Comp. Biochem. Physiol. Vol. 106A, No. 4, pp. 769–773, 1993
Printed in Great Britain

0300-9629/93 $6.00 + 0.00
Pergamon Press Ltd

THE EFFECT OF A TOXIC DINOFLAGELLATE (*ALEXANDRIUM TAMARENSE*) ON THE OXYGEN UPTAKE OF JUVENILE FILTER-FEEDING BIVALVE MOLLUSCS

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(*Received* 4 *January* 1993; *accepted* 5 *February* 1993)

Abstract—1. Oxygen uptake and grazing rates of juvenile bivalve molluscs *Mytilus edulis*, *Mya arenaria*, *Geukensia demissa*, *Placopecten magellanicus* and *Crassostrea virginica* were measured following 1 hr exposure to bloom concentrations (10^6 cells/l) of the toxic dinoflagellate *Alexandrium tamarense* (GT429) using a non-toxic clone of the same species (PLY173) as control.

2. For all bivalves, prefeeding estimates of $\dot{V}O_2$ were similar to postfeeding values and values recorded 24 hr after exposure to bloom conditions.

3. $\dot{V}O_2$ was similar for bivalves fed on both the toxic and non-toxic strains of *A. tamarense* suggesting that there were no adverse effects on $\dot{V}O_2$ following 1 hr exposure to toxic GT429.

4. Bivalves differed in their rates of grazing between toxic GT429 and non-toxic PLY173. Similar grazing rates were recorded for *M. edulis* and *G. demissa*. For *P. magellanicus* and *M. arenaria* reduced rates of clearance were recorded in GT429 compared with the non-toxic strain.

INTRODUCTION

There is much accumulated evidence showing that toxic dinoflagellates affect the physiology of bivalve molluscs. They are responsible for causing paralytic shellfish poisoning (PSP) in many parts of the world and can result in widespread mortality of shellfish populations (Shumway, 1990). One of the most studied species of toxic dinoflagellates is *Alexandrium tamarense* which has been recorded from the U.K., Venezuela, Spain, the Gulf of Maine and eastern Canada. Exposure to this species can result in a variety of responses including shell-valve closure, reduced or increased rates of particle clearance as well as causing changes to cardiac activity and byssus production (Shumway and Cucci, 1987; Gainey and Shumway, 1988). These responses are generally species-specific and may act to protect the shellfish from the effects of the toxins. One aspect of the research which has not attracted much study is the effect of *A. tamarense* on oxygen uptake. Preliminary work by Shumway *et al.* (1985) demonstrated variable changes of $\dot{V}O_2$ following 5 days of feeding on the toxic clone of *A. tamarense* (clone GT429). The responses of bivalves varied between species and also was dependent on whether they had prior exposure to toxic dinoflagellates. The present study was designed to assess the effect of short-term exposure to a toxic clone of *A. tamarense* (GT429) on the oxygen uptake of a number of juvenile bivalves using the non-toxic clone (PLY173) as a control. Not all of the chosen species had had previous exposure to the toxic dinoflagellates.

MATERIALS AND METHODS

Specimens of *Mytilus edulis* (24–32 mm) were obtained from Boothbay Harbor, Maine, *Mya arenaria* (19–27 mm) were collected from stony intertidal areas, Barnes Pt, Maine. These species may have had previous exposure to toxic dinoflagellates. *Geukensia demissa* (29–34 mm) were collected from mid- to upper tidal levels, Tiverton, Rhode Island, an area with no previous history of toxic dinoflagellates. Juvenile sea scallops, *Placopecten magellanicus* (28–22 mm), were grown in culture by H. Hidu at the Aquaculture Centre, Darling Research Station, Walpole, Maine, and *Crassostrea virginica* (9–12 mm) were cultured and supplied by Bill Mook of Mook Seafarms. Animals were scrubbed clean of epiphytes and maintained at 15°C over the summer in running seawater filtered to remove particles larger than 20 μm. No supplementary food was supplied.

Oxygen uptake was measured using a Gilson differential respirometer. This apparatus has been used previously to record aerial (Marshall and McQuaid, 1992) and aquatic oxygen uptake in molluscs (Newell and Pye, 1970) but has been criticized due to the shaking, normally required to facilitate gas exchange. A number of trial experiments were undertaken to provide background values and assess the effects of body size, temperature change and shaking on $\dot{V}O_2$.

The results of the preliminary studies showed that values for $\dot{V}O_2$ were similar to those recorded using other techniques and that it was unnecessary to shake the respirometer to facilitate gas exchange. All the bivalves being investigated opened quickly within the respirometer flasks and maintained steady gas exchange due to their own pumping activity. Because of their smaller size, oxygen uptake of *C. virginica* was measured on groups of three individuals and the machine was shaken.

Stock cultures of *Alexandrium tamarense*, toxic clone GT429 and the non-toxic clone PLY173 were provided by the Provosolli–Guillard Culture Centre for Marine Phytoplankton and grown in laboratory culture at 15°C with a photoperiod of 14 light:10 dark.

All experimental bivalves, excluding the oyster *C. virginica*, were individually marked using numbered plastic dots at least 3 days before experimentation.

The effects of the experimental manipulation on oxygen uptake were investigated in *P. magellanicus*, *M. edulis* and *G. demissa*. In the experiments a group of at least five individuals were transferred into a feeding chamber containing filtered seawater. Another group were held throughout this period within the respirometer (machine control). Values for oxygen uptake were measured prior to the transfer, 1 hr following return to the respirometer after the control feeding trial and then 24 hr after the initial measurements.

For the main experiments, prefeeding levels of oxygen uptake were measured for 15 individuals at 15°C following 1 hr equilibrium in the respirometer. Readings were taken every 5 min over a 1-hr exposure period. Groups of five individuals were transferred directly into 350 ml of control (filtered seawater; 0.45 μm), dinoflagellate GT429 or PLY173 at an initial density of 10^3 cells/ml at 15°C. Due to their smaller body size, for *C. virginica*, three individuals were placed in each respirometer vessel and the feeding chamber contained 200 ml of feeding mixture. After 1 hr exposure to the control or feeding media, a 10 ml sample was removed for particle counting to estimate the grazing rate. Cell counts were made using a microscope with a $\times 10$ objective and a Spiers–Levy haemocytometer following the procedure outlined by Guillard (1973). After feeding for 1 hr, bivalves were returned to respiration vessels containing filtered seawater. A one hour equilibration, oxygen uptake was measured as previously described. Bivalves were returned to aquaria conditions at 15°C overnight and the oxygen uptake reassessed 24 hr after the initial exposure to the dinoflagellate or control conditions. At the end of the experiment, dry tissue weights were obtained for all animals and filtering rates calculated following the method of Coughlan (1969).

Table 1. Effect of experimental manipulation on $\dot{V}O_2$ in bivalves expressed as μl O_2/mg/hr

Species	Manipulation	$\dot{V}O_2$	SD
P. magellanicus	Initial	0.153	0.094
	Machine control	0.208	0.066
	24 hr recovery	0.157	0.101
	Initial	0.106	0.057
	Transfer expt.	0.143	0.057
	24 hr recovery	0.136	0.077
M. edulis	Initial	0.280	0.061
	Machine control	0.290	0.057
	24 hr recovery	0.187	0.031
	Initial	0.316	0.097
	Transfer expt.	0.153	0.035
	24 hr recovery	0.225	0.097
G. demissa	Initial	0.141	0.04
	Machine control	0.126	0.10
	24 hr recovery	0.152	0.06
	Initial	0.141	0.03
	Transfer expt.	0.113	0.12
	24 hr recovery	0.110	0.03

RESULTS

For all experiments undertaken at the storage temperature of 15°C, observations made on the bivalves within the respirometer chambers showed normal valve opening and siphonal extension suggesting normal ventilatory patterns. In control exeriments where the vessels were not shaken, $\dot{V}O_2$ in *M. edulis*, *G. demissa*, *M. arenaria* and *P. magellanicus* was similar to values obtained when shaken gently. There was no decline in the oxygen uptake over the 1 hr during which measurements were recorded.

Table 1 shows the results from a series of preliminary trials to evaluate the experimental procedure used for the feeding experiment. Following measurement of the initial oxygen uptake, bivalves were either manipulated as in the feeding experiments or maintained in constant conditions within the respirometer. For *P. magellanicus*, *M. edulis* and *G. demissa*, there was no significant increase in oxygen uptake due to handling, and following 24 hr recovery, the values were similar to those recorded at the start of the experiment.

Table 2 summarizes the results of oxygen uptake in juvenile bivalves that had fed either on the toxic clone GT429 or the non-toxic clone PLY173. Initial rates of oxygen uptake varied between species with the oyster *C. virginica* showing consistently higher weight-specific oxygen uptake than the scallop *P. magellanicus* and the mussel *M. edulis*. The lowest weight-specific oxygen uptake was for *G. demissa*.

Oxygen uptake was similar for prefeeding, post-feeding and recovery periods for all species (Table 3). Three of the species showed significant differences ($P = 0.05$) but there was no consistent pattern contributing to the variation. Table 4 compares all values of oxygen uptake for each species of bivalves fed the toxic and non-toxic clones of *A. tamarense*. Only one species, *G. demissa*, showed a significant difference in oxygen uptake between feeding treatments. This was due to the lower oxygen uptake of the group used for the PLY173 experiment.

Table 2. Effect of *A. tamarense* on $\dot{V}O_2$ (μl O_2/mg dry tissue/hr ± SE) of bivalves

Species		Initial	1 hr after feeding	24 hr recovery	CR
M. edulis	Control	0.28 ± 0.06	0.28 ± 0.04	0.39 ± 0.07	—
	PLY173	0.29 ± 0.05	0.31 ± 0.04	0.36 ± 0.05	2.24 ± 0.09
	GT429	0.25 ± 0.04	0.31 ± 0.11	0.35 ± 0.05	2.65 ± 0.22
G. demissa	Control	0.16 ± 0.03	0.10 ± 0.02	0.17 ± 0.03	—
	PLY173	0.09 ± 0.04	0.11 ± 0.03	0.12 ± 0.03	1.11 ± 0.47
	GT429	0.14 ± 0.02	0.19 ± 0.03	0.17 ± 0.02	1.70 ± 0.46
M. arenaria	Control	0.24 ± 0.02	0.17 ± 0.02	0.27 ± 0.04	—
	PLY173	0.29 ± 0.12	0.20 ± 0.04	0.19 ± 0.04	0.58 ± 0.25
	GT429	0.21 ± 0.06	0.31 ± 0.06	0.29 ± 0.07	Negligible
P. magellanicus	Control	0.31 ± 0.04	0.31 ± 0.06	0.29 ± 0.04	—
	PLY173	0.25 ± 0.03	0.35 ± 0.06	0.35 ± 0.05	1.65 ± 0.80
	GT429	0.24 ± 0.07	0.37 ± 0.09	0.30 ± 0.05	1.00 ± 0.17
C. virginica	Control	0.38 ± 0.11	0.46 ± 0.17	0.31 ± 0.11	—
	PLY173	0.34 ± 0.01	0.33 ± 0.05	0.39 ± 0.39	Variable
	GT429	0.48 ± 0.13	0.25 ± 0.07	0.19 ± 0.01	Variable

CR, clearance rate (cells/mg dry tissue/hr ± SE).

The bivalves differed in their rates of grazing on *A. tamarense* (Table 2). The mussel *M. edulis* showed the fastest rates for both the toxic and non-toxic strains. Similar results, with a lower filtration rate, were evident for *G. demissa*. Contrasting with these results *M. arenaria* and *P. magellanicus* had reduced rates of food uptake in GT429 compared to the non-toxic strain. For the juvenile *C. virginica* the results were very variable between individuals of the group contributing to high variation in both treatments.

DISCUSSION

The present study showed that juvenile bivalves differed in their feeding responses to toxic and non-toxic strains of the dinoflagellate *A. tamarense*. While the mussels *M. edulis* and *G. demissa* had similar filtration rates, the others showed reduced or variable rates in the presence of the toxic strain. Regardless of their filtration responses, it was apparent that short-term exposure to a toxic strain of *A. tamarense* was not effective in increasing oxygen uptake, either 1 hr after feeding or following 24 hr recovery.

Many factors are known to affect the oxygen uptake of bivalves and there have been a number of previous studies on the species under investigation.

Table 3. ANOVA comparing the oxygen uptake at three time intervals during the feeding experiment

		F	*P*	$\bar{x}$
M. edulis	Control	3.94	ns	0.31
	PLY173	2.08	ns	0.31
	GT429	1.53	ns	0.30
G. demissa	Control	6.41	0.05	0.14
	PLY173	0.35	ns	0.11
	GT429	2.01	ns	0.17
M. arenaria	Control	2.07	ns	0.23
	PLY173	1.11	ns	0.22
	GT429	5.40	0.05	0.27
P. magellanicus	Control	0.71	ns	0.30
	PLY173	0.06	0.05	0.31
	GT429	0.15	ns	0.30
C. virginica	Control	0.24	ns	0.38
	PLY173	0.05	ns	0.36
	GT429	3.84	ns	0.30

P: probability level, ns: nonsignificant, $\bar{x}$: mean value (μl O_2/mg/hr) for combined results from the three time intervals.

For *M. edulis*, weight-specific oxygen uptake and the temperature effects on oxygen uptake in this study were within the range recorded by Bayne *et al.* (1973), Bayne (1976) and Widdows (1973, 1976). Oxygen uptake values in *G. demissa* and *M. arenaria* were more variable with values lower than *M. edulis*. Emerson *et al.* (1988) working on *M. arenaria* also found large variations in oxygen uptake of juvenile clams. In contrast, weight-specific oxygen uptake in the scallop *P. magellanicus* was similar to mean values given in Shumway *et al.* (1988a) at the same exposure temperature. Highest weight-specific oxygen uptake was recorded in the juvenile oysters, *C. virginica*. This result was consistent with their small size (dry weight less than 5 mg) and, although they were higher than previously recorded for this species (Shumway and Koehn, 1982), they occur within the range for other juvenile bivalves (Shumway, 1982).

There have been numerous studies on the feeding biology of bivalve molluscs, suggesting that feeding efficiency and growth are dependent on the food type and the morphology of the bivalve ctenidia (Jørgensen, 1966; Flaak and Epifanio, 1978; Enright *et al.*, 1986). Recent studies, however, suggest that some species are able to select particular food particles within mixed algal cultures or from natural suspensions including both algal cells and inorganic particles (Newell *et al.*, 1989; Cucci *et al.*, 1989; Lesser *et al.*, 1991). Within the present study there was considerable variation in the feeding rates not only between species but between the non-toxic and toxic clones of *A. tamarense*. The mussels *M. edulis* and *G. demissa* showed similar grazing rates on the two

Table 4. ANOVA comparing the oxygen consumption between two feeding regimes PLY173 and GT429

	$\bar{x}$	F Time interval	*P*	F Food type	*P*	F Interaction	*P*
M. edulis	0.31	2.16	ns	0.04	ns	0.20	ns
G. demissa	0.14	0.58	ns	5.73	0.05	0.34	ns
M. arenaria	0.25	0.04	ns	0.62	ns	1.20	ns
P. magellanicus	0.31	1.88	ns	0.07	ns	0.14	ns
C. virginica	0.33	1.08	ns	0.48	ns	1.79	ns

P: probability level, ns: non-significant, $\bar{x}$: mean value μl O_2/mg/hr.

clones, a feature also found for the New Zealand greenshell mussel *Perna canaliculus* (Marsden and Shumway, 1993). Contrasting with these results, *M. arenaria* and *P. magellanicus* showed reduced feeding rates on the toxic clone (GT429). While the grazing rates for *M. arenaria* were considerably less than those recorded by Shumway and Cucci (1987), results were consistent with previous studies and field data. These demonstrated reduction in filtration rates and lower toxicity in *M. arenaria* when compared with other species (Shumway *et al.*, 1985; 1988b; Hurst, unpublished information). At present, the reasons for these differences in grazing rates cannot be ascertained; however, since there are several likely selection sites (gills, siphon and palps) that may be able to distinguish between particles, any or all of these may be important in the selection procedure following short-term exposure to the toxic algae (Shumway *et al.*, 1990).

A number of previous studies have attempted to evaluate the metabolic cost of filtration in bivalve molluscs. For the mussels, *M. edulis* and *M. californianus*, the mechanical cost of filtration may represent up to 20% of the ingested ration (Bayne *et al.*, 1976; Bayne and Scullard, 1977). The increase in metabolic rate that is associated with feeding has been called the specific dynamic action (SDA) (Beamish, 1974). For the mussel, *M. edulis*, Langton (1975), Bayne (1976), Bayne *et al.* (1973) and Bayne and Scullard (1977) report increases in the oxygen uptake following feeding on the alga *Tetraselmis suecica*, although similar increases were not always apparent using other food sources. The observed increase in oxygen uptake was seen for up to 24 hr in these experiments and was thought to be associated with the metabolic costs due to digestion and ammonia excretion. Although increased metabolism was not a general feature found in the current research, previous studies have resulted in increases in oxygen uptake for some bivalves following exposure to toxic dinoflagellates.

Gainey and Shumway (1988) reported increased oxygen uptake in *Mya arenaria* contrasting with *P. magellanicus* which showed decreased oxygen uptake. Responses were also variable depending upon the previous history of the bivalves being investigated. For *M. edulis* that had had previous exposure to *A. tamarense*, oxygen uptake was unaffected, whereas those from an area without prior exposure had increased oxygen uptake (Cucci *et al.*, 1985; Shumway *et al.*, 1985). The results of the present study, however, do not support broad generalizations, as oxygen uptake was unaffected in both laboratory-reared individuals and those without likely prior exposure to the toxic alga. While it is probable that the short-term exposure to the toxic algae did not affect opening behaviour significantly, longer term exposure may have resulted in greater activity or valve closure. There may also have been modified filtration rates, increased cardiac activity, siphon retraction, increased mucus production or other physiological or neurophysiological effects.

The species used in this study differ in their nerve sensitivity to red tide toxins (Twarog and Yamaguchi, 1974). *C. virginica* appears to be one of the most sensitive with neurons inhibited by 0.01 μm STX with *M. arenaria* sensitive to 0.01 μm. In contrast, neurons of both *M. edulis* and *P. magellanicus* were unaffected by concentrations less than or equal to 0.1 μm STX. Twarog *et al.* (1972) suggest that those species that are most sensitive to STX may have a reduced filtration which would reduce the accumulation of red tide toxins. Results of the present study are consistent with this hypothesis with *C. virginica* and *M. arenaria* showing the lowest and most variable feeding rates.

Although short-term exposure of juvenile bivalves to the toxic strain of *A. tamarense* did not appear to act as a stress factor increasing oxygen uptake, longer term exposure may have a different effect. The physiological and other changes associated with toxin accumulation may affect any part of the energy balance equation through respiratory mechanisms, feeding, digestion and excretion. There is, therefore, a need for a fuller investigation into the effects of toxin accumulation on the metabolic energy expenditure of bivalve molluscs exposed to harmful or toxic marine phytoplankton.

Acknowledgements—The work was undertaken whilst I. D. Marsden was on study leave from the University of Canterbury, New Zealand. We thank Jan Barter for help in the maintenance of algal cultures. This study was funded in part by a U.S. Food and Drug Administration contract (22-89-4064) to the Massachusetts Health Research Institute and in part by grant/cooperative agreement (NA-90-AA-H-SK030) from the National Oceanic and Atmospheric Adminstration awarded to the New England Fisheries Development Association. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. This is Bigelow Laboratory for Ocean Sciences contribution number 93010.

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