

## NOTE

## Grazing in the heterotrophic dinoflagellate *Oxyrrhis marina*: size selectivity and preference for calcified *Emiliana huxleyi* cells

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**ABSTRACT:** Selective grazing on nanophytoplankton by the heterotrophic dinoflagellate *Oxyrrhis marina* was investigated in laboratory experiments. *O. marina* was offered 2 mixtures of differently sized algae: (1) *Micromonas pusilla* (2 µm Equivalent Spherical Diameter), *Emiliana huxleyi* (5 µm ESD), and *Tetraselmis suecica* (7 µm ESD); and (2) *Nannochloris* sp. (2 µm ESD), *Isochrysis galbana* (5 µm ESD), *Rhodomonas* sp. (8 µm ESD), and *Tetraselmis* sp. (10 µm ESD). *O. marina* grazed selectively on the larger algal species (ESD ≥ 7 µm), and also selected for the larger cells within each species. *O. marina* discriminated against *E. huxleyi*. To test this selection, *O. marina* was offered mixtures of equal concentrations of the similarly sized algae *E. huxleyi* and *I. galbana*. In these mixtures, *O. marina* preferred the calcified *E. huxleyi* cells over noncalcified *E. huxleyi* cells and discriminated against *I. galbana*. This result is also interpreted in terms of size-selective grazing.

**KEY WORDS:** Protozoa · Food selection · Prey size · Microphytoplankton · Coccoliths

Heterotrophic dinoflagellates are now recognized as a ubiquitous, important component of the pelagic protozoan community that feeds on pico- and nanophytoplankton (Lessard 1991). Size-selective grazing in protozoans (Fenchel 1980, Jonsson 1986, Rassoulzadegan et al. 1988) has been examined; however, little is known about the food preferences of heterotrophic dinoflagellates (Hansen 1992).

The widespread species *Oxyrrhis marina* was used as a model organism to study selective grazing in an omnivorous phagotrophic dinoflagellate. *O. marina*, which can reach high abundances in rockpools and salt lakes, has also been found in the White Sea, the western Baltic, the English Channel and in the Mediterranean Sea (Kofoid & Swezy 1921). This species has been reported to feed on a wide range of particle sizes, from small algae like *Nannochloris oculata* (2 to 4 µm)

to algae as large as *O. marina* itself, like *Cricosphaera elongata* (20 to 30 µm) (see Droop 1966). On the other hand, *O. marina* also seems to be able to discriminate between food species (Tarran 1992). The experiments presented here were designed to test (1) size-selectivity in *O. marina* grazing and (2) whether or not *E. huxleyi* may form an exception within its size class. In contrast to most previous dinoflagellate grazing studies, we used mixtures of food items.

**Material and methods.** *Oxyrrhis marina* and the algal species were obtained from the NIOZ culture collection (Netherlands Institute for Sea Research, Dept Biological Oceanography). They were grown semi-continuously in batch cultures in autoclaved f/2-medium (Guillard & Ryther 1962) at 15°C and illuminated 16 h light:8 h dark with 60 µE m<sup>-2</sup> s<sup>-1</sup>. *O. marina* was fed *Isochrysis galbana* and *Rhodomonas* sp.

In 3 incubation experiments *Oxyrrhis marina* (18 µm Equivalent Spherical Diameter, ESD) was offered different mixtures of algal species (Table 1). The experiments were performed in 600 ml glass bottles mounted on a rotating device (0.5 rpm), kept at 15°C and illuminated with 10 µE m<sup>-2</sup> s<sup>-1</sup> light (16:8 h). Prior to the experiments, *O. marina* was pre-adapted for 24 h to all experimental conditions, including food composition and concentrations. The algae used to restore the initial concentrations after the adaptation period, were also adapted to the low light conditions.

In the experimental and control bottles (i.e. with and without *Oxyrrhis marina*), cell concentrations and cell sizes of all species were followed for 48 h. Measurements of *O. marina* (Expts 1, 2, and 3) and algal concentration and size distribution (except *Micromonas pusilla*) in Expt 1 were made on unpreserved samples using a 128-channel electronic particle counter (Particle Data Inc.). Algae in Expts 2 and 3 were measured without preservation applying flow cytometry (Coulter Epics XL) on the basis of their fluorescence characteristics (Fig. 1a, b). Calcified *Emiliana huxleyi* cells were distinguished from noncalcified cells by their side-

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Table 1. Experimental set-up with initial *Oxyrrhis marina* biovolume concentrations and initial cell sizes and biovolumes of the food algae. n: number of replicates, ESD: equivalent spherical diameter

	<i>Oxyrrhis marina</i> ( $\mu\text{m}^3 \text{ml}^{-1}$ )	Food algae (species)	Size (ESD, $\mu\text{m}$ )	Cell volume ( $\mu\text{m}^3$ )
Expt 1 (n = 1)	$2.2 \times 10^6$	<i>Micromonas pusilla</i>	1.6	2
		<i>Emiliana huxleyi</i>	5.2	73
		<i>Tetraselmis suecica</i>	7.0	183
Expt 2 (n = 4)	$16.6 \times 10^6$	<i>Nannochloris</i> sp.	1.7	2
		<i>Isochrysis galbana</i>	5.0	64
		<i>Rhodomonas</i> sp.	7.8	250
		<i>Tetraselmis</i> sp.	9.8	492
Expt 3 (n = 4)	$12.3 \times 10^6$	<i>Emiliana huxleyi</i>	4.7	55
		<i>Isochrysis galbana</i>	4.7	56

scattering properties (flow cytometry, see Fig. 1c). Inverted microscopy was used to count preserved (2% acid Lugol's solution) samples of *M. pusilla* and to additionally control for the fraction of calcified *E. huxleyi* (1% glutaraldehyde).

Cell volumes of algae and *Oxyrrhis marina* were corrected by species-specific comparison with live cell volumes measured with an Image-Analysis-System (Leica Quantimet 570) at 500 $\times$  or 125 $\times$  magnification,

respectively. Grazing rates were calculated from concentration changes of all species, including *O. marina*, in the experimental bottles compared to the controls following Frost (1972). Electivity-indices ( $\alpha$ ) were calculated from clearance rates and statistically tested, as described by Chesson (1983) for selection experiments with changing food densities. For display purposes, the  $\alpha$  were transformed to  $\epsilon$ , with  $-1 \geq \epsilon \leq +1$ , following Chesson (1983).

**Results.** Due to the chosen light conditions, algal biovolume changes in the controls were insignificant (Figs. 2a, c & 3a); therefore, rates of changes in the experimental bottles containing *Oxyrrhis marina* reflect grazing rates, which are listed in Table 2. In the experimental bottles, biovolume concentrations significantly declined in the larger sized algae *Tetraselmis suecica*, *Rhodomonas* sp. and *Tetraselmis* sp. Within Expts 1 and 2, *O. marina* grazed on these larger algae with higher clearance rates than on the smaller algae (Table 2).

Due to the much lower algal and higher *Oxyrrhis marina* concentrations used in Expt 2, rates of biovolume changes were higher than in Expt 1. In Expt 1, large cells remained through the 48 h of the experiment (Fig. 2b), whereas in Expt 2 they were almost totally removed within the first 6 h (Fig. 2d). Despite higher maximum clearance rates, the ingestion rates and biovolume-specific daily rations of *O. marina* were higher in the Expt 1 (Table 2), in which food density

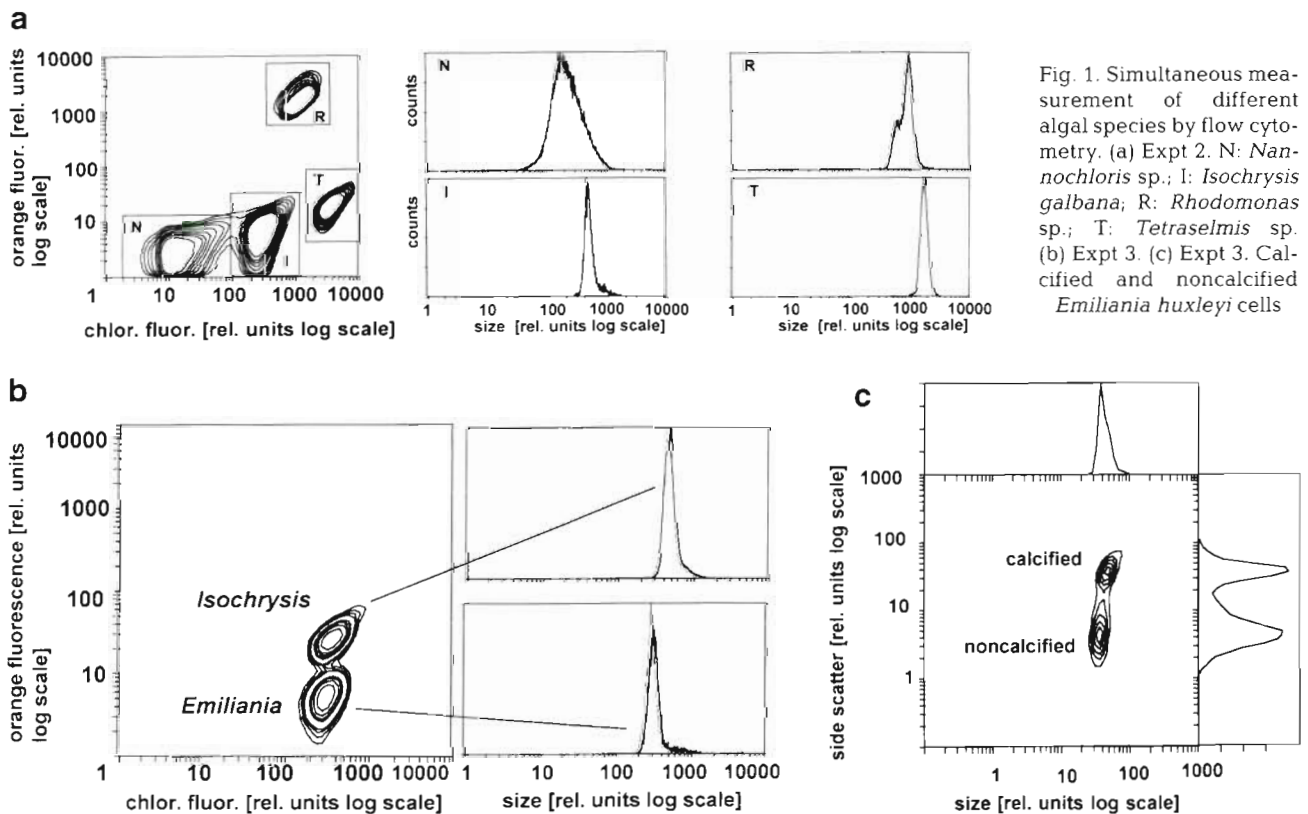


Fig. 1. Simultaneous measurement of different algal species by flow cytometry. (a) Expt 2. N: *Nannochloris* sp.; I: *Isochrysis galbana*; R: *Rhodomonas* sp.; T: *Tetraselmis* sp. (b) Expt 3. (c) Expt 3. Calcified and noncalcified *Emiliana huxleyi* cells

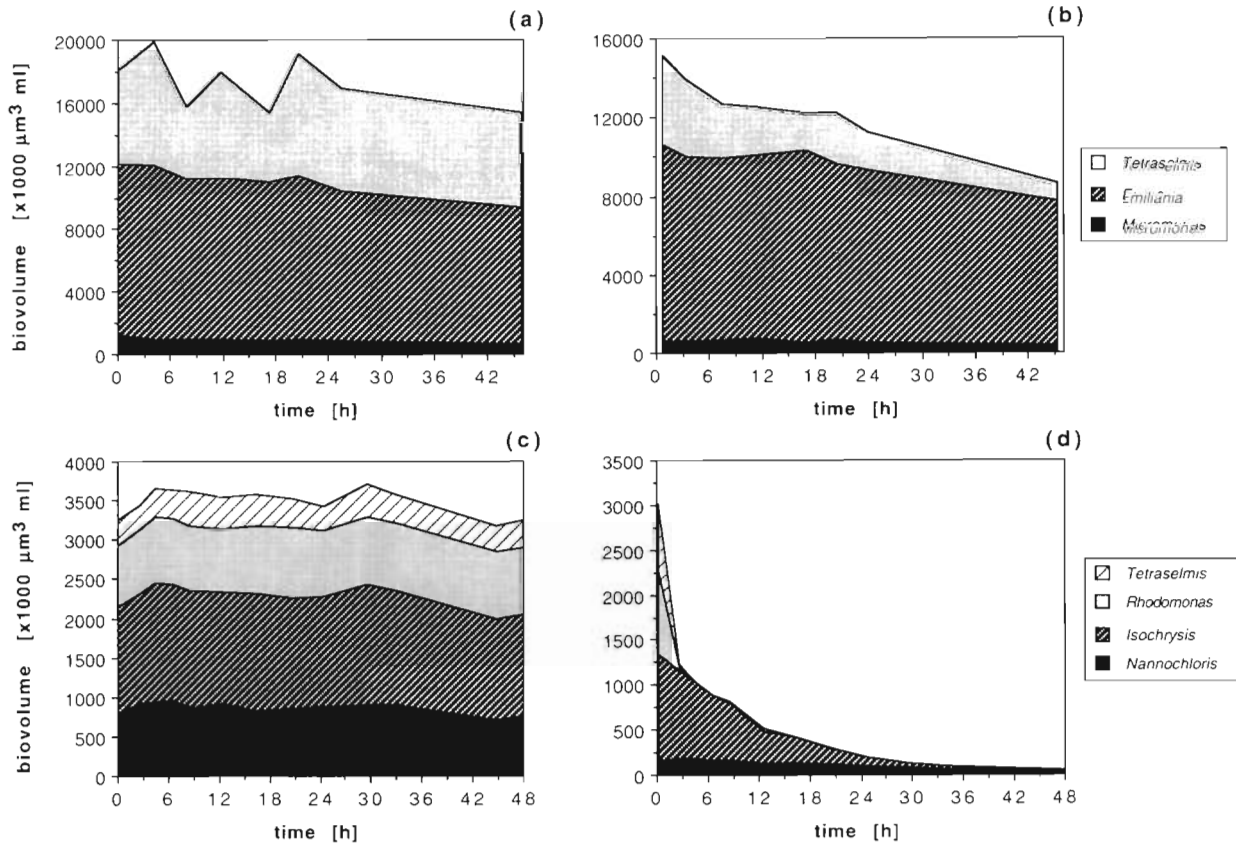


Fig. 2. Mean algal biovolume concentrations over 48 h in incubations without (a, c; controls) and with (b, d) *Oxyrrhis marina*. (a, b) Expt 1: *Micromonas pusilla* (2  $\mu\text{m}$ ), *Emiliana huxleyi* (5  $\mu\text{m}$ ) and *Tetraselmis suecica* (7  $\mu\text{m}$ ). (c, d) Expt 2: *Nannochloris* sp. (2  $\mu\text{m}$ ) *Isochrysis galbana* (5  $\mu\text{m}$ ), *Rhodomonas* sp. (8  $\mu\text{m}$ ) and *Tetraselmis* sp. (10  $\mu\text{m}$ ). Note: there were 2 *Tetraselmis* species which were different in size (different shading)

was much higher. In both experiments, the moderately sized algae (*Emiliana huxleyi* and *Isochrysis galbana*, respectively) declined at a slower rate than did the larger algae, and concentrations changed least in the smallest algae, *Micromonas pusilla* and *Nannochloris* sp. (Fig. 2b, d).

Positive selection of the larger cells is explicitly demonstrated by the Chesson-indices (Fig. 4a, b). As long as they were available at concentrations  $\geq 20$  cells  $\text{ml}^{-1}$ , the large *Rhodomonas* and *Tetraselmis* species were consumed in preference to the smaller algae. At even lower concentrations of these algae, *Rhodomonas*

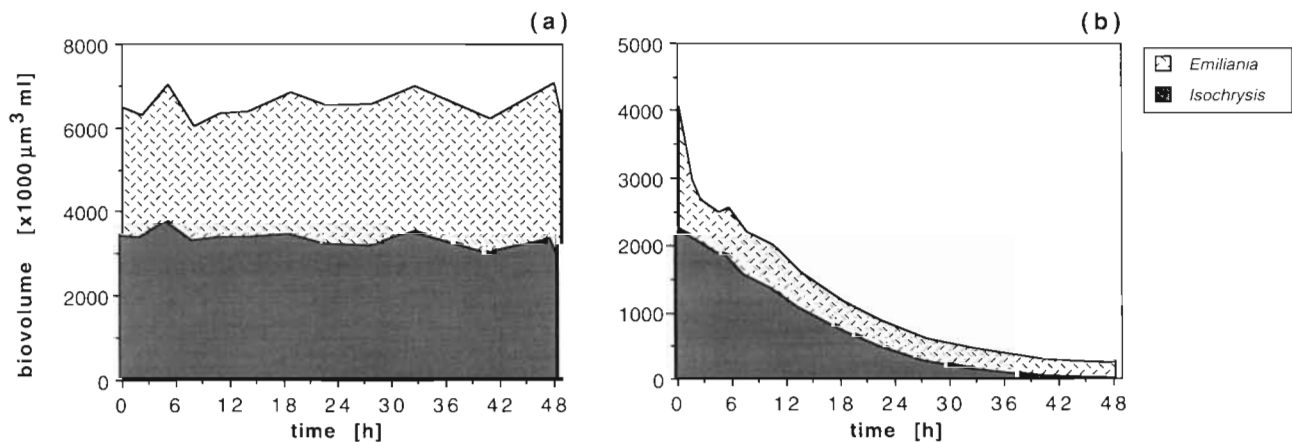


Fig. 3. Expt 3. Mean biovolume concentrations of *Emiliana huxleyi* and *Isochrysis galbana* over 48 h incubations without (a; control) and with (b) *Oxyrrhis marina*

Table 2. Mean algal concentrations ( $\times 1000 \mu\text{m}^3 \text{ml}^{-1}$ ), volume-specific clearance rates [ $\times 1000 \mu\text{m}^3 (\mu\text{m}^3 \text{Oxyrrhis})^{-1} \text{d}^{-1}$ ], ingestion rates ( $\text{cells Oxyrrhis}^{-1} \text{d}^{-1}$ ) and volume-specific daily rations ( $\% \text{d}^{-1}$ ) for *Oxyrrhis marina* feeding on 7 different algal species during 3 incubation experiments

Expt no.	Time	Food algae (species)	Algal conc.		Clearance rate		Ingestion rate	SDR ( $\% \text{d}^{-1}$ )
			Mean	SE	Mean	SE		
1	00–12 h	<i>Micromonas pusilla</i>	719	–	–45	–	–65	–3.3
1	12–24 h	<i>Micromonas pusilla</i>	617	–	76	–	96	4.7
1	24–48 h	<i>Micromonas pusilla</i>	449	–	54	–	51	2.4
1	00–12 h	<i>Emiliana huxleyi</i>	9447	–	–11	–	–6	–10.0
1	12–24 h	<i>Emiliana huxleyi</i>	9190	–	15	–	8	13.7
1	24–48 h	<i>Emiliana huxleyi</i>	7896	–	20	–	11	15.8
1	00–12 h	<i>Tetraselmis suecica</i>	3283	–	560	–	40	183.9
1	12–24 h	<i>Tetraselmis suecica</i>	2186	–	132	–	6	28.8
1	24–48 h	<i>Tetraselmis suecica</i>	1296	–	174	–	6	22.6
2	00–06 h	<i>Nannochloris</i> sp.	169	2	16	4	5	0.3
2	06–24 h	<i>Nannochloris</i> sp.	132	5	40	2	10	0.5
2	24–48 h	<i>Nannochloris</i> sp.	68	4	42	2	5	0.3
2	00–06 h	<i>Isochrysis galbana</i>	949	3	142	5	10	13.5
2	06–24 h	<i>Isochrysis galbana</i>	366	20	148	13	4	5.4
2	24–48 h	<i>Isochrysis galbana</i>	30	6	209	11	0	0.6
2	00–06 h	<i>Rhodomonas</i> sp.	126	2	1430	52	5	18.0
2	06–24 h	<i>Rhodomonas</i> sp.	1.3	0.0	225	31	0	0.0
2	24–48 h	<i>Rhodomonas</i> sp.	0.2	0.0	86	16	0	0.0
2	00–06 h	<i>Tetraselmis</i> sp.	77	6	1196	96	1	9.2
2	06–24 h	<i>Tetraselmis</i> sp.	6.1	0.5	–43	42	–0	0.0
2	24–48 h	<i>Tetraselmis</i> sp.	5.4	0.7	–27	38	–0	0.0
3	00–02 h	<i>Emiliana huxleyi</i>	1349	42	961	52	84	129.2
3	02–12 h	<i>Emiliana huxleyi</i>	663	12	–21	6	–1	0.0
3	12–48 h	<i>Emiliana huxleyi</i>	359	7	61	2	1	2.2
3	00–02 h	<i>Isochrysis galbana</i>	2185	16	87	6	11	18.9
3	02–12 h	<i>Isochrysis galbana</i>	1685	11	101	4	10	17.0
3	12–48 h	<i>Isochrysis galbana</i>	348	16	226	7	4	7.8

sp. was still positively selected, but grazing on *Tetraselmis* sp. ceased (Fig. 4b, Table 2). A multivariate test on the Chesson-indices of the first period of Expt 2, when all algal species were sufficiently abundant, showed the preference for the large algal species to be significant ( $p < 0.05$ , Hotelling  $t$ -test).

After 6 h, when the concentrations of the large algae were diminished to very low levels, *Oxyrrhis marina* fed primarily on the moderately sized *Isochrysis galbana* (Fig. 4b), which was grazed down during the rest of the experiment in preference to the small *Nannochloris* sp. (Figs. 2d & 4b). The (negative) Chesson-

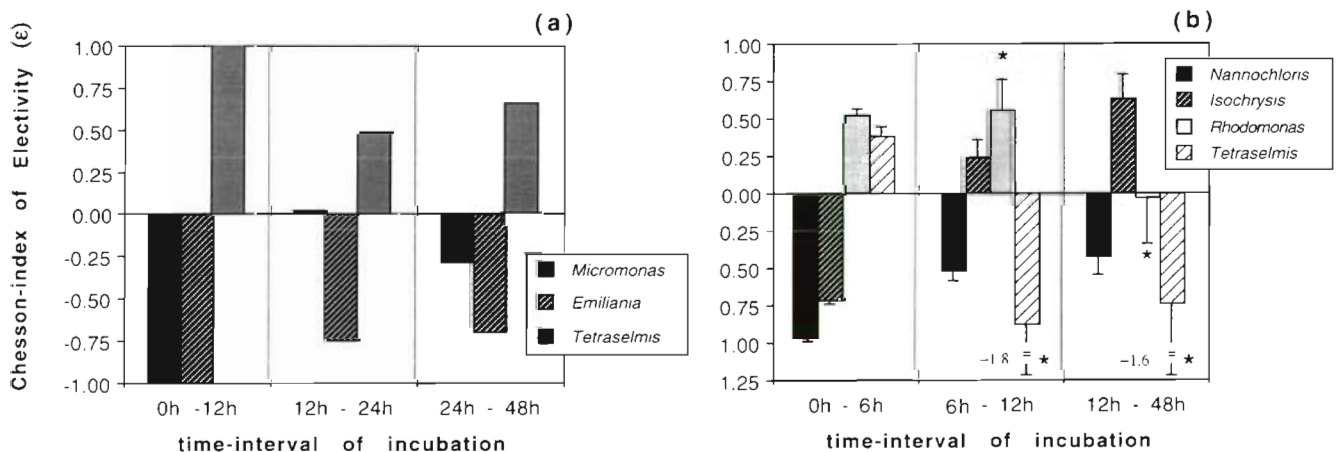


Fig. 4. Chesson-indices of Electivity ( $\epsilon$ ) for *Oxyrrhis marina* simultaneously offered differently sized algal species (see Fig. 2):  $-1 \leq \epsilon \leq +1$ , with  $\epsilon < 0$  indicating negative,  $\epsilon > 0$  positive, and  $\epsilon \approx 0$  no selective grazing. (a) Expt 1. (b) Expt 2. \*Large SD due to very low concentrations; mean  $\pm$  SD,  $n = 4$



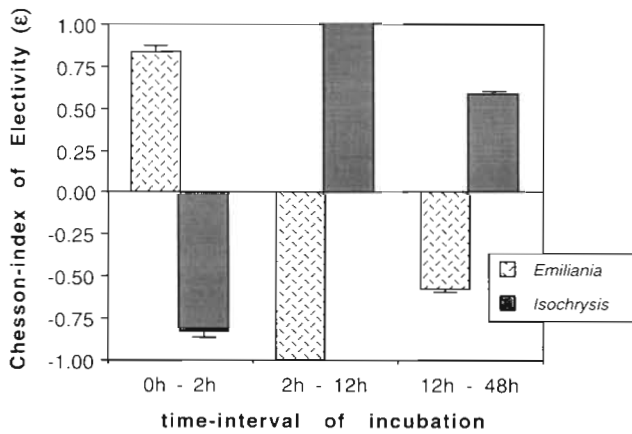


Fig. 5. Chesson-indices of Electivity ( $\epsilon$ ) for *Oxyrrhis marina* simultaneously offered *Emiliaia huxleyi* and *Isochrysis galbana*  $-1 \leq \epsilon \leq +1$ , with  $\epsilon < 0$  indicating negative,  $\epsilon > 0$  positive, and  $\epsilon = 0$  no selective grazing. Mean  $\pm$  SD, n = 4

indices of the smaller algae increased during the experiments, while the concentrations of the preferred, larger algae diminished. As a result, after 12 h the smallest species, *Micromonas pusilla*, was consumed almost in proportion to its abundance ( $\epsilon \approx 0$ , Fig. 4a). However, considerable discrimination remained against the moderately sized and most abundant alga *Emiliaia huxleyi* (Fig. 4a) and the small *Nannochloris* sp. (Fig. 4b).

In Expts 1 and 2, *Emiliaia huxleyi* was the only moderately sized alga that was selected against. More proof of a special feeding behaviour of *Oxyrrhis marina* towards *E. huxleyi* was demonstrated in Expt 3, where the similarly sized *Isochrysis galbana* and *E. huxleyi* were simultaneously offered. *O. marina* did not select against *E. huxleyi* in the first hours of the experiment. However, thereafter, *O. marina* preferred *I. galbana* (Figs. 3 & 5). All preferences were signifi-

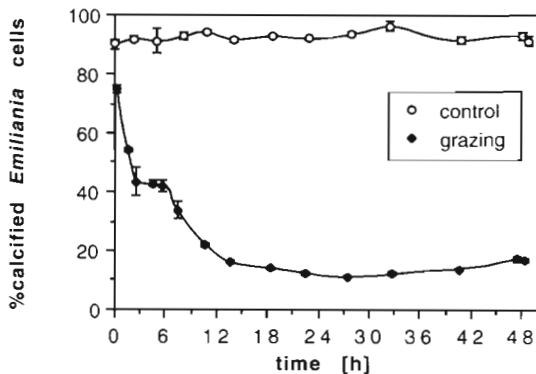


Fig. 6. Expt 3. Fraction of calcified *Emiliaia huxleyi* cells (% total *E. huxleyi* cell concentration) over 48 h incubations with (grazing) and without (control) *Oxyrrhis marina*. Mean  $\pm$  SD, n = 4. Where error bars are invisible, they fall within the size range of the symbols

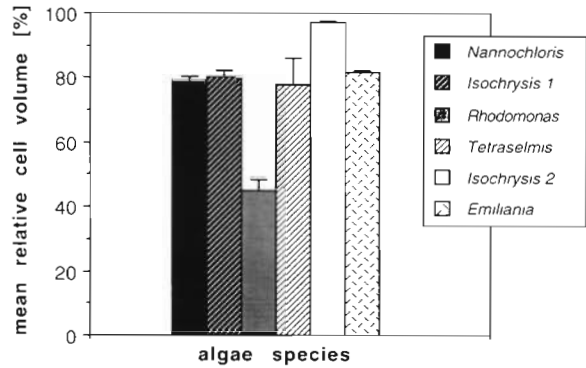


Fig. 7. Expts 2 and 3. Algal cell volume as % of cell volume in controls after 24 h grazing (for *Rhodomonas* sp. and *Tetraselmis* sp. after 12 h) by *Oxyrrhis marina*. Mean  $\pm$  SD, n = 4

cant (Student's *t*-test,  $p < 0.05$ ). While in the controls the percentage of calcified *E. huxleyi* cells remained constantly high ( $92 \pm 2\%$ ), the percentage in the experimental bottles declined sharply to 17% (Fig. 6), indicating a strong selection for calcified over noncalcified cells of *E. huxleyi*.

After 24 h grazing by *Oxyrrhis marina*, the mean cell size in all algal species was significantly reduced ( $p < 0.01$ , Student's *t*-test) in comparison to their sizes in the controls (Fig. 7). This indicates a preference of *O. marina* for larger cells within the species.

In Expt 3 controls, a daily rhythm in *Emiliaia huxleyi* cell size was found. *E. huxleyi* showed synchronized cell growth, with cell division at the end of the dark period (Fig. 8), which is in accordance with observations by van Bleijswijk et al. (1994). However, such a rhythm was missing in the bottles with grazing, indicating that *Oxyrrhis marina* fed selectively on the actively growing and dividing cells.

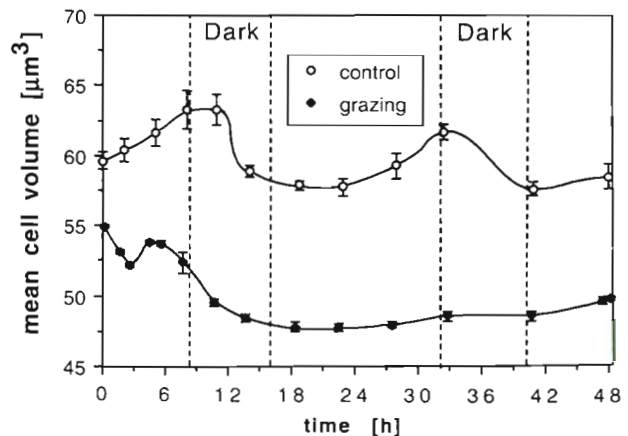


Fig. 8. Expt 3. Mean cell size in *Emiliaia huxleyi* over 48 h incubations with (grazing) and without (control) *Oxyrrhis marina*. Mean  $\pm$  SD, n = 4. Where error bars are invisible, they fall within the size range of the symbols

**Discussion.** In Expts 1 and 2, initial concentrations of the different algal species were not equal and their proportions changed during the incubations. We applied the Chesson-index, which is especially suited to measuring selectivity under these conditions. It measures any deviation from random foraging independent of changes in food item concentrations, and does not change unless the behaviour of the grazer changes (Chesson 1983). According to optimal foraging theory for a predator handling individual prey items, selective behaviour towards a less preferred prey ( $i$ ) is not influenced by the abundance of  $i$ , but by the abundance of the energetically more optimal, preferred prey (Charnov 1976). If the larger algae were the preferred prey, they would remain preferred irrespective of the abundance of the smaller algae. Thus, the relatively low biomass of the smallest algal species should neither have influenced the selective behaviour of *Oxyrrhis marina* towards themselves, nor towards the preferred, larger algal species.

The number of experiments and food species tested was limited, and food quality related properties other than size, e.g. biochemical clues (smell/taste), shape or mobility, may differ between the species tested and may also have affected grazing selectivity. Chemosensory ability has been shown to exist in flagellates (Bennett et al. 1988). However, selection experiments with *Oxyrrhis marina* grazing on a microalgae (*Dunaliella terticolata*) and flavoured and unflavoured latex beads suggested that *O. marina* is unable to distinguish particles on the basis of smell or taste (Tarran 1992). Cell shapes were not very different in our experiments: ovoid in case of *Rhodomonas* sp. and both *Tetraselmis* species and globoid in all other species. It is doubtful that *O. marina* could differentiate between such small differences in shape.

Grazing activity may be most directly documented by the clearance rate, which we expressed per unit biovolume of the grazer to account for differences in grazer size. Compared to Expt 1, maximum clearance rates were 2 to 3 times higher in Expts 2 and 3, indicating feeding saturation at the high initial food concentrations in the Expt 1 (Table 2). Maximum clearance rates and specific daily rations found in the first periods of the experiments were in the same range as reported in previous studies on *Oxyrrhis marina* (Tarran 1992 and references therein), and would allow growth rates up to 0.9 doublings  $d^{-1}$  (with ~50% gross growth efficiency, Davidson et al. 1995). The specific daily rations found during the remainder of Expts 2 and 3 were too low to support growth of *O. marina*, which is in accordance with the observed small changes in their biomass (not shown).

The selection for larger particles was consistently found in all experimental treatments of this study and,

obviously, size is a major selection criterium in *Oxyrrhis marina*. Size-selective grazing has also been shown for flagellates (Monger & Landry 1991, Hansen 1992), and ciliates (Fenchel 1980, Jonsson 1986, Ras-soulzadegan et al. 1988). Ciliates were shown to have an optimum prey size and their size-selectivity has been explained by the structure of their feeding apparatus (e.g. Fenchel 1980). In many flagellates such elaborate feeding structures are missing. The flagellate *O. marina* uses its transverse flagellum to contact and capture the prey particles (Dodge & Crawford 1971, 1974). This flagellum is equipped with hair-like projections, which may have a function in particle selection. Tarran (1992) observed differential feeding by *O. marina* on microalgae, but ascribed selectivity rather to feeding history than to prey size. Therefore, *O. marina* was pre-adapted to the food compositions used in the experiments of this study. Hansen (1992) found size-selective grazing to occur in the dinoflagellate *Gyrodinium spirale*. *G. spirale* was shown to have an optimum prey size, which is similar to its own size. The size-related preference of *O. marina* for large particles (this study) is in accordance with the results for *G. spirale*. However, in *O. marina*, there was some indication for, relative to the size of the grazer, a lower optimum food size.

In the present multispecies study, grazing on *Emiliania huxleyi* occurred but, in most cases, a negative selection was found. The observed discrimination against *E. huxleyi* in Expt 1 can not be explained by its size, since *E. huxleyi* was intermediate in size to *Micromonas pusilla* and *Tetraselmis suecica*. Perhaps deterrent substances played a role. Grazing on the microalga *Phaeocystis* cf. *globosa* by copepods (Hansen & van Boekel 1991) and by protozoans, including *Oxyrrhis marina* (Hansen et al. 1993), was also found to be very low, and DMSP (dimethylsulphoniopropionate)-related substances have been suggested to work as anti-grazing compounds (e.g. Estep et al. 1990). Whether a possible release of DMSP-related substances by *E. huxleyi* played a role in our experiments is not known and remains speculative.

An exception to the discrimination against *Emiliania huxleyi* was the selection of the calcified over noncalcified *E. huxleyi* and in preference to *Isochrysis galbana* (Expt 2). Since calcified *E. huxleyi* are bigger than both other cell types, 89  $\mu m^3$  compared to 55  $\mu m^3$  and 57  $\mu m^3$  (apparent ESD at  $t = 0$  h), the preference for the calcified cells could be explained by size-selectivity. The possession of coccoliths does not seem to be an effective defence mechanism, as has been suggested (Young 1994). On the contrary, coccoliths make the cells larger and, in this study, more susceptible to grazing by *Oxyrrhis marina*. Indeed, in experiments with *E. huxleyi* as the sole food or in bloom situations, graz-

ing on *E. huxleyi* by microzooplankton (Holligan et al. 1993), including *O. marina* (Tarran & Burkill 1995), has been shown.

One reason why microzooplankton may have a significant impact on *Emiliana huxleyi* populations is the preference, at least by *Oxyrrhis marina*, for the growing and dividing cells of *E. huxleyi*. If the grazers selectively remove the metabolically active fraction of an algal population, their impact would be much greater than would be estimated from numerical cell losses.

Hetero- and mixotrophic dinoflagellates form a substantial part of the herbivorous community. These organisms may show feeding behaviour like that observed for *Oxyrrhis marina*. However, it is clear that more investigations on selective grazing in heterotrophic dinoflagellates are needed.

*Acknowledgements.* We thank Mrs Anna Noordeloos for providing us with algal stock cultures. Dr Wim Klein Breteler and Dr Marcel Veldhuis are thanked for assistance in image-analysis and flow cytometry. Mr Jaap van der Meer is thanked for mathematical and statistical advice. Furthermore, we are indebted to Dr Wim Klein Breteler, Dr Roel Riegman, Dr Marcel Veldhuis and Dr Judith van Bleijswijk for their valuable comments and Mr Paul Boudreau for linguistic improvements of the manuscript.

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Responsible Subject Editor: J. Dolan, Villefranche-sur-Mer, France

Manuscript first received: September 25, 1995  
Revised version accepted: April 10, 1996