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EFFECTS OF TOXIC DINOFLAGELLATES ON CLEARANCE RATES AND SURVIVAL IN JUVENILE BIVALVE MOLLUSCS

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ABSTRACT Feeding and survival experiments using unialgal cultures of the toxic dinoflagellates, *Alexandrium* (=*Protogonyaulax*) *tamarense*, and *Gyrodinium aureolum*, were conducted on several species of juvenile bivalve molluscs. These experiments were designed to assess the potential impact of toxic algal blooms during the "grow-out phase" for the faster-growing juvenile stages. Mortality of juvenile bivalves after exposure to toxic dinoflagellates was dependent upon time after exposure and temperature during exposure, suggesting species specific patterns and an overall higher toxicity of *Gyrodinium aurelum* during both the winter and summer experiments. Feeding rates on unialgal cultures of toxic dinoflagellates during the winter of 1989 were uniformly low, and are correlated with the lower mortality observed in the survival experiments. Preference for the non-toxic microalgae, *Isocrysis* sp. was significant during these experiments for all bivalves except *Placopecten magellanicus*, which probably reflects more on the size of *Isochrysis* sp. and the functional morphology of the ctenidia of this species. Experiments conducted in the spring of 1990 reveal species-specific patterns which in some cases mirror the winter experiments. Other bivalve species show a significant preference for toxic dinoflagellates that is not always correlated with the survival experiments suggesting that some species can ingest and utilize toxic dinoflagellates without short-term effects.

KEY WORDS: toxic dinoflagellates, *Alexandrium, Gyrodinium, Mercenaria, Ostrea, Crassostrea, Argopecten, Mya, Mytilus, Placopecten, Geukensia*, clearance rates, survival

INTRODUCTION

Many coastal marine habitats are affected by periodic blooms of toxic microalgae that can have a significant impact on the shellfish industry, and public health (Shumway 1990). Historically, the primary focus has been on toxic dinoflagellates responsible for paralytic shellfish poisoning (PSP) associated with filter-feeding bivalve molluscs that accumulate toxins in their tissues, and can lead to PSP in human consumers.

What of the effect of these toxic dinoflagellates on the shellfish themselves, and the potential for economic loss due to a decrease in growth or outright mortality of shellfish? Recent studies have clearly demonstrated that exposure to toxic dinoflagellates has a significant effect on many physiological processes that include changes in feeding rates, respiration rates, shell valve closure, mucous production, and altered cardiac activity (Shumway and Cucci 1987, Gainey and Shumway 1988, Shumway 1990).

Almost all previous work on the effects of toxic dinoflagellates has been carried out using adult bivalve molluscs. For either the grow-out phase of juveniles suspended in the water-column or the introduction of juveniles onto bottom sites, the potential for exposure to blooms of toxic dinoflagellates is high, while the biological effects of these exposures for juvenile bivalve molluscs is presently unknown. During the juvenile phase, weight-specific metabolism is high (Griffiths and Griffiths 1987), and there must be sufficient phytoplankton available to cover the energetic costs of routine maintenance and growth. Exposure of juvenile bivalve molluscs to toxic dinoflagellates during this period could potentially affect feeding and, therefore, rates of growth as does exposure of adult blue mussels to toxic dinoflagellates (Nielsen and Strømgren 1991).

Two dinoflagellates commonly associated with toxic blooms are *Alexandrium* (=*Protogonyaulax*) *tamarense* and *Gyrodinium aureolum*. *Alexandrium tamarense* is well documented as a worldwide source of PSP toxins in shellfish and PSP outbreaks in humans (Shumway 1990). Toxins associated with *A. tamarense* may persist for months in the tissues of bivalves with unknown long-term consequences (Shumway and Cembella 1993, Cembella et al. in press). *Gyrodinium aureolum* has not been indicated in any outbreaks associated with human illness, but has been shown to cause mortalities in a number of shellfish species (Shumway 1990), and was recently associated with a massive shellfish kill in Maquoit Bay, Brunswick, Maine (Heinig and Campbell 1992). Widdows et al. (1979) demonstrated the direct cytotoxic effects of *G. aureolum* on adult *Mytilus edulis* when bloom concentrations of this dinoflagellate caused a decline in clearance rates and cellular damage to the gut after a short (<24 h) exposure. *Gyrodinium aureolum* has also been shown to inhibit feeding in the post-larvae of *Pecten maximus* and to cause mortalities in juvenile scallops (Lassus and Berthome 1988). The toxic effects of *G. aureolum* are not restricted to shellfish of commercial interest and affect a wide range of marine invertebrates and vertebrates (Cross and Southgate 1980, Shumway 1990).

Blooms of toxic *Alexandrium tamarense* are a seasonal and annual occurence in coastal Maine waters, and the incidence of *Gyrodinium aureolum* in these waters has recently increased. With the large investment in shellfish aquaculture in Maine we began an investigation on the effects of these toxic dinoflagellates on juvenile shellfish by examining the effects of bloom concentrations of *A. tamarense* and *G. aureolum* on survival and feeding in eight species of commercially important juvenile bivalves. We present here the results of survival and feeding experiments using unialgal cultures of toxic dinoflagellates. In a subsequent paper, we will address the feeding of juvenile bivalves on natural assemblages of particles in conjunction with bloom concentrations of toxic dinoflagellates.

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MATERIALS AND METHODS

Algal cultures were supplied from the Provasolli-Guillard Center for the Culture of Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences. *Alexandrium tamarense* (clone GT429) and *Gyrodinium aureolum* (clone PLY 497A) cultures were grown in mass cultures (20 l) using f/2 media at 15°C on a 14:10 light/dark photoperiod. Cells were harvested during exponential phase of growth.

Survival Experiment

Short- and long-term mortality associated with exposure to the toxic dinoflagellates, *Alexandrium tamarense* and *Gyrodinium aureolum* was assessed in juveniles of eight species of commercially important shellfish: *Mercenaria mercenaria, Ostrea edulis, Crassostrea virginica, Argopecten irradians, Mya arenaria, Mytilus edulis, Placopecten magellanicus,* and *Spisula solidissima* obtained from Mook Sea Farm Inc., Damariscotta ME. All animals were scrubbed free of any epibionts, and maintained in unfiltered, flowing sea water from Boothbay Harbor, Maine prior to use in experiments. Animals were not fed any supplementary food prior to the experiments. Bloom concentrations of *A. tamarense* (10^5 cells l^{-1}) and *G. aureolum* (10^6 cells l^{-1}) were maintained for one week in 175 l tanks using unfiltered sea water containing natural seston. Control tanks with just natural sea water were run simultaneously for all experiments. Mortality was assessed in control and treatment tanks at one week and six weeks post exposure. The experiment was run in the winter (5°C) of 1989 and spring (10°C) of 1990. Percentage of mortalities obtained were arcsine transformed prior to a Chi-square analysis at the 5% significance level, that compared bivalves exposed to toxic dinoflagellates and natural seston against controls exposed to natural seston only. During the time course of this experiment no *A. tamarense* or *G. aureolum* cells were present in natural sea water (D. Jacobsen, personal communication).

Feeding Experiments Using Unialgal Cultures of Toxic Dinoflagellates

Unialgal feeding experiments using bloom concentrations of *Alexandrium tamarense* and *Gyrodinium aureolum* were conducted on *Mercenaria mercenaria, Ostrea edulis, Crassostrea virginica, Argopecten irradians, Mya arenaria, Mytilus edulis, Placopecten magellanicus, Spisula solidissima,* and *Geukensia demissus* that were compared to feeding rates on *Isochrysis* sp. (clone TISO, [10^5 cells l^{-1}]). All animals were allowed to purge themselves in filtered sea water (0.7 μm Gelman glass filter) for 24 h prior to being used in feeding experiments. These experiments were also conducted in the winter (5°C) of 1989 and Spring (10°C) of 1990. Individual specimens were placed in aerated glass beakers containing 40–100 ml of the algal culture in filtered sea water. Control vials, without animals, were run simultaneously to correct for algal cell division during the experiment. Experiments lasted for 1 h, with samples taken at the end of the experimental period. Samples were analyzed with a Coulter counter model ZM fitted with a 100 μm orifice. Dry weights of soft tissues were obtained for all animals by constant drying at 60°C for 48 h. Clearance rates were calculated by the method of Coughlan (1969). Dry weight was used to normalize all data, while assuming a 100% retention efficiency for all algal species tested. Production of pseudofeces was not observed during these experiments. Differences in the weight specific clearance rates of total cells corrected for any cell division were evaluated using an ANOVA. No unequal variances were detected using the F_{max} test for the ANOVA (Sokal and Rohlf 1981), and where significant treatment effects occurred, the Student-Neuman-Keuls (SNK) multiple comparison test was applied at the 5% significance level to identify individual differences among the data sets.

RESULTS

No mortalities were noted after a one week exposure to *Alexandrium tamarense* or *Gyrodinium aureolum* during the winter of 1989 or spring of 1990 for any of the bivalve species tested. In 1989 no mortalities were noted six weeks after the one week exposure for bivalves exposed to *A. tamarense* while non-significant (Chi-square, $P > 0.05$) mortalities were noted for *Crassostrea virginica* and *Ostrea edulis* in the spring of 1990 six weeks after the one week exposure period (Table 1).

For bivalves exposed to *Gyrodinium aureolum* there were significant mortalities of *Mercenaria mercenaria* and *Argopecten irradians* after one week, while after the subsequent six weeks significant mortalities were noted in *Crassostrea virginica* and *Spisula solidissima* (Table 1) suggesting strong, specific-specific differences in mortality for time after exposure to toxic dinoflagellates and ambient water temperature during exposure.

During the winter of 1989 the unialgal experiments (Fig. 1a) all showed a significant within species ANOVA ($P < 0.001$) for feeding rates on the toxic dinoflagellates and the non-toxic microalgae

TABLE 1.

Percent mortality of juvenile bivalve molluscs six weeks after a one week exposure to bloom concentrations of the toxic dinoflagellates, *Alexandrium* (*-Protogonyaulax*) *tamarense*, and *Gyrodinium aureolum*.

Alexandrium tamarense				
Bivalve Species	**Winter 1989**	**Chi-square**	**Spring 1990**	**Chi-square**
Mytilus edulis	NM	NS	NM	NS
Crassostrea virginica	NM	NS	4%	NS
Ostrea edulis	NM	NS	4%	NS
Mercenaria mercenaria	NM	NS	NM	NS
Spisula solidissima	NM	NS	NM	NS
Argopecten irradians	NM	NS	NM	NS
Placopecten magellanicus	NT		NM	NS
Mya arenaria	NT		NM	NS
Gyrodinium aureolum				
Bivalve Species	**Winter 1989**	**Chi-square**	**Spring 1990**	**Chi-square**
Mytilus edulis	4%	NS	NM	NS
Crassostrea virginica	NM	NS	68%	$P < 0.05$
Ostrea edulis	12%	NS	4%	NS
Mercenaria mercenaria	44%	$P < 0.001$	NM	NS
Spisula solidissima	8%	NS	16%	$P < 0.05$
Argopecten irradians	100%	$P < 0.001$	8%	NS
Placopecten magellanicus	NT		NM	NS
Mya arenaria	NT		NM	NS

Temperatures for winter 1989 and spring 1990 were 5°C and 10°C respectively. Percentages were arcsine transformed prior to a Chi-square analysis at the 5% significance level, and compared bivalves exposed to toxic dinoflagellates and natural seston against controls exposed to natural seston only. NM = no mortalities, NS = not significant, NT = not tested.

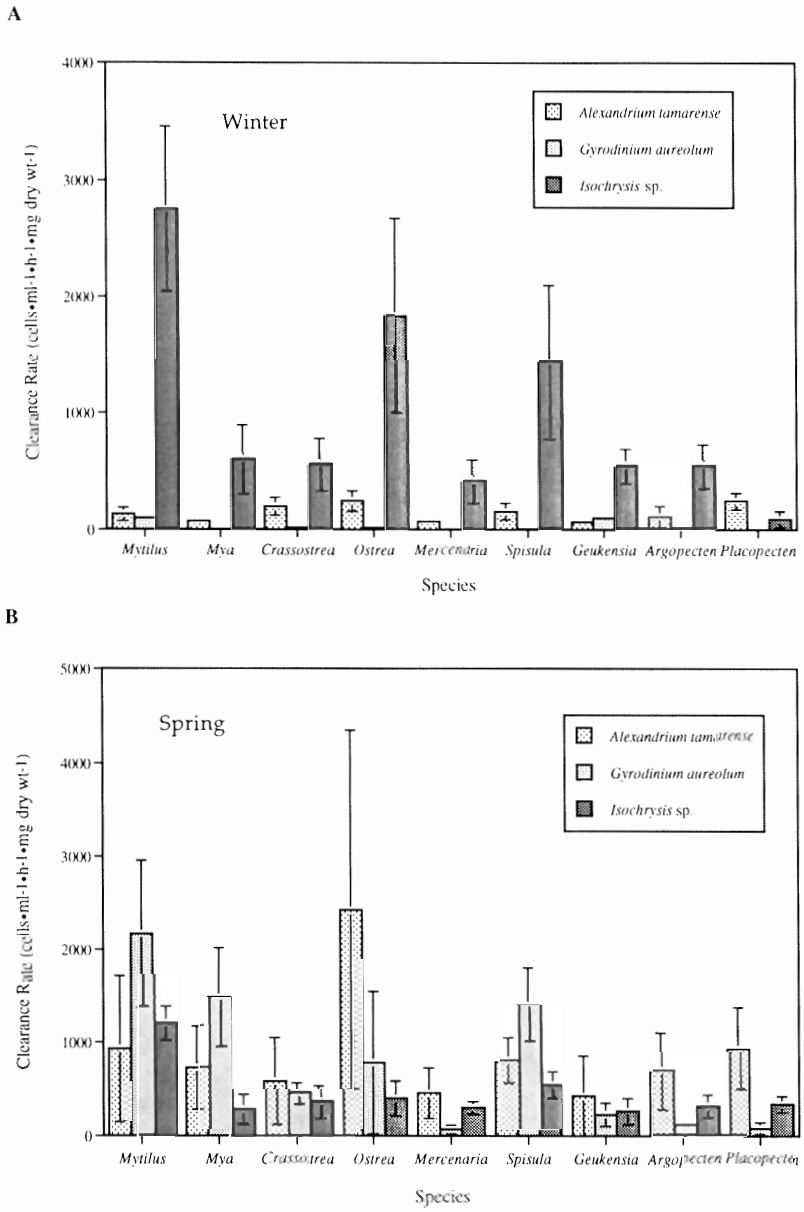

Figure 1. A: Clearance rates of nine species of juvenile bivalves fed pure cultures of *Alexandrium tamarense*, *Gyrodinium aureolum*, and *Isochrysis* sp. in the winter (5°C) of 1989. B: Clearance rates of nine species of juvenile bivalves fed pure cultures of *Alexandrium tamarense*, *Gyrodinium aureolum*, and *Isochrysis* sp. in the spring (10°C) of 1990.

Isochrysis sp. (Fig. 1a). In all species examined, except for *Crassostrea virginica* and *Placopecten magellanicus*, the post-hoc multiple comparison tests showed that the feeding rates on *Alexandrium tamarense* and *Gyrodinium aureolum* were grouped together (SNK; $P > 0.05$), but were significantly lower than the feeding rate on *Isochrysis* sp. (SNK; $P < 0.05$). For *C. virginica* and *P. magellanicus* the feeding rates between *A. tamarense* and *G. aureolum* were significantly different from one another (SNK; $P < 0.05$), but still significantly lower than the feeding rates on *Isochrysis* sp. as reported for the other species of bivalves. It should be noted that for *P. magellanicus*, exposure to *G. aureolum* induced the production of copious amounts of mucous and cessation of feeding. Analysis of between-species differences in clearance rates of *Alexandrium tamarense* and *Gyrodinium aureolum* showed a significant ANOVA ($P < 0.001$) for both species of toxic dinoflagellates with multiple comparison testing partitioning the feeding rates of the bivalve species tested in three groups for *A. tamarense* and two groups for *G. aureolum* (Table 2).

Experiments in the summer of 1990 (Fig. 1b) showed a similar significant ANOVA ($P < 0.05$) for the within bivalve analysis of feeding rates on the toxic dinoflagellates and *Isochrysis* sp. on all species tested except *Crassostrea virginica* and *Geukensia demissus* where no significant differences in clearance rates were detected (ANOVA; $P > 0.05$). Multiple comparison testing on *Ostrea edulis*, *Argopecten irradians*, and *Placopecten magellanicus* all showed a similar pattern with clearance rates on *Isochrysis* sp. being significantly higher than the two species of toxic dinoflagellates, which were grouped together, using multiple comparison testing. Comparisons for *Mytilus edulis*, *Mya arenaria*, and *Spisula solidissima* all showed a distinctively different pattern

TABLE 2.

Groupings of bivalves from significant ($P < 0.05$) post-hoc multiple comparison testing (SNK).

Alexandrium tamarense		
Bivalve Species	**Winter 1989**	**Spring 1990**
Mytilus edulis	B	B
Myra arenaria	C	B
Crassostrea virginica	A	B
Ostrea edulis	A	A
Mercenaria mercenaria	C	B
Spisula solidissima	B	B
Geukensia demissus	C	B
Argopecten irradians	C	B
Placopecten magellanicus	A	B

Gyrodinium aureolum		
Bivalve Species	**Winter 1989**	**Spring 1990**
Mytilus edulis	A	A
Mya arenaria	B	A
Crassostrea virginica	C	B
Ostrea edulis	C	A
Mercenaria mercenaria	B	B
Spisula solidissima	B	A
Geukensia demissus	A	B
Argopecten irradians	B	B
Placopecten magellanicus	B	B

Species with common letters exhibit equivalent rates of feeding.

where the feeding rates on *Gyrodinium aureolum* were significantly higher than feeding rates on *Alexandrium tamarense* or *Isochrysis* sp. which were grouped together using multiple comparison testing. Finally, *Mercenaria mercenaria* exhibited significant differences in feeding rates where *A. tamarense* and *Isochrysis* sp. were grouped together and exhibited higher rates of consumption of *A. tamarense* than *G. aureolum* (Fig. 1). Analyzing between-species differences in clearance rates for the spring of 1990 experiments again showed a significant ANOVA ($P < 0.001$) for both species of toxic dinoflagellates with multiple comparison testing dividing the bivalve species tested into two groups for both *A. tamarense* and *G. aureolum* (Table 2).

DISCUSSION

This study provides an initial assessment of the effects of two species of toxic dinoflagellates on survival and clearance rates in several species of juvenile bivalve molluscs. We were able to demonstrate that *Ostrea edulis* had significantly higher clearance rates of *Alexandrium tamarense* than did any other species of bivalve tested under spring conditions. These results are consistent with previous studies which showed that European oysters become toxic prior to any other species under field conditions, and selectively feeds on dinoflagellates under laboratory conditions (Shumway et al. 1985, Shumway et al. 1990). The feeding studies using *Gyrodinium aureolum* showed that *Mytilus edulis, Mya arenaria,* and *Spisula solidissima* exhibited the highest rates of consumption, while *Ostrea edulis* demonstrated feeding rates intermediate with the rest of the species examined.

The dinoflagellate, *Gyrodinium aureolum* has frequently been associated with fish kills, especially salmonids (see Turner et al. 1989, Jones et al. 1982, Roberts et al. 1982). Since the late sixties, *G. aureolum* has also been implicated in massive kills of marine fauna including shellfish (Partensky et al. 1989). *Gyrodinium aureolum* is the dinoflagellate implicated in the massive shellfish kills which occurred in Maquoit Bay, Maine, in September of 1988 (Heinig and Campbell 1992); however, the specific cause of death was not verified.

It seems likely that *Gyrodinium aureolum* may have a cytotoxic effect on shellfish, unlike other toxic dinoflagellates (e.g. *Alexandrium tamarense*) that normally induce neurotoxic responses (Shumway and Cucci 1987). Previous studies of the impact of *G. aureolum* on shellfish biology have demonstrated mortality in juveniles (Erard-LeDenn et al. 1990, Tangen 1977, Lassus and Berthome 1988, Helm et al. 1974), reduced shell growth (Nielsen and Stromgren 1991), reduced clearance rates (Widdows et al. 1979, Shumway unpublished) and marked cellular damage to the gut (Widdows et al. 1979). Preliminary studies carried out with Dr. Antonello Novelli (University of Oviedo, Spain) on isolates of *Gyrodinium aureolum* Clone PLY 497 provided little evidence for a neurotoxin in this species. Further, recent studies by Turner et al. (1987), Partensky et al. (1989), Gentien and Arzul (1990) and Gentien et al. (1991) all indicate that *G. aureolum* produces toxins. Partensky et al. (1989) confirmed the presence of at least one fat-soluble cytotoxin, and Gentien and Arzul (1990) determined that the toxic action proceeds from two different processes which are possibly associated with two types of toxic compounds.

Finally, it has been demonstrated that the harmful effects of *G. aureolum* can be reversed if the animals are returned to clean seawater before permanent damage has taken place (Widdows et al. 1979, Erard-LeDenn et al. 1990).

Recent, unexplained mortalities of hatchery-reared, juvenile oysters (Crassostrea virginica) began coincidentally with a bloom of another closely related dinoflagellate, *Gymnodinium sanguineum*. Further, during a second bloom of this dinoflagellate, mantle lesions were noted in the oysters with no mortalities. This species of dinoflagellate has not been previously demonstrated to be toxic to bivalves and was not directly linked to the oyster mortalities (Bricelj et al. 1992); however, it does implicate yet another species of dinoflagellate in harmful effects on shellfish.

As in previous studies on the effects of toxic dinoflagellates on shellfish, our results indicate that responses are species-specific, and that feeding-rates were significantly lower in the winter than spring. These differences are likely caused by the lower temperatures experienced in the winter, but for animals in the field both a decrease in temperature and lower food resources would contribute to decreased rates of consumption. Although exposure to toxic dinoflagellates during winter is unlikely under normal conditions, the combined results from the survival and feeding studies presented here would encourage aquaculturists to focus their attention on the possibility that exposure of *Placopecten magellanicus, Spisula solidissima* and *Crassostrea virginica* to outbreaks of *Gyrodinium aureolum* during early spring and late fall, where temperature conditions are similar to those used in this study, could result in substantial mortality and cessation of feeding. Cessation of feeding for extended periods of time is likely to have an effect on survivability and the time it takes to produce a marketable product. Our studies on the feeding of juvenile bivalves on natural assemblages with toxic dinoflagellate blooms (Shumway et al. in preparation) should provide additional information on the effects of these blooms on feeding.

Shellfish toxicity associated with blooms of toxic dinoflagellates is not novel, and is largely well defined due to the economic and public health issues. The increase in the occurrence of these, and other, noxious algal blooms have serious implications for the development and success of aquaculture. Shellfish toxicity monitoring programs ensure public safety and maximize harvesting time of adults ready for the market, but tell us nothing about the effects on future harvests. Comprehensive studies on the effects of toxic microalgae on juvenile bivalves of commercial importance are long overdue, and are more important than ever as aquaculturists seed juveniles into coastal waters with hopes of an ever increasing yield in the future.

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