NOTE

Relative grazing impact of microzooplankton and mesozooplankton on a bloom of the toxic dinoflagellate *Alexandrium minutum*

Albert Calbet*, Dolors Vaqué, Jordi Felipe, Magda Vila, Maria Montserrat Sala, Miquel Alcaraz, Marta Estrada

Institut de Ciències del Mar CMIMA (CSIC), Passeig Marítim de la Barceloneta 37–49, 08003 Barcelona, Spain

ABSTRACT: Grazing can be a substantial loss factor for harmful algal blooms (HABs) and a possible cause of their termination. There is, however, a considerable gap in our knowledge of the relative grazing impact of the different components of the planktonic community on a red tide. In this study, we examine the importance of grazing control on a naturally occurring bloom of the toxic dinoflagellate *Alexandrium minutum*. We estimated the grazing impact of microzooplankton (by the dilution method) and copepods (by 24 h incubations with cultured populations of *Acartia grani* and *Oithona davisae*) on a bloom of *A. minutum*. Grazing by microzooplankton ($0.84\ d^{-1}$) was equal to and even exceeded *A. minutum* growth rates ($0.79\ d^{-1}$). On the other hand, copepod impact on the *A. minutum* population was not significant, although they were actively feeding on the dinoflagellate, which accounted for 78 and 86% of the daily carbon intake of *A. grani* and *O. davisae*, respectively. Even if these results were extended to the highest realistic copepod abundance attainable in the area, the grazing impact on highly concentrated HABs would not be sufficient to significantly reduce the algal concentrations. In summary, grazing by microzooplankton can represent an important factor for the regulation of HABs.

KEY WORDS: Harmful algal bloom · *Alexandrium minutum* · Microzooplankton · Mesozooplankton · *Acartia grani* · *Oithona davisae* · Grazing

Harmful algal blooms (HABs) are becoming a commonly reported phenomenon in coastal and (semi-)confined waters, although uncertainty remains as to the causes of their apparently increased occurrence are still unknown (Anderson 1989, Hallegraeff 1993). Even more complex than the possible causes seem to be the factors controlling the development of these phenomena. There are different mechanisms that may act to regulate both the proliferation and the decline of a red tide. Hydrodynamism and meteorological events can act as concentrating agents for HABs, but can also rapidly disperse the bloom, their influence being determined by the topography of the area and the intensity of the physical stress (Steidinger 1973, Garcés et al. 1999, Vila et al. 2001). Inorganic nutrients are needed in the growth of HABs, their depletion resulting in cell mortality or in the formation of resting cysts (Anderson & Lindquist 1985). Interactions with other organisms are also important in determining the fate of algal populations. In this context, allelopathy, viruses, parasites and grazers are potential agents controlling red tides (Nagasaki et al. 1994, Zingone 1995, Coats et al. 1996, Turner & Tester 1997, Guisande et al. 2002, Johansson & Coats 2002). Amongst the biological factors influencing HABs, grazing pressure stands out as the most direct and widespread. Despite the importance of this trophic interaction, the role of grazing impact on HABs has been determined in relatively few studies (see review by Turner & Tester 1997), and most of them estimated the impact of grazers by indirect methods (Nakamura et al. 1995, 1996, Matsuyama et al. 1999). The outcomes of these studies are diverse and highly species- and site-specific (Turner & Tester 1997). In general, the effect of mesozooplankton grazing seems to be more relevant during the early stages of bloom formation, their influence being less decisive once the bloom is well established (Uye 1986). Microzooplankton grazing, on the other hand, has been shown to play a more active role in the decline of HABs (Nakamura et al. 1995, 1996, Matsuyama et al. 1999), although its impact has been seldom measured *in situ* (Gobler et al. 2002). There is, moreover, a clear lack of research comparing the effects of meso- and microzooplankton grazing impacts on the same HAB episode. The aim of this study was therefore to examine the importance of both micro- and mesozooplankton grazing as control agents for the proliferation of a naturally occurring HAB.

Materials and methods. *Community structure:* Experiments were conducted during January 2002, coincident with a bloom of *Alexandrium minutum* in the harbour of Arenys de Mar (40 km north of Barcelona, NW Mediterranean). The microplanktonic community structure was monitored monthly as part of a HAB detection program. Once the initiation of the bloom was evident, the sampling frequency was increased to 2 to 3 samples wk^{-1}. The standard method of sampling consisted of preserving 150 ml water from the patch of dinoflagellates with Lugol's solution (1% final concentration). Between 10 and 50 ml of the preserved samples were settled in Utermöhl chambers for 24 h and counted under an inverted microscope. Copepod abundance was assessed on the day of the experiment (January 29), using a 36 cm diameter plankton net with 53 µm mesh, hauled vertically from near the bottom to the surface. Samples were quickly preserved in buffered formalin (4% final concentration) for later analysis. In the laboratory, the species composition of the mesozooplanktonic community was estimated by counting and identifying all organisms in the sample.

Microzooplankton grazing impact: Microzooplankton grazing was assessed by the dilution method (Landry & Hassett 1982). Water was collected from the experimental site and transported in carboys to the laboratory within 1 h of collection. Once in the laboratory, duplicate bottles (500 ml) were filled with natural seawater (100%), previously screened through 150 µm mesh to remove mesozooplankton, and diluted with filtered (0.2 µm) seawater to obtain dilution fractions of 1, 0.75, 0.5 and 0.25. Samples were incubated in a culture room under temperature conditions similar to those *in situ* (15.5°C) for 24 h on a slow rotating (0.2 rpm) plankton wheel. Aliquots to assess *Alexandrium minutum* and ciliate abundance were collected at the beginning and at the end of the experiment and preserved with acidic Lugol (1% final concentration). To correct for ciliate losses due to preservation, a factor of 30% was applied (E. Broglio, E. Saiz, A. Calbet, I. Trepat, M. Alcaraz unpubl.). We did not amend the incubations with nutrients to avoid possible adverse effects on grazers (Gifford 1988), and because the sampling area presents high enough nutrient levels to guarantee saturating phytoplankton growth conditions (M. Vila et al. unpubl.).

Counts of *Alexandrium minutum* and ciliates were carried out using an inverted microscope on 10 ml Utermöhl settling chambers, after samples had settled for 24 h. More than 400 cells of *A. minutum* and 50 to 200 ciliates were counted per sample. Growth and grazing rates on *A. minutum* were calculated from the regression equation between net growth rate for each dilution bottle and dilution factor. The intercept of the equation is an estimation of the gross growth without predators and the slope coefficient corresponds to the community grazing rate (Landry & Hassett 1982).

To evaluate the extent of rotifer feeding impact on the bloom, *Synchaeta triophthalma* (the most abundant rotifer in the bloom) feeding rates on *Alexandrium minutum* were estimated with an incubation experiment using cultured organisms. The design consisted of 12 treatments, comprising 4 initial, 4 experimental and 4 control 75 ml polystyrene culture flasks (Corning). All flasks were filled with a suspension of *A. minutum* at a concentration of 3000 cells ml^{-1}. *S. triophthalma* was added to the experimental flasks at a concentration of 20 individuals ml^{-1}. Both experimental and control treatments simulated natural abundances, of predator and prey in the bloom. The flasks were incubated for 24 h on a rotating plankton wheel (0.2 rpm) at *in situ* temperature (15.5°C) and under a 12 h day/night light cycle. At the beginning and end of the incubations, the total flask contents were preserved with Lugol's solution (2% final concentration). As for the microplankton community structure monitoring, 10 ml of the preserved samples were settled in Utermöhl chambers for 24 h and counted under an inverted microscope.

Mesozooplankton grazing impact: Mesozooplankton grazing impact was estimated by copepod feeding experiments on the natural microplankton. The dominant organisms in the mesozooplankton community of the Arenys de Mar harbour were the copepods *Acartia grani* and *Oithona* sp. However, mesozooplankton were generally very scarce, precluding the use of wild animals for the experiments. Therefore, the experiments were conducted with cultured populations of *A. grani* (943.1 ± 10.19 [SE] µm in length), and *O. davisae* (327.9 ± 2.32 [SE] µm in length). These 2 species were originally collected from the Barcelona harbour and had been kept under controlled conditions for more than 2 yr. Around 100 *O. davisae* (males and females) or 25 *A. grani* (females) were incubated in triplicate with the natural seston community of the bloom for 24 h in 75 ml polystyrene culture flasks (Corning). Incubations took place on a rotating (0.2 rpm) plankton wheel under a 12h day/night light cycle at 15.5°C. The copepod concentration used in the experiments may seem too high for extrapolation of the resulting grazing rates to the natural community. However, considering the extremely high microplankton concentrations (3 × 10^3 cells ml^{-1} *Alexandrium minutum*, 23.4 ± 0.35 [SE] µm in diameter), an equally high abundance of predators was needed to detect the cell reduction by grazing effect. The experimental copepod:prey ratio allowed values close to the satiation of feeding (see 'Results') with a decrease at the end of the incubation of 40 and 20% of *A. minutum* concentration for *A. grani* and *O. davisae*, respectively. For the other microplanktonic

groups, reduction of abundance in the experimental flasks with respect to controls ranged from 30 to 57 % and 9 to 21 % for *A. grani* and *O. davisae* incubations, respectively. Copepod mortality was ≤1 % for the 2 species studied. Initial and final samples were preserved with Lugol's solution (1 % final concentration). Aliquots of 12 ml were settled in Utermöhl chambers for 48 h and counted under an inverted microscope. Ingestion and clearance rates on microplankton were calculated from cell disappearance using the equations of Frost (1972). Video images of 30 random cells of each dominant group were digitized with a Power Macintosh computer, equipped with a frame grabber and NIH Image analysis software (National Institute of Health, Bethesda, Maryland). The contour of the organisms was outlined, the area measured, and the length and width of the cell automatically estimated, assuming an ellipsoidal shape. For chain forming diatoms, each cell was counted as an individual organism.

Microplankton biovolumes were converted to cell carbon using a factor of 0.19 pg C μm^{-3} for ciliates (Putt & Stoecker 1989) and the equations provided by Menden-Deuer & Lessard (2000) for the other components of the community. Zooplankton carbon contents were obtained from the length-weight relationships of Uye (1982) and Uye & Sano (1998) for *Acartia grani* and *Oithona davisae*, respectively. Rotifer abundance was converted to carbon using a value of 18.12 ng C rotifer^{-1} (Egloff 1988).

Results and discussion. The natural evolution of the *Alexandrium minutum* bloom is shown in Fig. 1. *A. minutum* cells were recorded at low levels throughout the year in the Arenys de Mar harbour, but at the end of December the organisms began to increase their basal concentration in a patch at the northern part of the harbour. It was not until the end of January that they reached maximum concentrations in the sampled station and thereafter invaded the whole harbour. On the day of the experiment (January 29, 2002) the bloom was in the maintenance phase, although showing a decline in cell numbers, with abundance of *A. minutum* around 2000 to 3000 cells ml^{-1}. The composition of the microplankton community corresponding to the date of the experiments is shown in Table 1. At first glance, the data reveals a community numerically dominated by cells of *Skeletonema* sp. and *A. minutum*. However, when these values are expressed as carbon, *A. minutum* appears as the major contributor to microplankton biomass (80 % of total biomass). Other important components of the community were the dinoflagellate *Prorocentrum micans* and centric diatoms of the genus *Thalassiosira*. Ciliates (mostly *Mesodinium* spp., *Strombidium* spp., and tintinnida) and rotifers *Synchaeta triophthalma* were the dominant microplanktonic grazers. In contrast to the re-
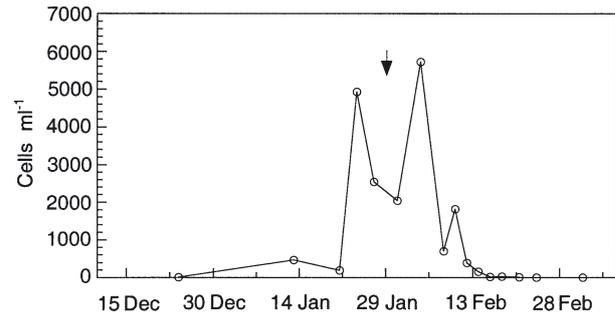

Fig. 1. *Alexandrium minutum.* Temporal pattern of abundance in the Arenys de Mar harbour from December 2001 to March 2002. Only the months in which the dinoflagellate was detected are shown. Arrow indicates day of the experiment (January 29)

markable abundance of micrograzers, larger predators, such as copepods, were very scarce, showing an average abundance in the harbour of 51 ind. m^{-3} for *Oithona* sp and 23 ind. m^{-3} for *Acartia grani*. No significant differences were found in the abundance of copepods in different locations of the harbour.

The results of the dilution experiment were evidence of an actively growing population of *Alexandrium minutum*, with growth rates (0.79 d^{-1}) comparable to those found during the exponential phase of previous blooms of this species in the studied area (0.9 d^{-1}, Garcés et al. 1998). The grazing by microzooplankton on *A. minutum* (0.84 d^{-1}) accounted for, and even exceeded, the growth rates of the dinoflagellates (Fig. 2). No clear effect of dilution treatments on the growth rates of potential protozoan grazers was evident during the experiments (ciliates r^2 = 0.06), and no satiation of the feeding was apparent (Gallegos 1989, Redden et al. 2002). According to the dilution experiment, the *A. minutum* bloom was in a slight recession phase, with an 11.3 % d^{-1} decline in the population. This result is consistent with the temporal evolution of the bloom, because the experiments were conducted during a decline in the abundance of cells (around 5 % d^{-1} from January 27 to 31, or 16 % from January 24 to 31).

Table 1. Microplanktonic community composition in terms of abundance and biomass, both expressed as mean ± SE

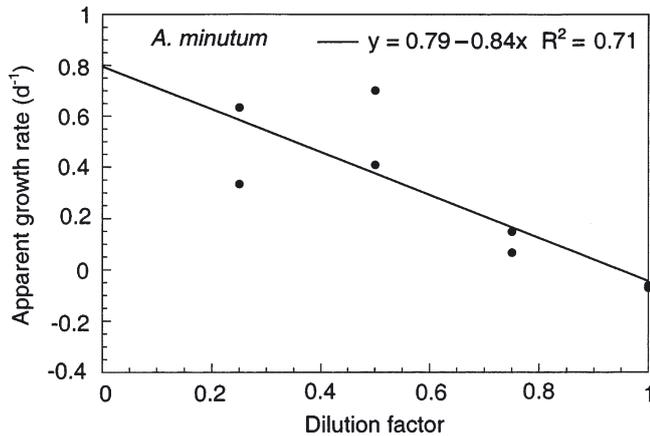| Organism	Cells ml^{-1}	μg C ml^{-1}
Alexandrium minutum	2887 ± 235	3.00 ± 0.25
Prorocentrum micans	117 ± 7	0.42 ± 0.03
Skeletonema sp.	8170[a] ± 667	0.20 ± 0.02
Thalassiosira sp.	35 ± 21	0.01 ± 0.01
Ciliates	53 ± 10	0.08 ± 0.01
Synchaeta triophthalma	21	0.38
[a]Each cell within the chain was considered as an individual organism		

Fig. 2. *Alexandrium minutum.* Apparent growth rate as a function of the dilution factor in the dilution experiment

The ingestion rates of the 2 copepod species tested are shown in Fig. 3A,B. *Acartia grani* ingestion rates were significant (*t*-test, $p < 0.05$) for all microplanktonic groups, except ciliates. *Oithona davisae*, on the other hand, only presented significant ($p < 0.05$) feeding rates on *Alexandrium minutum* and *Prorocentrum micans*. Ingestion rates on *Skeletonema* sp., although very high, were not significant due to strong variability within control bottles. Since feeding on ciliates was low and not significant for either of the copepod species, no attempt was made to correct for contribution of ciliate feeding on phytoplankton to the experiments (Nejstgaard et al. 2001). *A. grani* ingestion and clearance rates (Fig. 3C,D) were roughly 1 order of magnitude higher than those of *O. davisae*. The majority of the feeding was centered on the most abundant cells, *A. minutum* and *Skeletonema sp.* These feeding patterns do not seem to be the result of a selection for any specific group, but the consequence of the relative abundance of the different prey, as is evident from the homogeneity in clearance rates (Fig. 3C,D). Weight specific ingestion rates were high for both species, with values of 250% of the body carbon ingested per day for *O. davisae* (Fig. 3F), and 125% for *A. grani* (Fig. 3E). Consistent with the cell-based ingestion rates, most of the carbon ration resulted from the ingestion of dinoflagellates. Despite the considerable ingestion rates shown by the 2 species of copepods, their impact on the evolution of the bloom was not significant. The feeding of *A. grani* and *O. davisae* on *A. minutum*, estimated by multiplying the feeding rates obtained from experiments by the natural abundance of each copepod species, only resulted in a daily reduction of 0.007 and 0.003% of the standing stock, respectively.

The tight control exerted by microzooplankton grazing on the net growth rate of *Alexandrium minutum* is

the most evident result of the present study. This contrasts with the minor effect of mesozooplankton (copepod) grazing. Even when the feeding rates found in our study are extrapolated to the maximum attainable abundance of copepods observed in similar areas (15 copepods l^{-1}, M. Alcaraz unpubl.), their grazing on *A. minutum* does not represent a significant impact on the evolution of an established *A. minutum* bloom. For example, a grazing impact equivalent to the daily *A. minutum* growth would require 848 *Acartia grani* or 6193 *Oithona davisae* l^{-1}, which are unrealistic abundances. In contrast, microzooplankton can be numerically more important and have shorter generation times, thus enabling their grazing rates to impact on the growth rates of the dinoflagellates. Furthermore, the short microzooplankton generation times are a key factor in allowing fast proliferation of toxin-resistant species which benefit from the bloom. In our sampling, ciliates and rotifers were very abundant within the dinoflagellate patch (Table 1). *Synchaeta* spp. are active grazers on dinoflagellates, not presenting satiation of feeding within the range of prey concentration found in the present study (Egloff 1988). Our results show that *Synchaeta triophthalma* feeding on a culture of *A. minutum* at concentrations similar to *in situ* presented ingestion rates ranging from 44 to 80 cells ind.$^{-1}$ d^{-1} (average 58.4 ± 8.7 [SE]). Ingestion rates for tintinida feeding on a 23.4 µm diameter cell (equivalent to *A. minutum*) range from 40 to 50 cells ind.$^{-1}$ d^{-1} (Kamiyama & Arima 2001). Considering that only ∼30% of ciliates were able to feed on *A. minutum* (mostly tintinnids, and *Didinium* sp.), the combined feeding rates of both groups (54 to 85% of *A. minutum* standing stock) is consistent with the values of grazing obtained from the dilution experiments. Obviously, the former estimation of grazing impact is just a rough approximation, since clearance and ingestion rates are highly specific and dependent on prey size and concentration; however, it allows us to establish the fact that certain groups within the microzooplankton are able to produce most of the feeding impact detected. The results obtained here consolidate the robustness of the dilution method as an estimator of microzooplanktonic grazing. Further support of the reliability of the method is found in the close relationship observed between grazing estimates and temporal evolution of the dinoflagellate bloom at the sampled station. The slight difference between *A. minutum* growth and grazing rates, resulting in a decline of the population of 11.3% d^{-1}, is enough to explain the temporal evolution of the natural abundance of toxic dinoflagellates during the period of the experiments. However, patchiness at these high concentrations is sometimes important and could not be discarded as an effect masking the real abundance of *A. minutum* in the area, which makes relationships — such as the decline
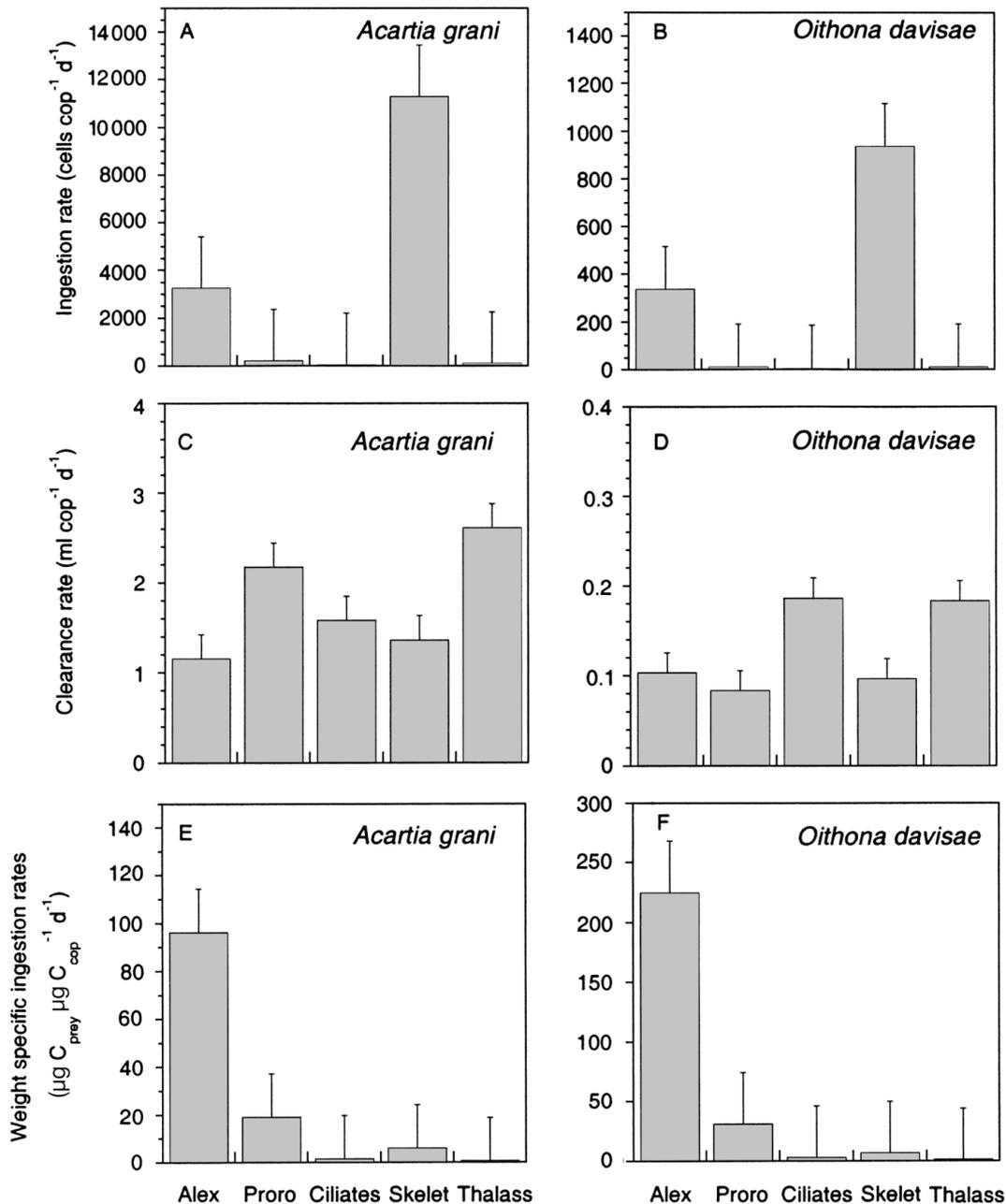
Fig. 3. *Acartia grani* and *Oithona davisae*. (A,B) Ingestion rates (cells copepod^{-1} d^{-1}), (C,D) clearance rates (ml copepod^{-1} d^{-1}) and (E,F) carbon based ingestion rates (µg C$_{prey}$ µg C$_{cop}^{-1}$ d^{-1}) on the different components of the microplanktonic community. Alex = *Alexandrium minutum*, Proro = *Prorocentrum micans*, Skelet = *Skeletonema* sp., Thalass = *Thalassiosira* sp., cop = copepod. Error bars represent SE.

of the bloom and the imbalance between dinoflagellate growth and mortality — speculative to some extent. Nevertheless, there is no doubt about the significance of microzooplankton grazing in shaping dinoflagellate net growth, which reinforces recent reports on the relative importance of microzooplankton over large metazoans as predators in highly productive environments (Calbet 2001, Strom et al. 2001, Calbet & Landry 2003).

Although active grazing by microzooplankton in marine communities is a common phenomenon (Strom et al. 2001 and references therein), studies reporting such tight coupling between phytoplankton growth and grazing under harmful algal bloom conditions are scarce (Buskey et al. 2001, Jeong et al. 2002). This coupling, as suggested by Strom et al. (2001), may be a result of the high potential growth and ingestion rates

of protist grazers. We extend this potential capability to other groups, such as rotifers (Mallin et al. 1995, the present study), which have been either often ignored or simply inadequately sampled in natural community grazing experiments; heterotrophic dinoflagellates (Nakamura et al. 1992, 1995, Jeong & Latz 1994), and meroplankton larvae (Turner & Anderson 1983) being among the most frequent.

It seems, therefore, that microzooplankters may be important agents in controlling HABs, whereas mesozooplankton appears, in general, to be unable to prevent the proliferation of a well-established HAB (see Turner & Tester 1997 for references). It is more probable that the mesozooplankton impact is significant in the initial phases of the bloom, either by feeding directly on the harmful algae or by reducing competition by selective feeding on competitors, parasites or other grazers of the algae (Uye 1986, Guisande et al. 2002, Johansson & Coats 2002). Nevertheless, it is evident that copepods actively feed on *Alexandrium minutum*, which apparently has no feeding deterrent effect despite its toxicity (presence of Isomers GTX4 and GTX1 of PSP toxins, analysed by HPLC with postcolumn oxidation and fluorescence detection, K. Van Lenning, pers. comm.). This view is consistent with previous studies (da Costa & Fernandez 2002, Guisande et al. 2002) showing that copepod feeding is inhibited only after several days of continuously ingesting *A. minutum*. The copepods we used in the experiments came from cultures and had never been exposed to any toxic dinoflagellate. It is probable that conducting the same experiments with the natural copepod community of the harbour would have resulted in much lower feeding rates. The long term feeding inhibitory effects could explain the low abundance of copepods in the Arenys de Mar harbour, which, according to parallel records in other harbours nearby, should show a peak of biomass at the time of the experiments (M. Alcaraz unpubl.). This harmful effect on copepods may be the result of direct ingestion of toxic dinoflagellates and of protozoa or small metazoa, the latter serving as vectors for the toxins. In a more favourable scenario, with other species at play, protozoans could act as detoxicating agents, allowing a safer carbon transfer from the toxic algae to higher trophic levels (Jeong et al. 2001).

In the present study, we do not present direct evidence of a bloom termination by microzooplankton grazing. There are other agents, not considered here, such as viruses, parasites, nutrient availability or climatic forcing that could have participated in ending the bloom. Most probably, there is no single mechanism involved in the termination of HABs. Moreover, our conclusions based on single day experiments in a particular bloom do not allow generalization to other areas. However, our study presents evidence of a tight coupling between microzooplankton grazing and a HAB forming dinoflagellate growth rate, and depicts a potentially important role for micrograzers in shaping the extent of toxic algae proliferations.

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