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DWARF SURFCLAM *MULINIA LATERALIS* (SAY, 1822) POPULATIONS AND FEEDING DURING THE TEXAS BROWN TIDE EVENT

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ABSTRACT In 1990, there was an unusual brown tide bloom of an aberrant Chrysophyte sp. in Baffin Bay and Laguna Madre near Corpus Christi, Texas. Coincident with the bloom was a dramatic loss of shellfish in Baffin Bay and Laguna Madre. The dominant clam, *Mulinia lateralis*, disappeared for about two years. We performed a series of experiments to determine if disappearance of *M. lateralis* was related to negative feeding interactions with the brown tide organism. Radioactive tracers were used to compare feeding rates on brown tide, *Isochrysis galbana*, *Dunaliella tertiolecta*, and *Heterocapsa pygmeae*. At low cell concentrations (<1,000 cells · ml^{-1}), *M. lateralis* grazing rates (cell · h^{-1}) increased with concentration and were similar among the microalgal species. At higher concentrations, grazing rates on *Isochrysis* were inhibited, but remained the same for the other microalgal species. Assimilation efficiency by *M. lateralis* was lowest on *Heterocapsa*, and was about the same for the three other species of algae. The high grazing and assimilation rates of brown tide by *M. lateralis* indicate that the loss of the clam population was not likely caused by a negative trophic effect of the brown tide. Other bloom factors, e.g. reproductive effects or toxic effects, may have contributed to the concomitant loss of the clam population and the occurrence of brown tide. It is also possible that non-bloom factors, e.g. natural population variability increased predation pressure, could have caused the population loss. The reduced populations of filter feeders could have been partially responsible for conditions conducive for the brown tide bloom.

INTRODUCTION

A monospecific bloom of a small chrysophyte alga began in January 1990 in Baffin Bay, Texas. This bloom caused water discoloration and is called a "brown tide." The bloom is chronic; it remains intense after 3 years, waning only during the winter months. The organism is an unknown species. It is a Type III Chrysophyte, 4–5 μm in diameter, similar (yet different) to *Aureococcus anophagefferens* and *Pelagococcus subviridis* (Stockwell et al. 1993). Chlorophyll content in the water column was about 10 μg · l^{-1} before the bloom, and it increased to 80 μg · l^{-1} during the apex of the bloom (Stockwell et al. 1993). Bottom light levels decreased 80% to 20% due to diffraction by the dense particulate matter in the water column (Dunton personal communication). The general ecological trends during the brown tide were a decrease in mesozooplankton (Buskey and Stockwell 1993), fish larvae (Holt personal communication) and benthic abundance and diversity (Montagna and Kalke in preparation). One interesting coincidence was a dramatic reduction in abundance of filter-feeding mollusks.

Other brown tides are known to have had catastrophic effects on bivalves (Shumway 1990). Effects have ranged from reproductive or recruitment failures (Bricelj et al. 1987, Tracey 1988), to adverse effects on feeding (Bricelj and Kuenstner 1989, Tracey 1988, Tracey et al. 1988) to a toxic effect (Draper et al. 1989, Tracey et al. 1990; Gainey and Shumway 1991). Mass mortalities of shellfish were usually reported. Although specific mechanisms for the mortality are difficult to ascertain, it is possible that one, or a combination of these effects is causing the population declines.

The dominant bivalve in the brown tide area, *Mulinia lateralis*, practically disappeared for 2 years. This caused great concern about the dominant finfishery, because *M. lateralis* is the predominant food source for black drum, *Pogonias cromis* (Martin 1979).

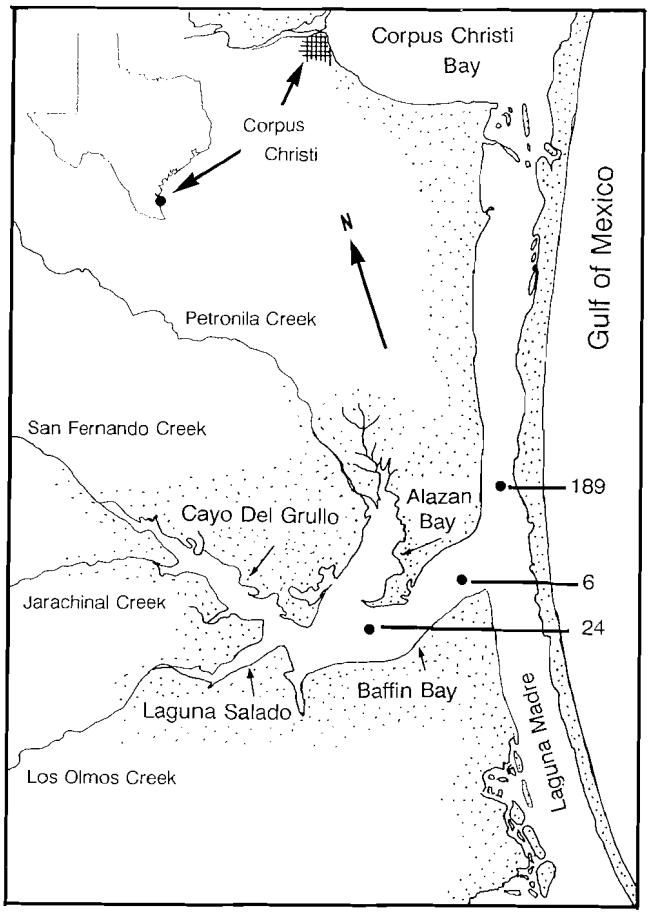

Figure 1. Study area.

TABLE 1.

Algae used in the two feeding experiments.

Division	Species	Cell Volume ($\mu m^3 \cdot cell^{-1}$)	Cell Biomass (pg C · $cell^{-}$)	Expt. 1 (10^3 cells · ml^{-1})	Expt. 2 (10^3 cells · ml^{-1})
Chrysophyte	Brown tide	33.5	3.685	2710	666
Chrysophyte	*Isochrysis galbana*	65.5	7.205	2450	765
Chlorophyte	*Dunaliella tertiolecta*	524	57.64	1045	322
Pyrrophyte	*Heterocapsa pygmeae*	720	79.20	142	32

The general concern was that there might be a major alteration of the ecosystem since carbon was tied up in a primary producer that was not being transferred into the food webs (Buskey and Stockwell 1993). Similar major ecological changes to the subtidal community occurred in Long Island, New York embayments experiencing *A. anophagefferens* blooms (Cosper et al. 1987). When *M. lateralis* reappeared in 1992, we initiated a feeding experiment to determine if the brown tide was causing feeding-related problems to the clam. We also document population change of *M. lateralis* during this period.

MATERIALS AND METHODS

Study Sites. The brown tide started in January 1990 in Alazan Bay, Laguna Salada, and Cayo de Grullo, which are three tertiary bays of Baffin Bay (Fig. 1). Each of the tertiary bays is fed by small creeks and rivers that contribute freshwater inflow intermittently in this drought-prone region. On average, evaporation exceeds river inflow, so these bays are often hypersaline. Salinity in Baffin Bay ranged from 40–60‰ during 1989, the year preceding the brown tide (Whitledge 1993). Four stations have been sampled

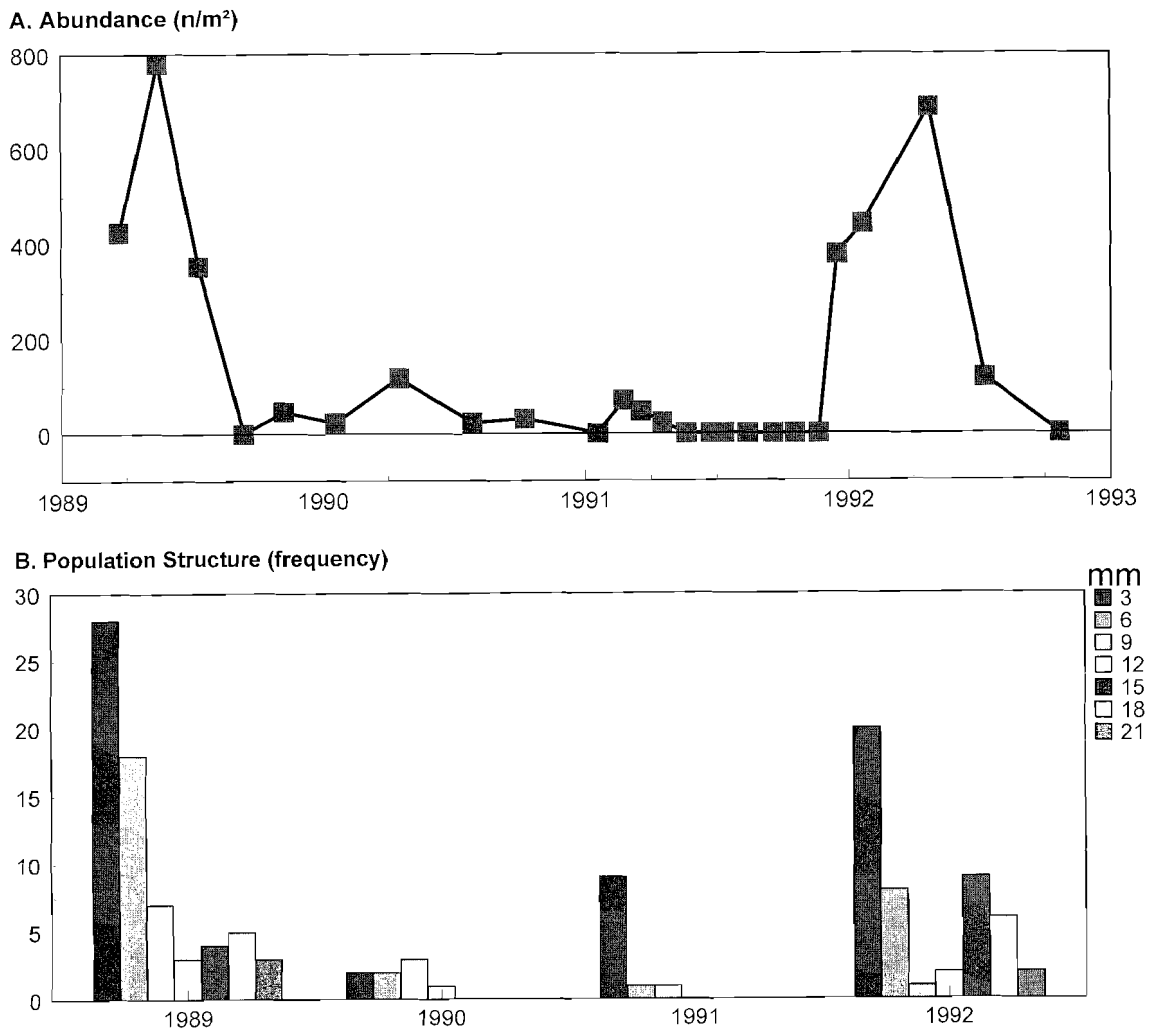

Figure 2. Population dynamics of *Mulinia lateralis* in Baffin Bay and Laguna Madre from 1989 to 1992. A. Average abundance at all stations sampled. B. Size structure of populations.

continuously since March 1988 (Fig. 1). Two of these stations are located near Markers 6 and 24 in Baffin Bay in open bay, mud bottoms at a depth of about 3 m. Two other stations are located west of marker 189 in the Intracoastal Waterway in the Laguna Madre. One of these stations is located in a seagrass bed, and the other in an adjacent unvegetated habitat. The brown tide did not reach the Laguna Madre until June 1990.

Population Study. Sediment at the four stations was sampled with core tubes held by divers. The tube was 6.7 cm inner diameter, and three replicates were taken within a 2-m radius. Sediment was sectioned at depth intervals of 0–3 cm and 3–10 cm. *Mulinia* was rarely present in the lower depth stratum. Samples were preserved with 5% buffered formalin. All macrofauna were extracted with 0.5 mm sieves, identified, and counted, but are reported elsewhere (Montagna and Kalke in prep.).

Feeding Experiments. Two experiments were performed where algae were pre-labeled with ^{14}C and fed to clams. The goal of the first experiment was to determine if there were functional responses of clam feeding rates to various algal concentrations. The goal of the second experiment was to determine if the algae were being assimilated. Four species of algae were used in each experiment (Table 1). The algae were prepared from stock cultures maintained at the University of Texas Marine Science Institute. A comparative approach was used to determine if responses to brown tide was different from responses to other algae that were not suspected of being poor food sources to the clams.

The first experiment was performed May 28, 1992. The brown tide was harvested from the field (2.71×10^6 cells $\cdot$ ml^{-1}), and was monospecific. A stock culture was made for each algal species and incubated with ^{14}C-bicarbonate overnight. Each stock culture was diluted to the following concentrations relative to the original: 100%, 75%, 50%, 37.5%, 25%, 18.75%, 12.5%, 6.25%, and 3.125%. The initial specific concentration of label was determined for each algal dilution (DPM_{algae}). Clams of similar size were collected (n = 72, mean length = 11.7 mm ± 1.0 mm SD, mean wet weight = 323 mg ± 82 mg SD). Each clam was offered 24 ml of algae in a sterile 50-ml centrifuge tube. After 1 h, the clam was harvested, rinsed with 1% HCl, and placed in 0.3 ml of Soluene tissue solubilizer for 24 h. Samples were counted by liquid scintillation spectrophotometry in 20 ml Insta-Gel (DPM_{clam}). The grazing rate fraction (F) was calculated by the following formula:

$$F = DPM_{clam}/(DPM_{algae} \times \text{Incubation Time}) \quad (1)$$

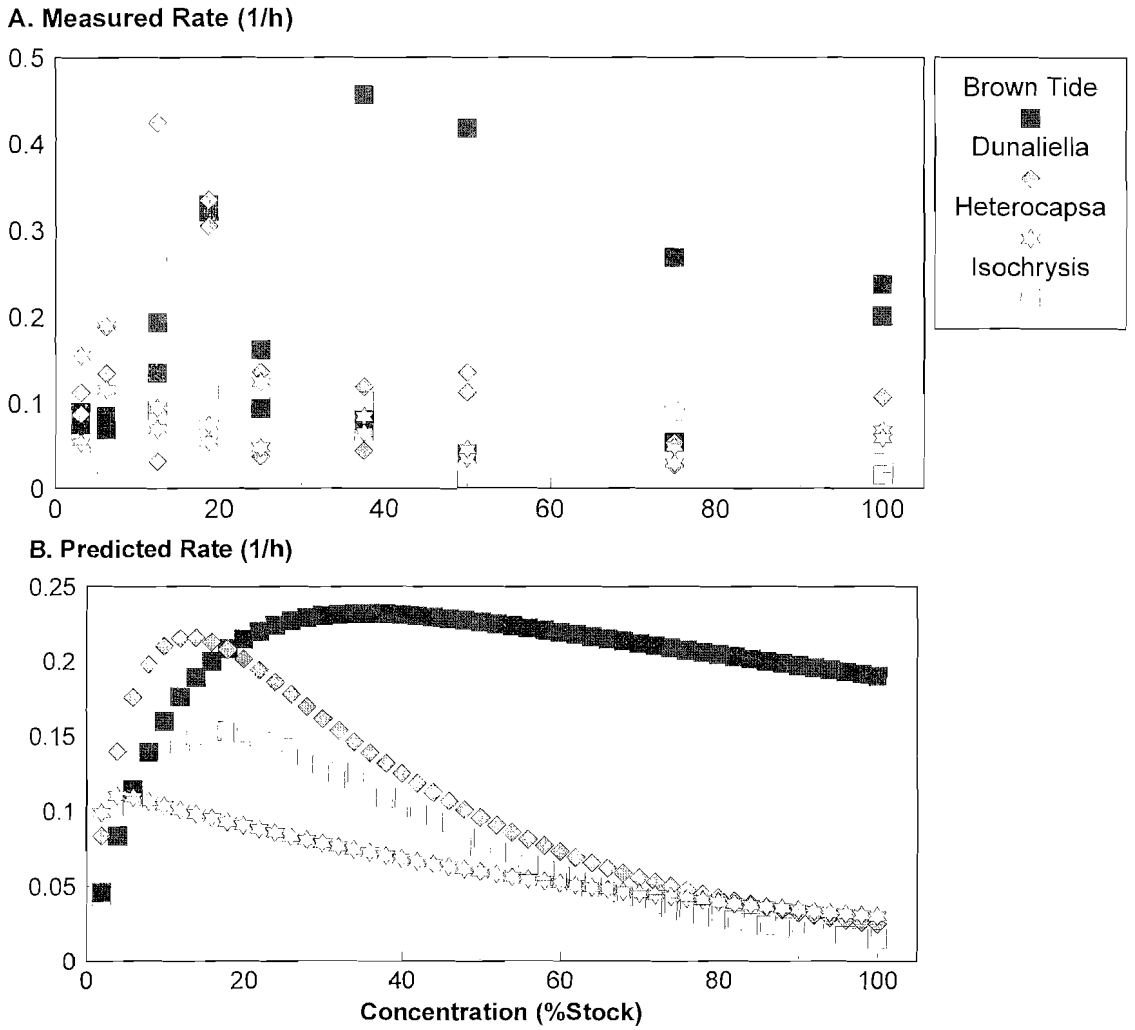

Figure 3. Grazing rate, F (h^{-1}), versus dilutions of stock cultures (% dilution of stock culture). A. Measured grazing rates for all four algal species. B. Predicted grazing rates by fitting raw data to the inhibition model.

The units of the grazing rate fraction are in h^{-1}. The feeding rates were normalized in various ways. F was multiplied by the number of cells offered to calculate feeding as cells $\cdot$ h^{-1} (I_{cell}):

$$I_{cell} = F \times \text{cell concentration} \times 24 \quad (2)$$

This number was multiplied by the cell carbon content to calculate biomass grazed per h as $\mu g\ C \cdot h^{-1}$ (I_C):

$$I_C = I_{cell} \times (\mu g\ C \cdot cell^{-1}) \quad (3)$$

The clearance rate (I_{clear}) was calculated as the volume of water swept clear of cells per unit time ($ml \cdot h^{-1}$):

$$I_{clear} = I_{cell}/\text{cell concentration} \quad (4)$$

The grazing rate data (F, I_{cell}, I_C, or I_{clear}) were fitted to a feeding rate inhibition model. The model assumes that grazing (I) increases exponentially as a function (k) of food concentration (cells or C) to some maximal value (I_m), and at high food concentrations the maximal value of feeding is inhibited as an exponential function (d):

$$I = I_m (1 - \exp^{(-k \times \text{concentration})}) \exp^{(-d \times \text{concentration}/I_m)} \quad (5)$$

The second experiment was performed June 2, 1992. The brown tide was harvested from the field (0.666×10^6 cells $\cdot$ ml^{-1}), and was monospecific. A stock culture was made for each algal species and incubated with ^{14}C-bicarbonate overnight, and the initial specific concentration of label was determined for each algal stock (DPM_{algae}). Clams of similar size were collected (n = 36, mean length = 7.4 mm ± 0.6 mm SD, mean wet weight = 374 mg ± 63 mg SD). Each clam was offered 24 ml of algae in a sterile 50-ml centrifuge tube. After 2 h, the clams were moved to 10 ml of an unlabeled culture of *Thalassiosira* and allowed to feed and depurate label for 2 h. There were 9 replicates for each algal treatment. At the end of the incubation, the clams were harvested, feces collected by filtration, and the culture media retained to trap respired $^{14}CO_2$. The media were acidified with 0.1 ml of 3M HCl to convert bicarbonate to carbon dioxide, then the carbon dioxide was trapped on a strip of filter paper that was impregnated with 0.15 ml of phenylethylamine (Hobbie and Crawford 1969). All sample types were counted by liquid scintillation spectrophotometry in 20 ml Insta-Gel. Total label uptake is calculated as the sum of the label in all three compartments:

$$DPM_{total} = DPM_{clam} + DPM_{feces} + DPM_{respired} \quad (6)$$

The percentage of the label in each compartment is calculated.

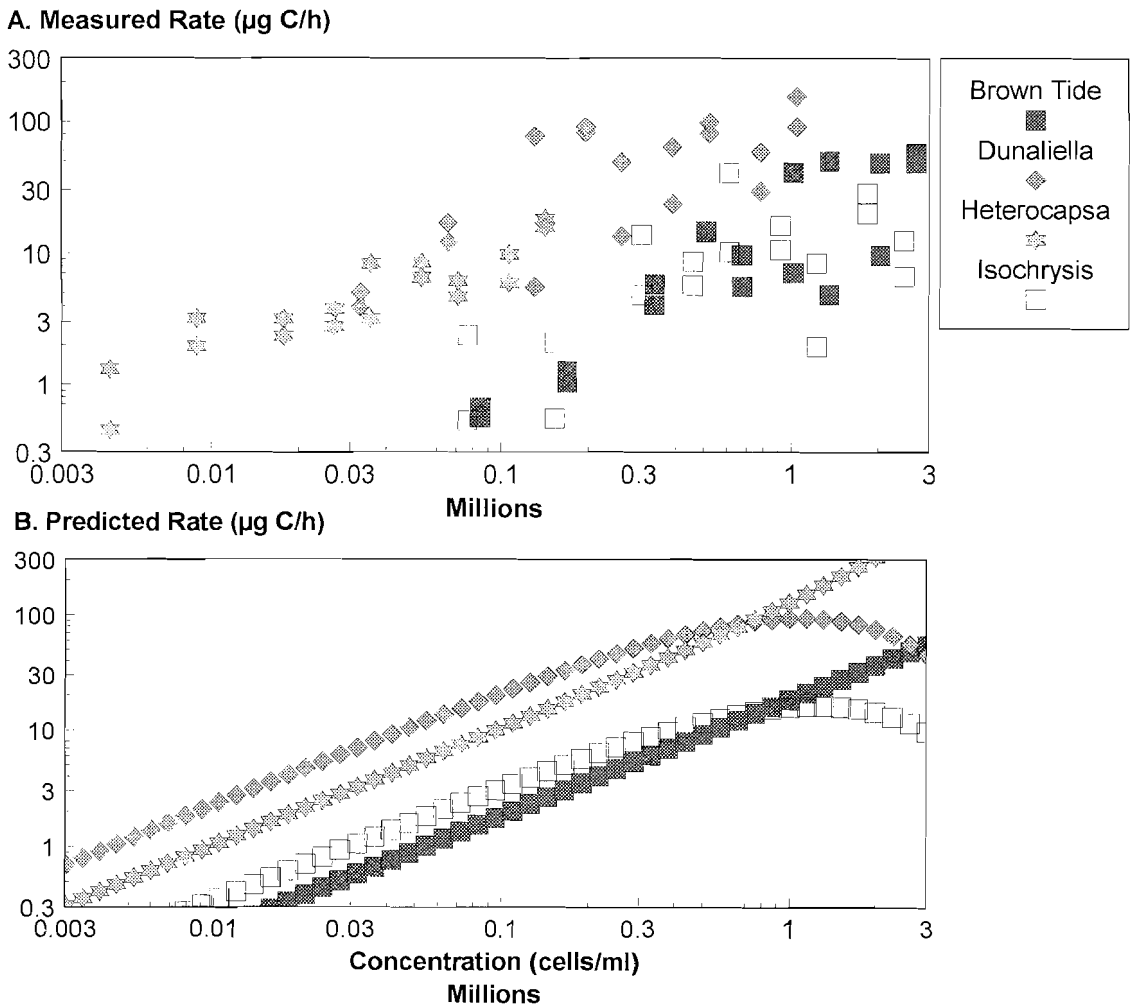

Figure 4. Carbon consumption rate, I_C ($\mu g\ C \cdot h^{-1}$), versus cell concentrations (10^6 cells $\cdot$ ml^{-1}). A. Measured grazing rates for all four algal species. B. Predicted grazing rates by fitting raw data to the inhibition model.

Assimilation of the label is calculated as the sum of incorporated and respired label:

$$\%\text{assimilation} = (\text{DPM}_{\text{clam}} + \text{DPM}_{\text{respired}})/\text{DPM}_{\text{total}} \quad (7)$$

RESULTS

In the Baffin Bay-Laguna Madre ecosystem, *Mulinia lateralis* usually recruits in the spring and has low densities during other seasons. In 1989, before the bloom, populations were dense (Fig. 2A), and there was a large spectrum of different sized individuals (Fig. 2B). During the years 1990 and 1991, when the brown tide bloom was at its greatest extent, population densities decreased to near extinction. The spring abundance peaks were very low, indicating a poor recruitment year. Large members of the population (>10.5 mm) were lost. When the population rebounded during 1992, large sized organisms were again present (Fig. 2B).

Feeding rates (equations 1–4), as a function of algal concentration, were measured in the first experiment (Figs. 3–7). These rates were fitted to the inhibition model (equation 5) and estimates for the three parameters were calculated (Table 2). The grazing rate fraction, F, increased for all four algal species to concentrations of stock culture of about 20–35%, and then declined (Fig. 3A). When fitted to the inhibition model, it appeared that maximal grazing rates were reached at the concentrations corresponding to 35% of the stock solution for brown tide, and 20% for two of the algal species: *Dunaliella* and *Isochrysis* (Fig. 3B). Grazing rates on *Heterocapsa* are best at the lowest concentrations (about 5% of stock). Surprisingly, inhibition of grazing rates at high stock culture concentrations was the least for brown tide. The stock cultures were started at very different densities (Table 1).

Grazing rates are presented in four other ways. The biomass consumed (I_C) and clearance (I_{clear}) rates were plotted versus the concentration of cells offered (cells · ml^{-1}) and the biomass offered (μg C · ml^{-1}) (Figs. 4–7). These rates and concentrations varied over several orders of magnitude, so are shown on logarithmic scales. The number of cells consumed (I_{cell}) generally had the same shaped curves as the biomass consumed (I_C), so are not shown. Parameters fit to all grazing models are shown in Table 2.

Biomass consumed (I_C) varied over four orders of magnitude from about 0.4 to 150 ng C · h^{-1} (Fig. 4A). Consumption rates increased with cell concentration offered (Fig. 4A). Inhibition (d) at the cell concentrations measured is obvious for *Dunaliella* and *Isochrysis* (Fig. 4B). Initial uptake rates (k) are very different for all four species. Maximal grazing rates (I_m) were highest for *Du-*

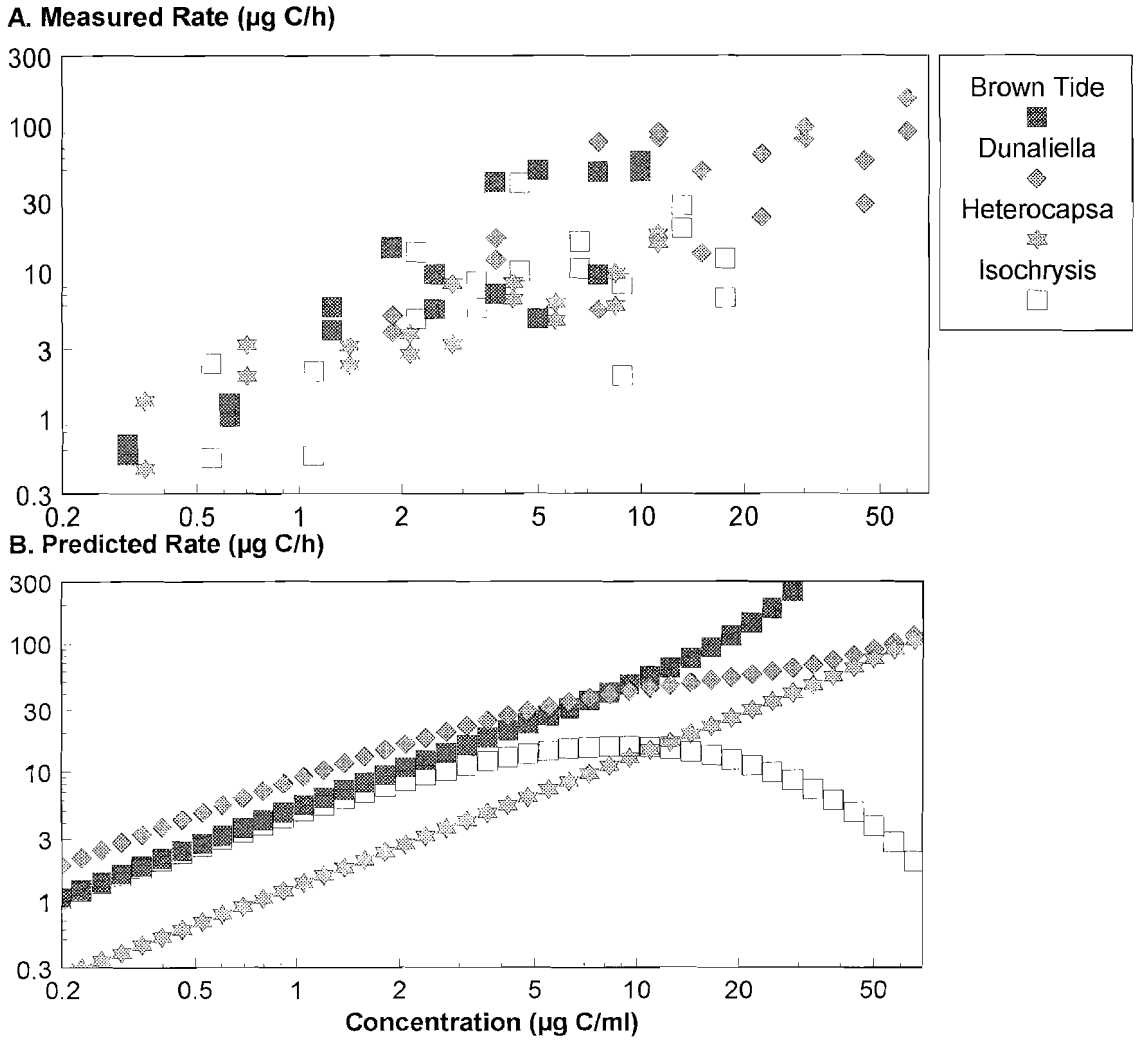

Figure 5. Carbon consumption rate, I_C (μg C · h^{-1}), versus carbon concentrations (μg C · ml^{-1}). A. Measured grazing rates for all four algal species. B. Predicted grazing rates by fitting raw data to the inhibition model.

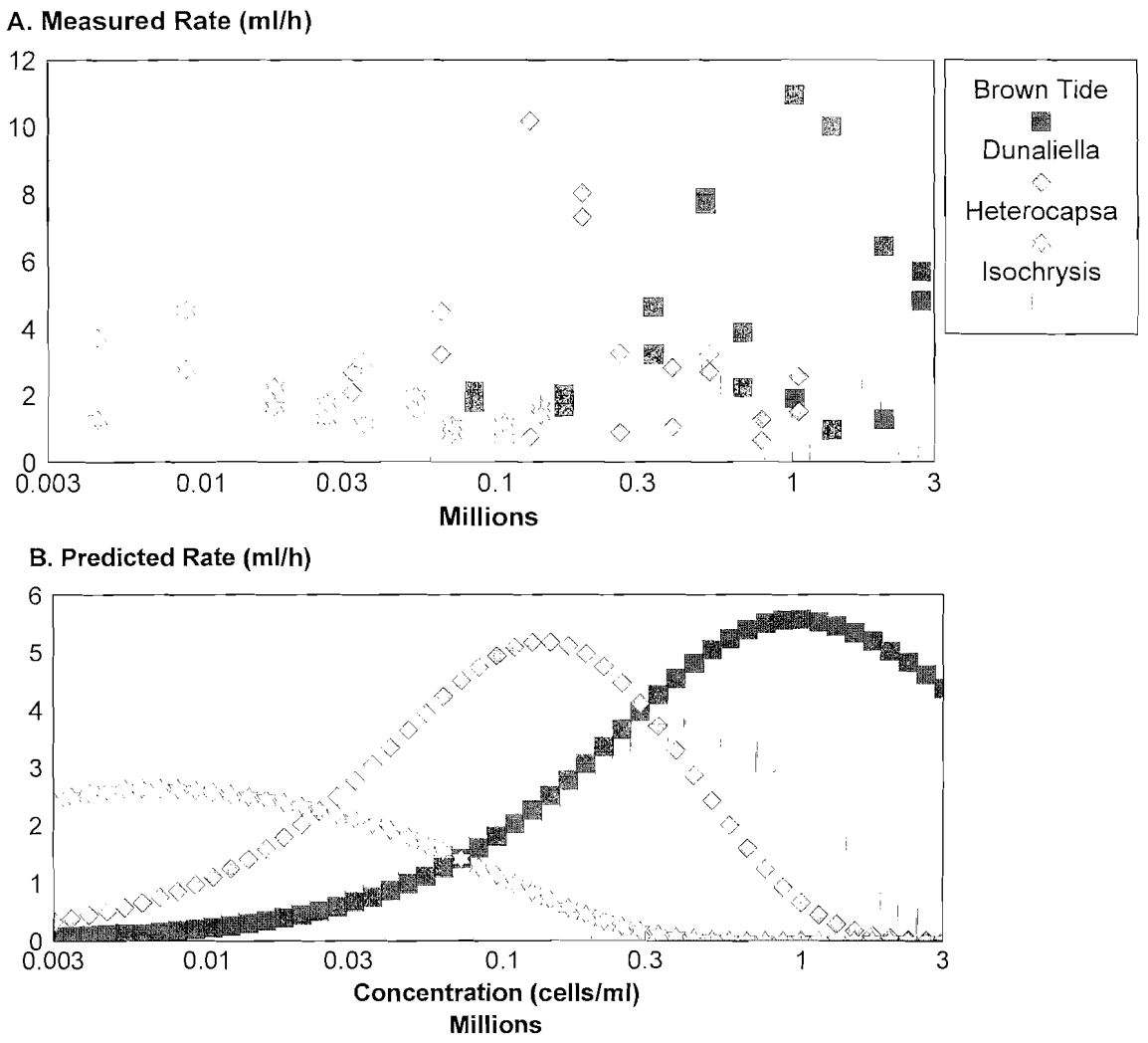

Figure 6. Clearance rate, I_{clear} (ml · h^{-1}), versus cell concentrations (10^6 cells · ml^{-1}). A. Measured grazing rates for all four algal species. B. Predicted grazing rates by fitting raw data to the inhibition model.

naliella (Fig. 4A), but the simulation indicates *Heterocapsa* also would have high maximal rates at high cell concentrations (Fig. 4B).

The different sizes of the algae means that different amounts of carbon were offered in each experiment (Table 1). This can be corrected for by presenting grazing rates versus the concentration of carbon offered (μg C · ml^{-1}) (Fig. 5A). Again, inhibition (*d*) at the carbon concentrations measured were obvious only for *Isochrysis* and to a lesser extent *Dunaliella* (Fig. 5B). Maximal grazing rates (I_m) were highest for brown tide, *Heterocapsa,* and *Dunaliella*. Initial uptake rates (*k*) were similar for three species: brown tide, *Dunaliella* and *Isochrysis,* which were higher than the rate for *Heterocapsa* (Fig. 5B).

Clearance rates (I_{clear}) generally had different shaped curves than the feeding rate curves. Clearance rates generally decreased with increased food offered. Peak feeding rates (I_m) occurred at different cell concentrations for all four species of algae (Figs. 6A and 6B). Inhibition (*d*) was high for *Dunaliella* and *Isochrysis,* but low for brown tide. Initial clearance rates (*k*) were highest for *Heterocapsa* and *Dunaliella*.

The shapes of the curves were similar when clearance rate is plotted against biomass offered (Fig. 7A). Inhibition (*d*) for all algal species was greatest for *Isochrysis* and *Heterocapsa* (Fig. 7B). Maximal clearance rates (K_m) were greatest for brown tide and *Dunaliella*. Initial clearance rates (*k*) were similar for all species.

The fate of algal carbon consumed was determined in the second experiment (Table 3). In general, assimilation rates are high, but this may be due to the short depuration time (2 h). Similar assimilation, respiration and defecation rates were found for brown tide, *Dunaliella,* and *Isochrysis*. *Heterocapsa* had the lowest assimilation rate, and highest defecation rate, indicating that this alga was not being utilized as efficiently as the other species.

DISCUSSION

Mulinia lateralis, of the family Mactridae, is an extremely hardy species, ranging from Prince Edward Island, Canada to Yucatan, Mexico and in salinities from 5 ppt to 80 ppt (Parker 1975). It is considered an opportunist, because it can colonize rapidly after a disturbance event such as dredging or heavy rain (Flint and Younk 1983, Flint et al. 1981). It is abundant in the low salinity zones of Gulf coast bays (Harper 1973, Montagna and Kalke 1992). In the current study area, the Baffin Bay-Laguna

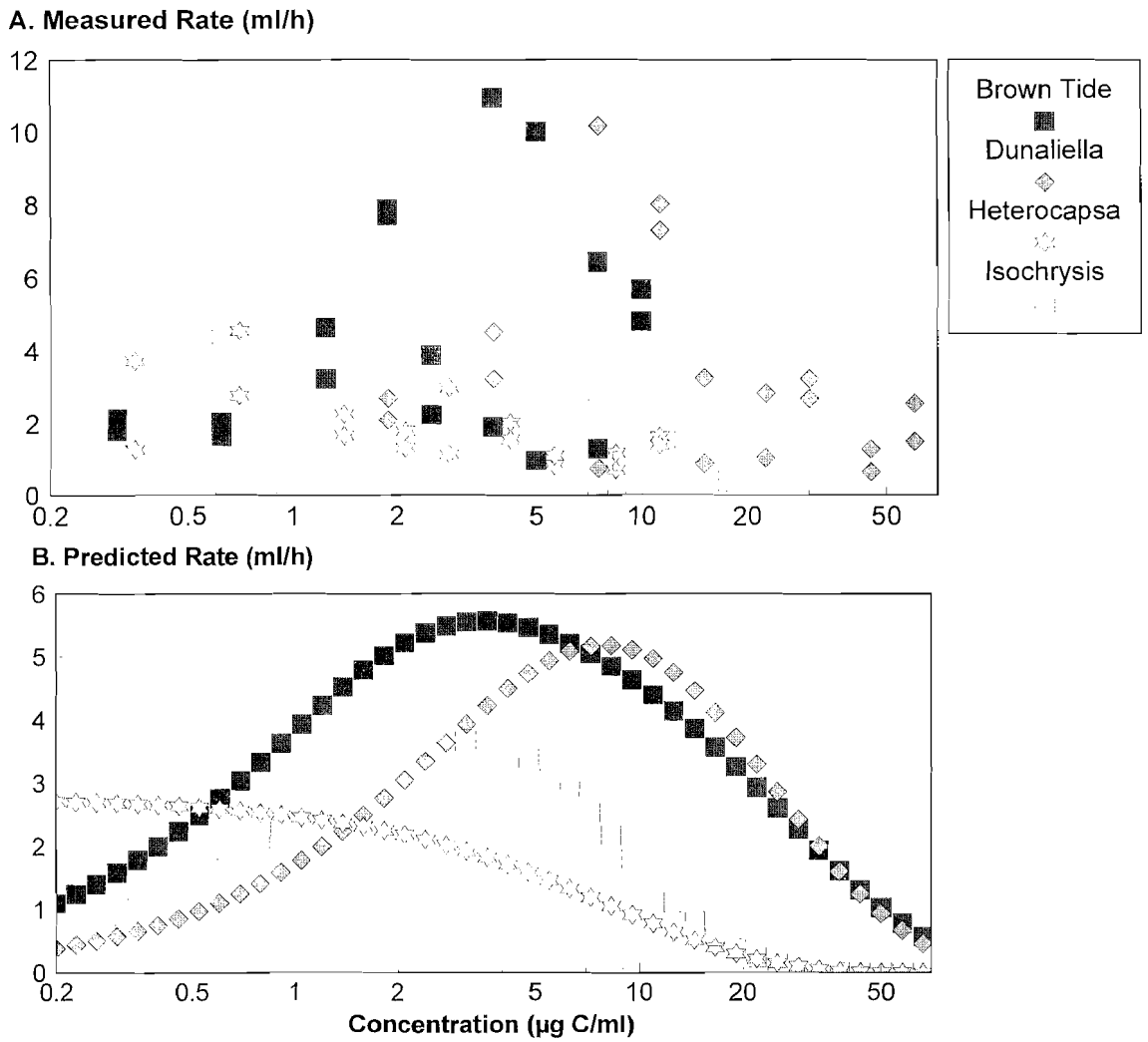

Figure 7. Clearance rate, I_{clear} (ml · h^{-1}), versus carbon concentrations (µg C · ml^{-1}). A. Measured grazing rates for all four algal species. B. Predicted grazing rates by fitting raw data to the inhibition model.

Madre ecosystem (particularly Alazan Bay), *M. lateralis* is the most abundant and widespread mollusk (Martin 1979, Cornelius 1984).

Mulinia lateralis spawning appears greatest in the spring in Baffin Bay and Laguna Madre (Fig. 2). However, it can have a continuous period of setting from a single spawning cycle from May through November in the Tred Avon River, Maryland and Chesapeake Bay (Shaw 1965, Holland et al. 1977). In Alazan Bay, Texas, Cornelius (1984) observed juveniles in all months except December, and Poff (1973) observed year-round spawning in Trinity Bay on the northern Texas coast. In San Antonio Bay, on the Central Texas coast, *Mulinia* population peaks occurred predominantly between January and April from 1987 through 1992 (Montagna unpublished data). It has a very short generation time and is capable of successfully spawning at 3 mm in length, which is approximately 60-days old (Calabrese 1969a). Embryo survival and development occurs over a wide range of salinity and temperature ranges. *Mulinia* develop into normal larvae throughout the salinity range of 15 to 35 ppt and the temperature range of 10 to 30°C (Calabrese 1969b).

Mulinia is an important food item for bottom feeding organisms, e.g., the black drum (Pearson 1929, Breuer 1957, Simmons and Breuer 1962, Martin 1979) and to the greater and lesser scaup ducks (Cronan 1957). Large rafts of scaup ducks were observed in upper San Antonio Bay, Texas in November 1988 corresponding to densities of 15,000 · m^{-2} of *Mulinia lateralis* (Kalke personal observation).

These three factors (wide-spread distribution and high densities, rapid population growth, and importance as a food source to fish and wildlife) indicate that *Mulinia* is an important species in the Laguna Madre-Baffin Bay ecosystem. There was great concern about the integrity of the ecosystem when the brown tide occurred, because brown tides may have negative effects on shellfish.

The brown tide bloom was most intense for two years, 1990–1991. During this time cell concentrations averaged 1.9 × 10^6 · ml^{-1} (Stockwell et al. 1993). During these two years, *Mulinia* populations suffered from very poor recruitment (Fig. 2). In both these years, there was a very small spring peak. This could be a coincidence, but the occurrence of brown tide occurred with the reduction of *Mulinia* populations. *Mulinia* populations declined during the last quarter of 1989 prior to the brown tide. The decline in late summer and fall appears to be a normal cycle that occurred in all four years. The low density in late 1989 is consistent with the trends found in earlier studies of Cornelius (1984). Although *Mulinia* ap-

TABLE 2.

Parameters fitted for grazing rates using the inhibition model. The variables are designated as Y versus X.

Variables	Alga	R^2	I_m	k	d
$F \times$ %stock	Brown tide	74%	2.75×10^{-1}	9.21×10^{-2}	1.02×10^{-3}
	Isochrysis galbana	63%	4.51×10^{-1}	5.49×10^{-2}	1.54×10^{-2}
	Dunaliella tertiolecta	73%	3.70×10^{-1}	1.36×10^{-1}	1.00×10^{-2}
	Heterocapsa pygmeae	85%	1.19×10^{-1}	9.66×10^{-1}	1.63×10^{-3}
$F_{cell} \times$ cells $\cdot$ ml^{-1}	Brown tide	79%	4.55×10^{8}	1.10×10^{-8}	2.22×10^{-7}
	Isochrysis galbana	65%	3.67×10^{6}	1.47×10^{-6}	1.03
	Dunaliella tertiolecta	80%	6.99×10^{5}	1.38×10^{-5}	-6.41×10^{-1}
	Heterocapsa pygmeae	91%	1.17×10^{9}	1.14×10^{-9}	1.02×10^{-9}
$F_{cell} \times \mu$g C $\cdot$ ml^{-1}	Brown tide	79%	6.54×10^{8}	2.07×10^{-3}	1.00×10^{-8}
	Isochrysis galbana	65%	3.67×10^{6}	2.04×10^{-1}	1.43×10^{5}
	Dunaliella tertiolecta	74%	8.00×10^{6}	5.41×10^{-3}	1.81×10^{4}
	Heterocapsapygmeae	91%	1.31×10^{9}	1.28×10^{-5}	1.10×10^{-8}
$F_C \times$ cells $\cdot$ ml^{-1}	Brown tide	79%	2.31×10^{6}	7.97×10^{-12}	1.59×10^{-2}
	Isochrysis galbana	64%	1.05×10^{6}	3.30×10^{-11}	8.25×10^{-1}
	Dunaliella tertiolecta	76%	9.48×10^{5}	2.44×10^{-10}	8.63×10^{-1}
	Heterocapsa pygmeae	91%	1.58×10^{6}	6.52×10^{-11}	-3.41×10^{-1}
$F_C \times \mu$g C $\cdot$ ml^{-1}	Brown tide	79%	2.56×10^{1}	2.10×10^{-1}	-2.03
	Isochrysis galbana	65%	2.64×10^{1}	2.04×10^{-1}	1.03
	Dunaliella tertiolecta	80%	4.03×10^{1}	2.40×10^{-1}	-6.41×10^{-1}
	Heterocapsa pygmeae	91%	1.08×10^{2}	1.20×10^{-2}	-9.37×10^{-1}
$F_{clear} \times$ cells $\cdot$ ml^{-1}	Brown tide	74%	6.60	3.40×10^{-6}	9.03×10^{-7}
	Isochrysis galbana	63%	1.09×10^{1}	2.23×10^{-6}	1.51×10^{-5}
	Dunaliella tertiolecta	73%	8.89	1.33×10^{-5}	2.31×10^{-5}
	Heterocapsa pygmeae	85%	2.85	6.79×10^{-4}	2.75×10^{-5}
$F_{clear} \times \mu$g C $\cdot$ ml^{-1}	Brown tide	74%	6.59	9.22×10^{-1}	2.44×10^{-1}
	Isochrysis galbana	63%	9.00	3.73×10^{-1}	1.49
	Dunaliella tertiolecta	73%	8.88	2.26×10^{-1}	3.99×10^{-1}
	Heterocapsa pygmeae	85%	2.77	9.77×10^{2}	3.22×10^{-1}

pears to have a cyclical life cycle in south Texas estuaries, it seems certain that recruitment and densities were unusually low in 1990–1991 during the peak of the brown tide bloom.

Mulinia is known to have cyclical life cycles, so it is difficult to prove that low abundances are directly related to the brown tide. Population declines could have been caused by the brown tide in at least three different ways: reproductive failure, feeding inhibition, or a toxic effect. Each of these events has been observed numerous times in shellfish in coincidence with other brown tide blooms on the east coast of the U.S. (Tracey 1988, Tracey et al. 1988, Gainey and Shumway 1991). The main goal of this study was to determine if feeding was affected adversely. The test is to determine if inhibition of grazing rates occurred at high densities as indicated by high values of the parameter d. Two other parameters of interest are the initial grazing rate (k) and the maximal grazing rate (I_m). Finally, food must be assimilated to be utilized.

The main approach in this study was comparative; therefore, the major assumption was that if feeding on brown tide was similar to that of other species, then there was no adverse feeding effect. Since the other algal species are kept in culture at the University of Texas Marine Science Institute to provide feed for animal cultures, this is not an unreasonable assumption.

There are many different ways of calculating a feeding rate and normalizing it to comparable units. Each different calculation and unitization would yield different interpretations. The basic measurement was the percent of label removed at each dilution level of a stock culture (Fig. 3). The concentrations of the stock cultures were at different levels of peak densities. When the dilutions were made, the result was experiments at differing concentrations for each species. The experiment was designed to determine how feeding varied as a function of food concentration. Dilutions were normalized to cell concentration to elucidate differences in cell concentration. Cell sizes among the four algae also differed. Although there are interspecific differences, generally bivalves retain larger particles more efficiently than smaller particles (Mohlenberg and Riisgard 1978). Differences in sizes of cells were ac-

TABLE 3.

Fate of algal ^{14}C in the second experiment. Average (±standard deviation) for $n = 9$.

Species	Incorporation	Respiration	Defecation	Assimilation
Brown tide	68% (±8)	8% (±5)	24% (±6)	78%
Isochrysis galbana	69% (±10)	11% (±3)	20% (±9)	82%
Dunaliella tertiolecta	64% (±10)	13% (±4)	23% (±7)	79%
Heterocapsa pygmeae	59% (±11)	11% (±3)	20% (±10)	73%

TABLE 4.

Summary of results of the feeding experiments.

Variables	I_m	k	d
$F \times$ %stock	Bt > (Du = Is) > He	(Du = He) > (Bt = Is)	(Du = Is) > He > Bt
$F_C \times$ cells · ml^{-1}	(Du = He) > (Bt = Is)	Du > He > Is > Bt	Is > Du > (Bt = He)
$F_C \times$ µg C · ml^{-1}	Bt > (Du = He) > Is	Du > (Bt = Is) > He	Is > Du > (Bt = He)
$F_{clear} \times$ cells · ml^{-1}	(Du = He) > (Bt = Is)	He > Du > (Bt = Is)	Is > (Du = He) > Bt
$F_{clear} \times$ µg C · ml^{-1}	(Bt = Du) > He > Is	He > Bt > (Is = Du)	Is > (Du = He) > Bt

Variables are designated as Y versus X in Figures 3–7 respectively.
Abbreviations used: Bt = brown tide, Du = *Dunaliella*, Is = *Isochrysis*, and He = *Heterocapsa*.

counted for by normalizing the ingestion rates by cell-carbon content (I_C) (Figs. 4 and 5). Generally, the functional response is that feeding rates increase with increased food concentrations (Figs. 4 and 5). Clearance rates are the volumes of water swept clear, and, in general, this rate decreases as the food concentration increases (Figs. 6 and 7).

The strongest inhibition of grazing rates is observed when the fraction removed (F) is plotted against the dilution series (% stock) (Fig. 3). The least amount of inhibition occurred with brown tide. This may be partially due to culture artifacts. At the time of this study, we had not learned how to culture the brown tide, therefore field populations were collected and used in the feeding experiments. The three cultured species had strong inhibition in experiments up to 20% of the stock solution and the brown tide sample showed only minor inhibition at full strength samples. This could be due to the build up of algal metabolites in the cultures, which are known to inhibit bivalve feeding (Ward and Targett 1989).

The cell density in the brown tide samples was high enough to discover the inhibition response. Tracey (1988) did not see feeding rate inhibition in *Mytilus edulis* until brown tide concentrations were at 10^5 cells · ml^{-1}. The concentrations of brown tide offered in this study were up to 2×10^6 (Table 1, Figs. 4 and 6).

Results appear to be different among the different ways to plot the data (Table 4), but some trends were consistent. *Isochrysis* was the only alga to have its feeding rate consistently inhibited by high food concentrations (Table 4). The only alga to have a low assimilation rate was *Heterocapsa* (Table 3). Brown tide never had the lowest maximal feeding rates (I_m) or initial rates (k) (Table 4). In all cases, brown tide did not appear to negatively affect feeding by *Mulinia*.

Mulinia appears to have the potential to control phytoplankton blooms. Clearance rates were near 10 ml · h^{-1} at peak brown tide densities of 10^6 cell · l^{-1} (Fig. 6A), thus at prebloom densities (800 · m^2, Fig. 2A) *Mulinia* could clear 8 l · h^{-1}. The average water column depth in the Baffin Bay-Laguna Madre ecosystem is 1.2 m (TDWR 1983); therefore, the clams associated with each square meter of sediment could clear the overlying water column in 150 h or about 6–7 days. Microzooplankton were common before the brown tide, but also nearly disappeared. Microzooplankton consumption decreased from 95% of the phytoplankton production to 5% consumed per day (Buskey and Stockwell 1993). With the loss of both the microzooplankton and the bottom filter feeding animals, there was almost no filtering capacity in the bay during the peak of the brown tide bloom, between 1990 and 1991.

Although we did not find negative feeding effects on adults, it is possible that there would be negative effects on juveniles or larvae. The east coast brown tide did cause negative feeding and locomotory behavior on scallop larvae (Gallagher and Stoecker 1989). We used individuals (6–12 mm) in the middle-size range (Fig. 2) in this study.

If feeding inhibition did not occur, then something else may have caused the population declines. It is well known that *Mulinia* population sizes have large natural variability, but brown tides on the east coast have been toxic to bivalves and have caused declines in reproductive potential. It is not known if these kinds of effects occur with *Mulinia*. Another possibility is increased predation pressure. When *Mulinia* populations declined in Texas, we were most concerned about how this would effect the food web that supported the black drum fishery. The black drum population has been increasing over the last five years, and reached 20-year record levels during the brown tide (Larry McEchron, Texas Parks and Wildlife Department, personal communication). It is possible that *Mulinia* populations were wiped out by the high populations of the predatory black drum. If this is true, there might have been a trophic cascade that led to conditions favorable for a bloom. In a trophic cascade, the predator reduced populations of the herbivore, which, in turn, allowed the primary producer populations to bloom uncontrollably. Since *Mulinia* feeds well on the brown tide alga, a trophic cascade is a plausible hypothesis for (at least partially) explaining the mollusk population declines and the occurrence of the bloom.

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