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Effects of the Texas (USA) 'brown tide' alga on planktonic grazers

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ABSTRACT: The Laguna Madre of south Texas, USA, has experienced a dense, nearly monospecific phytoplankton bloom since January 1990 referred to as the 'brown tide'. Zooplankton populations declined following the outbreak of the bloom and planktonic grazers have failed to bring the bloom under control. Laboratory studies of microzooplankton grazers feeding on brown tide indicate that this alga is nutritionally inadequate to support the growth of several species including the ciliate *Strombidinopsis* sp., the heterotrophic dinoflagellate *Noctiluca scintillans* or the rotifer *Brachionus plicatilus*. The presence of brown tide also inhibits the growth of some species (*Noctiluca scintillans*, *Brachionus plicatilus*) even when other nutritionally adequate food species are present. Some species that grow on brown tide grow best at low cell concentrations, including the ciliates *Fabrea salina* and *Euplotes* sp.; as algal densities increase, growth rates decrease. Laboratory studies of egg release of adult female *Acartia tonsa* indicate that the brown tide is a poor food for these copepods; egg release rates are similar to those of starved copepods and less than those of copepods fed other similarly sized phytoplankton. The brown tide is toxic to early naupliar stages of *Acartia tonsa* but not to adults. The brown tide alga appears to be toxic to some species of planktonic grazers and a poor food for others; the reduced grazing by the planktonic community may be a contributing factor to the persistence of this bloom.

KEY WORDS: Harmful algal blooms · Zooplankton · Brown tides

INTRODUCTION

A dense algal bloom referred to as the 'brown tide' has affected regions of the south Texas (USA) coast centered around the Laguna Madre since January 1990. This persistent algal bloom has reduced the penetration of sunlight, shading out seagrass beds and disrupting sport fishing activities. Having now persisted for over 5 yr, this is one of the longest phytoplankton blooms that has been scientifically documented. The probable causes contributing to the initiation of this bloom have been well documented; both a period of extended drought, causing abnormally high salinities, and a severe freeze in December 1989 caused an abrupt decline in the populations of both planktonic and benthic phytoplankton grazers (Buskey & Stockwell 1993, Montagna et al. 1993). The initiation of other major phytoplankton blooms have also been reported to develop as the result of the reduction or absence of zooplankton grazing (Granéli et al. 1989, Smayda & Villareal 1989). An extensive fish kill and die-off of benthic organisms associated with the freeze released a pulse of nutrients to fuel the initial bloom (Buskey & Stockwell 1993, DeYoe & Suttle 1994). The bloom has persisted without interruption since its initiation. The most important unanswered question is: why has the brown tide persisted for so long?

Phytoplankton bloom formation requires that growth of the algal species exceed the sum of all loss processes, including losses to sinking, mixing, advection, disease, grazing and other sources of mortality. The Laguna Madre is a shallow system with little water exchange with the Gulf of Mexico, so losses of phytoplankton due to physical effects of sinking, mixing and advection are extremely small. Before the brown tide bloom began, phytoplankton populations were held at low biomass due to grazing by zooplankton, which balanced daily phytoplankton production (Buskey & Stockwell 1993). Populations of the copepod *Acartia tonsa* appeared to be food limited, since enrichment studies showed increases in egg production rates with the addition of cultured phytoplankton to natural

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plankton assemblages (Buskey et al. unpubl.). After the brown tide began, microzooplankton community grazing rates decreased and copepod egg release rates measured in field incubations were reduced (Buskey & Stockwell 1993). Field studies indicated that populations of microzooplankton and mesozooplankton declined after the brown tide began (Buskey & Stockwell 1993). These changes in grazer populations during the brown tide were suspected to be due to the possibility that the brown tide was either a poor food for zooplankton or perhaps even toxic to some species. Disruption of zooplanktonic grazers on the brown tide may help explain the unusual persistence of this bloom.

The organism responsible for this bloom is a small (4 to 5 µm diameter) phytoplankton species which has not yet been formally classified. The Texas 'brown tide' alga is devoid of obvious diagnostic features, but examination of ultrastructure by transmission electron microscopy and of photosynthetic pigments by high performance liquid chromatography reveal that it is similar in morphology and pigments to *Aureococcus anophagefferens* (Sieburth et al. 1988, Stockwell et al. 1993), which has been responsible for recurrent blooms in Narragansett Bay and Long Island Sound (NE USA) since 1985 (Cosper et al. 1987). Recent molecular data indicate that both species belong to a newly recognized class *Pelagophyceae* (Anderson et al. 1993) but the 2 species appear to differ enough from one another to warrant placing them in separate genera (DeYoe et al. 1995). Densities of this alga in nature have reached as high as 5×10^6 cells ml^{-1}, but typical densities are 0.2 to 2×10^6 ml^{-1}.

In this study we investigate the suitability of the Texas brown tide alga as a food to support the growth of several species of protozoa and a rotifer. We also measure egg production rates of *Acartia tonsa* in the laboratory and survival of *A. tonsa* nauplii fed the brown tide.

MATERIALS AND METHODS

The ciliates and heterotrophic dinoflagellates used in this study were collected from the University of Texas Marine Science Institute's pier in the channel between the Gulf of Mexico and Aransas Bay, in Port Aransas, Texas. Samples were collected with a 30 cm diameter, 20 µm mesh net allowed to stream with the tide. These plankton samples were then screened through a 153 µm mesh sieve to remove mesozooplankton. Aliquots of these samples were then incubated in 1 l polycarbonate bottles and enriched with mixtures of cultured phytoplankton, including *Dunaliella tertiolecta*, *Heterocapsa niei*, *Isochrysis galbana*, *Pyrenomonas salina* and the Texas brown tide alga. These enrichments were then placed on a bottle roller rotating at ca 2 rpm and were incubated at 20°C at low light intensities for a period of several days. Enrichments were checked periodically for the growth of ciliates or heterotrophic dinoflagellates. When a species appeared to be growing well on the added phytoplankton species, individual cells were isolated under a stereo microscope and brought into culture. Ciliates brought into culture for this study include *Fabrea salina*, *Strombidinopsis* sp. and *Euplotes* sp. Heterotrophic dinoflagellates cultured for this study include *Oxyrrhis marina* and *Noctiluca scintillans*. Identification of ciliates and heterotrophic dinoflagellates are based on description in Lee et al. (1985). Cultures of the rotifer *Brachionus plicatilus* were acquired from the University of Texas Marine Science Institute's Fisheries and Mariculture Laboratory, and were originally isolated from local waters.

The large heterotrophic dinoflagellate *Noctiluca scintillans* and the copepod *Acartia tonsa* used for egg release and naupliar survival studies were collected using a 0.5 m diameter, 333 µm mesh net, which was allowed to stream with a gentle outgoing tide. The contents of the cod end were immediately diluted into a plastic bucket containing whole seawater. The zooplankton sample was returned to the laboratory and *N. scintillans* or adult female *A. tonsa* were sorted from the sample with a wide bore pipette.

Protozoan stock cultures were maintained in 'ciliate media' (Gifford 1985) in 50 ml tissue culture flasks held within a white PVC plastic cylinder on a bottle roller under the same conditions described for the enrichments. Cultures were fed every 3 to 4 d, and transferred into new media at 1 wk intervals. Cultures were maintained on mixtures of phytoplankton (*Fabrea salina*, *Euplotes* sp. and *Oxyrrhis marina*: *Isochrysis galbana* and brown tide; *Strombidinopsis* sp.: *Isochrysis galbana*, *Pyrenomonas salina* and *Heterocapsa niei*; *Noctiluca scintillans*: *Corethron criophilum*, *Ditylum brightwellii*, *Nitzschia thermalis*, *Thalassiosira* sp.; *Brachionus plicatilus*: *Isochrysis galbana*).

Phytoplankton for these studies were grown in f/2 culture media (Guillard & Ryther 1962), except for the Texas brown tide alga which was grown on ESAW artificial seawater medium (Harrison et al. 1980 as modified by DeYoe & Suttle 1994). Phytoplankton cultures were held in 250 ml polycarbonate flasks at 20°C on a 12:12 L/D cycle at approximately 120 µM photons m^{-2} s^{-1} (photosynthetically available radiation measured with a Biospherical Instruments QSL-100 quantum scalar irradiance meter). Only rapidly growing phytoplankton cultures were used. Phytoplankton cells for elemental analysis were filtered onto precombusted GF/F glass fiber filters, dried at 50°C and combusted in

a Carlo Erba EA 1108 elemental analyzer. The volumes of phytoplankton cells were determined from measurements made at 200× or 400× magnification using a Wild M20 microscope and appropriate geometric formulas. Brown tide concentrations used in these studies ranged from 0.05 to 5 mg C l^{-1} of brown tide, which corresponds to approximately 0.05 to 5×10^5 cells ml^{-1}, which is within the natural range of bloom concentrations.

Specific growth rates of protozoans (except *Noctiluca scintillans*) and rotifers on various concentrations of the brown tide alga and other phytoplankton species were measured by adding 2 or 3 organisms ml^{-1} to 150 ml of ciliate media containing the desired species and concentration of phytoplankton. Triplicate 10 ml samples were collected daily for 4 d. Samples of *Strombidinopsis* sp., *Fabrea salina*, *Euplotes* sp. and *Brachionus plicatilus* were preserved with Lugol's iodine. Samples were settled in Utermöhl chambers and enumerated using an inverted microscope (Olympus IMT-2). Specific growth rates (μ d^{-1}) were calculated from the linear portion of ln(organisms ml^{-1}) regressed against time (results were not used if growth was not exponential over a minimum of 3 d). Growth rates of *N. scintillans* were measured by placing 20 cells in a 50 ml plastic tissue culture flask with known phytoplankton concentrations. Flask were incubated on the bottle roller at 20°C for 3 d and the number of *N. scintillans* at the end of the experiment was counted under a dissecting microscope. Specific growth rates were calculated as:

$$\mu\ (d^{-1}) = 1/t \ln(N_t/N_0)$$

where N_0 and N_t are the observed number of *N. scintillans* at the beginning and end of a time interval t d long. Previous studies (Buskey 1995) have documented that *N. scintillans* maintains exponential growth at these food concentrations over a 3 d interval.

For egg release studies, 10 adult female *Acartia tonsa* were placed in each of ten 1200 ml wide-mouth glass jars, with cultured phytoplankton of a single species at a concentration of 1.5 mg C l^{-1} or 2 species at 1.5 mg C l^{-1} each. This food concentration was chosen because preliminary studies indicated that this was just below the concentration yielding maximum egg release rates for copepods fed diatoms. The jars were then placed on a plankton wheel rotating at ca 2 rpm within a walk-in growth chamber at 20°C on a 12:12 L:D cycle. After 24 h, the copepods were gently collected by pouring the sample through a 153 µm mesh sieve and transferred into fresh seawater containing the same phytoplankton concentration. After another 24 h the contents of the jar was again screened through a 153 µm mesh screen to remove the copepods, and then through a 20 µm mesh screen to collect eggs and nauplii produced over the past 24 h. The number of living *A. tonsa* adult females was counted and the number of eggs produced per adult female per day was calculated.

Newly hatched nauplii of *Acartia tonsa* were obtained by holding adult females within a 153 µm mesh plastic sieve in a large culture dish containing filtered seawater overnight. In the morning the sieve and adult copepods were removed and the eggs produced that night were allowed to hatch. Survival of *A. tonsa* nauplii on various phytoplankton foods was determined by placing a single N1 nauplius in each of 24 wells of a tissue culture plate containing 3 ml of phytoplankton culture at a concentration of 5 mg carbon l^{-1}. Each well was checked daily to monitor the survival of the copepod over a 5 d period. A second naupliar survival experiment was run by placing 50 newly hatched nauplii in a 50 ml tissue culture flask with a known concentration of phytoplankton (2, 3.5 or 5 mg C l^{-1}). These flasks were incubated on bottle rollers as described for protozoan cultures above, and the number of nauplii surviving after 5 d was determined.

RESULTS

Specific growth rates of the ciliate *Strombidinopsis* sp. fed *Pyrenomonas salina* increased with increases in food concentration until a maximum growth rate of 0.96 d^{-1} was achieved at a food concentration of 1 mg C l^{-1} (Fig. 1). When this same species was fed the Texas brown tide alga, all specific growth rates were negative, indicating mortality rather than growth on this food source. Since specific growth (death) rates became more negative as food concentrations of brown tide increased, it appears that the brown tide is toxic to this species.

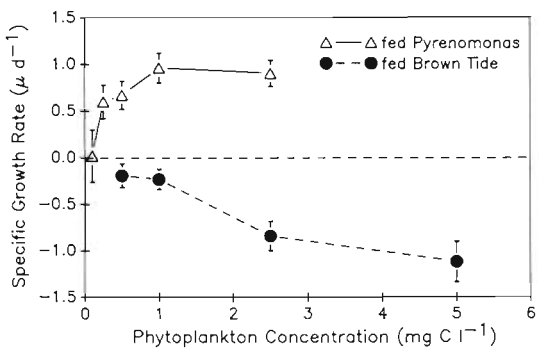

Fig. 1. Specific growth rate (d^{-1}) of the ciliate *Strombidinopsis* sp. on various concentrations of the Texas brown tide alga and on *Pyrenomonas salina*. Error bars represent the standard error of the slope of line for the natural logarithm of the number of cells regressed against time, used to determine specific growth rates

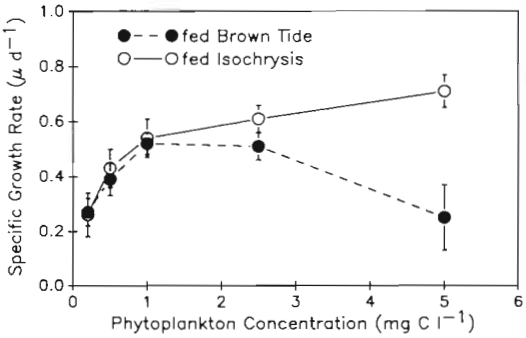

Fig. 2. Specific growth rate (d^{-1}) of the ciliate *Fabrea salina* on various concentrations of the Texas brown tide alga and on *Isochrysis galbana*. Error bars as in Fig. 1

In contrast, the ciliates *Fabrea salina* and *Euplotes* sp. grew well on the brown tide. Maximum specific growth rate for *F. salina* of 0.52 d^{-1} was achieved at 1 mg C l^{-1} of brown tide. However, the numerical response of *F. salina* to various concentrations of the brown tide alga shows a decreasing growth rate at food concentrations above 1 mg C l^{-1}, falling to 0.25 d^{-1} at 5 mg C l^{-1} (Fig. 2). In contrast, *F. salina* fed *Isochrysis galbana* showed a more typical numerical response curve, with growth rate remaining high at higher food concentrations (maximum specific growth rate of 0.71 d^{-1} at 5 mg C l^{-1}.) The ciliate *Euplotes* sp. showed a similar numerical response when fed the brown tide alga. Maximum specific growth rates of 0.5 d^{-1} were observed at a brown tide concentration of 1 mg C l^{-1}, but specific growth rates fell to 0.29 at 5 mg C l^{-1} (Fig. 3). Growth of *Euplotes* sp. was higher when fed *I. galbana* at 2.5 or 5 mg C l^{-1} than when fed similar concentrations of the brown tide.

The Texas brown tide alga did not support the growth of the heterotrophic dinoflagellate *Noctiluca scintillans*. However, there is no evidence that the brown tide alga is highly toxic to *N. scintillans*, since

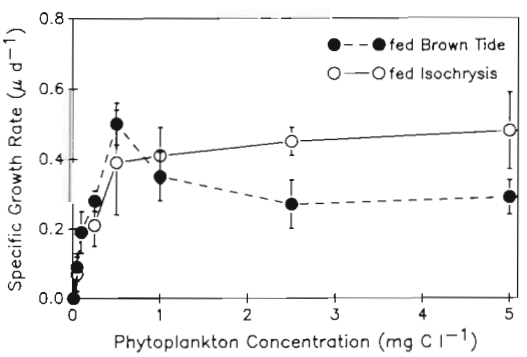

Fig. 3. Specific growth rates (d^{-1}) of the ciliate *Euplotes* sp. on various concentrations of the Texas brown tide alga and on *Isochrysis galbana*. Error bars as in Fig. 1

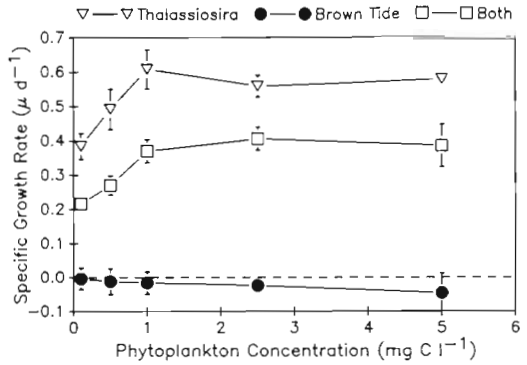

Fig. 4. Specific growth rates (d^{-1}) of the heterotrophic dinoflagellate *Noctiluca scintillans* on various concentrations of the Texas brown tide alga, *Thalassiosira* sp. or equal concentrations of both species (twice the total food concentration). Each point is the mean (±SD) of 3 growth experiments

growth (death) rate was only –0.04 d^{-1} at 5 mg C l^{-1} of brown tide. Specific growth rates of *N. scintillans* on *Thalassiosira* sp. ranged from 0.38 d^{-1} for 0.1 mg C l^{-1} to 0.6 d^{-1} (Fig. 4). When a mixture of *Thalassiosira* sp. and the brown tide alga was offered as food, the specific growth rate ranged from 0.22 to 0.38 d^{-1}. Even though total food concentration was twice as high when equal amounts of brown tide and *Thalassiosira* sp. were offered as food, growth rates were always lower than when *N. scintillans* were offered *Thalassiosira* sp. alone.

The small heterotrophic dinoflagellate *Oxyrrhis marina* did not grow on brown tide at concentrations below 0.1 mg C l^{-1}, but grew well on higher concentrations of this species (Fig. 5). Maximum specific growth rates of 0.55 d^{-1} were observed at a concentration of 5 mg C l^{-1}. However, growth rates of *O. marina* were higher when fed equivalent concentrations of *I. galbana* than when fed the brown tide alga at concentrations below 5 mg C l^{-1} (Fig. 5), with maximum growth on *I. galbana* at 0.5 mg C l^{-1}.

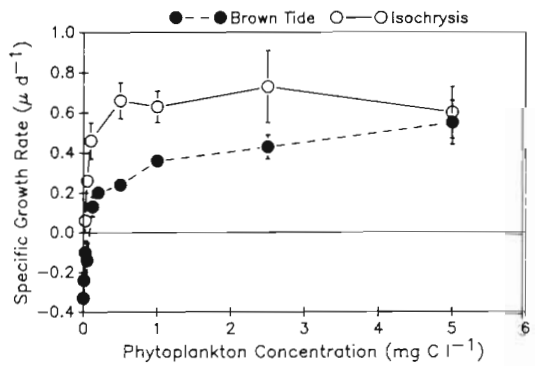

Fig. 5. Specific growth rates (d^{-1}) of the heterotrophic dinoflagellate *Oxyrrhis marina* on the Texas brown tide alga and on *Isochrysis galbana*. Error bars as in Fig. 1

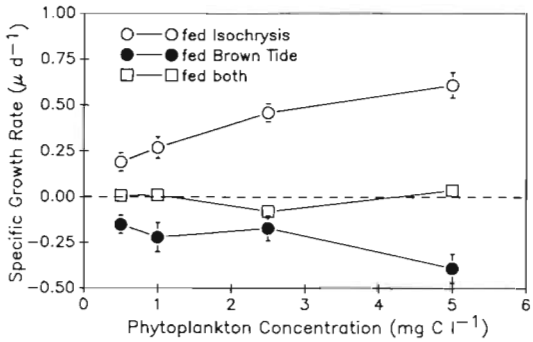

Fig. 6. Specific growth rates (d^{-1}) of the rotifer *Brachionus plicatilus* on the Texas brown tide alga, *Isochrysis galbana* and equal concentrations of each (twice the total food concentration). Error bars as in Fig. 1

The Texas brown tide alga did not support the growth of the rotifer *Brachionus plicatilus* at any food concentration. Specific growth (death) rates were similar to those for rotifers that were starved over the same 3 d period (ca -0.15 d^{-1}). At a brown tide concentration of 5 mg C l^{-1}, specific growth (death) rate decreased to -0.39. When the rotifers were fed *Isochrysis galbana*, specific growth rates ranged from 0.19 to 0.61 d^{-1} (Fig. 6). However, when *B. plicatilus* was fed an equal amount of both *I. galbana* and the Texas brown tide alga (yielding twice the total phytoplankton concentration), *B. plicatilus* showed little or no growth.

When groups of 36 *Acartia tonsa* nauplii were raised in 3 ml cell wells in tissue culture plates, the group held without any food exhibited daily mortality and were all dead by the end of a 5 d period. For a similar group of nauplii held in 3 ml of seawater containing brown tide at a concentration of 5 mg C l^{-1}, there was extensive mortality on Day 2, and all nauplii were dead by Day 3. For groups of nauplii raised on 5 mg C l^{-1} of *Isochrysis galbana*, *Pyrenomonas salina* or a combination of the 2 foods, over 85% of the nauplii were still

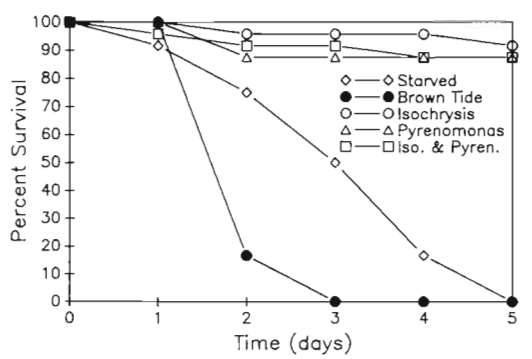

Fig. 7. Survival of groups of 24 nauplii of the copepod *Acartia tonsa* fed 5 mg C l^{-1} of the Texas brown tide alga, *Isochrysis galbana*, *Pyrenomonas salina*, a combination of *I. galbana* and *P. salina* or starved over a 5 d period

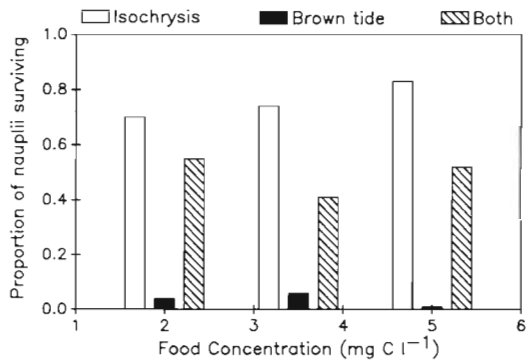

Fig. 8. Survival of groups of 50 nauplii of the copepod *Acartia tonsa* fed *Isochrysis galbana*, the Texas brown tide alga or a combination of both (twice the total food concentration) at food concentrations of 2, 3.5 and 5 mg C l^{-1} over a 5 d period. Each bar is the mean value of 2 replicate experiments

alive at the end of the 5 d period (Fig. 7). Since the brown tide appeared to settle to the bottom of the cell wells over the course of the experiment, subsequent experiments were done with groups of 50 nauplii in 50 ml tissue culture flasks rotated at 2 rpm to keep the algae in suspension. Replicate experiments were run at 2, 3.5 and 5 mg C l^{-1}. Survival of *A. tonsa* nauplii ranged from 1 to 6% on the brown tide alone, from 70 to 83% on *I. galbana* alone and from 41 to 55% on a combination of equal amounts of each food (twice the food concentration) (Fig. 8).

Egg release rates for adult female *Acartia tonsa* fed the Texas brown tide alga at a food concentration of 1.5 mg C l^{-1} was 3.4 ± 2.3 (mean ± 1 SD, n = 6) eggs $female^{-1}$ d^{-1}, which was not significantly different from the egg release rates of 1.7 ± 0.7 for *A. tonsa* that had been starved over the same 48 h period (*t*-test, α = 0.05) (Fig. 9). *A. tonsa* females fed similarly sized small phytoplankton species showed intermediate egg release rates of 9.3 ± 2.6 eggs $female^{-1}$ d^{-1} when fed

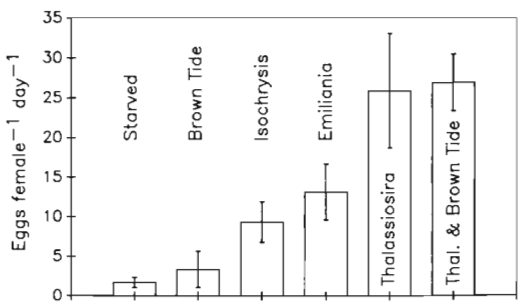

Fig. 9. Mean egg release rates (eggs $female^{-1}$ d^{-1}) of adult female *Acartia tonsa* fed 1.5 mg C l^{-1} of the Texas brown tide alga, *Isochrysis galbana*, *Emiliania huxleyi*, *Thalassiosira* sp., a combination of *Thalassiosira* sp. and brown tide, or starved. Each bar represents the mean (± SD) of 8 replicate experiments

1.5 mg C l^{-1} of *Isochrysis galbana* (5 µm diameter) and 13.1 ± 3.5 eggs $female^{-1}$ d^{-1} when fed 1.5 mg C l^{-1} of *Emiliania huxleyi* (4 µm diameter). Highest egg release rates of 25.9 ± 7.2 eggs $female^{-1}$ d^{-1} were measured for *A. tonsa* fed 1.5 mg C l^{-1} of the diatom *Thalassiosira* sp. When *A. tonsa* females were offered a combination of 1.5 mg C l^{-1} each of *Thalassiosira* sp. and the Texas brown tide alga (3 mg C l^{-1} total), egg release rates were 26.9 ± 3.6 eggs $female^{-1}$ d^{-1}, which is not significantly different from the release rate when the copepods were fed *Thalassiosira* sp. alone (*t*-test, $\alpha = 0.05$).

DISCUSSION

The Texas brown tide alga appears to be a poor food for a variety of zooplankton species. It supports no growth of the ciliate *Strombidinopsis* sp., the heterotrophic dinoflagellate *Noctiluca scintillans* or the rotifer *Brachionus plicatilus*. It is not unusual to find zooplankton that can not be cultured on a particular species of phytoplankton; some can only capture particles in a relatively narrow size range (Fenchel 1980). However, *N. scintillans* can be grown on a wide variety of phytoplankton species, including species of similar size (Buskey 1995), and *B. plicatilus* is very easy to culture and is widely used as a food for larval fish. Based on the results of this study, there is evidence that the brown tide may be directly toxic to some species of zooplankton, at cell concentrations similar to those found in nature. For the ciliate *Strombidinopsis* sp. (Fig. 1) and for the rotifer *B. plicatilus* (Fig. 6), mortality rates increase with increasing brown tide concentration. For one experiment with *Acartia tonsa* nauplii, mortality was faster in the presence of the brown tide than when no food was offered (Fig. 7). Additional evidence for toxicity of the brown tide to some species of zooplankton comes from the decrease in survival of *A. tonsa* nauplii when both a suitable food (*Isochrysis galbana*) and the brown tide are offered together (Fig. 8). In addition, when both *I. galbana* and the brown tide are offered together, growth of the heterotrophic dinoflagellate *N. scintillans* and the rotifer *B. plicatilus* are inhibited (Figs. 4 & 6). In contrast, there is little evidence that the related species *Aureococcus anophagefferens* is toxic to microzooplankton. No evidence was found for changes in protozoan grazing rate or for suppression of growth in protozoans fed *A. anophagefferens*, nor was there any evidence that *A. anophagefferens* caused a reduction in protozoan populations in nature (Caron et al. 1989)

The brown tide alga appears to be a poor food for *Acartia tonsa*, the dominant mesozooplankter in the Laguna Madre. Egg release rates of adult females fed the brown tide were not significantly different from those held without food over the same time interval. This may have been due in part to the small size of the brown tide cells (4 to 5 µm diameter), which is outside the optimum size range for particle capture by *A. tonsa* (Berggreen et al. 1988). However, *A. tonsa* females produced an intermediate number of eggs on 2 similarly small-sized algal species, indicating that size alone was not the problem. There was no evidence of brown tide toxicity to adult female *A. tonsa* at 1.5 mg C l^{-1}, since there was no direct mortality to adults and egg release was not lowered with the combination of *Thalassiosira* and brown tide. Lower egg release rates are reported for *A. tonsa* fed picoalgae during an *Aureococcus anophagefferens* bloom in Narragansett Bay (Durbin & Durbin 1989). In addition to lowering the egg release rates of adult females, the presence of the brown tide resulted in lower survival of *A. tonsa* nauplii, suggesting toxic effects. The Texas brown tide alga has also been shown to be toxic to yolk-sac and first feeding red drum and spotted sea trout larvae (G. J. Holt pers. comm.) but it does not appear to have adverse affects on adult fish populations.

Field evidence also supports the concept that the Texas brown tide alga is a poor food for zooplankton and disrupts trophic transfer in the planktonic food web. Mesozooplankton abundance (mainly *Acartia tonsa*) was lower in the Laguna Madre after the brown tide began than in the preceding year, and adult female *A. tonsa* were smaller and produced fewer eggs in field incubations than before the brown tide began (Buskey & Stockwell 1993). Microzooplankton abundances were also lower after the brown tide began, and microzooplankton community grazing rates of phytoplankton standing stock were reduced from ca 95% to less than 5% during the brown tide (Buskey & Stockwell 1993). It is still difficult to understand why species of microzooplankton capable of growing on the brown tide have not flourished and helped bring the brown tide under control. It is possible that *A. tonsa* may be exerting additional predation pressure on microzooplankton populations during the brown tide, due to the reduction of other species of phytoplankton in their preferred size range. It is well documented that *A. tonsa* also feed on microzooplankton (reviewed in Pierce & Turner 1992), so it is possible that they are holding microzooplankton populations below a level where they can exert sufficient grazing pressure to help control the brown tide.

The related brown tide species *Aureococcus anophagefferens* has been demonstrated to inhibit feeding and cause mass mortality of the mussel *Mytilus edulis* (Tracey 1988). Bricelj & Kuenster (1989) concluded that this mortality was due to toxicity and not to small size or nutritional inadequacy of this phytoplankton species. Laboratory studies also indicate that *A. anophag-*

efferens reduces growth and causes high mortality of bay scallop larvae (Gallager et al. 1989). *A. anophagefferens* was shown to inhibit the ciliary activity of isolated gills of some bivalve species such as *Mercenaria mercenaria* and *Mytilus edulis* but not others that were affected by brown tide in nature such as *Argopecten irradians* (Gainey & Shumway 1991). In contrast, the Texas brown tide alga is readily consumed by the dwarf surfclam *Mulinia lateralis* without adverse affects (Montagna et al. 1993) and there is no evidence that the Texas brown tide alga is toxic to adults of other species of invertebrates.

It seems likely that the Texas brown tide alga may produce a chemical that inhibits grazing or growth of microzooplankton, and/or may act as an allelopathic agent to reduce competition from other phytoplankton species. For example, both *Aureococcus anophagefferens* and the Texas brown tide contain high concentrations of dimethylsulfoniopropionate (DMSP), which is a precursor to dimethylsulfide (DMS) and acrylic acid (Keller et al. 1989, Stockwell et al. 1993). The role of DMSP in grazer inhibition is unclear, however. For example, *Phaeocystis pouchetii*, which also produces a large amount of DMSP (Keller et al. 1989), appears to be consumed by a wide variety of zooplankton (Admiraal & Venekamp 1986, Huntley et al. 1987), whereas *Chrysochromulina polylepis*, which also produces DMSP, reduces growth and feeding rates of the tintinnid *Favella ehrenbergii* (Carlsson et al. 1990). The polysaccharide-like layer on the surface of *A. anophagefferens* contains a bioactive compound responsible for the reduction in ciliary beat frequency in bivalve gills (Gainey & Shumway 1991) but no similar compounds have yet been identified in the Texas brown tide alga.

Many species of harmful and nuisance algae are toxic to a variety of marine organisms. Most of the toxins associated with harmful algal blooms were first noticed because of the extensive fish kills they caused or for the human health risk associated with consumption of contaminated seafoods. It is difficult to understand why algal species would evolve toxins that were specifically aimed at humans or fish species that do not directly consume these algal species. It is possible that in some cases these toxins might be substances that have evolved for some other physiological function in the cell, which coincidentally happen to be toxic to human or marine life. In the cases of *Aureococcus anophagefferens* and the Texas brown tide alga, it appears as if toxic substances may be targeted at benthic and planktonic grazers that feed on these species of phytoplankton, and although there are no direct threats to human health from these species, they may have a profound effect on the structure and function of the ecosystems in which they reside.

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