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EFFECTS OF TWO BLOOM-FORMING DINOFLAGELLATES, *PROROCENTRUM MINIMUM* AND *GYRODINIUM UNCATENUM*, ON THE GROWTH AND SURVIVAL OF THE EASTERN OYSTER, *CRASSOSTREA VIRGINICA* (GMELIN 1791)

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ABSTRACT Laboratory experiments were conducted to investigate the effects of the dinoflagellates *Prorocentrum minimum* and *Gyrodinium uncatenum* on the growth and survival of juvenile eastern oysters, *Crassostrea virginica*. In separate experiments lasting 30 d and 18 d for *P. minimum* and *G. uncatenum*, respectively, the dinoflagellates were offered to the oysters in both unialgal and mixed diets (with the diatom *Thalassiosira weisflogii*). Eight diets were used in each experiment: (i) the dinoflagellate at bloom density, (ii) the dinoflagellate at 33% bloom density, (iii) the dinoflagellate at 5% bloom density, (iv–vi) the diatom at the above densities, (vii) 50% dinoflagellate bloom density + 50% diatom bloom density, and (viii) 5% dinoflagellate bloom density + 95% diatom bloom density.

P. minimum at bloom density resulted in 100% mortality of juvenile oysters within 14 d and at 33% bloom density it resulted in 43% mortality within 22 d. Diets containing 5% *P. minimum* density did not cause mortality and supported good shell growth. No mortality was observed among oysters fed *G. uncatenum* and diets which included this dinoflagellate resulted in significantly greater growth than diets of the diatom *T. weisflogii*.

KEY WORDS: dinoflagellates, oysters, *Crassostrea virginica*, *Prorocentrum minimum*, *Gyrodinium uncatenum*, growth, survival

INTRODUCTION

Blooms of toxic and noxious algae are increasing worldwide in distribution, intensity and duration (Anderson, 1989; Cherfas, 1990; Smayda, 1990). While most of the attention focussed on toxic blooms has been related to species which pose public health risks, evidence is mounting that numerous species of algae, which apparently do not threaten human health, may nevertheless be noxious or harmful for bivalves (see Shumway, 1990; Shumway et al., 1990 and references therein).

In Chesapeake Bay, USA, no occurrences of PSP, DSP, or NSP have been recorded (VA Health Department) and the causative species (within the genera *Gymnodinium*, *Pyrodinium*, *Protogonyaulax*, *Dinophysis* and *Ptychodiscus*) have not been reported. Yet, substantial impacts on shellfish resources, particularly bivalve culture operations, have been observed. Anecdotal evidence from commercial hard clam (*Mercenaria mercenaria* (L.) and oyster (*Crassostrea virginica*) aquaculturists in Virginia suggests that dinoflagellate blooms in the late spring/early summer and in the late summer/early fall are responsible for widespread mortalities of juveniles (Cherrystone Aquafarms, Bagwell Enterprises, Intertidal Marine, pers. comm.). When they occur, late spring/early summer dinoflagellate blooms in this area are domi-

nated by *Prorocentrum minimum* (var. *mariae-lebouriae*) and late summer/early fall blooms by a *Gyrodinium-Cocclodinium-Gymnodinium* complex (Mackiernan, 1968; Zubkoff et al., 1979; Marshall, 1993; Sellner and Luckenbach, pers. obs.). At the Virginia Institute of Marine Science Oyster Hatchery, located on the York River estuary, Chesapeake Bay, Virginia, we have consistently observed impacts of dinoflagellate blooms on oyster reproduction, growth and survival. Conditioned adult oysters frequently do not spawn in the presence of bloom densities of *P. minimum*, and early larval development is impaired and high mortalities occur when *P. minimum* or the lysate from ruptured cells is present in larval culture tanks (V. Shaffer and M. Luckenbach, unpublished data). Juvenile oysters (from metamorphosis to ca. 2 cm shell height) within a land-based, flow-through nursery and an overboard floating nursery system exhibit little or no growth during the late summer bloom (M. Luckenbach, unpublished data).

The lack of quantitative evidence on the effects of these dinoflagellate blooms on oyster aquaculture in Virginia lead us to initiate investigations to (i) document the extent and composition of dinoflagellate blooms in the lower Chesapeake Bay, (ii) determine filtration and ingestion rates for selected bloom species in monocultures and in mixed diets, (iii) evaluate growth and survival of oysters feeding on two bloom-forming dinoflagellate spe-

cies, and (iv) quantify the effects of dinoflagellate blooms on oyster growth and survival in the field. This report addresses the third of these objectives by detailing results from laboratory experiments with juvenile oysters fed *P. minimum* and *G. uncatenum*.

MATERIALS AND METHODS

Separate experiments were run to investigate the effects of the dinoflagellates *Prorocentrum minimum* and *Gyrodinium uncatenum* on the growth and survival of juvenile oysters. Both experiments were conducted at the Virginia Institute of Marine Science Oyster Hatchery using single cohort oysters ranging in shell height from 2.5 to 3.8 cm. These oysters were reared for 6 to 9 months in ambient waters of the Chesapeake Bay then transferred to the hatchery where they were maintained for at least two weeks prior to experiments on cultures of *Isochrysis galbana* (Tahitian strain) and *Thalassiosira pseudonana* (clone 3-H) and suspensions of *Thalassiosira weisflogii* (clone T.FLUV) paste.

Dinoflagellates were cultured in the hatchery using unialgal stock solutions. *P. minimum* (HP9001) was supplied by the University of Maryland Laboratory at Horn Point and *G. uncatenum* (CCMP1310) was obtained from the Provasoli-Guillard culture collection. Cultures from 227 L Kalwall tubes were used to inoculate 2460 L vats and the phytoplankton were allowed to reach bloom levels. Daily cell counts and/or in vivo fluorescence measurements were made on samples from these vats to determine cell densities and the species composition of the vat assemblage. Bloom densities ranged from 8.9×10^3 to 2.5×10^5 cells · ml^{-1} and 1.6×10^3 to 1.0×10^4 cells · ml^{-1} for *P. minimum* and *G. uncatenum*, respectively. Growth and survival experiments were conducted as long as these densities were maintained and contamination by other species was minimal. The diatom *Thalassiosira weisflogii* was cultured in the hatchery and centrifuged (15,000 rpm for ca. 4 hrs) to produce a paste; resuspended cells from this paste provide a diet known to support oyster growth in the laboratory.

Eight diets were used in each experiment (Table 1). Bloom density of the dinoflagellate varied daily within the limits specified above, while bloom densities of *T. weisflogii* were achieved by resuspending an appropriate quantity of paste in filtered water to match daily counts from the dinoflagellate culture. Reduced densities were achieved by diluting bloom suspensions with filtered estuarine water.

The experimental design was similar for each experiment. Seven (for the *P. minimum* experiment) or 10 (for the *G. uncate-*

TABLE 1.

Algal diets used in each experiment with the dinoflagellates *Prorocentrum mariae-lebouriae* and *Gyrodinium uncatenum*. See text for cell concentration ranges at bloom densities.

Diet	Algae
I	100% bloom density, dinoflagellate
II	33% bloom density, dinoflagellate
III	5% bloom density, dinoflagellate
IV	100% bloom density, *T. weisflogii*
V	33% bloom density, *T. weisflogii*
VI	5% bloom density, *T. weisflogii*
VII	50% bloom density, dinoflagellate +50% bloom density, *T. weisflogii*
VIII	5% bloom density, dinoflagellate 95% bloom density, *T. weisflogii*

num experiment) individually numbered and pre-measured oysters were randomly allocated to each of 24 20-L plastic containers. Three of these were assigned to each of the eight diets above; a fourth container for each treatment received the algae diet, but no oysters. Twenty L of the appropriate algae suspension were added to each container. Light aeration helped maintain algae in suspension and precluded the development of hypoxia in the experimental containers. Water was changed and new rations provided daily between 0800 and 1030 for all treatments throughout the duration of the experiments. Additionally, the 5% bloom treatments were changed and fed between 1730 and 1830 daily. Preliminary measurements had revealed that densities approximating 33–100% bloom levels could be maintained for 24 hrs, but that 5% bloom treatments were substantially grazed down within 12 hrs. The *P. minimum* experiment was initiated on June 16, 1992 and terminated on July 20, 1992; the *G. uncatenum* experiment was run from Jan. 12–30, 1993.

Containers were inspected daily for moribund oysters and any dead oysters were removed and replaced with live ones. Water temperature and salinity were measured daily and dissolved oxygen occasionally throughout the experiments. In vivo fluorescence measures were made at various times throughout the day from each treatment replicate. Grazing rates were estimated according to Coughlan (1969) using regressions established between cell counts and fluorescence (*P. minimum*: $y = 11065x + 6920$, $r^2 = 0.71$; *G. uncatenum*: $y = 1215.6x + 31.5$, $r^2 = 0.87$; *T. weisflogii*: $y = 12344.4x + 0$, $r^2 = 0.85$). The no-oyster control containers provided a means of accounting for passive deposition and reproduction growth of algae.

All oysters were photographed (right valve up) at the initiation and termination of the experiment (or sooner if mortality occurred). Photographs were digitized (International Imaging Systems, Model 75 Image Processor) and shell growth computed as the change of shell surface area, expressed as mm^2 · d^{-1}. We analysed for differences in shell growth across diets and between containers within diet using a 2-way, nested analysis of variance followed by Tukey's a posteriori multiple comparisons tests where appropriate (Sokal and Rohlf, 1981).

RESULTS

Prorocentrum Experiment

Water temperature within the experimental containers ranged from 19.8–30.5°C and salinity varied from 15 to 18 ppt during the course of the experiment. Dissolved oxygen levels varied from 3.6–8.0 mg · L^{-1} with lowest levels recorded in bloom concentrations in early morning readings. There was no indication of low D.O. induced mortality.

Grazing rates indicate that oysters fed at reduced rates on *P. minimum* relative to the diatom *T. weisflogii* in the unialgal diets (Table 2). Clearance rates in the mixed diets could not be estimated in this study because of the differing regressions between in vivo fluorescence and cell counts for the two species. An inverse relationship between grazing rate and cell density was observed for *P. minimum*, but not *T. weisflogii* (Table 2).

Forty-seven percent mortality occurred in the 100% *P. minimum* bloom treatment on day 11 of the experiment and by day 14 100% of the original oysters in that treatment had died (Fig. 1). Mortality in the 33% dinoflagellate bloom treatment began on day 10 and stabilized at 43% on day 22. No mortality was observed in any of the other diets (Fig. 1).

TABLE 2.

Grazing rates on unialgal diets for (A) *Prorocentrum minimum* experiment and (B) *Gyrodinium uncatenum* experiment. Means and standard deviations are derived from estimates made for 3 replicate containers during 2–6 grazing periods per day for most days over the duration of the experiment; SD's represent variances between daily averages.

Algae	Diet	Mean Grazing Rate $(L \cdot Oy^{-1} \cdot Hr^{-1})$	SD
A. *P. miniumu*	100% bloom	0.030	0.074
	33% bloom	0.063	0.140
	5% bloom	0.117	0.159
T. weisflogii	100% bloom	0.301	0.224
	33% bloom	0.379	0.198
	5% bloom	0.388	0.233
B. *G. uncatenum*	100% bloom	0.051	0.115
	33% bloom	0.338	0.235
	5% bloom	0.310	0.039
T. weisflogii	100% bloom	0.252	0.145
	33% bloom	0.240	0.121
	5% bloom	0.224	0.105

Figure 2. Growth of *Crassostrea virginica* on unialgal and mixed diets with *Prorocentrum minimum* and *Thalassiosira weissflogii* expressed as changes in surface area of the right valve per day (see text). Diet designations are as in Table I. Error bars represent one standard deviation of the mean. Growth rates on diets not connected by a line are significantly different (experiment-wise error rate < 0.05, Tukey's multiple comparisons test).

Shell growth varied significantly among dietary treatments (F = 17.06, p < 0.0005), but not among containers within treatments (F = 1.40, p = 0.150). Rank orderings of treatment means revealed a surprising pattern with the diets containing 5% bloom concentrations of *P. minimum* having the greatest growth (Fig. 2). Tukey's multiple comparisons tests indicated clear differences between the growth rates on diets with minimal *P. minimum* densities (diets III, V, VI & VIII) and those on diets with high *P. mimimum* densities (I & II).

Gyrodinium Experiment

Water temperature varied from 20.5–27.5°C and salinity ranged from 8–14 ppt. Dissolved oxygen levels ranged from 6.98–9.64 mg · L^{-1}.

Grazing rate estimates reveal that *G. uncatenum* and *T. weisflogii* were both consumed in the unialgal treatments; again, graz-ing in mixed diets could not be estimated (Table 2). Lower clearance rates were observed in the bloom density of the dinoflagellate than in the reduced densities, but again no relationship between cell density and clearance rate was noted with the diatom (Table 2).

One oyster died in the 50/50 mixture of *G. uncatenum* and *T. weisflogii* (diet VII) on day 2 of the experiment. No further mortality occurred in any of the treatments during the feeding trials with *G. uncatenum*.

Significant variation in shell growth occurred between algal diets (F = 15.36, p < 0.0005), but not between replicate containers within a diet (F = 1.31, p = 0.19). Shell growth was greater in the diets which included *G. uncatenum* than in those lacking the dinoflagellate and the greatest growth was observed on the 33% bloom diet (Fig. 3).
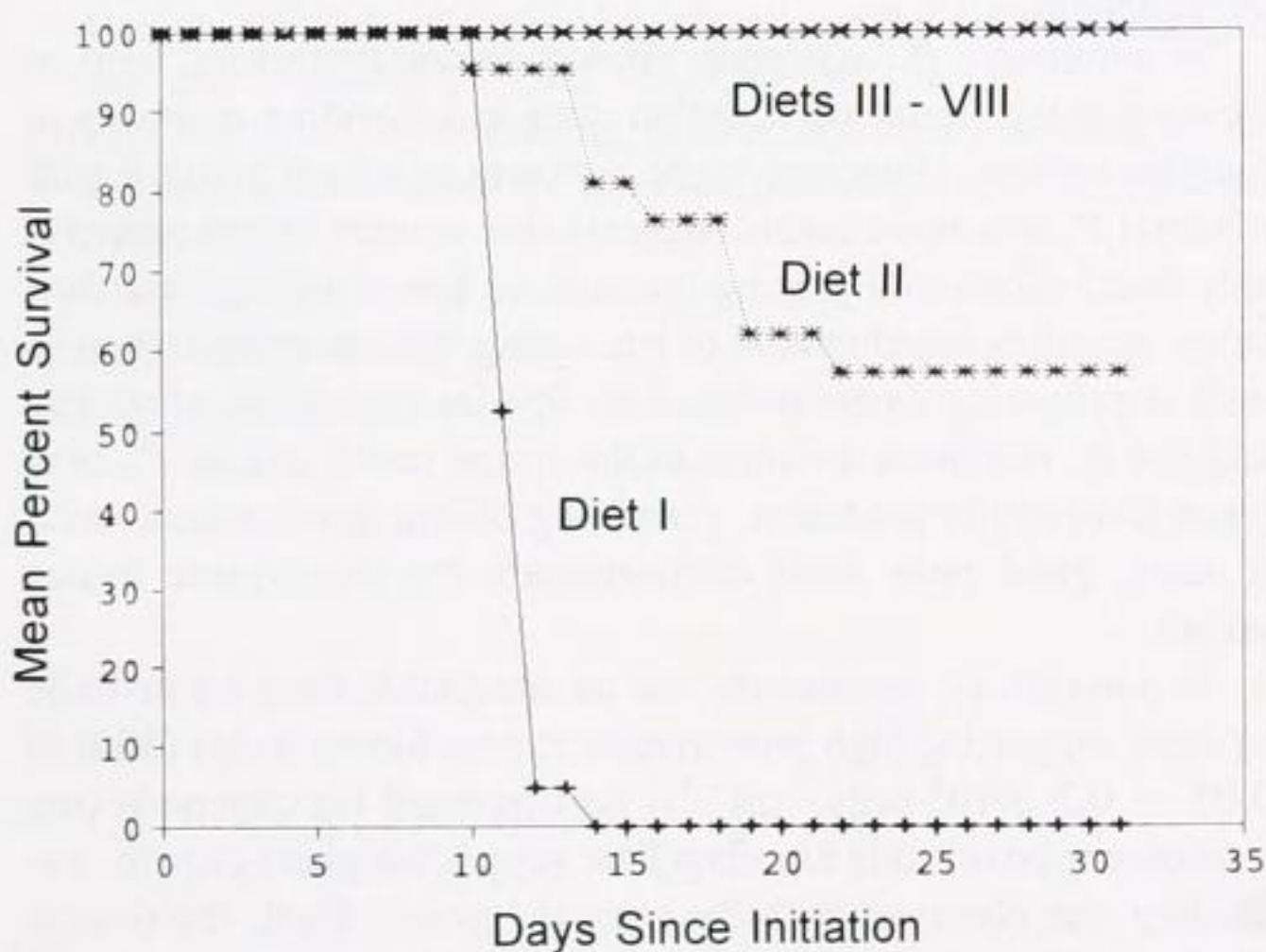

Figure 1. Survival of *Crassostrea virginica* in unialgal and mixed diets with *Prorocentrum minimum* and *Thalassiosira weisflogii*. Diet designations are as in Table I. Data are for oysters placed in each diet at the initiation of the experiment only and do not include replacement oysters.
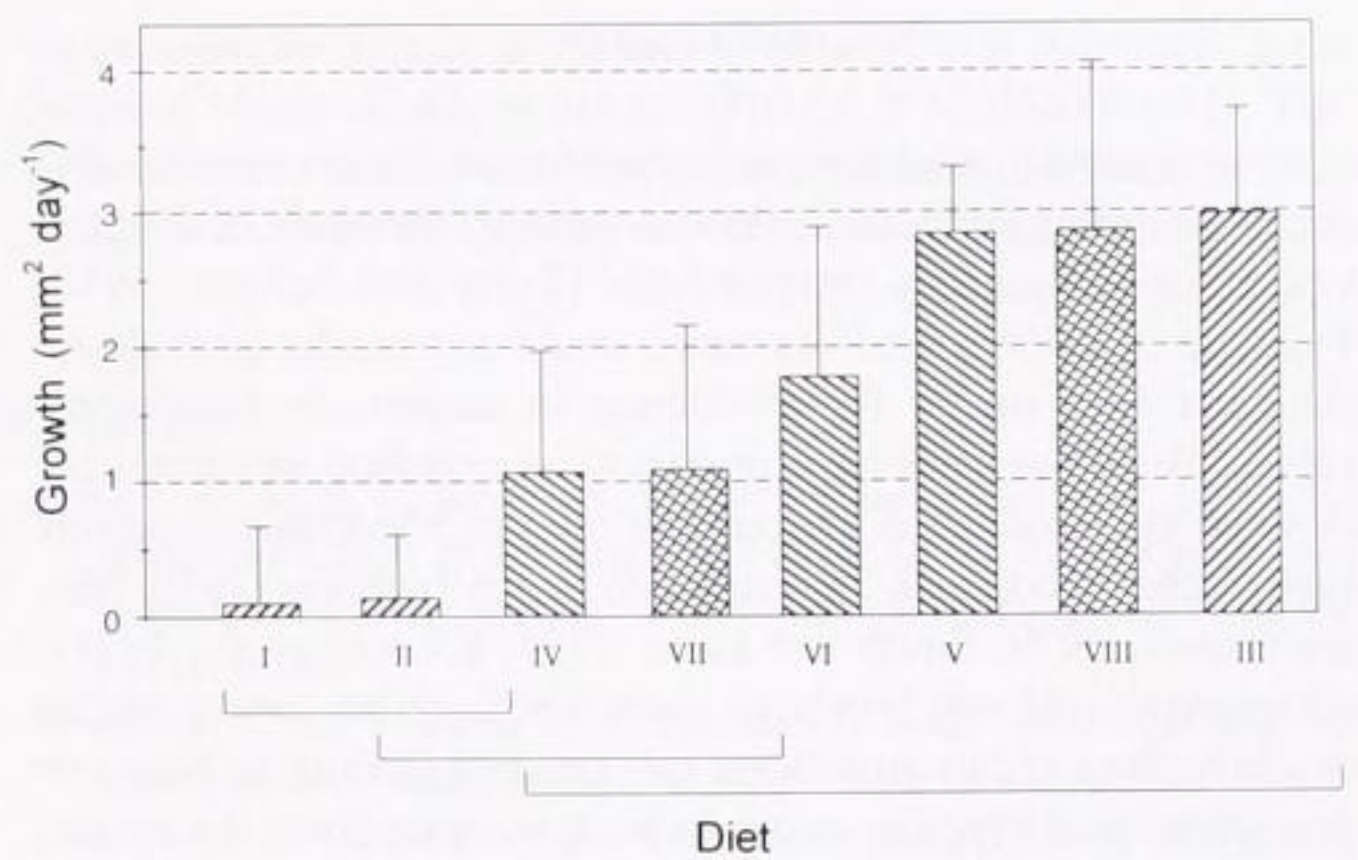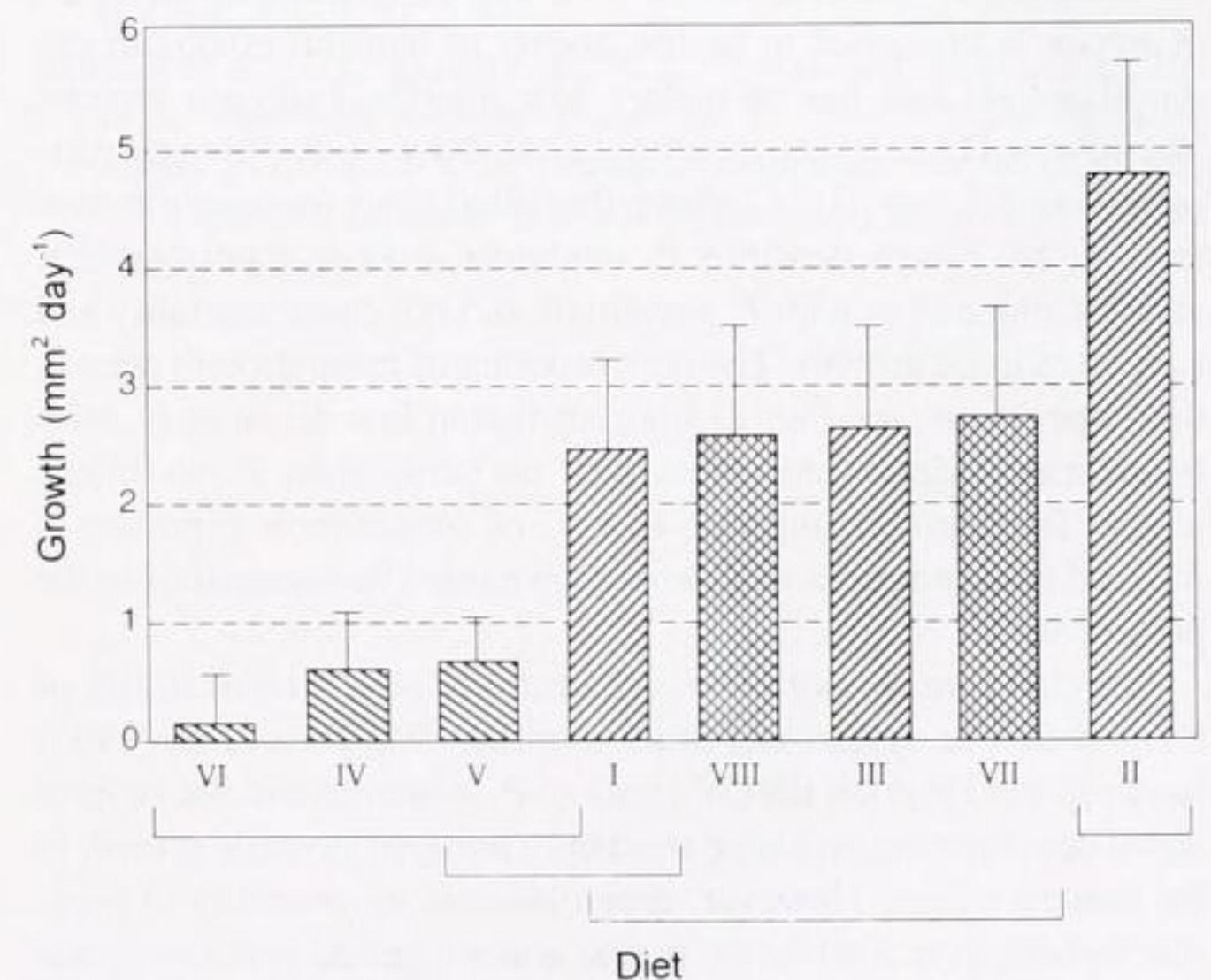

Figure 3. Growth of *Crassostrea virginica* on unialgal and mixed diets with *Gyrodinium uncatenum* and *Thalassiosira weisflogii* expressed as changes in surface area of the right valve per day (see text). Symbols as in Fig. 2.

DISCUSSION

Prorocentrum minimum and *Gyrodinium uncatenum* are frequent late spring and summer bloom-forming members of the phytoplankton community, respectively (Tyler and Seliger, 1978; Tyler, et al., 1982) and, as such, could potentially provide an abundant food supply for production in suspension feeding bivalves. Dinoflagellates have proven to be excellent substrates for elevated egg production and growth rates in planktonic copepods versus other foods such as diatoms (e.g., Paffenhofer, 1976; Morey-Gaines, 1979; Smith and Lane, 1985; Kleppel et al., 1991). Alternatively, bloom levels of each dinoflagellate could inhibit oyster feeding and/or growth via cell-induced feeding problems or development of hypoxic-anoxic habitats shutting down the oyster.

Juvenile oysters responded differently in this experiment to blooms of the two dinoflagellate species, dying at bloom and 33% bloom densities of *P. minimum* and growing well on *G. uncatenum*.

Positive clearance rates and the observations of fecal production indicate that *P. minimum* was ingested by oysters, but standard deviations on the order of the means indicate considerable daily variation. Mean grazing rates for *P. minimum* and *T. weisflogii* reported here are lower than those observed by Sellner et al. (in press). Using similar-sized oysters (shell height: 2.5–3.8 cm) in grazing experiments conducted between 21.5 and 25.0°C, with approximate concentrations of 10^4 cells mL^{-1}, Sellner et al. reported values of 1.95 and 3.73 L · (oyster h)$^{-1}$ for juvenile oysters fed on the dinoflagellate and the diatom, respectively. Unlike the present study, they used individual oysters in short-term feeding experiments (0.5–1.0 h) and analysed samples only for oysters which actually fed. The values reported in this study are means which reflect periods of non-feeding by some oysters. Additionally, high variability in daily densities for a given diet in these experiments would also increase variability in the grazing rates. For example, "bloom" levels of *P. minimum* ranged from 8.9 × 10^3 − 2.5 × 10^5 L^{-1}. Oysters may alter filtration rates accordingly, increasing filtration at lower cell densities. The principal utility of the clearance rates reported here lies in confirming that dinoflagellates were indeed cleared from suspension.

Mortality in the bloom and 33% bloom concentrations of *P. minimum* is presumed to be the impact of harmful effects of the dinoflagellate and not secondary low dissolved oxygen effects. The lowest D.O. levels measured near dawn in the bloom treatment was 3.6 mg · L^{-1}, above the lethal limit for juvenile oysters. At 5% bloom densities *P. minimum*, both in a unialgal diet and in combination with *T. weisflogii*, did not cause mortality and supported good growth. The rank ordering of mean growth rates in this experiment (see Fig. 2) suggests that at low densities *P. minimum* may support growth as well or better than *T. weisflogii* alone. The harmful impacts, if any, of longer-term exposure to reduced concentrations of *P. minimum* cannot be assessed from the present study.

Limited data are available on harmful effects of other strains of *P. minimum* to oysters and other shellfish. Wickfors et al. (1993) have reported that the EXUV strain of *P. minimum* did not support larval development and supported only minimal juvenile growth in the eastern oyster. However, they observed no mortality of juvenile oysters over a six-week period and suggested that nutritional deficiency or digestive interference, rather than acute toxicity, was responsible for the observed patterns. This strain of *P. minimum* is also a poor food source for juvenile hard clams, *Mercenaria mercenaria*, but it is apparently highly toxic to juvenile bay scallops,

Argopecten irradians (Lamarck, 1819) (Wickfors and Smolowitz, 1992). *P. minimum* has been implicated in the mortality of adult oysters on the French Atlantic coast (Lassus and Berthome, 1988). Nakazima (1965a; 1965b; 1956c; 1968) credited *P. minimum* with causing outbreaks of shellfish poisoning in *Tapes japonica* (Gmelin, 1791) which have been lethal to humans.

G. uncatenum, alone and in mixed diets with *T. weisflogii*, supported oyster growth which was greater than or equal to the diatom alone. Growth on *T. weisflogii* alone was lower in the experiment with *G. uncatenum* than in the one with *P. minimum* (compare diets IV, V & VI in Figs. 2 & 3), presumably a result of lower rations in the former experiment. "Bloom" levels for the diatom were achieved by matching cell concentrations with daily counts from the dinoflagellate cultures; since *G. uncatenum* bloom densities were generally lower than those for *P. minimum*, lower concentrations of the diatom were offered in the former.

On day 2 of the *G. uncatenum* experiment one oyster died in the 50/50 dinoflagellate/diatom diet. This was presumably not in response to the diet, since no other deaths occurred during the experiment. The 18 d duration of the experiment was set by our ability to maintain bloom levels of *G. uncatenum*; it is possible that longer term exposures might have produced other effects. The apparent lack of toxic impacts of *G. uncatenum* on juvenile oysters suggests that field observations of oyster mortalities and reduced growth during late summer/early fall blooms in the lower Chesapeake Bay are the result of other dinoflagellate species. Two major components of these blooms *Cochlodinium heterolobatum* and *Gymnodinium splendens* have been reported to be toxic to oysters (Woelke, 1961; Cardwell et al., 1979; Ho, and Zubkoff, 1979).

Species-specific and density-dependent effects of bloom-forming dinoflagellates on *C. virginica* will warrant further attention by fishery resource managers and aquaculturists in Chesapeake Bay. Shumway (1990) noted that there are few practical options for reducing bloom impacts on shellfish culture, but that early warning systems are requisite for the continued growth of shellfish aquaculture. Variable responses of oysters to bloom-forming species in this region point to the need for reliable monitoring in support of aquaculture to track bloom composition and development.

In summary, *P. minimum* proved an unsatisfactory food at elevated levels, reducing filtration rates and elevating mortality in juvenile oysters. However, highest growth in a food mixture with minimal *P. minimum* levels suggests that oysters might conceivably exact substantial grazing pressure on low dinoflagellate densities, retarding development of late spring blooms of this taxon as well as enhancing oyster production. Spatial decoupling of oysters and low *P. minimum* densities in the spring could release *P. minimum* from oyster predation, permitting bloom development, and, in turn, yield poor food environments for subsequent oyster growth.

In contrast, *G. uncatenum* was an acceptable food for juvenile oysters, supporting high growth rates at near bloom levels (33% of 0.05 − 0.3 ×10^4 cells · ml^{-1}). As discussed for copepods (see references above), this dinoflagellate supports highest growth, exceeding that observed with the normal "good" food, the diatom *Thalassiosira weisflogii*. Spatial overlap of this dinoflagellate and oyster populations would be expected to lead to substantial losses of *G. uncatenum* to herbivory. Frequent *G. uncatenum* blooms on the Bay might therefore reflect the paucity of healthy oyster populations in the Bay over the last decade.

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