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Inter-annual variations of planktonic food webs in the northern Adriatic Sea

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Abstract

The temporal dynamics of microphytoplankton, microzooplankton and mesozooplankton were monitored over 37 months in the Adriatic Sea in order to identify alterations in the plankton structures, which can lead to, or enhance the production of macro-aggregates, that affected the entire northern basin in summers 2000 and 2002, and to assess any negative effects of mucilage on plankton temporal patterns. Samples were collected monthly, from June 1999 to July 2002, on three transects at 9 stations across the northern and central Adriatic Sea. Besides the high year-to-year variations in abundances and taxonomical composition, plankton communities only showed a clear seasonal succession during 2001, when since April a grazing food web developed and was able to control large sized phytoplankton increase. In spring–summer 2000 and 2002 consumer abundances remained quite low and the dominant mesozooplankton summer species (*Penilia avirostris*) did not reach its usual summer maximum. The lack of an efficient top control was more evident on the northernmost transect, where generally grazing food web prevails over the microbial one. A large part of the microphytoplankton blooms, although not particularly intense, was exported to the bottom in the particulate phase, where it was processed by bacteria, enhancing the production of refractory dissolved material.
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1. Introduction

Plankton size and functional classes play essential roles in the organic carbon flux through pelagic food webs (e.g., Legendre and Le Fevre, 1992). The size of photosynthetic producers, i.e. large (>2–5 μm) or small

(<2–5 μm) phytoplankton, and the nature of dissolved organic carbon (DOC) produced (labile or refractory), can strongly influence the partitioning of biogenic carbon between the short-lived (microbial food web), long-lived (grazing food chain; Azam, 1998) or sequestered pools (refractory DOC and biogenic sedimented matter; Legendre, 1996).

Remarkably, in shallow turbulent environments, like the northern Adriatic, where increased nutrient availability is episodic, the microbial or the grazing food

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web can alternately dominate in the carbon flow over short time periods. In spring, as a result of episodic nutrient enrichment of the euphotic zone and insufficient grazing, as a controlling factor of their population size, large-sized phytoplankton blooms occur. On the opposite, microbial food web is typical of low energy environment, mostly based on regeneration processes (Kiørboe, 1996). As a consequence, the final fate of photosynthesised carbon can strongly change over time in the same environment as a function of the planktonic food web structures.

The northern Adriatic is one of the most productive Mediterranean regions at several trophic levels, from phytoplankton to fish. Particularly, the area of marked, but variable, plankton standing crop and production was quantified off the Po River delta and related to the spreading of its plume (Franco, 1973; Gilmartin and Revelante, 1981; Smodlaka and Revelante, 1986; Degobbis et al., 2000). All plankton biomasses show a strong decreasing gradient from the Po River eastwards, as well as from northern Adriatic southwards, whereas a reverse gradient is evident for plankton diversity (Fonda Umani, 1996).

Microphytoplankton is mostly constituted by diatoms that vary temporally and spatially with intermittent riverine inputs and generally show two maxima (winter–spring and autumn) throughout the water column, more evidently in the coastal waters. Nanoplankton is numerically dominant throughout the entire Adriatic Sea, more abundantly in the northern part and along the coasts. Coccolitophorides are associated with Ionian input waters and are more abundant in the southern part. Dinoflagellates are characteristic of the summer period, although their abundance never reaches high values, with the exception of "red tide" phenomena that were reported almost every year during the 1970s, along the western coast (Emilia Romagna Region, Italy), and less frequently in other northern Adriatic coastal areas (Sellner and Fonda Umani, 1999). In the 1970s, nutrient loading by the Po River significantly increased, reaching the highest concentration in the early 1980s (Harding et al., 1999). At the end of the 1980s, we observed a shift from red tides to mucilage phenomena, which affected the whole northern basin in 1988, 1989, 1991, 1997, 2000 and 2002 (Degobbis et al., 1995, 1999; Precali et al., 2005—this issue).

Microzooplankton composition in the northern Adriatic is characterized by the dominance of ciliates other than tintinnids (Revelante and Gilmartin, 1983, 1985), southwards tintinnids become more important.

In the northern basin, mesozooplankton is characterized by high percentage of meroplankton, and strictly

neritic copepod and cladoceran species, low diversity, and clear prevalence of *Penilia avirostris* in the summer and *Acartia clausi* during the rest of the year. Southwards diversity increases as well as abundance of the "oceanic" species, and *Paracalanus parvus* becomes prevalent (Malej, 1979; Hure et al., 1980; Specchi and Fonda Umani, 1983, 1987; Lučić et al., 1988; Ghirardelli et al., 1989; Fonda Umani et al., 1992, 1994; Fonda Umani, 1996; Hure and Kršinić, 1998).

Regarding the food web structure, Del Negro et al. (2001) found a high number of relationships among different classes of prey and predators in the coastal northern Adriatic area in the spring, when the increase of primary production enhances the predation rates, thus resulting in a more efficient transfer of energy towards the upper level consumers.

The main goal of this paper was to define the structural changes of the plankton community that occurred in the northern Adriatic Sea over a 37-month period (from June 1999 to July 2002), as well as to highlight possible significant differences among the years with (i.e. 2000 and 2002) and without mucilage events (i.e. 1999 and 2001). We analyzed the temporal evolution of microphytoplankton, microzooplankton and mesozooplankton communities, their mutual relationships, as well as total abundance and taxonomical composition.

Analyses of the plankton system were carried out bearing in mind that

(1) the mucilage appears all along the water column and impacts the entire northern Adriatic sub-basin
(2) alterations in the plankton structures, which can lead to, or enhance the production of macro-aggregates, must be recognizable at the same spatial and temporal scale
(3) negative effects of mucilage on the temporal plankton dynamics has to be noted at a sub-basin wide scale.

2. Material and methods

Samples were collected monthly, from June 1999 to July 2002, on three transects at 9 central stations (A03, A07, A11, B06, B10, B13, C04, C07, C12), across the northern (transect A) and central (transects B and C) Adriatic Sea (Fig. 1). Water samples (5 L) for microphytoplankton and microzooplankton analysis were collected with Van Dohrn (transect A) and Niskin (transects B and C) bottles at three standard depths (surface, 10 m and 2 m above the bottom).
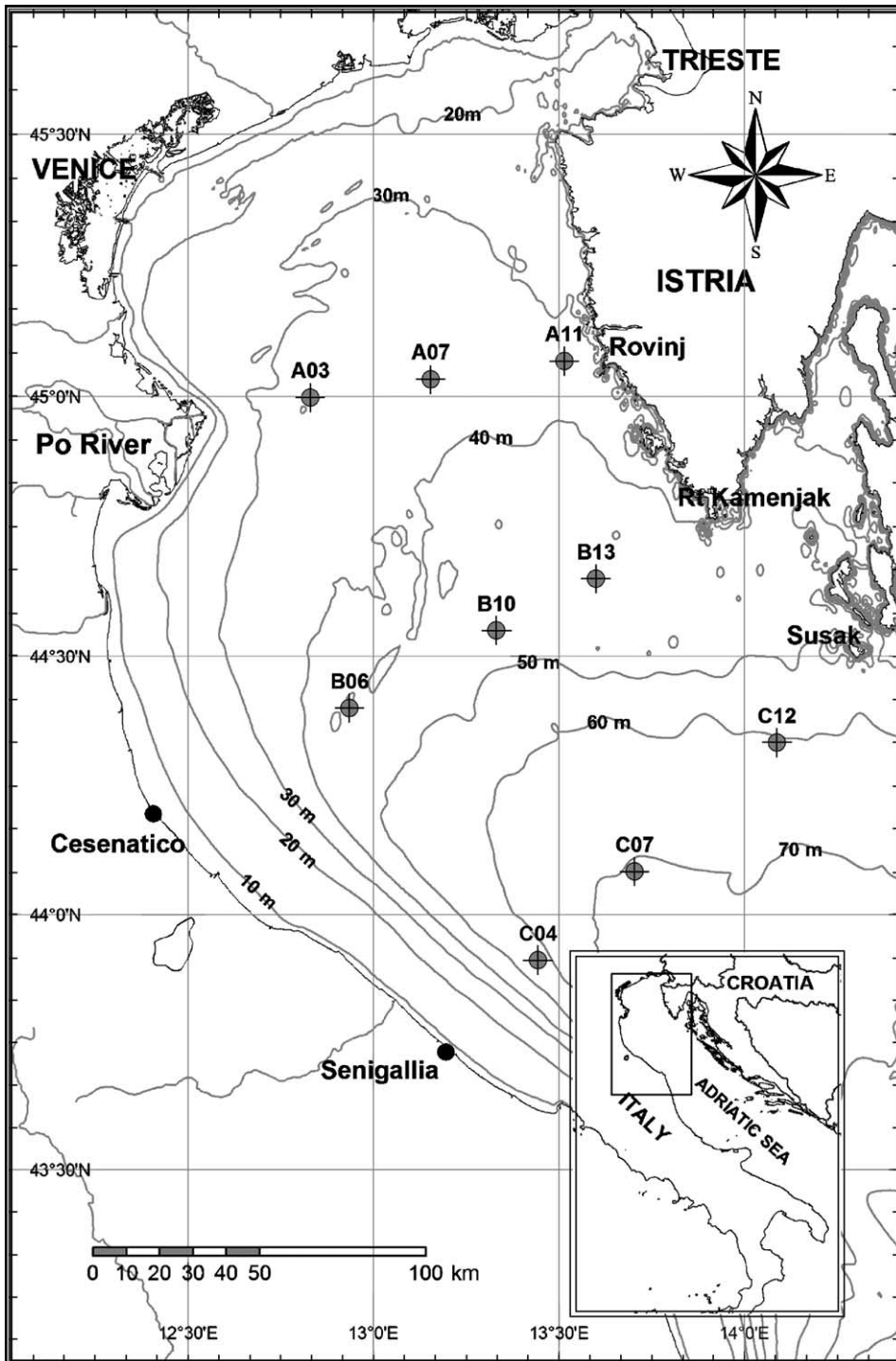
Fig. 1. Map of the sampling area.

Microphytoplankton samples were preserved with neutralized Lugol's solution (transects A—200 mL) and buffered formaldehyde (transects B and C—2% final concentration; 500 mL), and stored in dark bottles.

When counted only autotrophic microphytoplankton (>20 μm) fraction was considered.

Microzooplankton samples were preserved with formaldehyde neutralized with $Ca(CO_3)_2$ (1.5% final

concentration). In the laboratory, samples were concentrated by sedimentation and 50–100 mL sub-samples of the initial 2 L (transects B and C) and 5 L (transect A) were analyzed. Heterotrophic dinoflagellates were distinguished according to literature (Tomas, 1997) and to observations by epifluorescence microscopy.

Species composition and abundance, both for microphytoplankton and microzooplankton, were determined

on an inverted microscope according to Utermöhl (1958).

Mesozooplankton samples were collected by vertical tows (from 3 m above the bottom to surface) with a 0.25 m² sampling area, 200 μm mesh plankton WP2 net. Samples were preserved with buffered formaldehyde (2% final concentration) until laboratory analysis. Taxonomic analyses were performed on the total sample or on a sub-sample (at least 1000 individuals were counted).
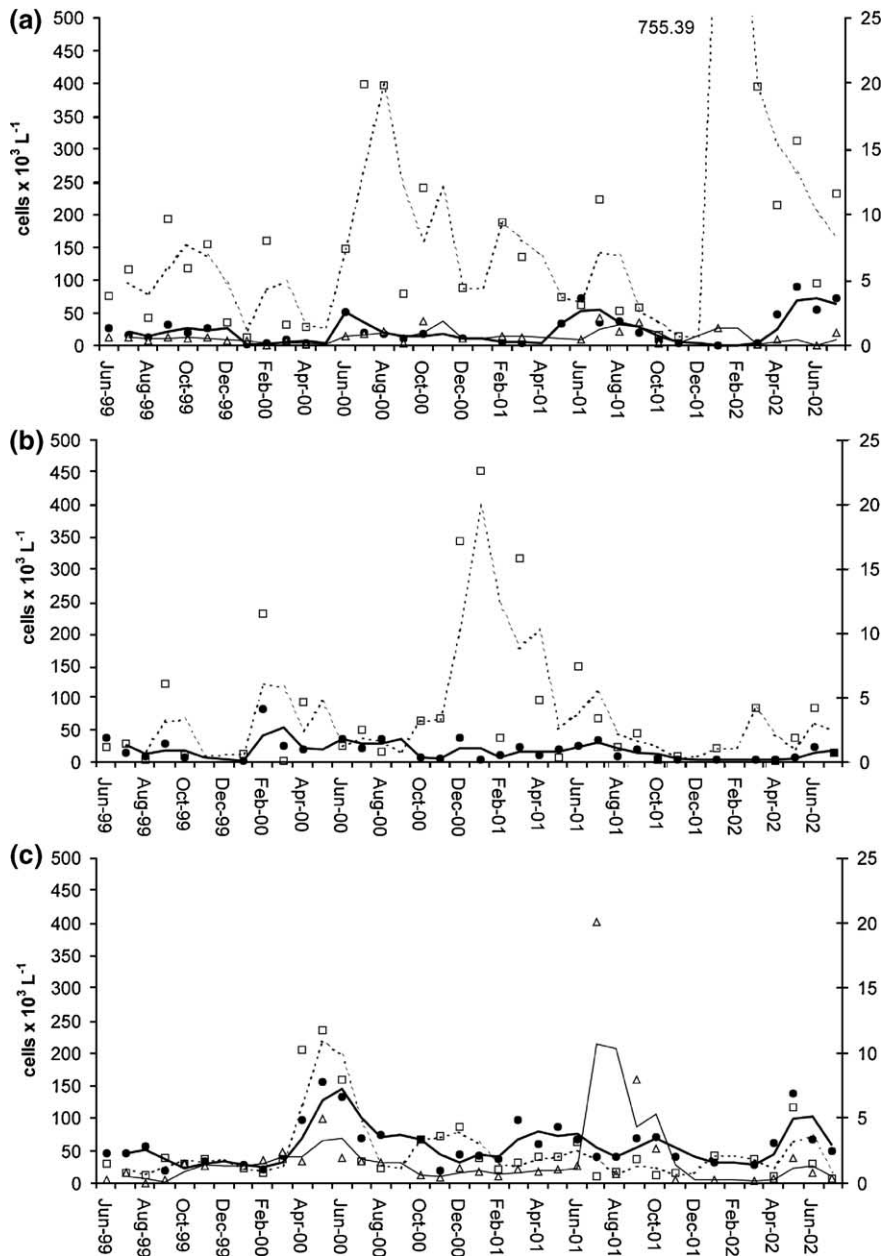

Fig. 2. Abundances of diatoms (□) scale on the first axis; autotrophic dinoflagellates (●) and other phytoplankton (△) scale on the second axis, on transects A (a), B (b) and C (c).

2.1. Data elaboration

Microphytoplankton and microzooplankton data have been expressed as mean integrated values, after integration using the trapezoid sum. Being differences among stations of the same transect lower than differences among transects, mean integrated values of each of the three stations have been further averaged for each transect to highlight different patterns among transects.

Theoretic grazing impact on phytoplankton was calculated using seasonal clearance rates experimentally obtained for the Gulf of Trieste through dilution experiments for microzooplankton (Fonda Umani and Beran, 2003) and grazing experiments using *A. clausi* as model for mesozooplankton (Fonda Umani, 2001) multiplied by microzooplankton and mesozooplankton biomass as individual numbers.

Principal component analysis (PCA) was computed by MATEDIT (Burba et al., 1992) for each station on a matrix where rows were the main taxonomic groups: diatoms (DT), autotrophic dinoflagellates (AD), other phytoplankton (OP); heterotrophic dinoflagellates (HD); aloricate ciliates (AC), tintinnids (TN), copepod nauplii (CN); copepods (CP), cladocerans (CD), eggs and larvae (EL), other mesozooplankton (OM), and columns of the sampling dates.

3. Results

3.1. Temporal dynamics

3.1.1. Microphytoplankton

Diatoms were the most important group all over the basin and all year round, and they caused several blooms of different intensity along all three transects.

The blooms in the second half of 2000 were particularly intense in the western-central part of transects A and B, although strictly confined to the surface layer. Usually in summer, dinoflagellates increased; coccolithophorids (other phytoplankton in the graph) reached relevant abundances only along transect C (Fig. 2). For other details on species composition, see Totti et al. (2005—this issue).

Fig. 3 shows the temporal dynamics of the mean integrated microphytoplankton abundances for all three transects. The highest abundance was observed on transect A in January 2002, when the averaged integrated value amounted to 755×10^3 cells L^{-1}. This maximum was due to the *Asterionellopsis glacialis* bloom registered in the western and central area, which affected the entire column water. All the other maxima did not exceed 400×10^3 cells L^{-1}. The timing of the blooms as well as dominating species composition was homogeneous in the entire area. Winter bloom appeared in January–February due to *Skeletonema costatum* in 2001, while in 2002 winter bloom was due to *A. glacialis*, which was replaced in March by *Chaetoceros* spp., with a minor presence of *S. costatum*. High abundances observed on transect A, from July to November 2000 and from January to May 2002, were not registered on other two transects. On the contrary, the increase registered in December 2000–January 2001 was clearly evident on transect B, less evident on C and totally absent on A.

3.1.2. Microzooplankton

Microzooplankton communities were dominated by aloricate ciliates, with the exception of May 2000 on transect C and in the central basin in summer 2001, when heterotrophic dinoflagellates reached the same
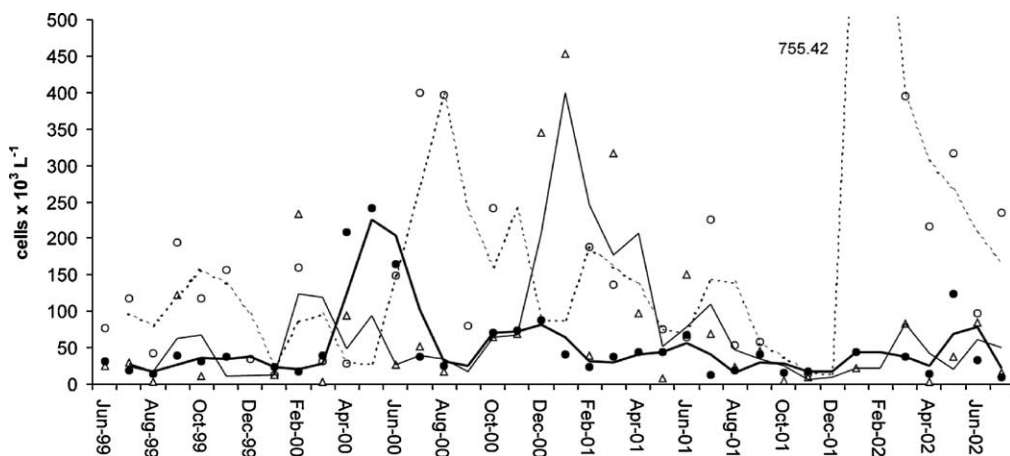

Fig. 3. Temporal dynamics of the mean integrated microphytoplankton abundances on transects A (○), B (△) and C (●).

densities of aloricate ciliates (from 100 to 400 ind. L^{-1}). Over the entire basin, the most frequent and abundant heterotrophic dinoflagellates belonged to *Gymnodinium/Gyrodinium* group and to genus *Protoperidinium* (*P. diabolum*, *P. depressum*, *P. oblongum*, *P. oceanicum*, *P. divergens*, *P. conicum*, *P. pyriforme*, *P. steinii*) and *Diplopsalis* group. The latter was particularly abundant with small cells on transect A. In late

summer–fall, *Hermesinum adriaticum*, a small ebriida, probably a mixotrophic species because of numerous endosymbiotic cyanobacteria, reached high abundances. Contrary to the past aloricate ciliates contribution in total microzooplankton increased southwards. Usually they showed spring–summer maxima, which was totally absent in summer 2000 on transect A where the entire year was characterized by low abundances
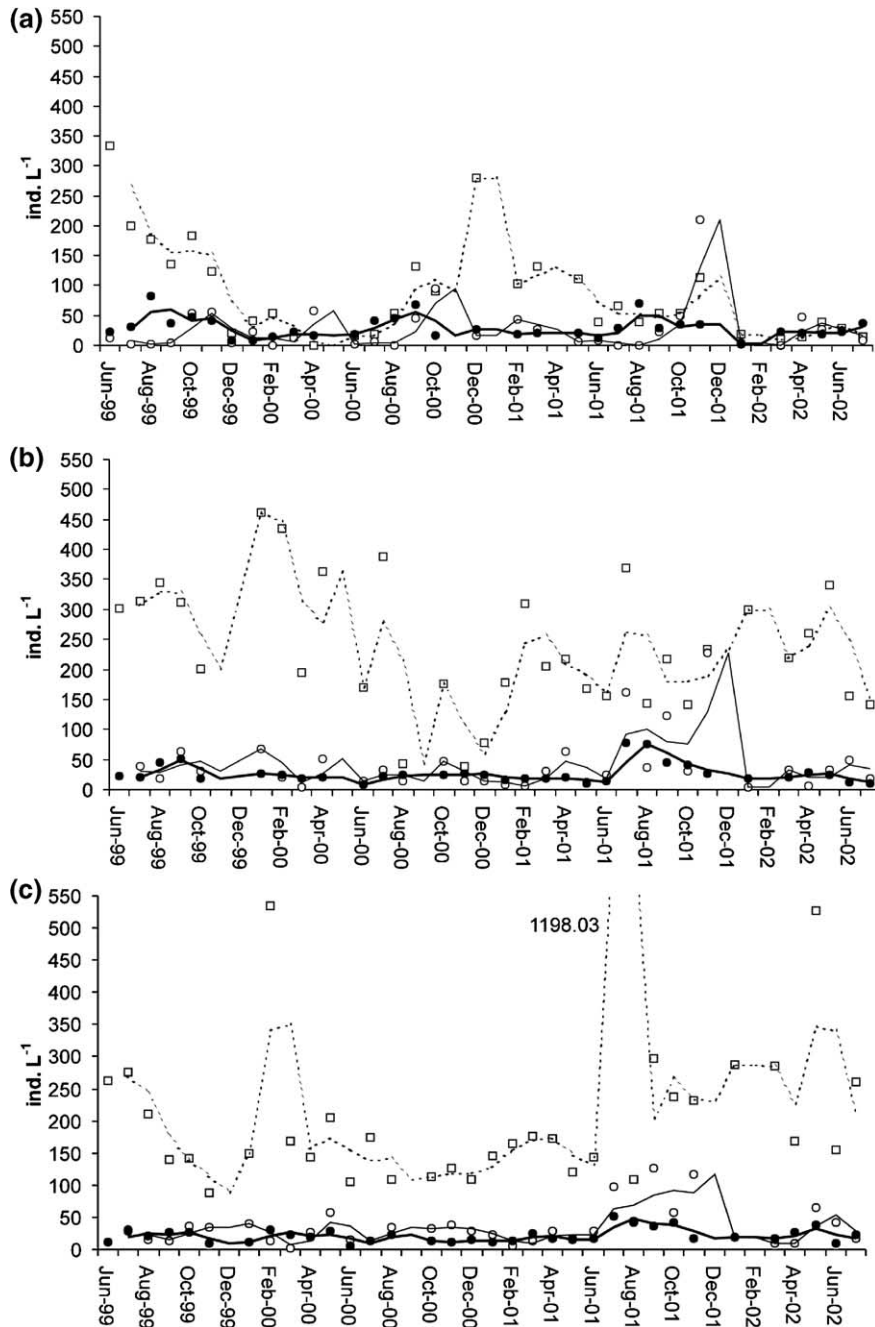

Fig. 4. Abundances of aloricate ciliates (□), tintinnids (○), copepod nauplii (●) on transects A (a), B (b) and C (c).

(Fig. 4). Tintinnids were scarce until autumn 2001 when a significant increase occurred, which lasted until January 2002. Usually autumn maxima were less evident on the southern transect. The species *Stenosemella nivalis* was present throughout the whole period, more abundantly in winter. *Tintinnopsis nana* was also almost constantly present on transect A. Genus *Salpingella* characterized summer and fall. *Steenstrupiella steenstrupii* was present in summer. In summer 2000, in the southeastern part of the basin, species *Dadayiella ganymedes*, *Eutintinnus lusus undae*, *Rhabdonella spiralis* and *Xystonella longicauda*, which characterize warm and salty waters, significantly contributed to the total abundance. *Helicostomella subulata* and *Tintinnopsis compressa*, which were typical of the northern basin in the past and almost completely absent in the last years, appeared again in summer 2002 on the southern transects. Copepod nauplii were constantly present throughout the year on all three transects, although they never reached high abundances, with only slight increase in summer 2001.

Mean integrated abundances of microzooplankton were not particularly high, usually under 400 ind. L^{-1} (Fig. 5). On transect A total microzooplankton was lower than on transects B and C. Only in January–February 2000, July–August 2001 and May 2002 microzooplankton reached higher values on transects B and C. Temporal pattern was very similar on the southern transects, but differed on A: in 2000 and 2001 spring–summer, maxima were observed on B and C, but they were absent on A, where maximum occurred in December 2000 and November 2001; the spring maximum of 2002 was of lesser significance on transect A. Temporal pattern was substantially the same in the

southern transects: spring–summer maximum and winter minimum.

3.1.3. Mesozooplankton

In the entire basin, copepods prevailed during the entire period, with the exception of summer (Fig. 6). Most abundant species throughout the year were *P. parvus*, *A. clausi*, *Oithona similis*, *Ctenocalanus vanus* and *Temora longicornis*; while in spring and particularly in the last year *Calanus helgolandicus* became relevant. Cladocerans, namely *P. avirostris*, were dominant in summer. Their prevalence was significantly more important in summers 1999 and 2001 and in the northern part of the basin, whereas in summer of 2000 and 2002 their swarming started only in July instead of May–June and was less intense. Generally, cladocerans' contributions in total abundance decreased southwards.

On all three transects, mesozooplankton temporal dynamics were characterized by maxima in the late spring–summer (with evident dropping off in June 2000 and May 2002) and fall–winter minima. Total mean integrated abundances were very similar on transects A and B, whereas on C they significantly decreased, particularly during the summer peaks (Fig. 7). Summer maxima were particularly relevant in 2001 when they exceeded 20,000 ind. m^{-3} on transects A and B. In June 2002, high abundance registered on transect B was due to a heterotrophic dinoflagellate *Noctiluca scintillans* bloom. A less intense bloom of *N. scintillans* was registered on transects A and B also in April–May 2001.

We calculated the ratio between the average total abundances of microzooplankton and cladocerans that preferentially use the same dimensional class of prey,
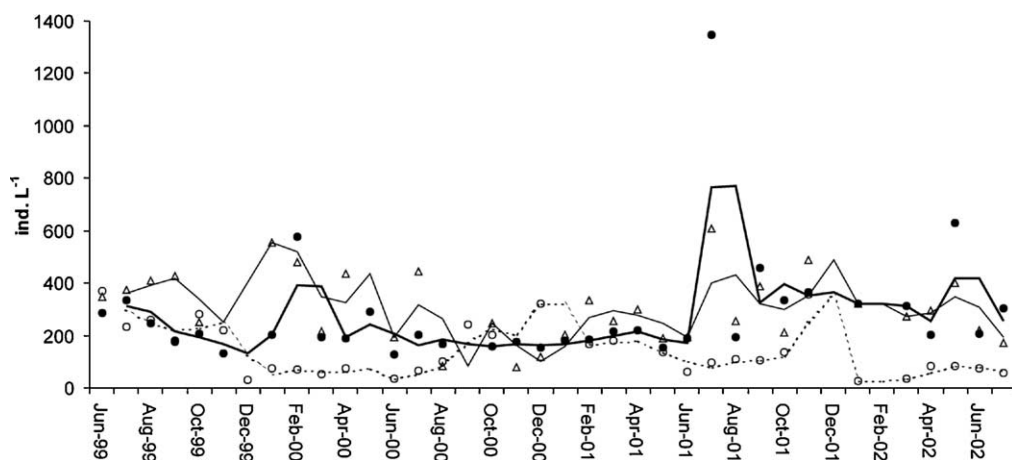

Fig. 5. Mean integrated abundances of microzooplankton on transects A (○), B (△) and C (●).
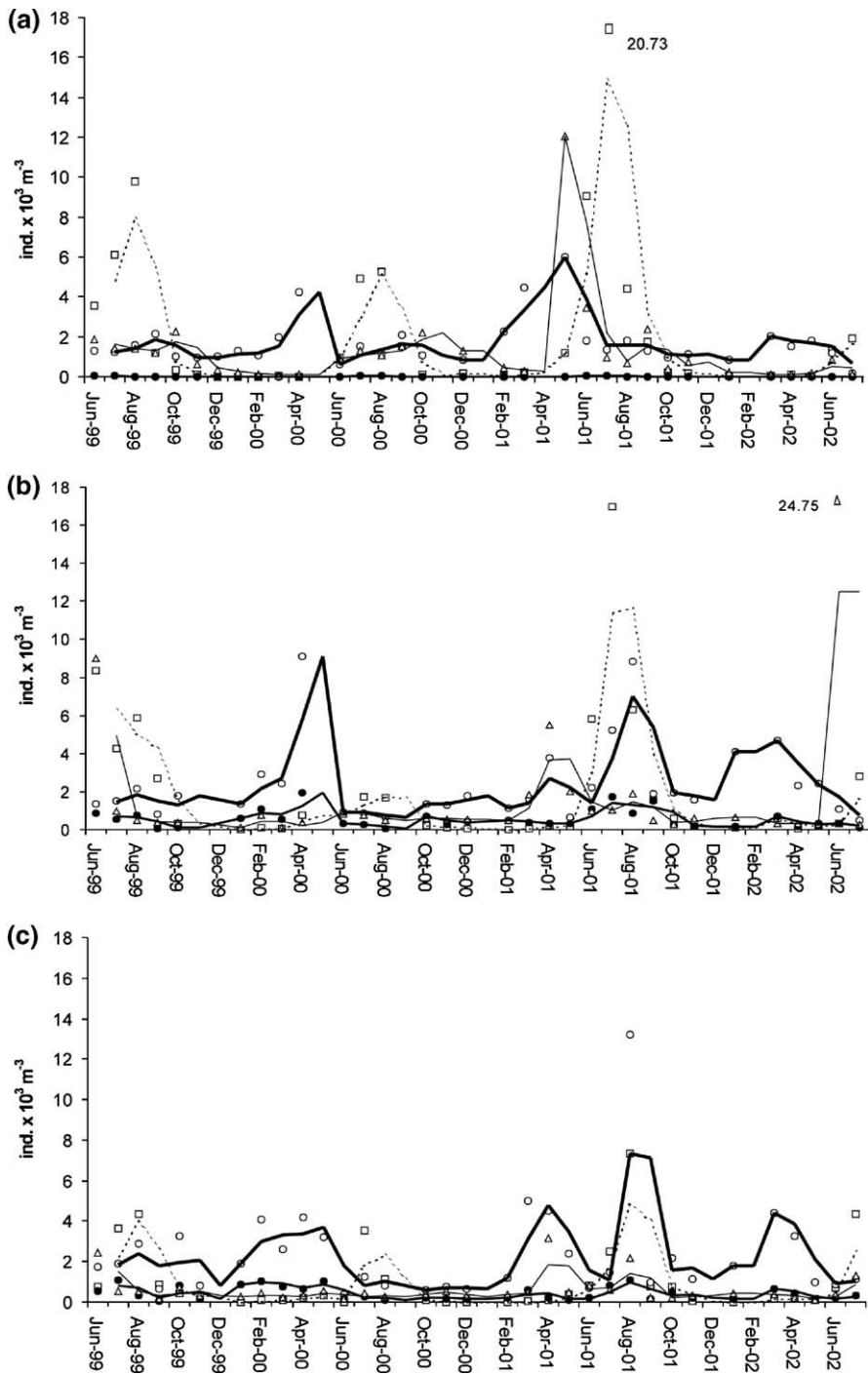
Fig. 6. Abundances of cladocerans (□), copepods (○), eggs and larvae (●), other mesozooplankton (△) on transects A (a), B (b) and C (c).

namely nanoplankton, for all three transects. The relative importance of cladocerans decreased southwards, where microzooplankton clearly prevailed (Fig. 8), indicating a shift from the grazing to the microbial food web from the Northern basin southwards.

Theoretical grazing impact on microphytoplankton (Fig. 9) usually did not exceed 20% and it was particularly low on transect A because of the higher ratio between prey and predators. Grazing removal considerably increased in summer 2001, and particularly on
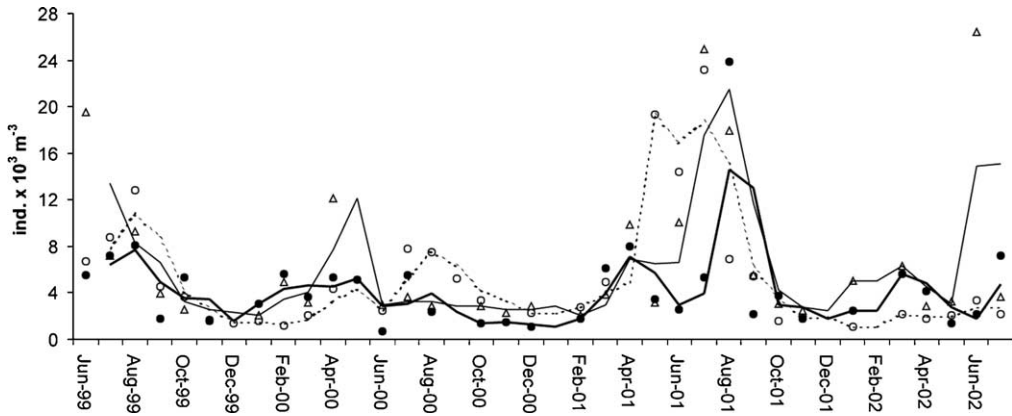
Fig. 7. Total mean integrated abundances of mesozooplankton on transects A (○), B (△) and C (●).

transects B and C where it reached 70% and 50% of total phytoplankton biomass, respectively.

3.1.4. PCA analysis

Results of PCA analyses allowed us to recognize a common pattern for all stations; only monthly samples of 2001 distributed in all four quadrants, identified by the first two axes (in Fig. 10 we reported three examples of PCA ordination). The succession was particularly regular at station A03, where cladocerans (CD), and eggs and larvae (EL) clearly characterized June and July, whereas copepods (CP) were associated with May sample. Tintinnids (TN) appeared related to fall samples. Cladocerans resulted associated all along the transects A and B with July samples, whereas August samples were more related to cladocerans along the

transect C. At all stations, data from June, July and/or August 2001 occupied the most distant position from the axis origin in the diagrams, which indicates the most relevant differences in the plankton community composition. On the contrary, no clear succession can be recognizable for the other 2 years (2000 and 2002). All monthly samples were weakly ordered by PCA analyses. They were all distributed close to the origin and appeared mostly similar to fall–winter samples of 2001.

4. Discussion

Plankton communities showed high year-to-year variations in abundances and taxonomical composition, as was previously reported for the northern Adriatic Sea
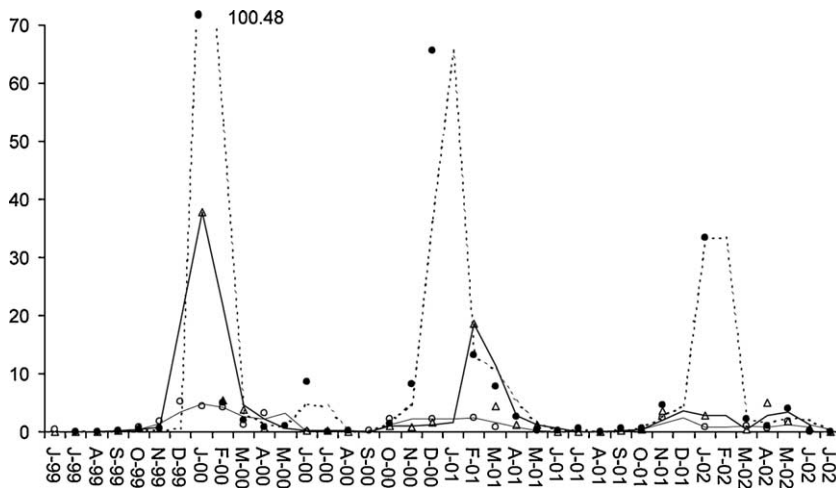

Fig. 8. The ratio between average total abundances of microzooplankton (ind. L^{-1}) and cladocerans (ind. m^{-3}) on transects A (○), B (△) and C (●).
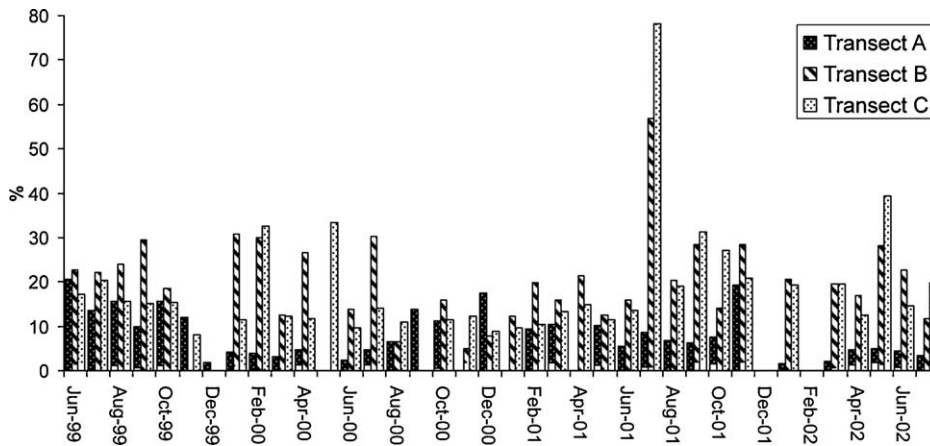
Fig. 9. Theoretical grazing impact on microphytoplankton expressed as percentage on transects A, B and C.

(e.g., Kršinić, 1995; Mozetič et al., 1998; Harding et al., 1999; Mioković, 1999; Degobbis et al., 2000; Totti et al., 2002; Fonda Umani et al., 2004). The most variable fraction was phytoplankton, which exhibited different annual patterns depending on the areas. Phytoplankton succession was more regular on the southern transects than on transect A, where it showed a very high abundance in the second half of 2000, due to the long flood of the Po River, and it was strictly confined to the surface, which only slightly enhanced density integrated over the whole water column. Conversely, the integrated abundance significantly increased on transect A in January 2002 due to the homogeneous distribution of the vernal bloom in the mixed water column. Besides this vernal bloom, phytoplankton abundances remained very low over the 3 years, particularly if compared with data obtained in the same area during the 1970s–1980s (e.g., Fonda Umani et al., 1992). This implies that phytoplankton biomass, which we can only indirectly estimate based on phytoplankton abundances, should be quite low as well. In spring–summer 2000, when the most intense and widespread mucilage event affected the whole northern Adriatic (Precali et al., 2005—this issue), phytoplankton abundances did not show any significant increase. This was particularly evident in the northern sub-basin (transect A) where abundances started to increase only from July.

Conversely nanophytoplankton significantly increased in 2000 (Totti et al., 2005—this issue), but this fraction was not able to produce any substantial contribution to total autotrophic biomass neither to exuded DOC due to the small cell volume.

Research on mucilage has been dominated by the idea that it consists of exuded algal polysaccharides copiously produced during phosphorus-limited growth

of diatoms (e.g., Myklestad, 1999 and references therein) or, more recently, of dinoflagellates (MacKenzie et al., 2002; Pompei et al., 2003). Our findings on low phytoplankton abundances, and thus biomass as well, at a basin scale, cannot support the idea of a direct and fast release of polysaccharide-rich exudation by the scarce phytoplankton. The likely source of mucilage is the dissolved organic matter (DOM) pool because of its sufficiently large size and variability (Azam et al., 1999): dissolved organic carbon (DOC) in the northern Adriatic ranged from 53 μM to 281 μM, giving ~200 μM carbon as average in summer and ~100 μM carbon in winter (Pettine et al., 2001). This pool size translates into ~40–80 g C m^{-2}. Malej et al. (2001) calculated for the summer 2000 mucilage event in the northernmost part of the Adriatic Sea (Gulf of Trieste), that concomitant with the maximum extension of mucilage coverage (as surface creamy layer, clouds and spider web structures), the total integrated mucilage-associated particulate carbon was 82 g C m^{-2}.

The DOC pool in the marine systems can be divided as autochthonous, i.e. produced in situ, or allochthonous, i.e. delivered from the land. The major identified sources of autochthonous DOM to the oceans, besides phytoplankton exudation, are sloppy feeding and excretion by grazers, viral lysis of bacteria, and more generally microbial activities on dissolved and particulate organic matter (OM). The terrestrial inputs reach the marine system mainly via river and sewage outfalls. The rivers draining into the northern Adriatic are the major sources of land derived DOM: the Po River alone can bring 1.65 tons km^{-2} year^{-1} (Pettine et al., 1998). According to Søndergaard and Middelboe (1995), only 19% (as average) of DOC rivers is labile; in the Danube–Black Sea mixing zone, Becquevort et al.

(2002) recently found that only 9% of the DOC was labile. Besides the river borne refractory DOC, which can only partially be accounted for producing huge

aggregates at a basin scale, there must be autochthonous sources of organic carbon, which are not efficiently used by both high level consumers and bacteria.
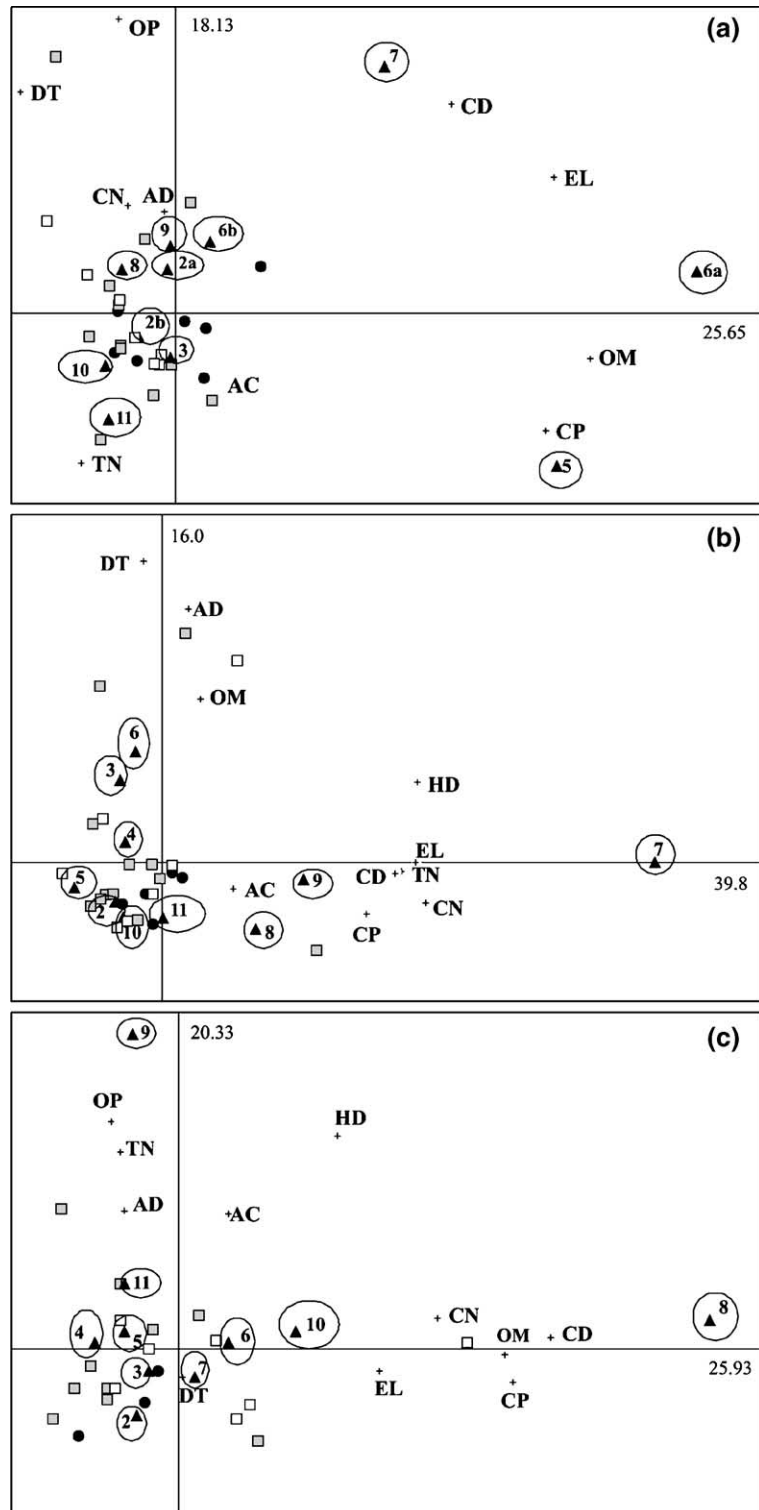
To focus on the role played by microzooplankton and mesozooplankton consumers, our findings suggest that only during 2001 the export via grazing of the photosynthesised carbon was efficient, whereas the phytoplankton biomass, although not particularly high in 2000 and 2002, was not controlled by the removal of both microzooplankton and mesozooplankton. Consumers and particularly mesozooplankton increased since April in 2001 and high abundances persisted until the end of the year, whereas in 2000 and 2002 consumers and particularly mesozooplankton remained low throughout spring and summer. In 2001 since April, a grazing food web developed and it was able to control large sized phytoplankton increase. This had a particularly relevance on transect A, because of the observed shift from the grazing to the microbial food web from the Northern basin southwards.

We can assume that a large part of the blooms was exported to the bottom in the particulate phase because non-predatory death of algae is a large-scale process (Brussaard et al., 1995; Berges and Falkowski, 1998). Bacteria acting on detritus demineralise P in preference to C due to "enzymatic fractionation" (Smith et al., 1992) and produce high C/P organic matter, leading to an enhanced production of C-enriched DOM, highly resistant to bacterial uptake, which can be seen as the precursor of the gel-like material that through aggregation produce mucilage of impressive dimension.

Once formed in summers 2000 and 2002, large aggregates dramatically impact the whole plankton community. As already stated, they can influence the microzooplankton and mesozooplankton temporal and spatial variability directly by decreasing naupliar copepod population (Kršinić, 1995), altering feeding capability (Bochdansky and Herndl, 1992; Malej and Harris, 1993) or indirectly by altering food web structure and function (e.g., Cabrini et al., 1992; Milani and Fonda Umani, 1992; Cataletto et al., 1996). Our findings are in agreement with previous results: microzooplankton did not show any relevant increase in summers of 2000 and 2002. Impact on mesozooplankton was even more evident because mucilage particularly affects the behavior of the summer dominant species *P. avirostris* (Acri et al., 1999), which in summer 2000 and 2002 did not reach its usual summer maximum. Consequently, for these 2 years it was impossible to recognize any regular seasonal succession, which on the contrary was very clear for the year 2001.

5. Conclusions

Summing up in summers 2000 and 2002, when the northern Adriatic was impacted by widespread mucilage formations, we did not observed any significant increase at a basin scale of producers, almost in the microphytoplankton fraction, which is the most likely source of exudates. On the other hand removal by grazers was lower than in spring–summer of 1999 and 2001, thus probably in 2000 and 2002 sedimentation rates of ungrazed spring diatom blooms were higher. Once at the bottom detrital carbon might have enhanced bacterial production of recalcitrant DOC. Negative effects of mucilage on microzooplankton and mesozooplankton were particularly evident in summer 2000 and more important along the transect A, where mucilage aggregates were more dense.

Acknowledgements

Fig. 10. The ordination scattergram (the first two principal components) obtained by PCA applied on the main taxonomic groups of microphytoplankton: diatoms (DT), autotrophic dinoflagellates (AD), other phytoplankton (OP); microzooplankton: heterotrophic dinoflagellates (HD), aloricate ciliates (AC), tintinnids (TN); mesozooplankton: copepod nauplii (CN); copepods (CP) cladocerans (CD), eggs and larvae (EL), other mesozooplankton (OM); on stations A03 (a), B06 (b) and C12 (c) from June 1999 to July 2002. The values reported on the axes represent the percentage of variance explained by the first two principal components. Symbols relate to years 1999 (●), 2000 (□, grey), 2001 (▲) and 2002 (□). The encircled numbers indicates the months, from February (number 2) to November (number 11) of year 2001.

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