

A COMPENDIUM OF THE RESPONSES OF BIVALVE MOLLUSCS TO TOXIC DINOFLAGELLATES

LOUIS F. GAINNEY, JR.¹ AND SANDRA E. SHUMWAY²

¹Dept. of Biological Sciences
University of Southern Maine
Portland, Maine 04103 U.S.A.

²Maine Department of Marine Resources
W. Boothbay Harbor, Maine 04575

INTRODUCTION

The biology of toxic dinoflagellates, and the threat to public health caused by their presence, have been studied in great detail by a number of workers (see LoCicero 1975, Taylor and Seliger 1979, Anderson et al. 1985). Until recently, however, little attention has been given to the effects of these organisms on their molluscan hosts. A number of authors have, in fact, states that the dinoflagellates have little effect on the host animals (e.g., Prakash et al. 1971, Quayle 1969, Arafiles et al. 1984, Estudillo and Gonzales 1984). Although there are data to the contrary, this belief has prevailed and has been reiterated often in the literature.

In a recent series of papers, Shumway and co-workers have studied the behavioral and physiological responses of bivalve molluscs to the presence of the toxic dinoflagellate, *Protogonyaulax tamarensis*. We have shown that not only are the host organisms affected by the presence of the dinoflagellates, but that the effects are species specific, geographically specific and often dramatic. In this review, we summarize the data on the effects of various species of toxic dinoflagellates on the behavior and physiology of bivalve molluscs.

Shell Valve Closure

Perhaps the most widely reported effects of red tide organisms upon bivalve molluscs is isolation from the environment either by valve closure or reduced filtration. Differential valve closure has been reported in *Brachiodontes recurvis* and *Crassostrea virginica*: valve closure increased in the presence of *Gymnodinium monilata* but was normal in the presence of *G. breve* (Sievers 1969). Differential valve closure has also been reported in *Mytilus edulis* by Shumway and Cucci (1987). While *M. edulis* from Maine showed no response to the addition of *Protogonyaulax tamarensis* (clone GT429), *M. edulis* from Rhode Island showed varying degrees of shell-valve closure when presented with GT429 (Figure 1). While 3 animals were shown to continue normal activity patterns (Figure 1b), the majority (15) exhibited at least partial shell-valve closure.

Echalent siphons were closed and the mantle edges in otherwise "open" animals were retracted. Similar patterns of shell-valve activity were noted in Spanish *M. edulis* in the presence of GT429 (Figure 1d, e). Two-thirds of these animals tested showed initial, erratic shell-valve closure followed by complete closure.

Both *Crassostrea virginica* and *Ostrea edulis* remained open in the presence of GT429 (Figure 2). *O. edulis* normally had the shell valves open and the mantle edges were visible. Addition of GT429 caused partial adduction of the shell valves in only four of the 14 animals studied (Figure 2a). Figure 2b shows the typical response of *O. edulis* to the introduction of GT429. There was an initial, partial adduction of the shell valves followed by periodic "snaps." This activity pattern continued until clean sea water was introduced. *C. virginica* exhibited an initial shell-valve closure when GT429 was presented. This closure was followed by a gradual reopening (Figure 2c) and the pattern repeated, although complete closure never occurred. (Shumway and Cucci 1987). Ray and Aldrich (1976) reported that *C. virginica* rarely opened when exposed to *Gonyaulax monilata* (= *Gessnerium monilatum*, Loeblich), but opened frequently in the presence of *Gymnodinium breve* (= *Ptychodiscus brevis*, Steidinger). Dupy and Sparkes (1968) reported valve closure accompanied by vigorous "clapping" of the valves in *C. gigas* upon exposure to *Gonyaulax washingtonensis*.

Placopecten magellanicus showed the most striking behavioral responses of any species studied by Shumway and Cucci (1987). While 2 animals showed no response, the majority (14) exhibited an immediate closure of the shell valves followed by either violent swimming activity, partial, sustained shell-valve closure, or a combination of the two (Figure 3a). Swimming/clapping activity patterns were never observed to last for more than 30 min.-1 hr. On addition of clean sea water, the activity ceased (Figure 3b) and the animals remained open with the mantle edges and tentacles freely exposed.

Spisula solidissima, *Modiolus modiolus*, *Artica islandica* and *Guekensia demissa* showed no change in valve activity upon exposure to GT429, while *Mercenaria mercenaria* showed a pronounced valve closure (Figure 3), Shumway and Cucci 1987).

*Publication No. 282 of the Tallahassee, Sopchoppy & Gulf Coast Marine Biological Association.

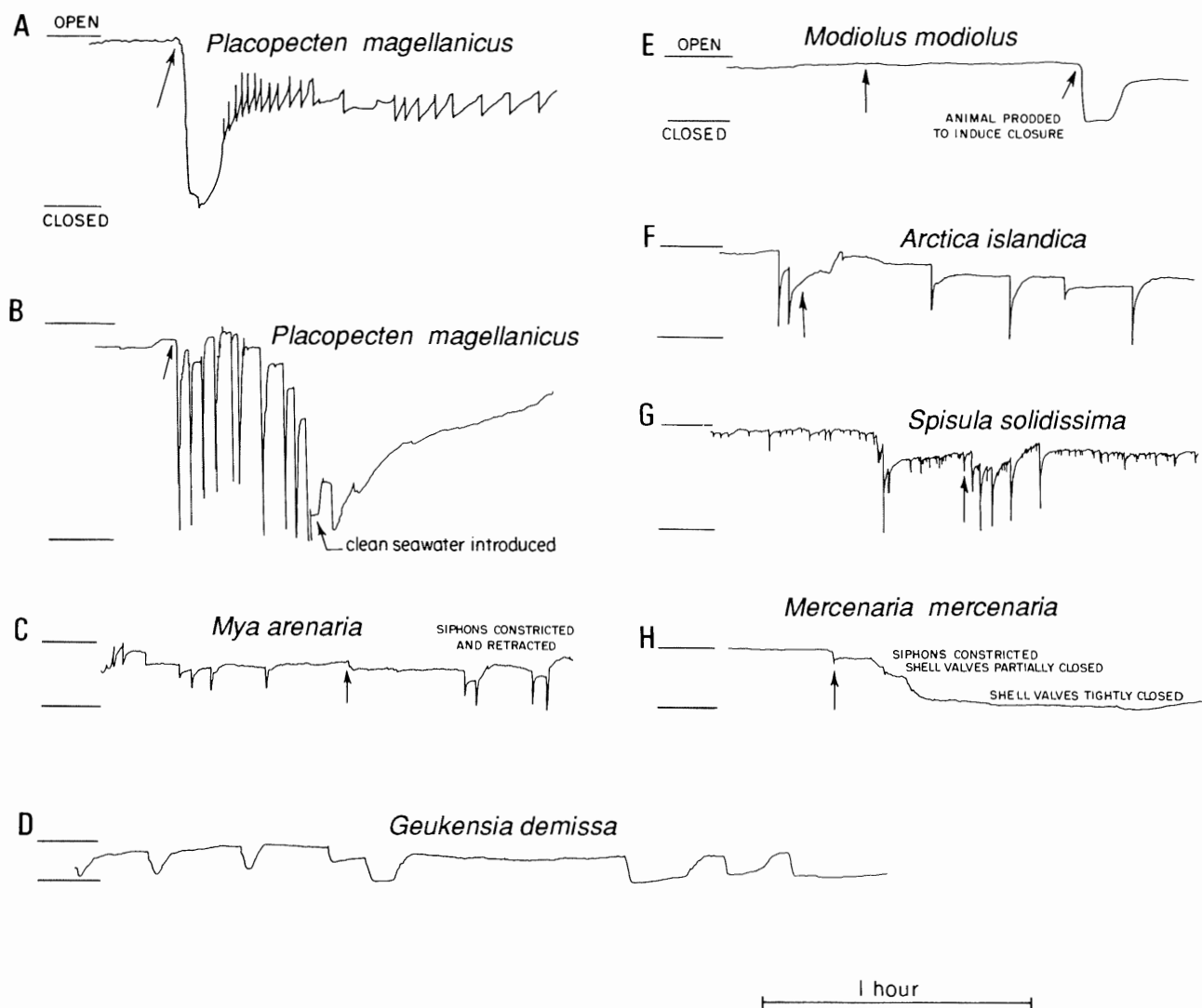


Figure 1. Tracings of shell-valve activity patterns of bivalve molluscs after exposure to *P. tamarensis*. Arrows indicate addition of GT429. After Shumway and Cucci (1987).

Effects on Filtration Rate

Reduced filtration rates have been reported for a number of bivalves exposed to a variety of toxic dinoflagellates. In general, those animals that showed increased valve or siphon closure also showed decreased filtration rates, e.g., *Mytilus edulis* from Rhode Island, *Mya arenaria* (Shumway and Cucci 1987), *Crassostrea virginica* (Ray and Aldrich 1967, Shumway and Cucci 1987), *Crassostrea gigas* (Dupuy and Sparkes 1968), and *Mercenaria mercenaria* (Dupuy and Sparkes 1968, Shumway and Cucci 1987). Filtration rates increased significantly in *Ostrea edulis* and *Mytilus edulis* from Maine, while filtration rates were unchanged in *Placopecten magellanicus*, and *Spisula solidissima* upon exposure to GT429 (Table 1, Shumway and Cucci 1987).

Effects on Feeding

In a series of feeding experiments, Shumway and Cucci (1987) found that *Mytilus edulis*, *Crassostrea virginica*,

Ostrea edulis, *Placopecten magellanicus*, and *Modiolus modiolus* showed no preferential selection either for or against GT429, and the dinoflagellate appeared in both the pseudofeces and feces. GT429 appeared in the pseudofeces of *Mya arenaria* but was excluded from the feces, demonstrating preingestive selection (Figure 4). Exposure of *Spisula solidissima* to GT429 resulted in an increase in pseudofeces production, with GT429 appearing in both the pseudofeces and feces (Figure 5).

Byssus Production

The effects of *Protogonyaulax tamarensis* on byssus production by three species of mussels (*Mytilus edulis*, *Geukensia demissa*, *Modiolus modiolus*) were reported by Shumway et al. (1987, Table 2). Byssus production was inhibited in both *M. edulis* and *G. demissa*; moreover, there were geographic differences in the response of *M. edulis*, i.e., animals from areas previously exposed to toxic algal blooms (Maine) showed less decrease in byssus pro-

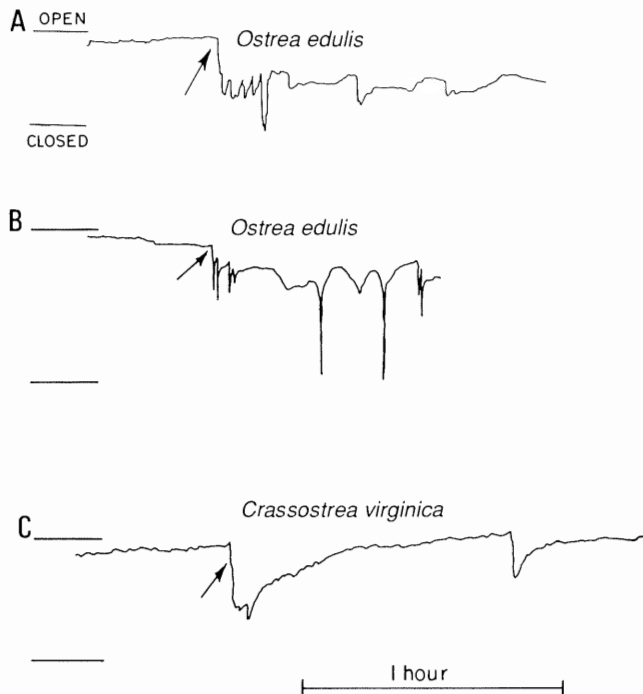


Figure 2. Tracings of shell valve activity of oysters after exposure to *P. tamarensis*. (Arrows indicate addition of GT429.) After Shumway and Cucci (1987).

duction than did mussels from areas never exposed to such blooms (Rhode Island). Only *M. modiolus* was unaffected. Shumway et al. (1987) suggested that, while the presence of toxic dinoflagellates has a definite effect on byssus production, the reduced production is not necessarily a response to the presence of toxins *per se*, or to the interruption of the byssus function in particular, but is more likely an indication of physiological stress by individual animals.

Oxygen Consumption

Oxygen consumption, after exposure to GT429, has been measured in 4 species of bivalves by Shumway et al. (1985), and the relationship between oxygen consumption and other physiological responses to red tide is not clear. For example, *Placopecten magellanicus* showed no change in filtration rate, an increase in valve activity, yet showed a decrease in oxygen consumption. *Spisula solidissima* showed no change in filtration or valve activity, yet showed a decrease in oxygen consumption. *Mya arenaria* showed a decrease in filtration rate yet an increase in oxygen consumption. *Mytilus edulis* from Rhode Island showed an increase in valve closure and an increase in oxygen consumption. Not surprisingly, *Mytilus* from Maine, which had prior exposure to *Protogonyaulax tamarensis* showed no change in oxygen consumption yet had increased clearance rates. The effects of red tide on oxygen consumption may be due to indirect effects, such as increased activity or repayment of an oxygen debt, although a direct effect on cellular metabolism cannot be ruled out in species such as *Placopecten* or *Spisula* which either showed an increase, or

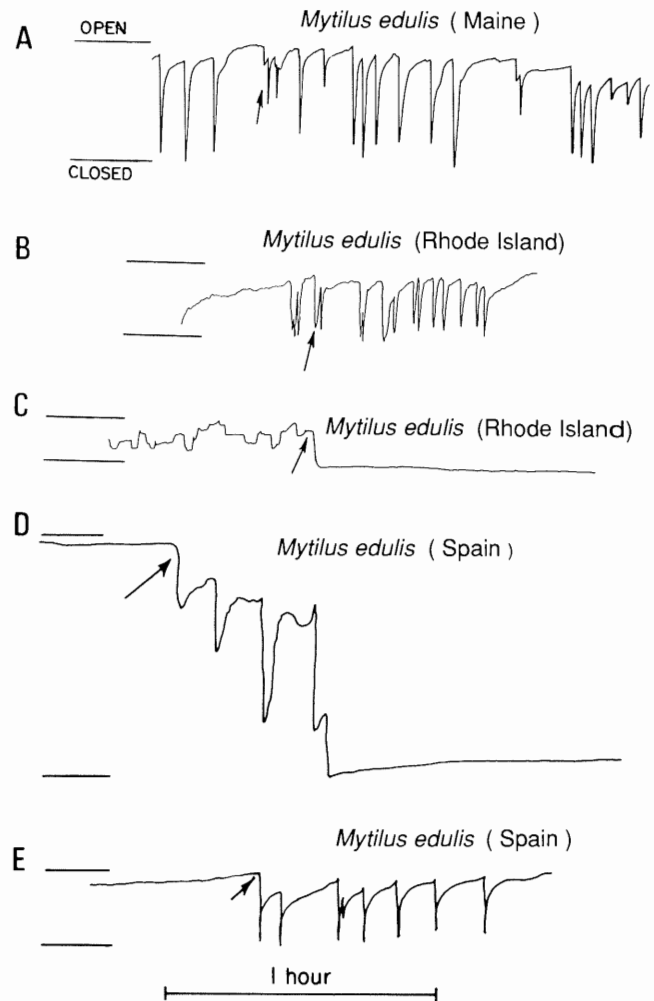


Figure 3. Tracings of shell-valve activity of mussels from various localities after exposure to *P. tamarensis*. Arrows indicate introduction of GT429. After Shumway and Cucci (1987).

no change, in activity yet had a decrease in oxygen consumption (Figure 6).

Cardiac Activity

Gainey and Shumway (1988) measured cardiac activity in 8 species of bivalves exposed to GT429. Cardiac activity was unaffected in *Spisula solidissima*, *Mercenaria mercenaria*, *Placopecten magellanicus* and *Artica islandica*. In *Mya arenaria*, there was a transient decrease in heart rate between 30 min. and 3 hr. after exposure to GT429 in 4 of 10 individuals. The rates returned to normal within 24 hr., and were presumably related to increased siphon closure, which resulted in depressed heart rates in untreated individuals.

Exposure of *Ostrea edulis* to GT429 affected 2 out of 9 animals: these 2 had a significant decrease in heart rate. These animals also experienced cardiac arrhythmias.

Exposure of *Geukensia demissa* to GT429 resulted in a significant decrease in heart rate in 1 out of 10 animals tested. In addition, 3 animals had a transient increase in

TABLE 1.

The clearance rates of 6 species of bivalve molluscs estimated assuming 100% retention efficiency of algal cells. Animals were fed a mixture of algal cells (*Prorocentrum minimum*, *Phaeodactylum tricornutum* and *Chroomonas salina*) initially. The same animals were later fed on the same mixture with the toxic dinoflagellate, *Protogonyaulax tamarens* (GT429) added. See Shumway et al. (1985) for details.

Species	Clearance rate (cells $1^{-1} h^{-1} \times 10^3$)	
	Before exposure to GT429	After exposure to GT429
<i>Ostrea edulis</i>	4220*	6160
<i>Placopecten magellanicus</i>	5000	4980
<i>Mya arenaria</i>	6240*	4500
<i>Mytilus edulis</i> (Maine)	9020*	9900
<i>Mytilus edulis</i> (Rhode Island)	7470	7940
<i>Spisula solidissima</i>	5420	5310
<i>Crassostrea virginica</i>	8320*	7720

* Rate is significantly different from animals exposed to GT429 ($P \leq 0.05$)

heart rate, which appeared within 1 day after exposure, and disappeared within 2 days after exposure. After this transient increase, the heart rate returned to normal in 1 animal and was lower in the other 2.

The response of *Mytilus edulis* to GT429 was divided into one of 3 categories: maximal, transient and minimal. Of the 17 *Mytilus* from Maine exposed to GT429, 6 had a maximal response. Two of these animals had a significant decrease in heart rate, while 2 animals had a significant increase in heart rate. Two animals had a transient increase in rate, followed by a prolonged decrease. Four of the 6 animals died within 6 days of exposure. In addition to the change in heart rate, cardiac arrhythmias were present in 5 of the 6 animals. Five of the 17 *Mytilus* had a transient response to GT429. The pre- and post-treatment heart rates were not different, but these animals had cardiac arrhythmias, and depressed rates, but actively returned to

normal within 3 days of exposure to GT429. Six of the *Mytilus* were unaffected by exposure of GT429.

Eleven *Mytilus* from Long Island were exposed to GT429. Three animals had a maximal response: 2 had a significant decrease in heart rate, and 1 had a significant increase. The 2 animals that had depressed heart rates also had pronounced arrhythmias within 2 days of exposure. These arrhythmias lasted for 8 days. Two of the animals had a transient response consisting of periods of cardiac arrhythmia that appeared within 4 days after exposure and lasted until 5 days after exposure. Six animals had no response to GT429.

The 3 species that had an unequivocal response to GT429 are pteriomorphs (Table 3). The only heterodont that had a response to GT429 was *Mya arenaria*: 40% of the individuals tested had a reduced heart rate for several hours after exposure. In *Mya*, siphon closure is accompanied by bradycardia prior to exposure to GT429, and this transient reduction in heart rate probably was due to closing of the siphons in response to GT429. The different response of pteriomorphs and heterodonts to the presence of GT429 is reflected in other aspects of their cardiac physiology (reviewed in Painter and Greenberg 1979).

Neurophysiological Effects

The effect of red tide toxins on bivalve neurons has been investigated by Twarog and Yamaguchi (1974, Table 4). They found a graded response that varied according to species. *Mytilus edulis*, *Placopecten magellanicus*, and *Mercenaria mercenaria* were unaffected by concentrations of saxitoxin (STX) less than or equal to 0.1 mM. *Mya arenaria* neurons were inhibited by 0.01 mM, while *Crassostrea virginica* neurons were inhibited by 0.1 uM STX. Twarog and Yamaguchi hypothesized that those animals that are most sensitive to STX either are not regularly exposed to the toxin, or have a reduced filtration rate which would reduce accumulation of toxin. This hypothesis is borne out by the fact that *Mytilus edulis* rapidly accumulates toxin and is insensitive to STX, whereas the rate of accumulation in *Mya* is less (Shumway and Cucci 1987).

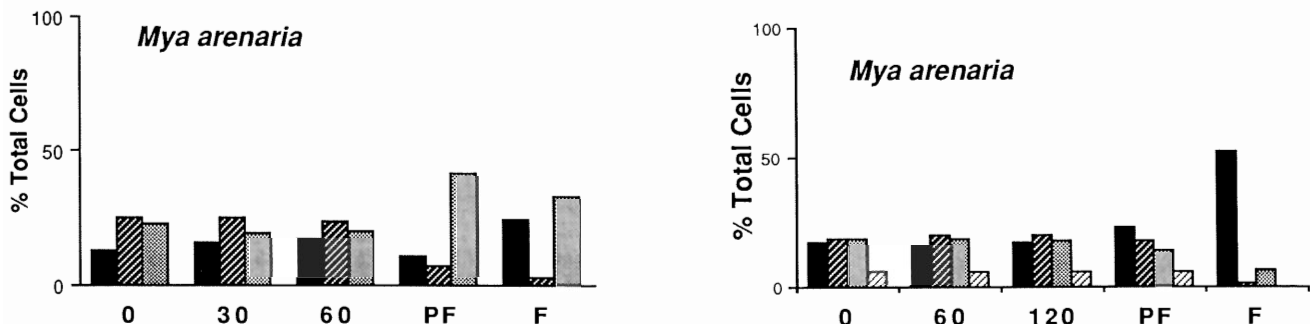


Figure 4. Percentages of the total cell count within an algal mixture of the clones 3H (solid bars), 3C (dark stripes), Exuv (hatched) and GT429 (light stripes) at time 0 and after 60 and 120 min. and within the pseudofeces (PF) and feces (F) during feeding experiments. After Shumway and Cucci (1987).

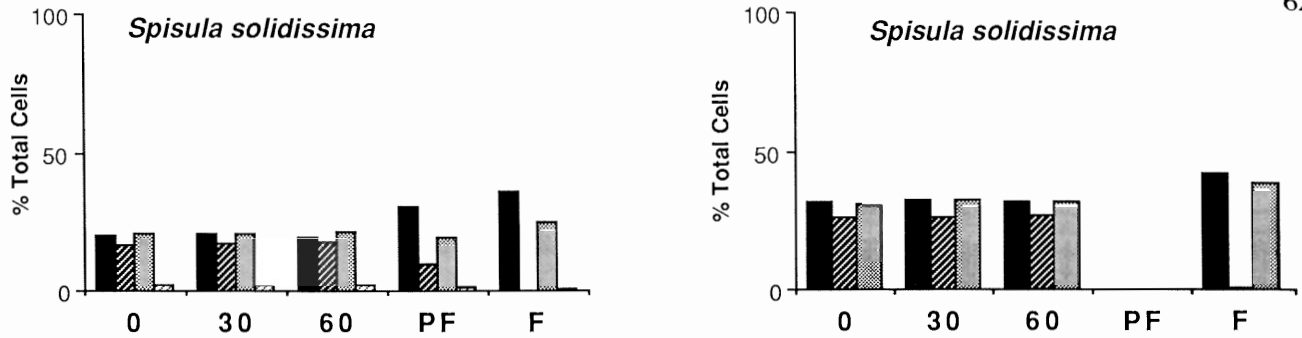


Figure 5. Percentages of the total cell count within an algal mixture of the clones 3H (solid bars), 3C (dark stripes), Exuv (hatched) and GT429 (light stripes) at time 0 and after 60 and 120 min. and within the pseudofeces (PF) and feces (F) during feeding experiments. After Shumway and Cucci (1987).

TABLE 2.

The production of byssus threads by three species of mussels before (control) and after exposure to *Protogonyaulax tamarensis* and after a 1 week recovery period. Results are expressed as number of threads produced per mussel per day \pm standard deviation (from Shumway et al. 1987).

Species	n	Control	After exposure to GT 429	After recovery
<i>Mytilus edulis</i> (Maine)	94	15.5 \pm 2.1	7.1 \pm 3.4*	13.4 \pm 4.5
<i>Mytilus edulis</i> (RI)	91	6.2 \pm 1.2	1.9 \pm 0.8†	2.4 \pm 1.0†
<i>Modiolus modiolus</i>	92	21.9 \pm 4.9	23.2 \pm 3.5	23.6 \pm 4.8
<i>Geukensia demissa</i>	86	19.4 \pm 4.1	10.6 \pm 1.1*	16.3 \pm 3.3

* Significantly different from control at $p < 0.05$.
 † Significantly different from control at $p < 0.01$.

TABLE 3.

Summary of effects of the toxic dinoflagellate, *Protogonyaulax tamarensis*, on cardiac activity in bivalve molluscs. Inh: Inhibition; Exc: Excitation; Tran: Transient; None: No effect (From Gainey and Shumway, 1988).

Subclass	Species (n)	Response: %
Pteriomorpha	<i>Mytilus edulis</i> (Maine n = 17)	Tran. Inh: 29%
		Inh: 24%
		Exc: 12%
		None: 35%
		Tran. Inh: 18%
<i>Mytilus edulis</i> (Long Island n = 11)	Inh: 18%	
	Exc. 9%	
	None: 55%	
<i>Geukensia demissa</i> (n = 10)	Tran. Inh: 10%	
	Inh: 10%	
	Tran. Exc. 40%	
	None: 40%	
<i>Ostrea edulis</i> (n = 9)	Inh: 22%	
	None: 73%	
<i>Placopecten magellanicus</i> (n = 6)	None: 100%	
Heterodonta	<i>Mya arenaria</i> (n = 10)	Tran. Inh: 40%
		None: 60%
	<i>Spisula solidissima</i> (n = 4)	None: 100%
		None: 100%
	<i>Mercenaria mercenaria</i> (n = 16)	None: 100%
<i>Arctica islandica</i> (n = 6)	None: 100%	

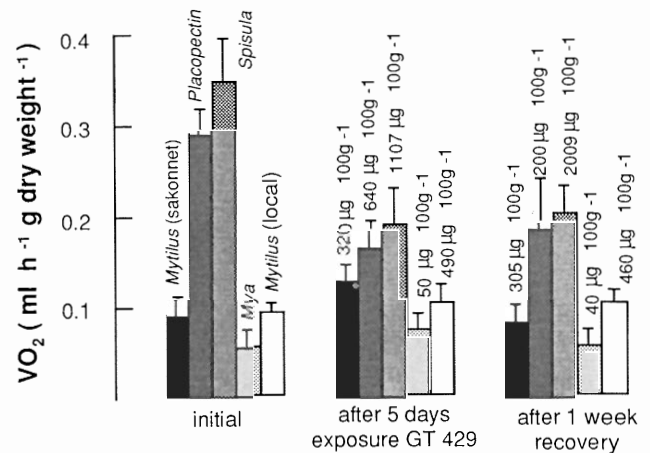


Figure 6. Rates of oxygen consumption for 4 species of bivalve molluscs exposed to the toxic dinoflagellate, *P. tamarensis*. After Shumway et al. (1985).

TABLE 4.

Block of action potential by saxitoxin (STX) (From Twarog and Yamaguchi, 1974).

Species	10 ⁻⁸	10 ⁻⁷	10 ⁻⁶	10 ⁻⁵	10 ⁻⁴
<i>Mytilus edulis</i>	-	-	-	-	-
<i>Placopecten magellanicus</i>	-	-	-	-	-
<i>Mercenaria mercenaria</i>	-	-	-	-	-
<i>Modiolus demissus</i>	-	-	-	-	+
<i>Pecten irradians</i>	-	-	-	-	+
<i>Mya arenaria</i>	-	-	-	+	+
<i>Crassostrea virginica</i>	-	+	+	+	+
<i>Elliptio complanata</i>	-	+	+	+	+

The species are listed in order of increasing sensitivity to STX.
 + = Full Block.

Mortality

There have been periodic reports in the literature of mass mortality of a variety of bivalves exposed to a variety of toxic dinoflagellates. However, the effects of the various red tide organisms are variable. For example, Sievers (1969) reported that *Carassostrea virginica* showed increased mortality when exposed to *Gonyaulax poleydra*; similarly, Reish (1963) reported increased mortality of *Mytilus edulis* exposed to *Gonyaulax poleydra*, while Adams et al. (1968) reported no deaths for *Mytilus* exposed to *Protogonyaulax tamarensis*. In a laboratory study, there was 75% mortality in *Mytilus edulis* from Rhode Island and Spain upon exposure to *P. tamarensis*. These mussels had had no prior to exposure *P. tamarensis*. In contrast, there was no mortality in *Mytilus edulis* from Maine upon expo-

sure to *P. tamarensis*. These mussels had had prior exposure to the toxic dinoflagellate (Shumway and Cucci 1987).

SUMMARY

The most common effect of red tide upon bivalves is a decrease in exposure to the environment either by reducing filtration, or increasing valve closure. The other physiological effects noted, such as changes in oxygen consumption and cardiac activity, may be associated with the former responses and may not be a direct effect of exposure to red tide organisms. However, whether or not toxic dinoflagellates exert their physiological effects directly, or indirectly, they clearly cause physiological stress in a variety of bivalve molluscs.

REFERENCES CITED

- Adams, J. A., D. D. Seaton, J. B. Buchanan & M. R. Longbottom. 1968. Biological observations associated with the toxic phytoplankton bloom off the East coast. *Nature* 220:25-27.
- Anderson, D. M., A. W. White & D. G. Baden. 1985. Toxic dinoflagellates. Elsevier, Amsterdam. 561 pp.
- Ararfiles, L. M., R. Hermes & J. B. T. Morales. 1984. Lethal effect of paralytic shellfish poison (PSP) from *Perna viridis*, with notes on the distribution of *Pyrodinium bahamense* var. *compressa* during a red tide in the Philippines. In White, A. W., Anraku, M. & Hooi K. (eds.) Toxic red tides and shellfish toxicity in southeast Asia, pp. 43-51.
- DuPuy, J. L. & A. K. Sparks. 1968. *Gonyaulax washingtonensis*, its relationship to *Mytilus californianus* and *Crassostrea gigas* as a source of paralytic shellfish toxin in Sequin Bay, Washington. *Proc. Nat. Shellfish Assn.* 58:2.
- Estudillo, R. A. & C. L. Gonzales. 1984. Red tides and paralytic shellfish poisoning in the Philippines. In White, A. W., M. Anradu & Hooi, I. (eds.) Toxic red tides and shellfish toxicity in southeast Asia, pp. 52-79.
- Gainey, L. F., Jr. & S. E. Shumway. 1988. Physiological effects of *Protogonyaulax tamarensis* on cardiac activity in bivalve molluscs. *Comp. Biochem. Physiol.* 91C:159-164.
- LoCicero, U. R. 1975. Proceedings of the First International Conference on Toxic Dinoflagellate Blooms, Massachusetts Science and Technology Foundation, Wakefield, MA. 541 pp.
- Painter, S. D. & M. J. Greenberg. 1982. A survey of the responses of bivalve hearts to the molluscan neuropeptide FMRFamide and to 5-hydroxytryptamine. *Biol. Bull.* 162:311-332.
- Ray, S. M. & D. V. Aldrich. 1967. Ecological interactions of toxic dinoflagellates and molluscs in the Gulf of Mexico. In Russell, F. E. & R. P. Saunders (eds.) *Animal Toxin*. Pergamon Press, N.Y., pp. 75-83.
- Reish, D. 1963. Mass mortality of marine organisms attracted to the "red tide" in Southern California. *Ca. Fish and Game* 49:265-270.
- Shumway, S. E., T. L. Cucci, L. Gainey & C. M. Yentsch. 1985. A preliminary study of the behavioral and physiological effects of *Gonyaulax tamarensis* on bivalve molluscs. In Anderson, D. M., A. W. White & D. G. Bader (eds.) *Toxic Dinoflagellates*. Elsevier, Holland, pp. 389-394.
- Shumway, S. E. & T. L. Cucci. 1987. The effects of the toxic dinoflagellate *Protogonyaulax tamarensis* on feeding and behavior of bivalve molluscs. *Aquatic Toxicol.* 10:9-27.
- Shumway, S. E., F. C. Pierce & K. Knowlton. 1987. The effect of *Protogonyaulax tamarensis* on byssus production in *Mytilus edulis* L., *Modiolus modiolus* Linnaeus, 1758 and *Geukensia demissa* Dillwyn. *Comp. Biochem. Physiol.* 87A:1021-1023.
- Sievers, A. M. 1969. Comparative toxicity of *Gonyaulax monilata* and *Gymnodinium breve* to annelids, crustaceans, molluscs and a fish. *J. Protozool.* 16:401-404.
- Taylor, D. L. & H. H. Seluger. 1979. Toxic Dinoflagellate Blooms. Elsevier, Amsterdam, 505 pp.
- Twarog, B. M. & H. Yamaguchi, 1974. Resistance to paralytic shellfish toxins in bivalve molluscs. In: Proceedings of the First International Conference on Toxic Dinoflagellate Blooms, November 1974. Boston, Massachusetts. (ed. V. R. LoCicero), Mass. Science and Technology Foundation, Wakefield, MA, pp. 381-393.