	n.s.	**	**	n.s.	*	**	**
time	n.s.	**	n.s.	**	n.s.	*	n.s.	n.s.
depth	**	**	n.s.	n.s.	**	**	**	n.s.
depth x time	n.s.	n.s.	n.s.	n.s.	*	**	*	*
depth x station	n.s.	**	n.s.	n.s.	n.s.	**	**	**
time x station	n.s.	n.s.	*	**	*	n.s.	n.s.	n.s.
station x time x depth	**	**	*	n.s.	**	*	**	*

Table II.12: Results of the Monte-Carlo permutation tests restricted for split-plot design using pRDA testing the effect of station, time, depth and the interactions between these factors on the absolute densities of the most important species, * $p < 0.05$, ** $p < 0.01$

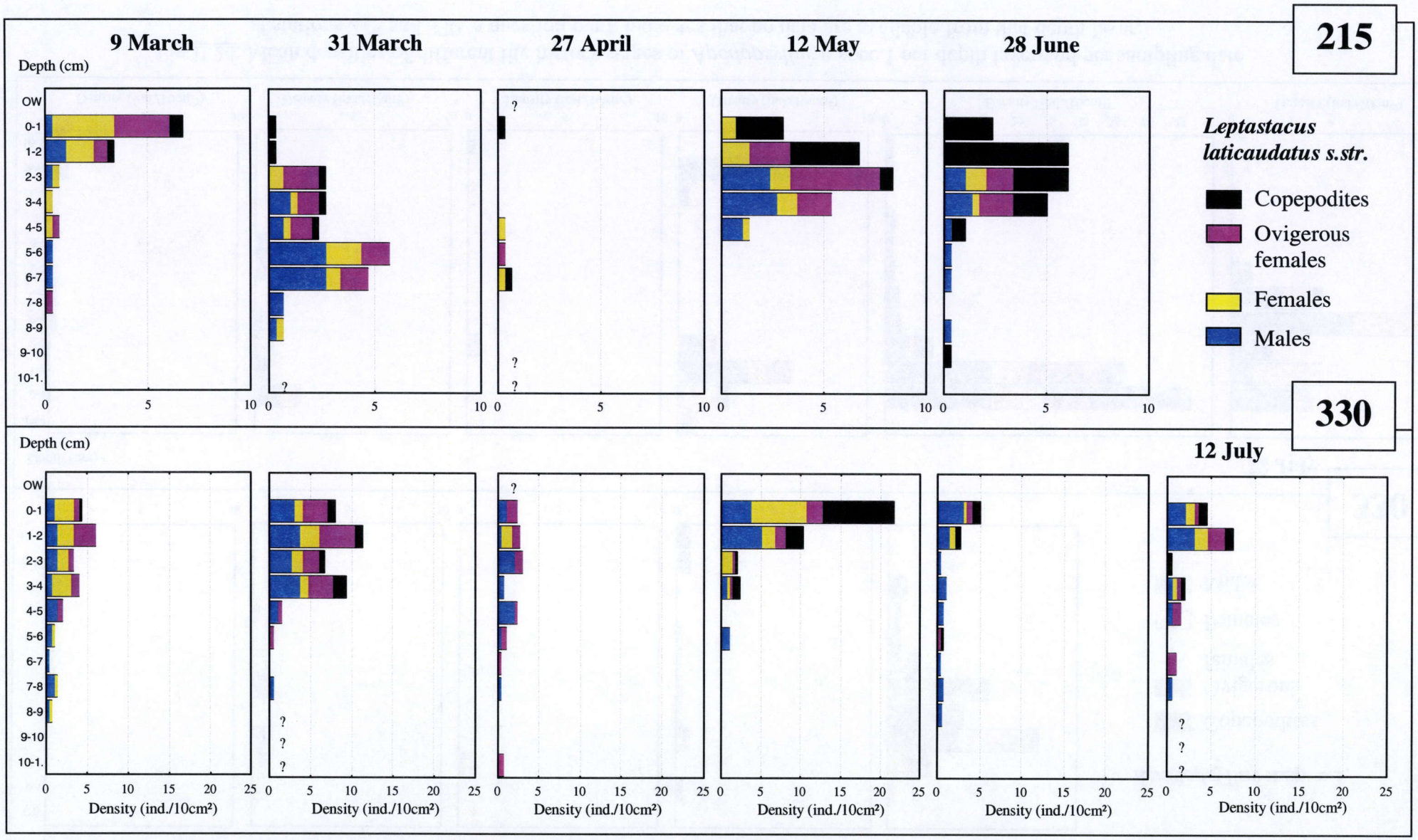

Fig.II.23: Mean densities of different life history stages of *Leptastacus laticaudatus s.str.* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

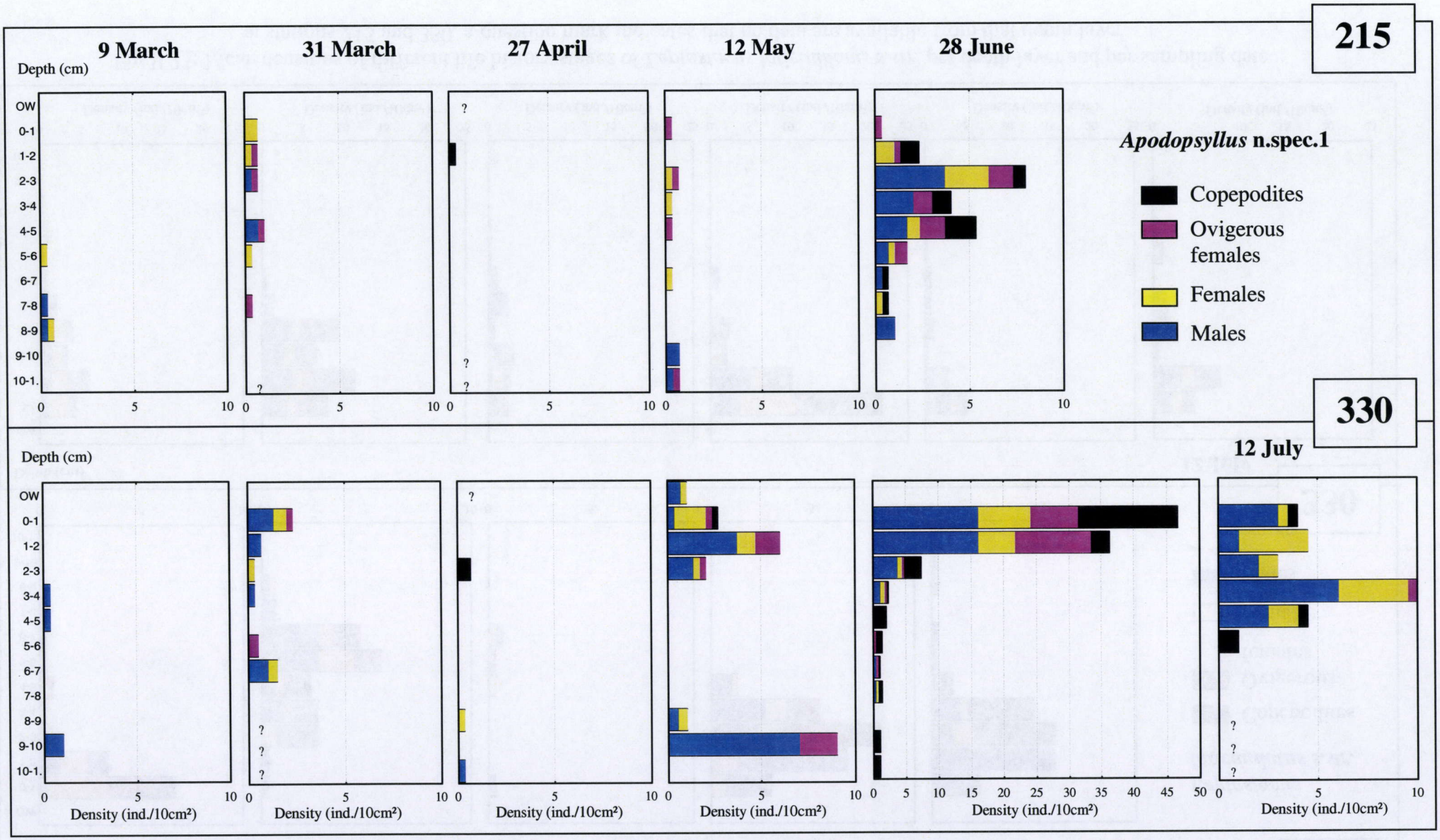

Fig.II.24: Mean densities of different life history stages of *Apodopsyllus* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

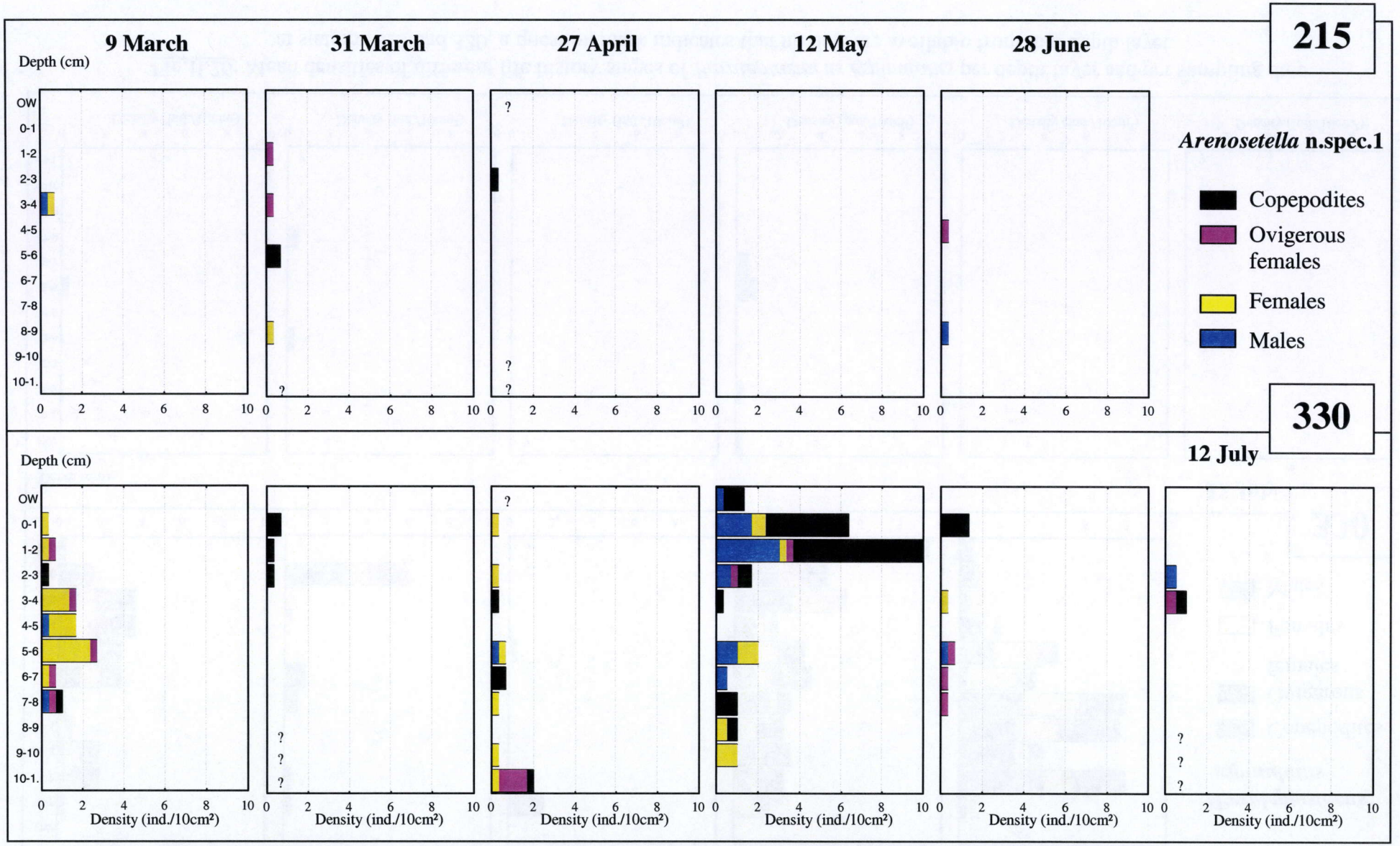

Fig.II.25: Mean densities of different life history stages of *Arenosetella* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

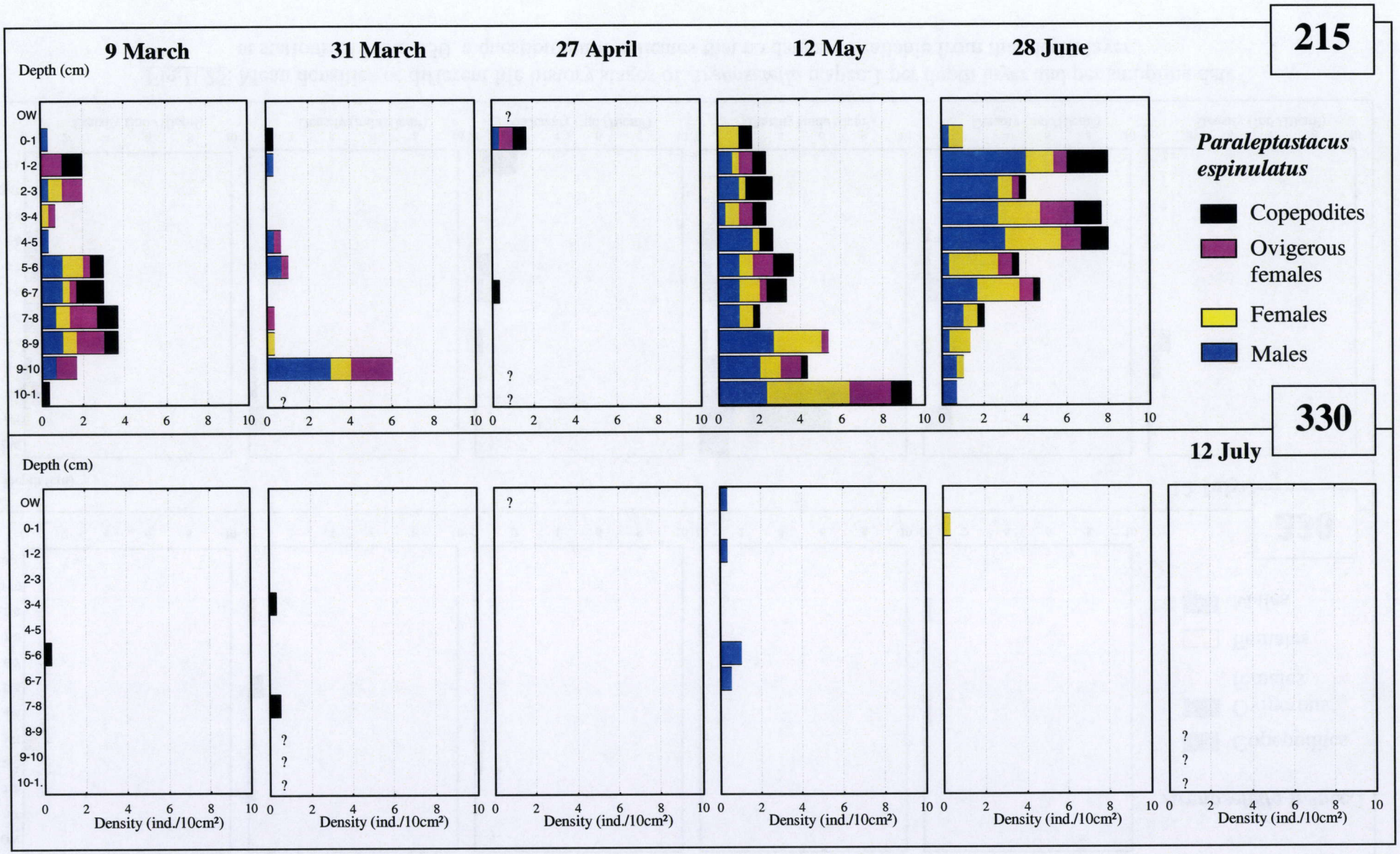

Fig.II.26: Mean densities of different life history stages of *Paraleptastacus espinulatus* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

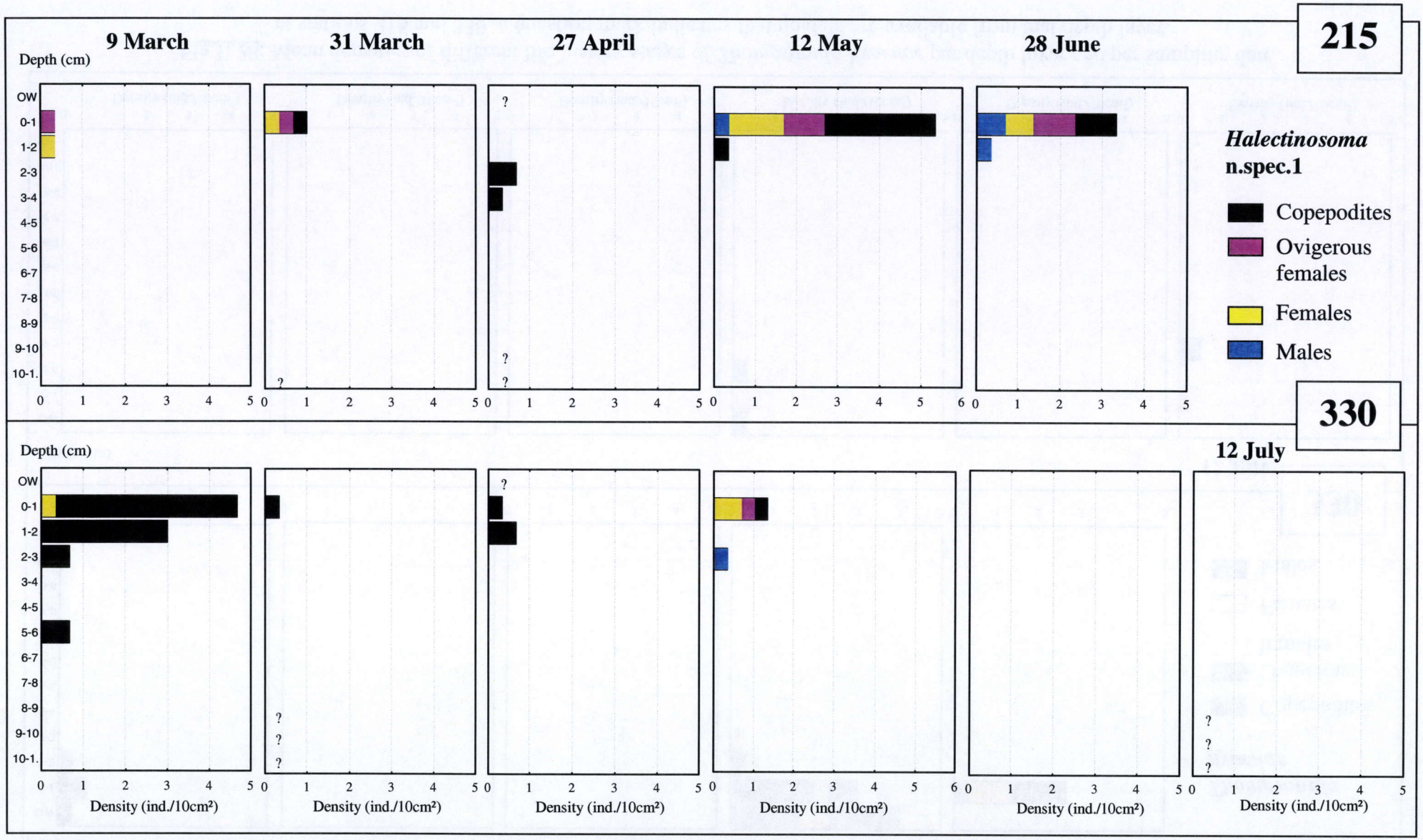

Fig.II.27: Mean densities of different life history stages of *Halectinosoma* n.spec.1 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

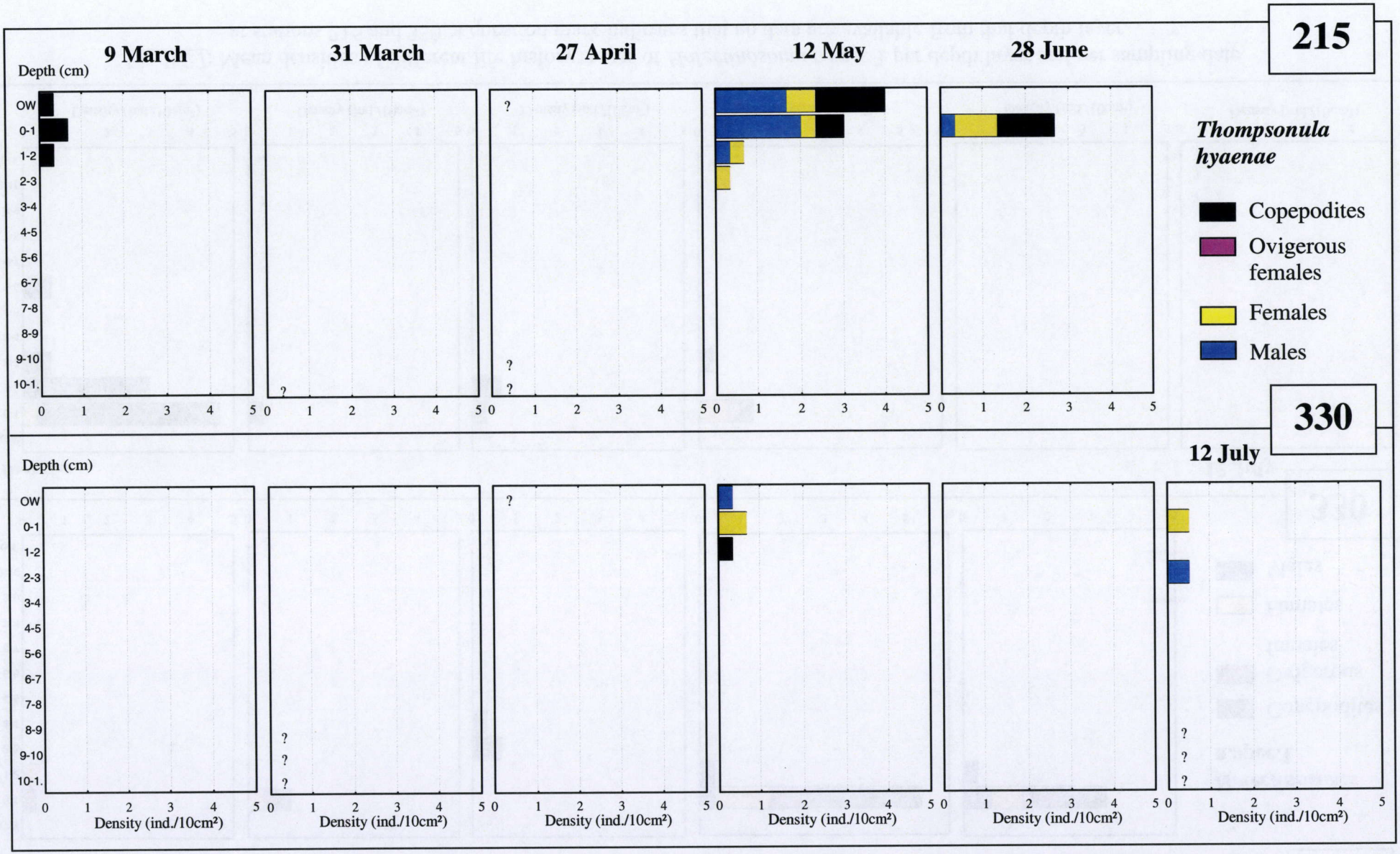

Fig.II.28: Mean densities of different life history stages of *Thompsonula hyaenae* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

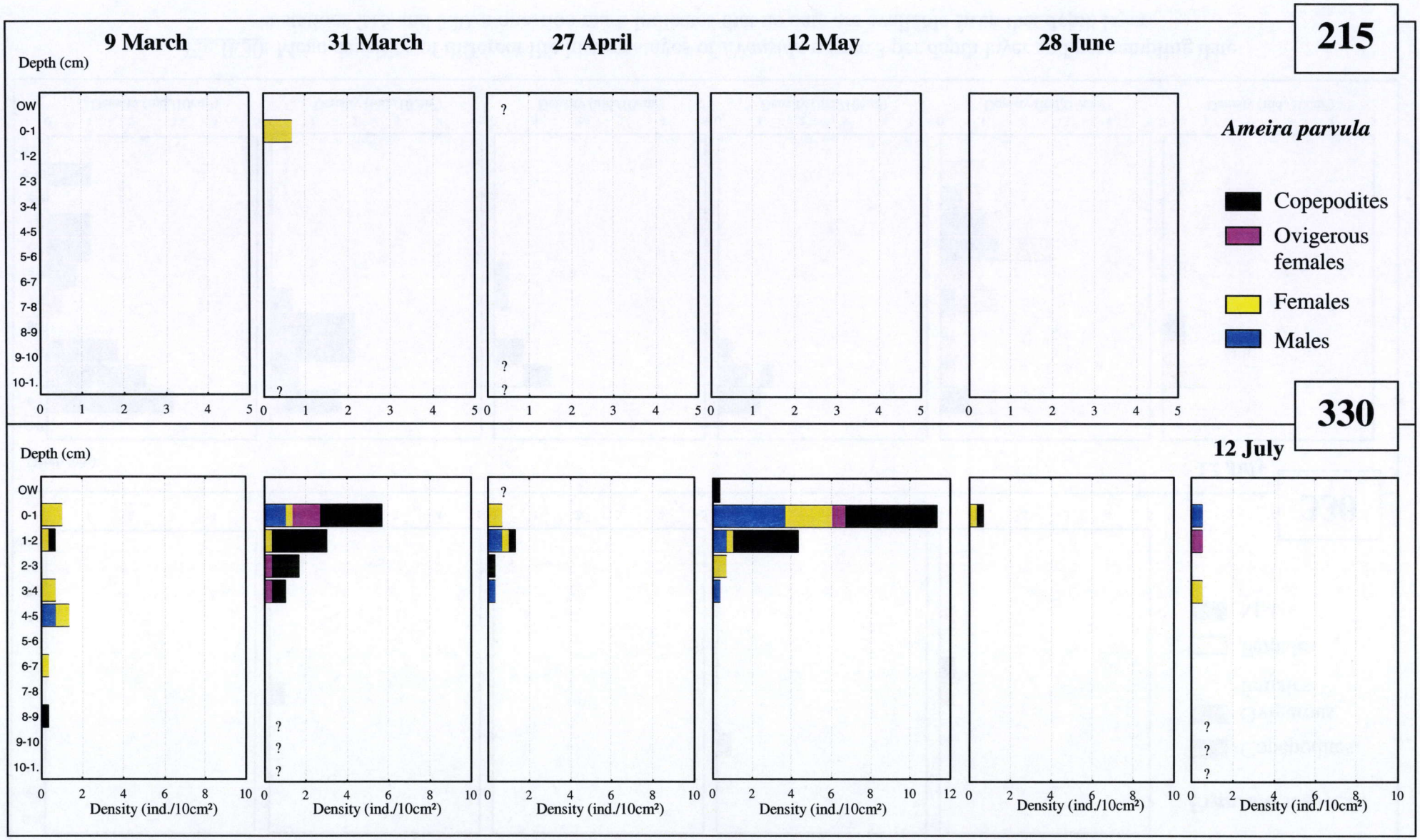

Fig.II.29: Mean densities of different life history stages of *Ameira parvula* per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

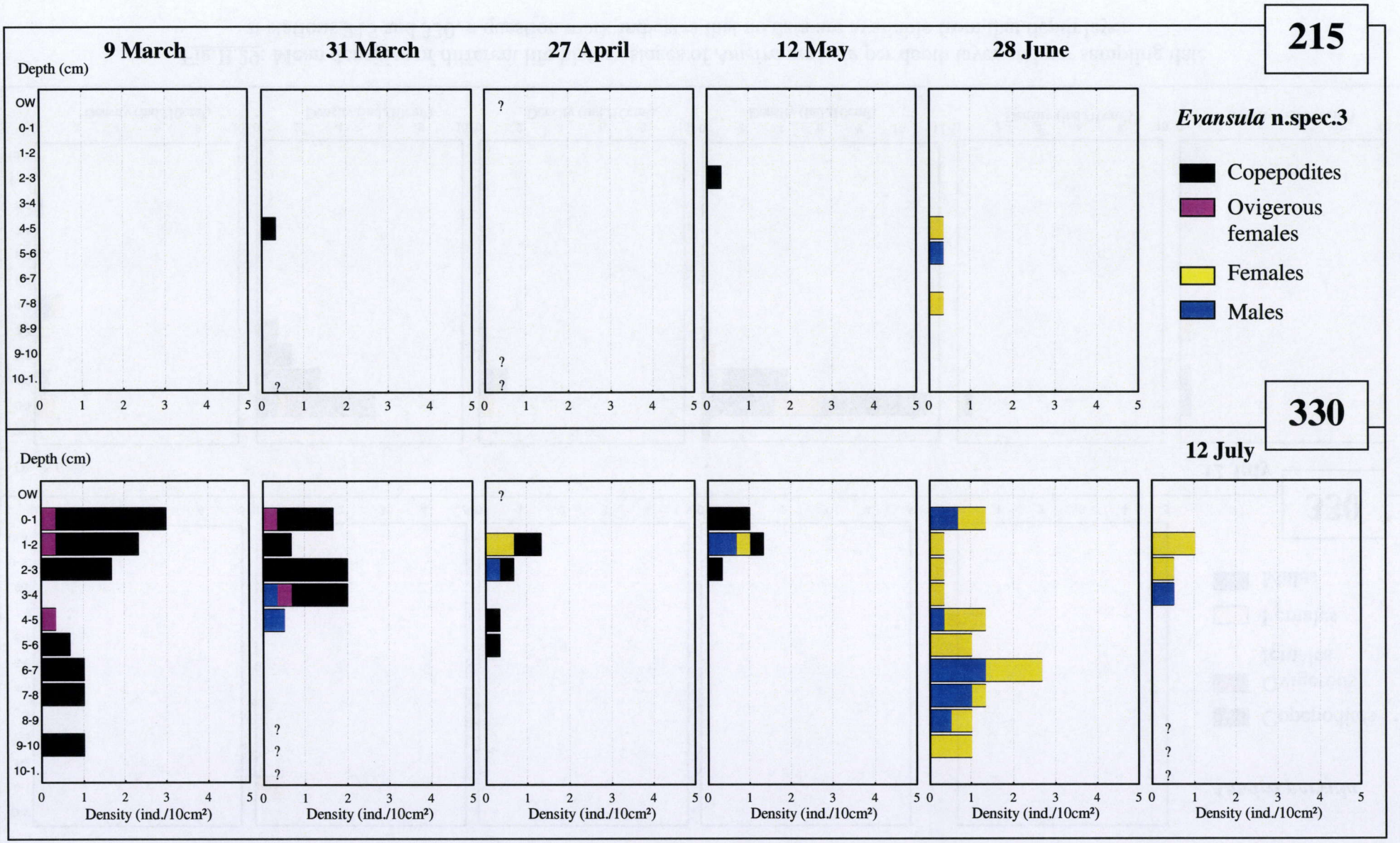

Fig.II.30: Mean densities of different life history stages of *Evansula* n.spec.3 per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

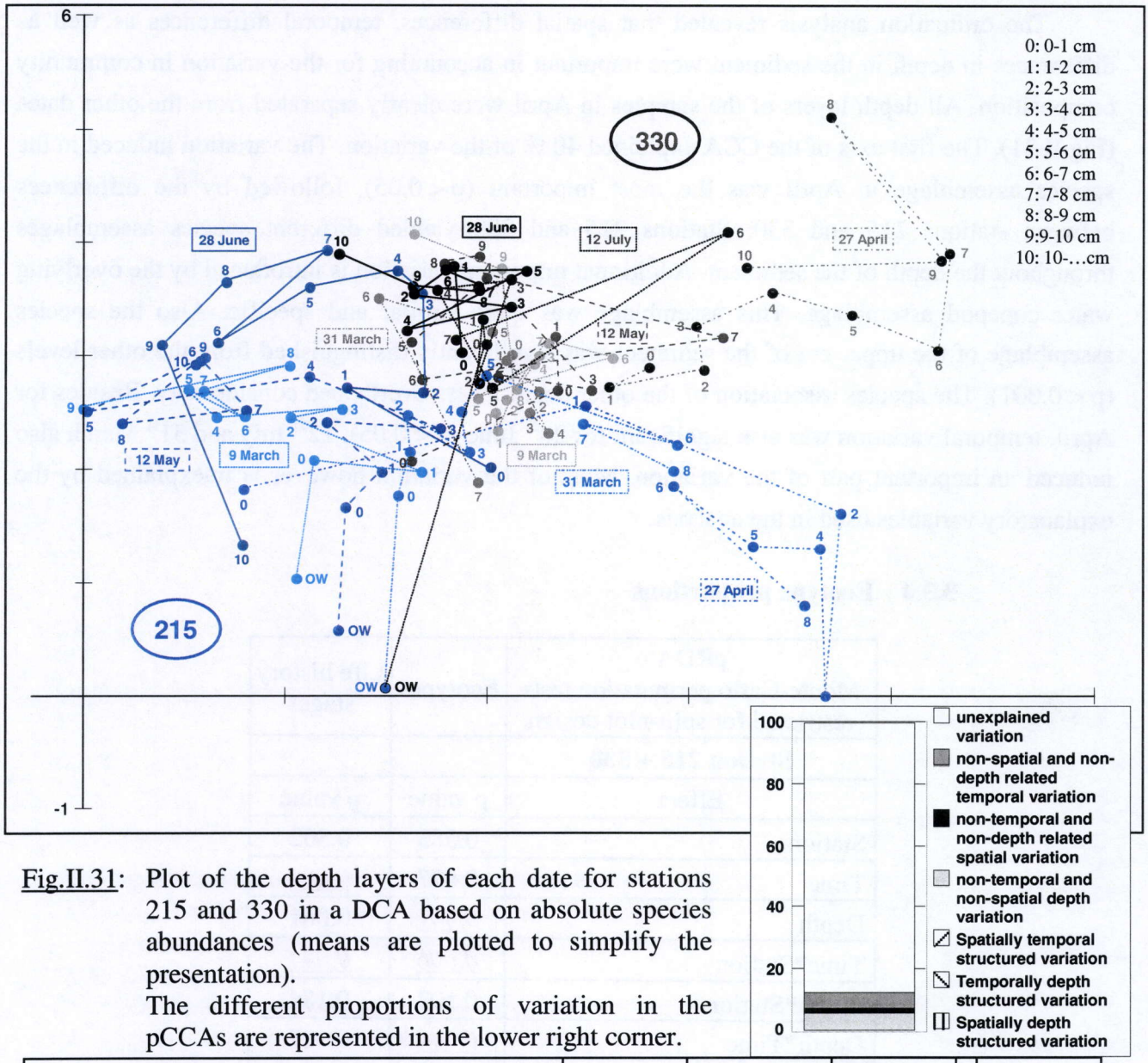

Fig.II.31: Plot of the depth layers of each date for stations 215 and 330 in a DCA based on absolute species abundances (means are plotted to simplify the presentation).
The different proportions of variation in the pCCAs are represented in the lower right corner.

	Analysis	Eigenvalue	% of total variation		p value [1]
Total variation	CA	19.509			
Spatial + temporal + depth structured variation	CA	2.464	12.63		
Non-temporal and non-depth related spatial variation	pCCA	0.352	1.80		*0.026*
Non-spatial and non-depth related temporal variation	pCCA	0.933	4.78		*0.001*
Non-temporal and non-spatial depth variation	pCCA	1.131	5.80		*0.002*
Spatially temporal structured variation = effect station*time	pCCA	0.005	0.03		*0.029*
Spatially depth structured variation = station*depth	pCCA	0.009	0.05		0.097
Temporally depth structured variation = time*depth	pCCA	0.034	0.17		0.465
Spatially and temporally depth structured variation = effect station*time*depth	pCCA	0.002	0.01		0.259
[1] Monte-Carlo permutation tests restricted for split-plot design					

Table II.12: Results of the analyses of the effect of station, time, depth and the interactions between these factors on species composition

The ordination analysis revealed that spatial differences, temporal differences as well as differences in depth in the sediment were important in accounting for the variation in community composition. All depth layers of the samples in April were clearly separated from the other dates (Fig.II.31). The first axis of the CCA explained 40 % of the variation. The variation induced in the species assemblage in April was the most important ($p < 0.05$), followed by the differences between stations 215 and 330. Stations 215 and 330 yielded different species assemblages throughout the depth of the sediment. Additional important variation is introduced by the overlying water copepod assemblage. This assemblage was quite similar and specific. Also the species assemblage of the upper cm of the sediment was significantly distinguished from the other levels ($p < 0.001$). The species association of the other depth layers overlapped considerably. Besides for April, temporal variation was also significant for 28th June ($p < 0.05$). 12th July and 31st March also induced an important part of the variation. Most of the variation however is unexplained by the explanatory variables used in the analysis.

3.3.4 Ecotype proportions

pRDA Monte-Carlo permutation tests restricted for split-plot design	Ecotypes	Life history stages
Station 215 + 330		
Effect	p value	p value
Station	0.583	0.302
Time	0.477	*0.004*
Depth	*0.001*	0.061
Time*Station	*0.006*	*0.043*
Depth*Station	0.102	0.184
Depth*Time	*0.044*	0.127
Station*Time*Depth	*0.002*	*0.027*

Table II.13: Results of the analyses of the effect of station, time, depth and the interactions between these factors on ecotype proportions and on the proportions of life history stages

Depth was an important structuring variable for ecotype distribution (Table II.13). Endobenthic species were significantly more abundant in the upper cm of the sediment in comparison with deeper levels, whereas it was the other way around at 7-8 cm depth. Yet, the typical sediment surface inhabiting epi- and endobenthic species were not restricted to the upper sediment layers (Fig.II.32 and II.33). Especially epibenthic species often occurred in deeper layers of the sediment, reducing the relative abundance of the interstitial species. These fluctuations in vertical distribution were responsible for the significant effect of depth*time. The presence of epibenthic species in deeper levels was more important at station 330 than at station 215, resulting

in the significant effect of station*time*depth. The endobenthic species were more restricted to the upper sediment layers than the epibenthic species at station 215, where they were not encountered anymore below 3 cm depth. They were very abundant in the upper cm in May and June. At station 330 they were also frequently found in the surface layers of the sediment in May but their abundance in the upper 2 cm was reduced in June. They were still frequently found in the deeper layers from 4 to 10 cm depth at that moment, contributing to the significant effect station*time*depth. The higher relative abundances of epi-and endobenthic species at station 215 in comparison with station 330 in April explain the significant effect of time*station ($p < 0.01$ for April). A significant effect of the interaction between time and station was also observed in May ($p < 0.05$) because more epi- and endobenthic species were then found at station 330. Some free-swimming species were also encountered in the deeper layers of the sediment. Another peculiarity is that in May even interstitial species were present in the overlying water.

3.3.5 Life history stages

Depth does not influence the distribution of males, (ovigerous) females or juveniles of the total species assemblage in the sediment (Table II.13). In general adults do not make excursions into the sediment or to the surface over time and copepodites were not found to be concentrated at the surface layers (Fig.II.34). In April the latter were even more abundant in the deeper layers of the sediment. In April the lower contribution per depth layer of all adults in favour of copepodites at station 215 in comparison with station 330 resulted in a significant effect time*station ($p < 0.01$ for April). This kind of interaction also comprised differences in May ($p < 0.05$) between both stations due to the higher contribution of males at the expense of females and ovigerous females at station 330. The significant temporal pattern was already illustrated by the total percentages per sample (see 3.2.4) and was confirmed by the proportions per depth layer ($p < 0.05$ for 31st March). On 31st March more ovigerous females and less females and copepodites were encountered per depth layer than at the other sampling dates ($p < 0.05$).

The distribution of the life history stages of the most important species is illustrated in figures II.23 up to II.30. *Leptastacus laticaudatus s.str., Apodopsyllus* n.spec.1 and *Arenosetella* n.spec.1 showed enhanced recruitment in May and/or June. At station 330 the highest number of juneniles of *Evansula* n.spec.3 and *Halectinosoma* n.spec.1 was found on 9th March. Juveniles of *Leptastacus laticaudatus s.str.* and *Arenosetella* n.spec.1 are concentrated in the upper layers of the sediment, whereas the relative distribution of the different life history stages of *Apodopsyllus* n.spec.1, *Paraleptastacus espinulatus* and *Evansula* n.spec.3 was similar throughout the depth of the sediment.

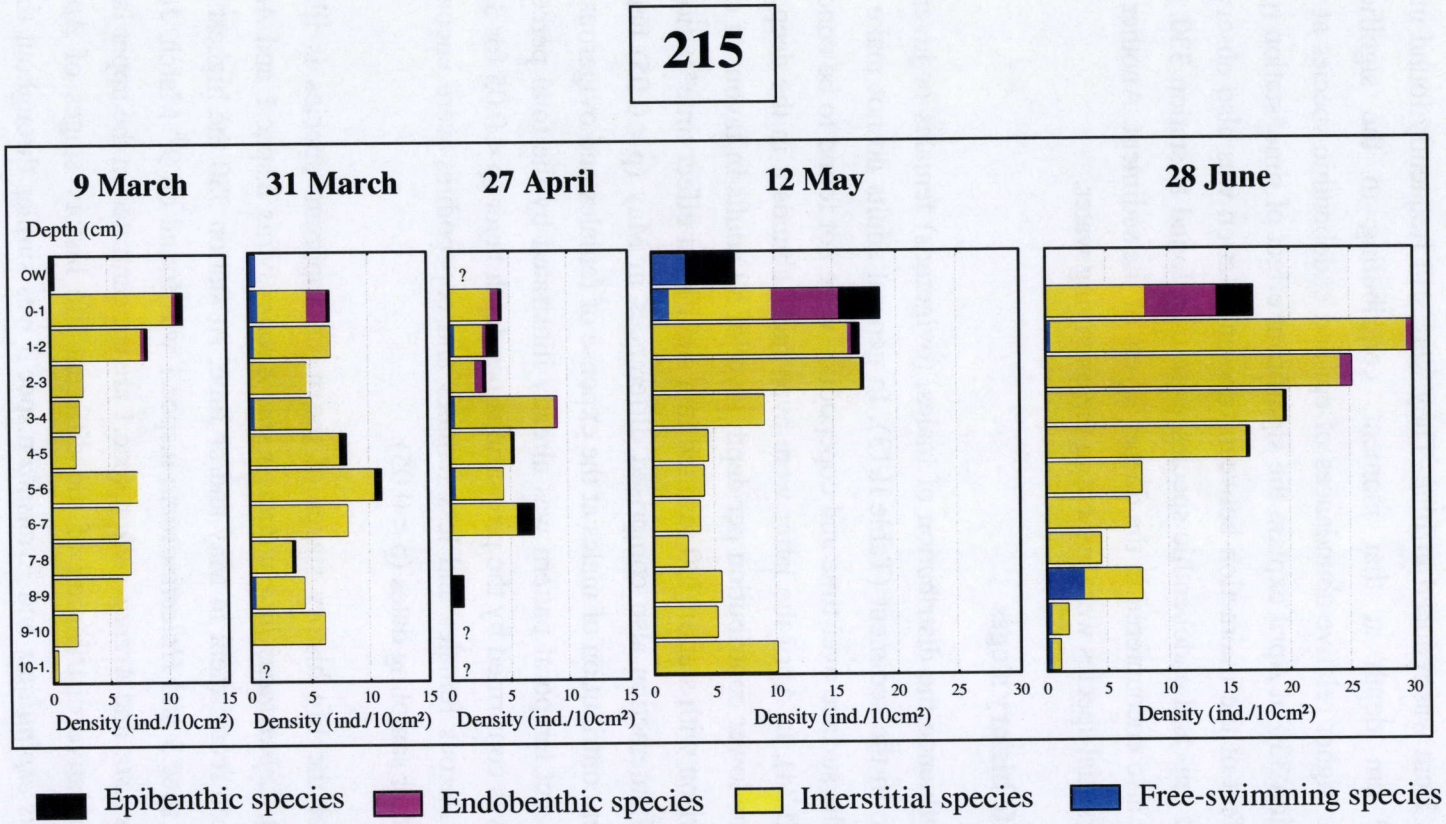

Fig.II.32: Mean relative abundances of different ecotypes per depth layer and per sampling date at station 215, a question mark indicates that no data are available from that depth layer.

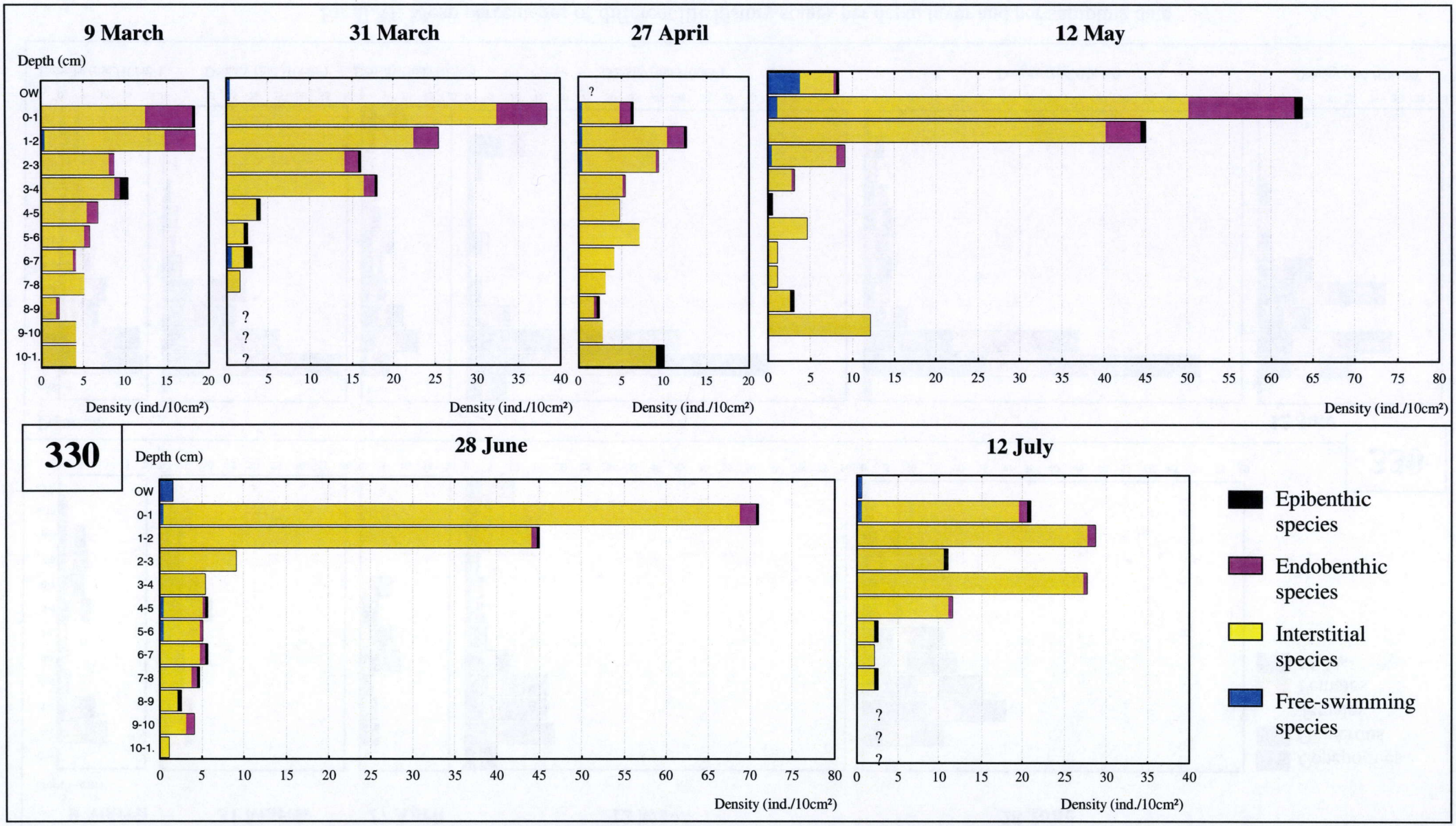

Fig.II.33: Mean relative abundances of different ecotypes per depth layer and per sampling date at station 330, a question mark indicates that no data are available from that depth layer.

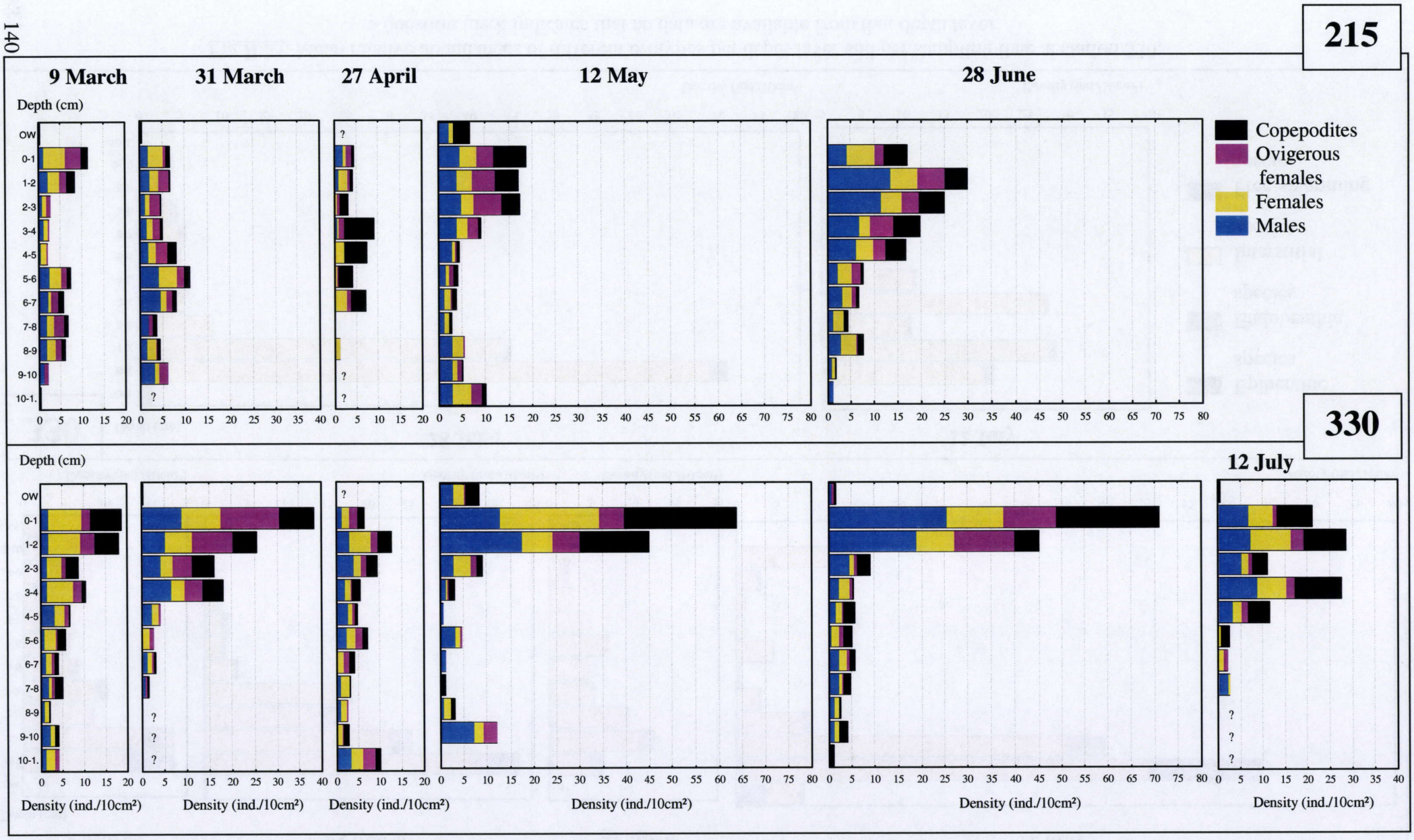

Fig.II.34: Mean percentages of different life history stages per depth layer and per sampling date at stations 215 and 330, a question mark indicates that no data are available from that depth layer.

4 Discussion

4.1 Environmental data

4.1.1 High chlorophyll *a* background signature near and in the sediment

Surprisingly, the highest chlorophyll *a* concentration in the sediment was recorded on 9th March at both stations. At station 330, the chlorophyll *a* and fucoxanthin concentration in the overlying water showed a peak as well, whereas this was not visible in the surface water. The chlorophyll *a* and fucoxanthin concentrations point to the presence of diatoms, Chrysophyceae, Prymnesiophyceae or brown macroalgae. Several reasons may explain elevated chlorophyll *a* and fucoxanthin concentrations near and in the bottom unrelated to primary production in the water column: 1) lateral advection of deposited organic matter such as macroalgae (Graf, 1992); 2) benthic primary production of bottom-dwelling algae such as diatoms or 3) presence of diatom spores in the sediment.

Lateral advection and accumulation of a great amount of deposited phytoplankton from the water column is impossible as diatoms or *Phaeocystis* cells (Prymnesiophyceae) were not observed yet (in high numbers for diatoms) in the water column at that time. Vanaverbeke (2003) ascribed the high chlorophyll *a* concentration at station 330 on 9th March to the deposition of slowly decaying macroalgae, because the phytopigment signature disappeared slowly. Macroalgae increase organic matter content in sediments during winter, when thalli are torn off by storms and are transported to deeper areas (Price & Hylleberg, 1982; Graf *et al.*, 1983; Abele, 1988). In the Kiel Bight sediments 73 % of the organic matter is derived from macrophytes (Liebezeit, 1986). The Kiel Bight is a relatively non-turbulent enclosed body (Smetacek, 1984; Boon & Duineveld, 1996), where macroalgae may accumulate and sink. The sandbank system is definitely not. At station 215 still much higher chlorophyll *a* concentrations were reported on 9th March, throughout the depth of the sediment. The recurrence of this observation cast doubt on the possibility of the deposition of macroalgae. Deposition and burying of macroalgae would happen rather exceptionally because of the high hydrodynamics of the area and the remoteness of areas with dense patches of macroalgae. An accumulation of macrophytes might occur at places with reduced current velocity in the gullies but very unlikely on the sandbanks themselves. Both observations at station 215 and station 330 may also be unrelated and caused by a different kind of organic supply.

At a depth of 12 m at station 215 there might also be an effect of benthic primary production (Rosenfeld, 1979). In shallow areas benthic algae sometimes overrule the phytoplankton: in the Wadden Sea, for instance, the mean benthic primary production is of the same magnitude as the phytoplankton production (Postma, 1982). Sufficient light intensity reaching the bottom is the ultimate requirement for autotrophic activity on the bottom. Euphotic depths in the Belgian and Dutch coastal waters range respectively between 70 and 8 m in offshore areas (Gieskes & Kraay,

1975, 1977; Lancelot & Mathot, 1987). Gieskes & Kraay (1975) observed that the onset of the growing season was related to a mean light intensity over the mixed water column of 0,03 gcal/cm²min. In general this is attained in February-March in the Belgian and Dutch offshore waters. Irradiance measurements on 9th March at station 215 show that the euphotic depth was 9.5 m, i.e. approximately 2 meters above the bottom and benthic diatoms were not observed in the sediment samples (Bonne & Muylaert, pers. obs.). Benthic primary production could hence not have been important. Moreover, benthic primary production would only take place at the sediment surface, whereas the high concentrations were found through the depth of the sediment.

Yet, pelagic diatoms and a lot of tychopelagic diatoms were frequently encountered in the sediment samples (Bonne, Muylaert & Sabbe, pers. obs.). The exact life form of the latter kind of diatoms is little known (Sabbe, 1997). A lot of diatoms rely on physical mixing to sustain production and some of them are known to migrate with the tide between sediment and water column in estuaries (Lauria *et al.*, 1999). The presence of these diatoms have contributed to the fluctuations in the pigment signature but the observed amount of tychopelagic diatoms is probably not high enough to explain the high values of the pigment profile on 9th March (Bonne & Muylaert, pers. obs.). Diatom spores cannot give such a strong pigment signature either (Muylaert, pers. comm.).

A high background level of organic matter may also be related to non-active autotrophs. Hansen & Josefson (2003) found comparable concentrations in aphotic sediments prior to the spring phytoplankton bloom in the Baltic, due to the presence of predominantly spore-forming diatoms. The diatom pool sizes supported the idea that diatoms do survive for long periods in sediments and that diatoms buried in the sediment have very slow degradation rates (Hansen & Josefson, 2001). Upon the death of diatoms, remineralization of the frustules occurs slowly in aerobic conditions (Van Bennekom *et al.*, 1974). The grazing upon diatoms somewhat enhances Si remineralization (Johnston, 1973). Finally Sun *et al.* (1991) suggested that more than one pool of chlorophyll exists and that some of the chlorophyll in the sediment is unrelated to fresh phytodetritus. The present organic matter may constitute a non-reactive, refractory fraction which has already reached the maximum degree of degradation (Graf, 1992). It is concluded that the background level on 9th March is mainly due to older buried phytoplankton derived material. This phytodetritus may have accumulated during autumn and winter and not have been processed completely due to low temperatures (Rudnick *et al.*, 1985). Yet, under oxic conditions it is most likely that a settling autumn bloom can be completely consumed by a well established benthic community (Graf *et al.*, 1983).

4.1.2 Diatom and *Phaeocystis* bloom

Diatom and *Phaeocystis* C biomass data expressed a diatom bloom from mid March until the end of April, followed by a *Phaeocystis* bloom from mid April until mid May in 1999. This succession is common in the southern North Sea (Nelissen & Stefels, 1988; Reid *et al.*, 1990; Lancelot *et al.*, 1987; Lancelot *et al.*, 1998; Rousseau, 2000). The developing diatom bloom was also reflected by the declining Si concentrations from the beginning of March to the end of April in the bottom water at station 330 (Lancelot & Mathot, 1987; Rousseau *et al.*, 2000). Si concentration increased again through remineralization from the end of April to mid June, being processed again in a second moderate diatom bloom in July. Very low nitrate and phosphate concentrations in the surface water at the end of April confirmed the *Phaeocystis* bloom peaked at that moment and also marked the end of the bloom (Van Bennekom *et al.*, 1975; Gieskes & Kraay, 1975; Veldhuis *et al.*, 1987). The drop in salinity at both stations indicated a high input of fresh water from the river Scheldt (Yang, 1998; Rousseau, 2000) and Yser (for station 215), probably enhanced by heavy rainfall (Rousseau, 2000). The high input of river water may be enhanced by the storm on 27th April and probably even increased the biomass of *Phaeocystis* offshore, as these runoff waters are characterized by a high nutrient load (Nelissen & Stefels, 1988).

4.1.3 Sedimentation of primary production

Direct sedimentation of phytoplankton cells in the North Sea has been shown to be very important, particularly during and at the end of phytoplankton blooms (Fransz & Gieskes, 1984; Gieskes & Kraay, 1984; Cadée, 1985). Sedimentation of *Phaeocystis* colonies has already been described in the Southern Bight of the North Sea for long time (Savage & Hardy, 1934). Sedimentation was also found to be the main loss factor in other areas (Wassmann *et al.*, 1990; Wassmann, 1994; Riebesell, 1993). Not only at the end of the bloom but also during bloom periods higher diatom as well as *Phaeocystis* concentrations were recorded near the bottom than in the surface water (Peperzak *et al.*, 1998). Settling rates of *Phaeocystis* colonies were probably enhanced by pinnate colonization because these diatoms have a higher specific density than *Phaeocystis* colonies (van Ierland & Peperzak, 1984). Sedimentation has even been proposed to be an important factor in the life cycle of *Phaeocystis* (Peperzak, 1993). Nevertheless, Rousseau *et al.* (2000) calculated that at station 330, the organic material originating from the *Phaeocystis* bloom was consumed before reaching the benthic system and that all organic material was remineralized in the water column. According to these findings, no effect of the spring bloom would have been observed in the benthos. The observations and measurements in the present study however point in the direction of substantial fluxes of phytoplankton derived material toward the bottom. An accurate estimate of phytoplankton sedimentation is essential from an ecological point of view as it determines available food for higher trophic levels in the seabed. Interpretation of the existing field data on primary production and pigment and nutrient concentrations near and in the bottom is however complicated, due to the interplay of environmental and physiological factors.

4.1.3.1 Sedimentation of diatom blooms

The ammonium concentration is one of the most obvious indicators of the extent of organic matter decomposition (Nelissen & Stefels, 1988). A peak of NH_4 near the bottom was recorded on 31st March at station 330. NH_4 must have been recently formed because this N compound is an unstable intermediate form (Johnston, 1973). Fauna activity may have enhanced this benthic ammonification (Postma *et al.*, 1984). The highest concentration of NO_3 at this time reflected the stock of nitrate enriched in the water column during winter (Rousseau *et al.*, 2000). NO_3 concentration decreased during the sampling period as the phytoplankton bloom progressed.

The spring diatom bloom started between the 9th and 19th March and lasted until 27th April. Smetacek (1980) estimated that the time interval between a bloom in the water column and material arriving on the bottom was one to two weeks. The settling of diatoms after bloom development has been discussed as a seeding behaviour of these organisms, i.e., diatoms leave the euphotic zone and settle rapidly as clumped aggregates, which disintegrate at the sediment surface and release spores (Smetacek, 1985). Graf *et al.* (1983) observed that there was a considerable loss of cells already during early to mid March, when the diatom bloom was still growing vigorously. At least in shallow waters, diatoms reach the sediment surface as intact cells providing high quality food for benthic organisms (Graf, 1992). Zooplankton grazing is low at the beginning of the diatom bloom (Rousseau *et al.*, 2000) and with low temperatures, the rapidly sinking diatoms are not susceptible to extensive bacterial decomposition in the water column (Smayda, 1970; Iturriaga, 1979; Hobbie & Cole, 1984). This scenario is consistent with the presence of pelagic as well as tychopelagic diatoms in the sediment samples from 9th March until 12th May (Bonne, pers. obs.). Graf *et al.* (1982) demonstrated that the benthic response to such pelagic events is immediate. As a result an efflux from the sediment by diffusion includes in the liquid phase dissolved organic matter as well as dissolved inorganic nutrients derived from decomposition products (Graf, 1992). In mesocosms response in terms of ammonia release of the sediment was recorded in less than 5 days (Kelly & Nixon, 1984). Consequently, the increased ammonium concentrations at the end of March may reflect decomposition of diatoms on the sediment in the early stage of the diatom bloom, whereas decomposition processes near the bottom were less important during April.

The apparently lower decomposition activity near the bottom in April may be attributed to increased grazing pressure in the water column, most of the sinking diatoms being eaten before reaching the bottom. Rousseau *et al.* (2000) described the food web structure in the water column at station 330, activated by the early spring diatom and *Phaeocystis* production. Bacterial production increased in early March 1998 almost in concert with diatom production, utilising organic products derived from the diatoms. Microprotozooplankton started their growth and reached a first peak at the end of the diatom bloom. Mesozooplankton grazing was also stimulated by the early spring diatom bloom, with a short delay as well. This finding is consistent with the presence of *Temora longicornis* and *Acartia clausi* at the end of March at the sediment surface at

station 215 and 330 respectively. Whether phytoplankton settles out in the form of fresh algal material or as degraded material may also vary from year to year depending on the abundance and composition of the zooplankton (Reigstad *et al.*, 2000). On 27th April a moderate storm (wind force 7 beaufort, wind speed 14.7 m/s) may have washed away any evidence of potentially deposited material near the bottom.

In the sediment the background signature of chlorophyll *a* completely disappeared at both stations in April. At station 330 the older organic matter present in the sediment was metabolized during March, reflected in the higher NH_4 concentration at that moment near the depth of the earlier measured peak in chlorophyll *a* in the sediment. If a part of the background signature at station 215 may have been attributed to primary production of tychopelagic diatoms, this may have been hampered by the huge proliferations of *Phaeocystis* in the water column at the end of April, because light penetration in the water column is determined by suspended matter content and phytoplankton biomass (Reid *et al.*, 1990).

Another peak of NH_4 concentration near the bottom at station 330 was observed on 12th July, coinciding with high numbers of diatoms and elevated values for fucoxanthin and chlorophyll a in the water column as well as near the bottom. The organic decomposition in July was probably mainly derived from the moderate diatom bloom at that moment.

4.1.3.2 Sedimentation of *Phaeocystis* colonies

4.1.3.2.1 Station 330

The highest chlorophyll *a* concentration near the bottom was recorded at the same moment as the *Phaeocystis* bloom peaked (29th April), followed by a clear peak in total organic matter at the bottom on 3rd May at station 330. The latter observation has to be treated with caution, as this measure may not reflect organic carbon that is not consumed yet by benthic organisms. The highest density of macrobenthic organisms during the sampling campaign (2480 ind./m²) was recorded in the macrobenthic samples of 3rd May, due to the very high abundance of *Spiophanes bombyx* (1102 ind./m²) and juveniles of *Scoloplos armiger* (347 ind./m²), both deposit feeders (Van Hoey, 2000). The highest density of juveniles of *Ophelia limacina* (deposit feeder), *Lanice conchilega* (deposit feeder, grazer and filter feeder), *Anaitides maculata-mucosa* (predator) and *Pectinaria koreni* (deposit feeder or grazer) was also found at this moment. Some of these polychaetes may have been present in the sediment that was burned to measure total organic carbon in the sediment. Their high abundances however point to the presence of a lot of detrital material. Van Hoey (2000) excluded this sampling event from the analyses because of the finer sands that were sampled, assuming that another area was sampled in comparison with other dates. The sampling point on 3rd May was indeed located at 200 m from the exact coordinates of station 330 but it was situated in between the areas sampled at 19th March and 31st March. The latter samples were not characterized by another community than at station 330 proper. Moreover the

species and juveniles abundantly found on 3rd May were also encountered at succeeding sampling events, though in lower numbers. The sampling point on 3rd May was not situated in a large pit where finer material could have been accumulated, because depth on 3rd May was the same as the surrounding points sampled. On 3rd and 6th May the nets were completely clogged with *Phaeocystis* colonies and a thick layer of living and dead *Phaeocystis* colonies were observed on top of the sediment in the core samples (Bonne, pers. obs.). The huge increase of deposit feeders indicates enhanced food availability through the settlement of this phytoplankton material (Widbom & Frithsen, 1995). Larval settlement of some polychaetes seems to be timed so that the population can significantly benefit from the sedimentation of the phytoplankton bloom (Rumohr, 1980). Although *Spiophanes bombyx* is often spatially distributed, sudden and huge increases in densities following the spring phytoplankton bloom have recently been observed at the Middelkerkebank as well (Van Hoey, unpubl. data). Phytoplankton can be readily assimilated by the benthos, without needing bacterial intermediaries (Tenore *et al.*, 1982; Findlay & Tenore 1982). Davies & Payne (1984), Graf *et al.* (1984) and De Wilde *et al.* (1984) assumed that the sedimentation of the spring phytoplankton bloom acted as a triggering mechanism for the lifecycle of macrobenthic fauna. The peak in organic carbon at 3rd May, probably including some polychaete biomass, is regarded as a result of phytoplankton deposition. At station 330 sedimentation most probably occurred en masse in the beginning of May. No doubt exists whether the majority of the settled material is derived from the *Phaeocystis* colonies, as the peaks of chlorophyll *a* at the bottom coincided with the peaks of chlorophyll *a* and *Phaeocystis* biomass in the water column and because *Phaeocystis* colonies were observed at the bottom. On 12th and 20th May the nets were still clogged with *Phaeocystis*. Still, some diatom biomass may be deposited at that time as well.

Fucoxanthin concentration peaked at the same moment in the water column as chlorophyll *a* and *Phaeocystis* biomass (Bonne & Van Gansbeke, unpubl.data). The same was observed near the bottom. Fucoxanthin has been widely accepted to be a diatom-specific pigment (Hansen & Josefson, 2003) but the close relation between fucoxanthin and chlorophyll *a* concentrations indicates dominance of fucoxanthin-containing microflagellates such as Prymnesiophyceae (Gieskes & Kraay, 1984), which class *Phaeocystis* belongs to. Consequently it is not clear which portion is made up by diatom sedimentation in the beginning of May as a result of the end of the diatom bloom. Si concentrations near the bottom peaked at 20th May, indicating the end of remineralization processes of diatom material through the food web. With the available data it is impossible to define when these diatoms must have been consumed. Silicon is not rapidly recycled (Reid *et al.*, 1990), so a considerable time span between uptake of diatoms and release of silicon is assumed. It's possible that diatoms still settled in May, as the species taking over the lead after an initial diatom bloom cannot reduce the diatoms to ecologically negligible quantities (Van Bennekom *et al.*, 1975; Officer & Ryther, 1980). Diatoms are always present and contribute significantly to the phytoplankton community throughout the vegetative season including periods of *Phaeocystis* occurrence (Lancelot *et al.*, 1998; Rousseau *et al.*, 2000). In the present study low

abundances of diatoms in the water column were still recorded until 12th May. Pelagic diatoms were also present in the sediment samples of 12th May but were absent in the samples of 28th June (Bonne, pers. obs.). Van Ierland & Peperzak (1984) demonstrated that diatoms are also associated with decaying *Phaeocystis* colonies.

High NH_4 concentrations near the bottom on 12th May indicated an increased decomposition of organic material, most probably originating from decaying *Phaeocystis* colonies. A fluff layer was discerned on top of the sediment in the cores at that moment (Bonne, pers. obs.). Also in the sediment NH_4 concentrations increased in May and June.

4.1.3.2.2 Station 215

The clogging of nets and the presence of *Phaeocystis* colonies on top of the sediment in the beginning of May was observed at station 215 as well. Yet, the peak in total organic matter in the sediment was not observed on 3rd May, implying that deposition of *Phaeocystis* derived material would not have taken place in a similar extent as at station 330 or that deposition had taken place at another moment. Currents and bottom topography create advection and non-synchronisation of bulk sedimentation of the spring bloom causing uneven deposition in different water masses (Graf, 1992; Hansen & Josefson, 2003). Considerable variability in the supply of organic matter to the sediment also results from spatial and temporal differences in rates of primary production, zooplankton grazing and chemical regimes in the water column (Gee *et al.*, 1985). Resuspension could be another mechanism by which the material was removed from the sediment surface just after deposition (Hansen & Josefson, 2003). Although no evidence was found near the bottom for phytodetritus deposition, contrasting observations were made in the sediment. On 12th May chlorophyll *a* concentrations greatly exceeded all maximum recordings of station 330 and were comparable to the concentrations in the beginning of March at station 215. This pigment signature may be a sum of *Phaeocystis* derived detritus and tychopelagic diatoms, since the latter were also very numerous in the sediment at that moment. *Phaeocystis* colonies accompanied by amphipods and cumaceans were present in the overlying water on 12th May (Bonne, pers. obs.).

4.1.4 Tidal induced resuspension and redeposition

Chlorophyll *a* concentrations at station 215 were always higher than at station 330, except on 27th April when almost no chlorophyll *a* was observed beneath 1 cm depth at station 215. On any date (except 27th April) the chlorophyll *a* profile was uniform to a depth of about 5 cm at station 215, whereas this was not observed at station 330. Evidence exists that wave action, hydrodynamics and tidal sediment transport create a more dynamic environment on the southern part of the Kwintebank than at the investigated site at the Gootebank (Langhorne, 1982, Vlaeminck *et al.*, 1989; Lanckneus *et al.*, 1993; De Moor *et al.*, 1993). As a result, the sediment at station 215 in the sandwave area (Lanckneus *et al.*, 1992a) may be subject to continuous tidal depositions and resuspensions. The different hydrodynamic activity may be reflected in the poorer

sorted sediments at station 215 in comparison with the well-sorted sediment at station 330, situated in a flattened area (Vlaeminck *et al.*, 1989). At station 215 high concentrations of chlorophyll *a* may have been rapidly homogenised through the top 5 cm of the sediment due to more intensive hydrodynamics. At beaches the chlorophyll per g of sand was uniform to a depth of about 20 cm as a result of the sand being mixed to a depth of between 2 and 10 cm on any tide (McIntyre *et al.*, 1970). Also in estuarine waters, the concentration of organic matter is kept constant, since currents and waves often rework the top centimetres of the sediments (Rice & Rhoads, 1989). In regions where tidal mixing is important, sediment resuspension and redeposition will serve to complicate the picture of sedimentation events (Smetacek, 1984). Jennes & Duineveld (1985) provided marvelous evidence of the effect of the tidal cycle on the amount and composition of near-bottom suspended material in offshore sandy habitats. During flood the current velocity is strong enough to erode the sediment, whereas algae and other particles are deposited during the slack following the flood. Ebb current velocities move the sediment but they are not strong enough to resuspend the sediment. As a result, deposited algae and particles are buried in the sediment down to a depth of 5 cm. The presence of sand ripples enhance this process, since algae and other particles tend to move towards the lee side of the ripple where they are buried by heavier sand particles descending from the crest of the ripple. This process is repeated when the stronger flood current velocities resuspend buried algae and particles again. Resuspension during high tidal currents and resedimentation was also observed by Boon & Duineveld (1998) in the German Bight.

Weather conditions and tide of the sampling events are illustrated in table II.14. The highest chlorophyll *a* values at station 215 were observed in samples taken at low water. At station 215 the previously mentioned tychopelagic diatoms were more abundant on 9th March and 12th May in comparison with other dates, with the highest numbers on 12th May. At station 330 they were most numerous on 31st March, sampled with low water as well, but the amount was not as high as on 12th May at station 215. The estimates of diatom quantities are very rough since the samples were not processed for diatom enumeration. The higher abundances of tychopelagic diatoms might result from sinking under stable conditions during the tide, while they are mixed throughout the water column during periods of intense mixing. This process will be enhanced with good weather whereas no settling will take place during bad weather, as was indeed recorded on 27th April. Hence, the interpretation of the chlorophyll *a* and nutrient concentrations are very likely influenced by fluctuations resulting from tidal currents, especially at station 215. It will be hardly possible to report sedimentation of phytoplankton near the bottom at high current velocities during flood. Yet, phytoplankton may have settled and have been buried in the sediment at other moments of the day. Jennes & Duineveld (1985) performed an experiment in which they observed that algae soon became buried even though no surface deposit could be detected. This may be the reason why a peak in organic matter or chlorophyll *a* was not found near the sediment in the beginning of May at station 215, whereas elevated chlorophyll *a* concentrations were present in the sediment. The concentrations of chlorophyll *a* that can be buried in this way range from 400 µg/l to 3500 µg/l

sediment (Jennes & Duineveld, 1985). These values are consistent with the high concentrations found in this study at station 215, ranging between 347 ng/g and 881 ng/g, which is similar to 1509 µg/l and 3830 µg/l. It can be concluded that tidal processes buried tychopelagic diatoms and some older detritus on 9th March and buried tychopelagic diatoms and *Phaeocystis* detritus on 12th May at station 215.

The resemblance with the observations of Jennes & Duineveld (1985) confirm that this mechanism might be quite widely spread on the sandbanks of the North Sea.

	215			330	
	sampling	wind speed		sampling	wind speed
9th March	at low water	3 beaufort (4.0 m/s)	9th March	2 h. before low water	3 beaufort (3.5 m/s)
31st March	3 h. before low water	2 beaufort (3.0 m/s)	31st March	at low water	2 beaufort (3.3 m/s)
28th April	3 h. before low water	?	27th April	2 h. before low water	7 beaufort (14.7 m/s)
11th May	at low water	4 beaufort (6.7 m/s)	12th May	2.5 h. after low water	6 beaufort (13.7 m/s)
29th June	2.5 after high water	6 beaufort (13 m/s)	29th June	1.5 h. before low water	6 beaufort (13.8 m/s)
12th July	/		12th July	0.5 h. before high water	5 beaufort (10.2 m/s)

Table II.14: Weather conditions and sampling moment in relation to the tidal cycle for the samples at stations 215 and 330

Whereas at station 215 frequent resuspension of the upper sediment layer most likely determines the distribution of chl *a* and chemical compounds in the sediment, the sediment at station 330 is not reworked that intensively and other mechanisms regulating pore water flow and particle concentrations may be more important than tidal resuspension and redeposition. Sedimentological structures such as ripples, which are present in the study area, may influence the boundary layer flow by creating advective transport processes through the sediment near the ripples (Ziebis *et al.*, 1996; Thibodeaux & Boyle, 1987). The transport is driven by pressure gradients generated when bottom flows are deflected by small surface structures of e.g. hydrodynamical origin (Huettel *et al.*, 1996) and is much faster than diffusional transport (Ziebis *et al.*, 1996). In natural sands, particulate organic matter constitutes the most fine-grained and easily suspendable part of the sediment and is therefore likely to follow pore water flows through the sand matrix (Rusch *et al.*, 2000). Hence, the topography-related interfacial particle transport can be a key process for organic matter uptake and cycling in seabeds with sandlike permeabilities. The layers of advective pore-water flows may produce zones of enhanced microbial decomposition activities (Huettel *et al.*, 1996), resulting in the higher NH_4 concentrations in the top layers of the sediment in comparison with deeper layers, as clearly distuinguished on 27th April and 12th July at station 330. This mechanism may also have been responsible for the increased availability of diatoms and bacteria and particles originating from the decaying *Phaeocystis* colonies, into the upper layers of the sediment, resulting in a reaction of the interstitial fauna. The spatial pattern of the ripples introduces spatial variability of the advective porewater flows (Huettel & Gust, 1992) and may explain why different vertical concentration patterns are also observed.

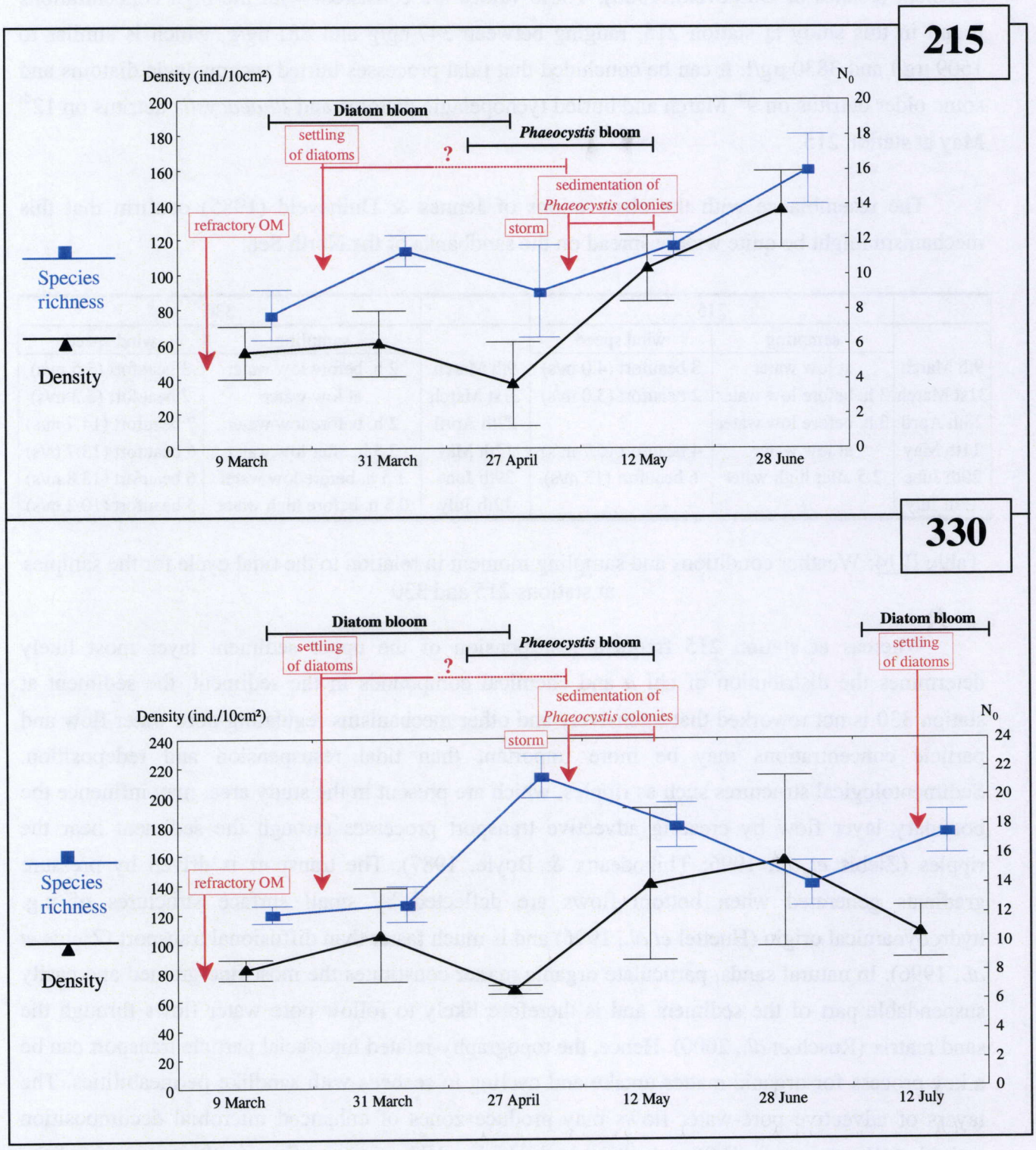

Fig.II.35: Representation of phytoplankton sedimentation and observed (storm) processes during the sampling period, plotted on the graph of density and diversity at stations 215 and 330.

4.2 Response of the harpacticoid community

While sandy sediments of low organic-matter content are widely distributed in high-energy nearshore and offshore areas, little is known of the response of benthic fauna in low organic-content sands to the deposition of phytodetrital organic matter to the sediment surface (Webb, 1996). The majority of studies investigating the response of harpacticoids to diatom or phytodetrital sedimentation have been conducted in fine, often organic-rich sediments with significant silt-clay contents in both field (e.g. Rudnick *et al.*, 1985; Decho & Fleeger, 1988a; Fleeger & Shirley, 1990; Olafsson & Elmgren, 1997) and laboratory settings (e.g. Montagna, 1984; Decho & Castenholz, 1986; Gee *et al.*, 1985; Rudnick, 1989; Widbom & Elmgren, 1988; Widbom & Frithsen, 1995). Some field records also exist from harpacticoid responses on very high organic loads such as sludge disposal (e.g. Moore & Pearson, 1986). The response of harpacticoids in sandy sediments was investigated in an experiment with sediments from a salt marsh (Webb, 1996) or in a field study in an estuary (Montagna *et al.*, 1983) and on beaches (Hockin, 1983). Field studies of the harpacticoid response on sedimentation of primary production in comparable offshore clean sands are lacking.

The previously discussed phytoplankton sedimentation events are represented in Fig.II.35 as potential triggering mechanisms responsible for the changes in the harpacticoid communities. Direct correlations were not detected and it is not known for how long specific conditions had prevailed but an attempt is made to indicate the varying importance of the changing physical environment and the food supply to the benthos within the entire period observed. Although the underlying processes cannot be identified from the available data, the analyses give some information about important shifts in community composition during the spring phytoplankton bloom.

4.2.1 Winter population

In the beginning of March a typical winter population was found at station 215 in comparison with the species assemblage of January 1997 at the same station (Chapter I). *Halectinosoma* n.spec.2, *Arenosetella* n.spec.1, *Kliopsyllus constrictus s.str.*, *Kliopsyllus* n.spec.2, *Kliopsyllus* n.spec.4, *Leptastacus laticaudatus s.str.*, *Paraleptastacus espinulatus*, *Arenocaris bifida*, *Arenocaris reducta* and *Membranastacus* n.spec.1 were common species for both sampling events, accounting for 71 % of the species and 92 % of the total density in March 1999. A stable community was outlined in the southern part of the Kwintebank, encompassing spatial sediment differences from fine to medium median grain size (Chapter I). The species assemblage of the even coarser sediments on 9th March (median grain size 384 µm with 13 % very coarse sand and 4 % gravel) did not deviate from this previously defined community pattern. The comparable medium sand (median grain size 351 µm) at station 330 yielded a similar density and species richness as station 215 in the beginning of March. They had half of the species in common but the very high dominance of *Paraleptastacus espinulatus* at station 215 resulted in a clearly lower eveness than at

station 330 throughout the depth of the sediment. Both communities were evenly distributed among the different depth layers. Deeper levels yielded significantly more copepods in comparison with later sampling events. During periods of adversity, interstitial species have an avoidance advantage by vertical migration into deeper sand layers (Hicks, 1979). Though the subsurface feeding benthos may depend upon detritus that is buried during winter in order to survive (Rudnick *et al.*, 1985), the present organic material is unlikely to be palatable food for the present community. At both stations the highest chlorophyll *a* concentrations were measured on 9th March and corresponded with a quite low density and species richness. Despite the much higher chlorophyll *a* values in the sediment at station 215 in comparison with station 330, the former even yielded less individuals and species than the latter. Beneath the surface flocculent layer, detrital particles are generally in a compacted form within faecal pellets or bulk sediment (Moore, 1931; Young, 1971; Rhoads, 1974) and are certainly, on average, of greater age and poorer nutritional quality than surface particles. Nevertheless, benthic heterotrophic bacteria, associated with the buried detritus, may have acted as a trophic buffer providing some food for the present community during this season of low primary production.

4.2.2 Early spring population during diatom bloom

From the end of March to the end of April a completely different community evolved at both stations. At station 215 an intermediate situation between the beginning of March and the end of April was already observed on 31st March, diversity in the upper sediment layers being increased, whereas this was not the case yet at station 330. At station 330 diversity increased dramatically at the end of April. Sediment composition differences and the occurrence of a storm however render the interpretation of the changed community characteristics in April more difficult. At station 215 finer sands were sampled, while the median grain size at station 330 was significantly coarser than the other samples at this station. The community typical of the southern part of the Kwintebank occurs over a range of sediments with a median grain size from fine to medium sand (Chapter I). The sediments sampled in April at station 215 fell into this range. The same community should therefore be expected, all the more since this community was also encountered on 9th March in coarser sediments.

The variation in the harpacticoid species assemblage between April and the other sampling events was more important than the differences between both stations, belonging to two different sandbanks. The observed changes thus exceed clear spatial differences and are therefore not only attributed to slight changes in sediment characteristics but very likely to other environmental changes as well. Adverse effects of disturbances by the storm may have impoverished the fauna but cannot have changed the species assemblage completely. The insignificant lower abundances may be related to these environmental conditions.

The community shift may be related to the developing diatom bloom in the water column, diatoms settling rapidly (Graf *et al.*, 1983; Smetacek, 1985). Several epibenthic (Sellner, 1976; Ustach, 1982; Decho, 1986, 1988; Decho & Fleeger, 1988a) and endobenthic harpacticoids (Decho & Fleeger, 1988b) are found to feed upon diatoms as well as phytodetritus (Rudnick, 1989). Even interstitial species are observed to ingest diatoms and diatom exudates (Decho & Castenholz, 1986). Moreover, harpacticoids are able to exponentially increase feeding rates as a function of increased microphytobenthos (Montagna *et al.*, 1995). Nevertheless, no evidence was found for associations between diatoms and total harpacticoid abundances in correlative field studies (Montagna *et al.*, 1983) or in laboratory experiments (Webb, 1996). This finding is confirmed in the present study since harpacticoid abundances did not show a clear trend in early spring. Species composition however changed dramatically. The sudden increase of subordinate species may explain the emergence of a different community. Numerically subordinate species which are incapable of feeding flexibility, are likely to be constrained to a narrow specialized range of food items which might only be available at certain times of the year. Inflexible species will therefore tend towards a lower numerical carrying capacity with breeding seasons limited to surplus periods of preferred foods (Hicks, 1979). The otherwise dominant species is both incapable of the utilization of the food resource and of outcompeting the subordinates (Hicks & Coull, 1983).

Lee *et al.* (1977) found some interstitial harpacticoids to be highly selective in forming patches around certain types of algae. They suggested that algal colonies or blooms can selectively attract specific species and may be a factor causing the non-random distribution of these harpacticoids. Yet, Montagna *et al.* (1983) only found one out of four dominant species to be strongly correlated with the standing stock of diatoms at a sand site. Although diatoms are implicated in the feeding of interstitial and epibenthic species, it has also been shown that bacteria are important dietary constituents (Rieper, 1978), which may be more important as food than the diatoms proper. Feeding data of an interstitial harpacticoid species suggest that attraction to algae (diatoms) may be only to find bacteria associated with the algal patch, since the animals ingested diatoms with associated heterothrophs but only retained the heterothrophic fraction (Decho & Castenholz, 1986).

Graf (1992) has put forward that the response of the small organisms, bacteria (Meyer-Reil, 1983) and foraminiferans (Altenbach, 1985) may be so fast that no food remains for the slower larger animals. The high conversion efficiency of this first response, especially of bacteria, however provides significant amounts of bacterial food to higher trophic levels. Although harpacticoids are able to grow and reproduce on an exclusive diet of bacteria (Rieper, 1978), some of them produced more eggs on a mixed diet of algae and bacteria than either diet alone (Heinle *et al.*, 1977). Montagna (1984) found copepods ingesting diatom carbon faster than bacterial carbon. Although assimilation rates of bacteria were 8-10 times that of diatoms in other laboratory experiments (Heinle *et al.*, 1977; Brown & Sibert, 1977), the species may be highly dependent on diatoms for the provision of necessary trace nutrients required for breeding – emphasizing food

quality rather than quantity as the necessary prerequisite for successful reproductive performance (Hicks, 1979). Intact diatoms may still have been available in the early phase of the diatom bloom when heterotrophic activity in the sediment is minimal (Nixon *et al.*, 1976; Hobbie & Cole, 1984). The presence of diatoms in the sediment and of ovigerous diatom eating *Enhydrosoma* (Hicks & Coull, 1983) indicate that nutritional requirements were probably met. High diversity of food particles, including diatoms, diatom exudates, bacteria and other heterothrophs, faecal pellets and other organic compounds may have contributed to the diversity of the community. With the sedimentation of the *Phaeocystis* bloom the favourable conditions for many of the subordinate species may have vanished and these species disappeared again.

4.2.3 Late spring - early summer population after Phaeocystis sedimentation

In May a clear response was observed in the upper layers of the sediment, being even more pronounced in June, when the community characteristics were significantly different. At the sediment surface the significant higher number of *Temora longicornis* in May may have been feeding on *Phaeocystis* colonies (Jones & Haq, 1963; Weisse, 1983). The presence of a thick fluff layer of *Phaeocystis* colonies was also reflected in the presence of even interstitial species in the overlying water, probably feeding on the rich bacteria or heterotrophic cultures on the decaying colonies.

After sedimentation lysis of the *Phaeocystis* cells is an important mechanism for release of dissolved organic carbon (Osinga *et al.*, 1996). Van Duyl *et al.* (1992) and Osinga *et al.* (1995) found that bacteria responded rapidly to addition of fresh *Phaeocystis* material in experimental benthic systems. Also in the field, sedimentation of phytoplankton blooms increased bacterial biomass significantly (Meyer-Reil, 1983, 1987). Bacterial utilization of the carbon substrates and microheterotroph grazing of bacteria and uptake of dissolved organic carbon may form an important link to higher trophic levels (Davidson & Marchant, 1992).

The surface feeders observed in the upper centimetres of the sediment (e.g. the epibenthic harpacticoid *Thompsonula hyaenae* and the endobenthic *Halectinosoma* species) in May may have been directly assimilating sedimented phytodetritus (Rudnick, 1989). Yet, the significantly increased abundance of these species did not result in a significant effect of the sedimentation process on total epi- or endobenthic densities or on total harpacticoid densities in May. A high degree of utilization of fresh detritus was also shown by harpacticoids in a mesocosm experiment of Widbom & Frithsen (1995), whereas they did not respond quantitatively within the 5 months of the experiment.

Significantly higher total harpacticoid densities and an altered species composition were reported more than one month later, in June. At that moment the more abundant harpacticoids were concentrated in the upper 2 cm and strongly dominated by a single interstitial species, *Apodopsyllus* n.spec.1. This bacteria grazer may have increased bacterial consumption and

reproduction as a result of increased food density (Rieper, 1978). Gray (1969) and Decho & Castenholz (1986) found a strong experimental or field relationship between the distribution of specific harpacticoid species and certain microbial flora. Very high densities of *Apodopsyllus* n.spec.1 in spring were also recorded at coastal stations along the Belgian coast (Herman, 1989) and this species was frequently found in sand enriched with silt (Willems, 1989). The high reproductive potential, the small body size and the large fluctuations in population size are characteristics of a typical r-strategist and provide a selective advantage in unpredictable or short-lived environments (Heip, 1995). *Apodopsyllus* n.spec.1 has probably a capacity for the utilization of a wide variety of food sources of different origin, including *Phaeocystis*. Opportunists of organic enrichment have been found among the epibenthic and phytal copepods (*Bulbamphiascus* and *Tisbe* (Moore & Pearson, 1986; Marcotte & Coull, 1974, Gee *et al.*, 1985)). *Apodopsyllus* n.spec.1 is an interstitial representative of an opportunist utilizing an increased organic input through an indirect pathway. *Apodopsyllus* n.spec.1 may be the harpacticoid counterpart of *Capitella capitata* and *Polydora* species. These opportunistic macrobenthic species are able to persist in areas where periodic anoxic conditions exist (Heip, 1995). *Apodopsyllus* species also display preference for anoxic environments (Wieser *et al.*, 1974; Moore, 1979b, Willems, 1989). Anoxic conditions may not have favoured this species in the present study since the sediment was oxidized at any time.

Increased reproductive effort in May and June in the present study was observed for other interstitial species as well. Also Fleeger & Shirley (1990) found that the reproductive cycles in the dominant harpacticoid species were related to the spring bloom sedimentation event. While not denying the role of temperature, the results suggest that breeding periodicity is also strongly related to food resource availability as a result of phytoplankton deposition. For some species migratory behaviour and reproductive activity were interrelated, egg development taking place in the surface layers of the sand (Huys *et al.*, 1986a), whereas the total distribution of life history stages per depth layer did not reveal any changes in the vertical distribution over time. A lack of response at major taxon level (Fleeger *et al.*, 1989) may be misleading, if individual species within the taxon react differently to environmental change (Warwick *et al.*, 1988; Olaffson, 1992).

The dense interstitial fauna in the upper sediment layers reflects that deposited organic matter is effectively assimilated and incorporated in the sediment, very likely through the microbial food web since the main source of energy for the interstitial harpacticoids is the bacterial flora (McIntyre *et al.*, 1970). Also the increase in nematode selective deposit feeders was suggested to be the result of increased numbers of bacteria and protozoa in the sediment following the spring bloom (Olafsson & Elmgren, 1997). The significant vertical migration took place after the bloom reached the sediment surface in May and June, animals from deeper sediment layers moving to the sediment surface attracted by the fresh food supply (Schulz, 1983). In June deeper levels harboured more harpacticoids than in May as a result of particle and pore-water transport by bioturbation, providing food particles at greater depth (Graf, 1992). A significant structuring effect

is thus recorded in the interstitial community, which relies indirectly on sedimented phytoplankton, and not in the directly assimilating epibenthic harpacticoids, although these copepods are regarded as very mobile and may colonize food patches very quickly (Decho & Fleeger, 1988a).

Changes in total densities were not regarded as significant at station 330 due to the considerable patchiness. Yet, organic matter reaching the bottom is patchy distributed as well (Plante *et al.*, 1986) and the high variability in densities was reported in these months in which a clear sinking of organic matter was demonstrated.

With the available data it is impossible to define how important the contribution of diatoms must have been in May and June. It is very likely that the most important contribution to the bacterial production was based on *Phaeocystis* sedimentation. The clear response in the upper centimetres in June may also be partly due to post-bloom sedimentation of largely amorphous carbon-rich material, accumulated in the surface layer in the course of the bloom. Post-bloom mucilage sedimentation could be a secondary pathway for the vertical flux of *Phaeocystis*-derived organic matter (Riebesell *et al.*, 1995).

4.2.4 Similarities and differences between the stations

The response of the harpacticoid fauna observed in June was clearly different from the community changes in April at both stations. The high eveness in April after the moderate diatom sedimentation contrasts with the high dominance in June after the clear and more extensive *Phaeocystis* sedimentation. A clear picture emerges of increasing dominance and decreasing diversity with increased organic enrichment and potentially with the change in nutritive value of the deposited organic matter.

Species richness was however not negatively affected at station 215 after *Phaeocystis* deposition. Species richness increased from the beginning of March toward the end of June, implying an increasing positive effect of the sedimentation events on species richness. Species richness patterns differed significantly between both stations. At station 330 species richness increased dramatically from the beginning of March toward the end of April, whereas it decreased after the sedimentation of the *Phaeocystis* bloom. Densities increased during the entire period at both stations. The trend in species richness at station 330 is consistent with the results of the laboratory experiments of Gee *et al.* (1985), while abundances behaved differently. His experiments showed that, at levels of organic enrichment common in nature, not only the abundances of many species increased but also the number of species, compared with the controls. At high levels of organic enrichment there was a decrease in both the abundance and species richness and an increase in species dominance. Harpacticoids also showed negative responses in abundance in organic enrichment experiments of Widbom & Elmgren (1988) and Widbom & Frithsen (1995). Van Damme *et al.*, (1984) also recorded a drastic decrease in harpacticoid fauna along the Dutch and Belgian coast as a result of intensive organic enrichment. In the present study however organic enrichment was not that severe yet to negatively affect densities.

According to the scenario at station 330 and in Gee *et al.* (1985) the increasing species richness at station 215 suggests that organic enrichment was less intensive at this station. Yet, chlorophyll *a* concentrations in the sediment at station 215 were much higher than at station 330 on 12th May and 28th June, whereas the faunal responses to high organic loads (increased abundance versus decreased diversity) were clearer at station 330. This apparent discrepancy may be refuted by the hypothesis that the response on organic enrichment is also dependent on mixing in the sediment. One consequence of tidal mixing is that very little of the primary production in the water column becomes incorporated in the sediment (Jennes & Duineveld, 1985) and may hamper an efficient assimilation of the organic matter by the benthos. In areas where the top centimetres of the sediments are often reworked by currents and waves, the total concentration of metabolizable organic matter in the sediments is critically dependent on how fast the animals work the organic matter into the sediment (Rice & Rhoads, 1989). Despite the higher chlorophyll *a* concentrations at station 215, the fauna may not have been fast enough to incorporate as much organic matter as at station 330. Consequently, the interstitial fauna was not as densely concentrated in the top centimetres of the sediment as at station 330 after phytoplankton deposition.

Resuspension and advection of deposited organic matter at station 215 may also result from sand extraction activities (Newell *et al.*, 1998), since the Kwintebank is a heavily exploited sandbank (Chapter III). Station 215 however is located in an area of low sand extraction intensity. Table II.15 illustrates the extraction activities in spring 1999 near station 215. Extraction activity was most frequent in April but still fairly low to rework the sediment considerably. Just before sampling on 28th April a sand extraction vessel had been in the neighbourhood only for a very short while. Yet, on more heavily exploited areas on the Kwintebank (Chapter III) the importance of resuspension and redeposition may be significant in diluting the organic enrichment in the sediment at specific places and concentrating it at other places. On top of the bill, these extractions do not only reduce the food availability by resuspension but also directly impact fauna densities by removing the fauna. The possible confusion between effects of increased organic matter inputs and effects of sand extraction (or fisheries in Heip, 1995) is an unexplored problem that requires careful consideration in a number of other dredged areas as well.

1999	January	February	March		April	May	June	July
Days	14,20,28	4	23,30,31		6,7,16,21, 22,23,28,29	5,6,10	0	0
Number of days	3	1	3		8	3	0	0
Mean duration of disturbance (min.)	4,5	1	0,5		1,7	1,7	0	0
m² disturbed	540	120	60		204	204	0	0
Sampling	/	/	9th March	31st March: sand extraction on 31st March after sampling	28th April	11th May	29th June	/
Last sand extraction event before sampling			35 days before sampling	23 h. before sampling	5 h. before sampling	20 h. before sampling	50 days before sampling	

Table II.15: Sand extraction activities in spring 1999 near station 215 on the Kwintebank

4.2.5 Differences between meiofaunal taxa

The obvious differences in harpacticoid community structure in April were not as clearly observed for other meiofaunal organisms such as nematodes. For nematode abundances and community structure at station 330 significant differences were found between 9th March and later sampling events (Vanaverbeke, 1993). Differences in density and community structure between April and succeeding months were also observed but they were not as pronounced as for harpacticoids. Copepod community structure was more sensitive to low dose enrichment than the nematode species assemblage, in agreement with the findings of Gee *et al.* (1985). They demonstrated that there were no detectable differences in nematode community structure between different levels of organic enrichment but that there was a clear response in the high dose treatments. The copepods, on the other hand, separated out into well-defined communities and were obviously the most important group in determining the total meiofaunal community pattern Gee *et al.* (1985).

Yet, in April nematode densities increased significantly in comparison with 9th March, whereas this was not the case for harpacticoid densities. Nematodes reached maximum densities in May whereas harpacticoids in June. Montagna *et al.* (1989) suggested that the two groups occupy different trophic niches, nematodes being linked to a short, detrital/bacterial-based food chain. In the case of organic enrichment their number would increase rapidly. In the present study nematode abundances responded more rapidly to the pulses of organic matter in April as well as in May, while copepods lacked behind but were also able to assimilate a considerable amount of the detrital/bacterial-based food sources. The differences in abundance maxima between nematodes and copepods may be due to competition, both being dependent on the same input from the water column. During the diatom bloom, nematodes and polychaetes may have more quickly assimilated diatoms than (epibenthic) harpacticoids. Montagna *et al.* (1983) found positive correlations between diatoms and ciliates or nematodes or polychaetes but not between diatoms and harpacticoids. Nematodes may also suffer from competition with polychaetes, like harpacticoids. Widbom & Elmgren (1988) and Widbom & Frithsen (1995) found that the meiofauna showed remarkably little response to the increased organic input to the sediment because they were limited by biotic interactions with the opportunistic polychaete species that completely dominated the benthic fauna in the eutrophied mesocosms. Their results suggest that a few opportunistic species may, at least temporarily, prevent species that are more dependent on fresh detritus from utilizing an increased input of such phytodetritus to population growth (Widbom & Frithsen, 1995). Experimental evidence that such negative interactions occur, and can be more important than predation or physical disturbance, has been presented by Alongi & Tenore (1985); additions of a subsurface feeding polychaete decreased surface meiobenthic abundance.

5 Conclusions

During the spring phytoplankton bloom temporal changes in the harpacticoid community were clearly discerned with high diversity in April and high density and dominance in June. Changes in community structure and density followed the same pattern while diversity behaved differently at both stations. At station 215 the organic matter is probably mixed trough the upper layers of the sediment and reworked continuously. A great part of the deposited matter is resuspended during flood and hence not assimilated in a great extent by the infauna. The fraction of the deposited matter that is consumed by the harpacticoids continuously increased density and species richness. Yet, the *Phaeocystis* derived material increased the dominance in the community. At station 330 the deposited organic matter is not reworked as intensively, resulting in a more stable food supply to the benthos. The harpacticoid fauna was more concentrated in the upper centimetres of the sediment at this station. Diversity increased remarkably during the diatom bloom, whereas the community was completely dominated by the most successful opportunistic interstitial species, *Apodopsyllus* n.spec.1, which exploits the detrital/bacterial food sources after *Phaeocystis* deposition.

Popeye of the North Sea = *Apodopsyllus*