



## Sublethal effects of Texas brown tide on *Streblospio benedicti* (Polychaeta) larvae

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### Abstract

The Texas brown tide bloom is noted for a concordant decline in benthic biomass and species diversity. However, the link between harmful effects induced by Texas brown tide and benthos has not been demonstrated. It has been proposed there may be a larval bottleneck, where larvae, but not adults, suffer adverse effects. This study was performed to test the effect of brown tide alga, *Aureoumbra lagunensis*, on mortality, growth and behavior of *Streblospio benedicti* larvae. Growth rates and swimming speeds, but not mortality rates, of polychaete larvae were reduced in cultures with brown tide relative to *Isochrysis galbana*, which is about the same size as brown tide. Results from this research indicate that brown tide does have harmful sublethal effects for one dominant species of meroplanktonic larvae, which could help explain reduced adult population size. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Brown tide; Polychaete larvae; Meroplankton; Growth; Mortality; Swimming speed; Turning rates

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### 1. Introduction

The Texas brown tide is a harmful algal bloom occurring in estuaries of the southern Texas coast, USA. The bloom was first noted in January 1990 in Baffin Bay and spread to Upper Laguna Madre in July 1990, where it persists as of this writing. The bloom increases intensity in summer months, slackens in winter and spring (Buskey et al., 1996). A small (4–5  $\mu\text{m}$  diameter) pelagophyte alga, *Aureoumbra lagunensis* (DeYoe et al., 1997) is responsible for the bloom. Densities as high as  $1 \times 10^7$  cells  $\text{ml}^{-1}$  have occurred and brown tide effectively outcompetes other phytoplankton (Stockwell et al.,

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1993). High salinities (due to drought) and high ammonia concentrations (due to fish killed by a freeze) are thought to be conditions that triggered the bloom (Stockwell et al., 1993; Buskey et al., 1998). Disruption of grazer control apparently has contributed to persistence of the bloom (Buskey et al., 1997).

Associated with the occurrence of brown tide has been a dramatic decline of benthos in Laguna Madre (Montagna et al., 1993; Conley, 1996; Buskey et al., 1997). There has been a decrease in biomass and diversity of benthic invertebrates in Laguna Madre. The dominant bivalve, *Mulinia lateralis* virtually disappeared after onset of brown tide (Montagna et al., 1993). The dominant polychaete, *Streblospio benedicti*, had very high populations prior to brown tide (about 10 000 individuals  $m^{-2}$ ) then declined two orders of magnitude (Buskey et al., 1997). What caused these changes is not clear. Feeding inhibition by brown tide alga, *Aureococcus anophagefferens*, is known to occur in other bivalves (Bricelj and Kuenstner, 1989), but did not occur with *M. lateralis* fed *Aureoombra lagunensis* (Montagna et al., 1993). Brown tide carbon also appears to support the benthic food web in Baffin Bay and Laguna Madre (Street et al., 1997). One possible mechanism by which brown tide can harm benthos is by effects on planktonic larvae, which can reduce recruitment success. For example, *A. lagunensis* is toxic to early naupliar stages of the calanoid *Acartia tonsa*, but not to adults (Buskey and Hyatt, 1995). Most infauna have a planktonic larval stage, and it is possible that harmful effects exist for larvae, but not adults.

The present study was performed to test for lethal and sublethal effects of brown tide, *Aureoombra lagunensis*, on larvae of the dominant polychaete, *Streblospio benedicti*. Mortality, growth rates, and behavioral responses of larvae were measured in several concentrations of brown tide and one concentration of *Isochrysis galbana*, which is about the same diameter as *A. lagunensis*.

## 2. Materials and methods

### 2.1. Test organisms

*Streblospio benedicti* were collected from surface sediments (3–4 cm depth) in Rincon Bayou, TX, USA (salinity 16 psu) to start cultures. The station in Rincon Bayou (27° 53.927' N, 97° 36.250' W) is in the Nueces delta. The samples were stored on ice to keep organisms cool during transport, which lasted about 1 h. Additional sediment from the site was collected by shovel, frozen at  $-5^{\circ}C$  to kill infaunal organisms, and stored for maintaining *S. benedicti* cultures in the laboratory. Cultures were maintained at the University of Texas at Austin, Marine Science Institute with running (0.5 l  $min^{-1}$ ) filtered seawater from Aransas Pass (about 28°C). Adult *S. benedicti* were extracted from sediment on a 60  $\mu m$  sieve, rinsed with filtered seawater into a 250 ml beaker, and pipetted into culture dishes. Cultures were maintained in eleven small (80  $\times$  40) mm and four large (120  $\times$  60) mm culture dishes. Fifty adult worms of varying sizes were added to each culture dish so that males and females were present in each culture. Frozen sediment was thawed, 10 ml were added to small culture dishes and 15 ml were added to large dishes as culture medium. Filtered seawater (22 psu) was added and each dish was

aerated using aquarium tubing and a series of capillary tubes. Sediment was changed biweekly in culture dishes by sieving worms on a 60  $\mu\text{m}$  sieve and adding fresh, recently thawed mud to each dish. Salinity was checked daily with a Leica TS meter refractometer and it was necessary to add deionised water to culture dishes every 3rd day to replace evaporated water. The salinity change in the dishes was 2–4 psu every 3 days.

*Isochrysis galbana* cultures were grown in f/2 culture media (Guillard and Ryther, 1962) at 25°C on a 12:12 light–dark cycle at a light intensity of about 120  $\mu\text{M}$  photons  $\text{m}^{-2} \text{s}^{-1}$ . *Aureoumbra lagunensis* was cultured under the same temperature and light regime, but at a salinity of 33 psu in a modified f/2 culture media (Buskey et al., 1998).

## 2.2. Bioassay test procedure

Planktotrophic larvae were collected on 23 July 1997 by decanting overlying water from culture dishes into a 400-ml beaker. This was 2 days after larvae became free swimming, and at the 7-setiger stage. Larvae were concentrated by pipetting individuals into a 250-ml beaker containing filtered seawater (33 psu). Larvae were transferred by pipette into culture plates, where 15 larvae were placed in each of the six 15-ml wells. Ten ml of brown tide cells were added to three different culture plates at concentrations of  $2 \times 10^5$ ,  $1 \times 10^5$  and  $2 \times 10^4$  cells  $\text{ml}^{-1}$ . A fourth plate of larvae was established with 10 ml of *I. galbana* diluted with autoclaved seawater to a concentration of  $2 \times 10^5$  cells  $\text{ml}^{-1}$ . The *I. galbana* test acts as a positive control, because it is common and about the same size as brown tide. By positive control, we mean that we assume larval growth, development, and behavior should be relatively normal in these cultures. A fifth plate for a negative control was established with larvae placed in 10 ml of autoclaved seawater and no phytoplankton food. By negative control, we mean that we assume growth, development, and behavior would be impaired for planktotrophic larvae where food is not present. Plates were stored and maintained in an incubator under 24 h light at 25°C.

Each replicate was checked daily for 8 days to measure mortality, growth stages, and behavior of larvae. Larval mortality was determined by counting the number of live larvae present in each well using a dissecting microscope. Larval growth stage was determined by counting the number of setigers using a compound microscope (Dean, 1963).

Swimming behavior of *S. benedicti* larvae was quantified in each well of two experimental treatments (brown tide and *I. galbana* at  $2 \times 10^5$  cells  $\text{ml}^{-1}$ ) using an Expertvision Cell-Trak motion analysis system. Videotaped experiments were digitized with a Motion Analysis VP-110 video-to-digital processor and outlines of larvae were sent to a personal computer at a rate of 15 frames  $\text{s}^{-1}$ . The digitized images were then processed to produce paths following the motion of larvae over time. Only paths exceeding 15 frames (1 s duration) were used in analysis, and paths for a single larvae rarely remained within the field of view for more than 5 s. From these records mean behavioral parameters, including swimming speed ( $\text{mm s}^{-1}$ ) and rate of change of direction (RCDI,  $^\circ \text{s}^{-1}$ ), were calculated for all larvae in each treatment replicate (Buskey, 1997).

### 2.3. Statistical analyses

A total of six independent replicates of 15 larvae each for five experimental treatments were examined on 8 successive days to measure growth and mortality. Because replicate wells were reexamined through time, a repeated measures analysis of variance model was used to analyze data. A linear contrast procedure was used to test for differences among specific treatment levels, i.e. to compare mortality of brown tide and *I. galbana* grown at  $2 \times 10^5$  cells  $\text{ml}^{-1}$ . The swimming behavior experiment had only two treatments, brown tide and *I. galbana* at  $2 \times 10^5$  cells  $\text{ml}^{-1}$ , so results were examined using a *t*-test. The number of larvae captured in a video frame could not be controlled, so sample size varied in each of the six replicates.

## 3. Results

All larvae were at the 7-setiger growth stage at the beginning of mortality, growth, and behavior experiments. There was no growth in any culture for the first 3 days (Fig. 1). There was a significant difference in development among the cultures (ANOVA,  $F_{4,28} = 9.65$ ,  $P = 0.0001$ ). There was no growth in control experiments, where larvae remained at the 7-setiger growth stage for the entire duration of the 8-day experiment (Fig. 1). Growth was most rapid in the *I. galbana*  $2 \times 10^5$  cells  $\text{ml}^{-1}$  treatment, where larvae reached 9-setiger stage by day 4, and 11-setiger stage by day 5. In all brown tide cultures, greater than 50% of larvae remained at the 7-setiger stage until day 4, and grew to the 9-setiger stage at which they remained for the rest of the experiment. In all cases, larvae grew by two setigers and all were at the same stage within a treatment (Fig. 1).

There was almost no mortality in cultures during the 4-day period of any treatment, but mortality began in all at day 5 (Fig. 2). There was a significant difference in mortality among cultures over time (ANOVA,  $F_{20,175} = 2.56$ ,  $P = 0.0027$ ). The control culture and the *I. galbana*  $2 \times 10^5$  cells  $\text{ml}^{-1}$  treatment had the highest mortality, averaging 1.2 and 2.8 larvae alive, respectively, on day 8. The mortality in these two cultures were significantly different at different concentrations, in contrast to brown tide cultures at different concentrations which were the same (ANOVA, linear contrast,  $P = 0.0027$ ).

*Streblospio benedicti* larvae grown in brown tide had a 55% slower average swimming speed ( $0.385 \text{ mm s}^{-1}$ ) than those grown in *I. galbana* ( $0.597 \text{ mm s}^{-1}$ ) at the same concentration (Table 1). The difference in swimming speed rates, however, were only slightly non-significant (*t*-test,  $t = 1.996$ ,  $P = 0.0738$ ). The rate of change in direction (RCDI) of larvae in brown tide was 290% slower ( $59^\circ \text{ s}^{-1}$ ) than those grown in *I. galbana* ( $232^\circ \text{ s}^{-1}$ ) (*t*-test,  $t = 8.219$ ,  $P < 0.0001$ ).

## 4. Discussion

*Streblospio benedicti* larvae exposed to brown tide had a slower growth rate than those exposed to *I. galbana*. One possible explanation is larvae were feeding on the

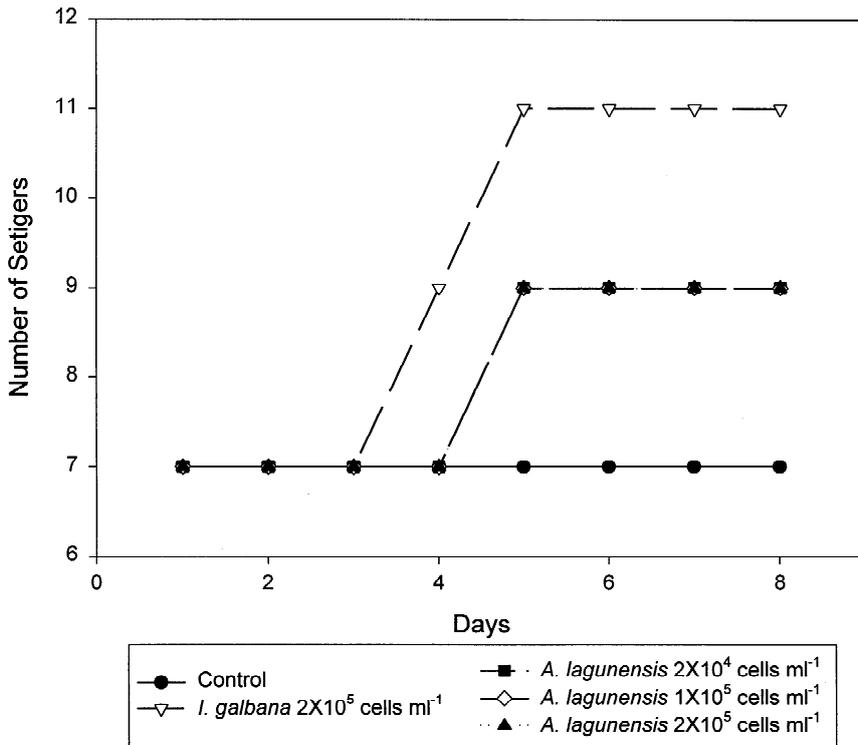


Fig. 1. *Streblospio benedicti* larvae growth in different culture treatments over 8 days. Growth is indicated by the number of setigers found on the larvae. All cultures were started at the 7-setiger stage and grown in different concentrations of brown tide, *Aureoumbra lagunensis* or *Isochrysis galbana*.

brown tide organism, but not gaining as much nourishment as obtained from *I. galbana*. *Aureoumbra lagunensis* is nutritionally inadequate to support growth of the ciliate *Strombidinopsis* sp., the heterotrophic dinoflagellate *Noctiluca scintillans*, or the rotifer *Brachinous plicatilis* (Buskey and Hyatt, 1995). Stable isotope analyses indicate that adult *S. benedicti* incorporate brown tide under bloom conditions in Alazan Bay, TX (Street et al., 1997). There was virtually no microphytobenthic production during the height of the Texas brown tide (Blanchard and Montagna, 1995), so brown tide was the only source of microalgal carbon. Higher growth rates in cultures are probably due to higher nutritional value of the prey offered. When provided increased organic enrichment, *S. benedicti* grows at higher rates and produces more larvae (Levin, 1986). Another possible explanation of reduced growth in the presence of brown tide is stress. *Aureoumbra lagunensis* is toxic to *A. tonsa* nauplii (Buskey and Hyatt, 1995). Stress in cultures can alter demographic parameters of *S. benedicti* (Levin et al., 1996). Hydrocarbons caused delayed maturation and reduce fertility whereas blue-green algae (*Spirulina* sp.) caused reductions in juvenile survival and fertility. Stress could be caused by brown tide if the alga exudes an alleopathic chemical.

Regardless of the mechanism, slower growth rates and delayed maturation in brown

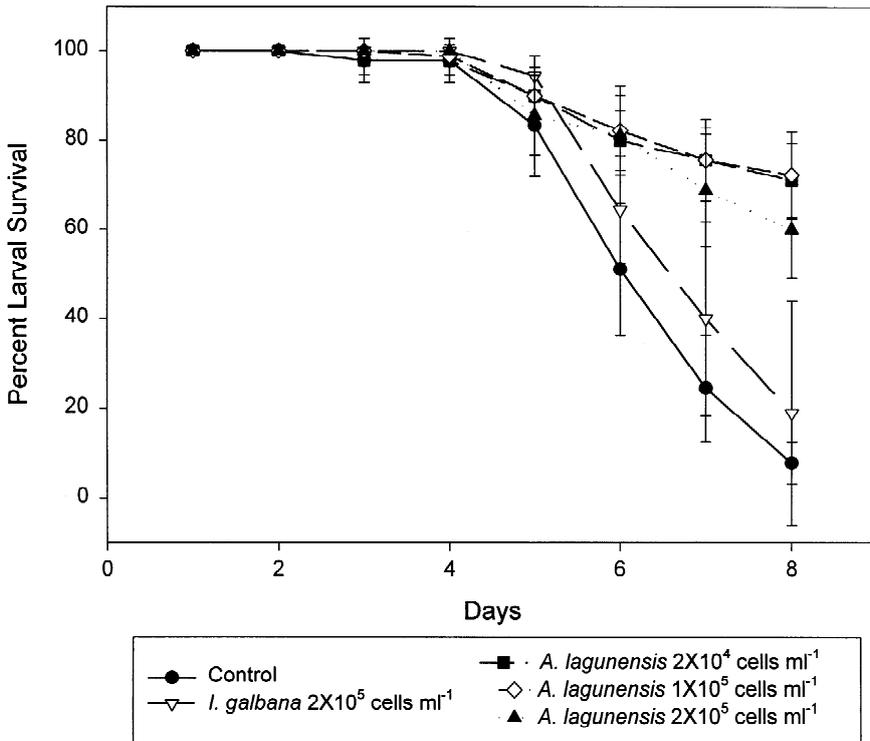


Fig. 2. *Streblospio benedicti* larvae mortality in different culture treatments. All larvae were grown in different concentrations of brown tide, *Aureoumbra lagunensis* or *Isochrysis galbana*. Percentage of the original culture remaining. Mean and standard deviation given for six replicates.

tide cultures caused larvae to spend more time in the swimming stage. If this occurs in the field as well, then larvae are in the plankton longer as well. Larval stages are subject to high predation rates, thus longer planktonic stages would increase exposure to

Table 1  
*Streblospio benedicti* larvae behavior in two culture treatments<sup>a</sup>

Exposure	Larval behavior		
	Number of larvae	Speed (mm s <sup>-1</sup> )	RCDI (° s <sup>-1</sup> )
<i>A. lagunensis</i>	471 ± 190	0.385 ± 0.170	59.45 ± 31.98
<i>I. galbana</i>	376 ± 217	0.597 ± 0.200	232.35 ± 40.41
$P >  t $	0.4384	0.0738	< 0.0001

<sup>a</sup> Number of larvae videotaped per replicate, swimming speed, and rate of change of direction (RCDI) in *Aureoumbra lagunensis* (Texas brown tide) and *Isochrysis galbana* at the same concentration ( $2 \times 10^5$  cells ml<sup>-1</sup>). Mean and standard deviation given for six replicates.

predation. A loss of larvae prior to recruitment could explain a decline in density of *S. benedicti* in Laguna Madre and Baffin Bay during the height of the bloom.

Mortality began after larval growth peaked at 5 days in both brown tide and *I. galbana* cultures. After 5 days, mortality was very high in control (unfed) and *I. galbana* cultures, but for different reasons. Organisms were starving in the control cultures and larvae had grown to the point that they were ready to settle in the *I. galbana* cultures. Planktotrophic larvae are typically released at the 3–5-setiger stage and feed in the plankton for 10–21 days (Levin, 1984; Levin and Huggett, 1990). After 5 days following development to 7-setiger stage, all larvae raised in *I. galbana* reached the 11-setiger stage. At the 11-setiger stage, larvae begin to settle and mortality rates are high if no suitable substrate is present for settlement (Dean, 1963). At experimental day 5, larvae in brown tide cultures were still in the planktonic, 9-setiger, pre-settling stage and did not experience sudden high mortality rates. This indicates larvae have the ability to sustain longer time periods in the plankton during less favorable brown tide blooms.

Growth or mortality rates of *S. benedicti* larvae did not vary over the tested concentration range of Texas brown tide, *Aureoumbra lagunensis*, over 8 days. There was only a slight increase in mortality at the highest brown tide concentration, but it was not statistically significant (Fig. 2). However, concentrations of brown tide in the cultures were slightly below bloom conditions, which can reach up to 0.5 to  $5 \times 10^6$  cells  $\text{ml}^{-1}$  (Buskey et al., 1996, 1997). It is possible that if higher or lower concentrations of brown tide were used, then a greater or lesser effect could have been recorded. Grazing rates by the bivalve *Mulinia lateralis* increases with increasing *A. lagunensis* cell density over a range of 0.02 to  $2 \times 10^6$  cells  $\text{ml}^{-1}$  (Montagna et al., 1993). Although, no responses were found among brown tide concentration treatments, there were differences in larval growth, mortality, and behavior between cultures of brown tide and *I. galbana* at the same concentration.

Behavior of larvae grown in brown tide was different from that grown in *I. galbana*. Larvae had 55% slower swimming speeds and 290% lower turning rates than larvae grown in *I. galbana*. The lack of a statistically significant result (i.e.  $P = 0.07$ ) does not mean that swimming speed was not affected by brown tide. Overall, there is a reduced behavioral response of larvae exposed to brown tide. Stress is known to cause altered swimming responses in planktonic larvae. Barnacle larvae and copepod larvae exposed to sublethal levels of pollutants, e.g. copper and cadmium, also exhibit reduced swimming speed and other behavioral changes (Lang et al., 1980; Sullivan et al., 1983). In contrast, larvae of the scallop *Argopecten irradians* do not have different swimming behavior when exposed to *I. galbana* and *Aureococcus anophagefferens* (Gallager et al., 1989). The slower swimming response in the presence of Texas brown tide could effect fitness of *S. benedicti* in Laguna Madre or Baffin Bay. If high swimming speeds or high turning rates are necessary to either avoid predators or obtain food, then the larvae would have increased exposure to predation and decreased ability to obtain food in the presence of brown tide.

Other brown tide species are known to affect invertebrate behavior. The effect of brown tide alga, *Aureococcus anophagefferens*, on bivalves has been studied in detail. Exposure to this species causes decreased activity of lateral cilia in five of eight bivalves tested (Gainey and Shumway, 1991). Reduced grazing rates by adults (Bricelj and

Kuenstner, 1989; Gainey and Shumway, 1991) and larvae (Gallager et al., 1989) are also known to occur. Disrupted grazing pressure is thought to be partly responsible for persistence of brown tide blooms (Bricelj and Kuenstner, 1989; Buskey et al., 1997).

Brown tide, at densities less than bloom conditions, appears to have a negative affect on *S. benedicti* larvae. The trend in mortality and growth data indicates larvae will spend longer periods of time in the plankton. The trend in behavior data indicates that larvae will have less ability to move in the plankton. Together, the longer period in the planktonic stage and reduced ability to avoid predation or capture food indicates that *S. benedicti* larvae should be more susceptible to high rates of mortality. Successful recruitment requires survival through the larval, metamorphosis and early settlement stages. The data presented here demonstrates it is likely that brown tide indirectly causes decreased survival in the planktonic stage. *Streblospio benedicti* is known to have alternative reproductive modes (Levin and Huggett, 1990). It is not known if lecithotrophic larvae of *S. benedicti* would suffer the same effects when exposed to brown tide. Lecithotrophic populations of *S. benedicti* are known to have a survivorship advantage in larval and juvenile stages (Levin and Huggett, 1990). Therefore, it is not likely that lecithotrophic populations would have responses to brown tide that are similar to those exhibited by planktotrophic populations.

In summary, the initial (5 day) course of the experiment demonstrated that brown tide is not lethal to *S. benedicti* larvae. Sublethal effects were observed, including decreases in swimming speed and rate of change in swimming direction. A second sublethal effect is decrease in growth rate, and thus delayed development when larvae are cultured in brown tide. The net effect of slower growth and slower behavioral responses could contribute to increased mortality of *S. benedicti* larvae and reduced recruitment in the natural environment during brown tide bloom conditions.

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## References

- Blanchard, G.F., Montagna, P.A., 1995. Assessment of a brown tide impact on microalgal benthic communities in Baffin Bay (Texas) in 1990 using a primary production simulation model. *Oceanologica Acta* 18, 371–377.
- Bricelj, V.M., Kuenstner, S.H., 1989. Effects of the 'brown tide' on the feeding physiology and growth of bay scallops and mussels. In: Coper, E.M., Bricelj, V.M., Carpenter, E.J. (Eds.), *Coastal and Estuarine Studies*, Springer-Verlag, Berlin, pp. 491–509.
- Buskey, E.J., 1997. Behavioral components of feeding selectivity of the heterotrophic dinoflagellate *Protoperidinium pellucidum*. *Mar. Ecol. Prog. Ser.* 153, 77–89.

- Buskey, E.J., Hyatt, C.J., 1995. Effects of the Texas (USA) 'brown tide' alga on planktonic grazers. *Mar. Ecol. Prog. Ser.* 126, 285–292.
- Buskey, E.J., Montagna, P.A., Amos, A.F., Whitley, T.E., 1997. Disruption of grazer populations as a control factor to the initiation of the Texas brown tide algal bloom. *Limnol. Oceanogr.* 42, 1515–1522.
- Buskey, E.J., Stewart, S., Peterson, J., Collumb, C., 1996. Current status and historical trends of brown tide and red tide phytoplankton blooms in the Corpus Christi Bay National Estuary Program study area. Publication CCBNEP-07, Texas Natural Resource Conservation Commission, Austin, TX, 174 pp.
- Buskey, E.J., Wysor, B., Hyatt, C.J., 1998. The role of hypersalinity in the persistence of the Texas 'brown tide' in the Laguna Madre. *J. Plankton Res.* 20, 1553–1565.
- Conley, M.F., 1996. Effect of a persistent brown tide bloom on macroinfaunal communities in Baffin Bay and Laguna Madre, Texas. Master of Arts Thesis, University of Texas at Austin, 79 pp.
- Dean, D., 1963. On the reproduction and larval development of *Streblospio benedicti*. *Biol. Bull.* 128, 67–76.
- DeYoe, H.R., Stockwell, D.A., Bidgare, R.R., Latasa, M., Johnson, P.W., Hargraves, P.E., Suttle, C.A., 1997. Description and characterization of the algal species *Aureoumbra lagunensis* gen. et sp. nov. and referral of *Aureoumbra* and *Aureococcus* to Pelagophyceae. *J. Phycol.* 33, 1042–1048.
- Gainey, Jr. L.F., Shumway, S.E., 1991. The physiological effect of *Aureococcus anophagefferens* ('brown tide') on the lateral cilia of bivalve mollusks. *Biol. Bull.* 181, 298–306.
- Gallager, S.M., Stoecker, D.E.K., Bricelj, V.M., 1989. Effects of the brown tide alga on growth, feeding physiology and locomotory behavior of scallop larvae (*Argopecten irradians*). In: Cosper, E.M., Bricelj, V.M., Carpenter, E.J. (Eds.), *Coastal and Estuarine Studies*, Springer-Verlag, Berlin, pp. 511–541.
- Guillard, R.R.L., Ryther, R.H., 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Detonula confervacea* Cleve Gran. *Can. J. Microbiol.* 8, 229–239.
- Lang, W.H., Forward, Jr. R.B., Miller, D.C., Mercy, M., 1980. Acute toxicity and sublethal behavioral effects of copper on barnacle nauplii (*Balanus improvisus*). *Mar. Biol.* 58, 139–145.
- Levin, L.A., 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull.* 166, 494–508.
- Levin, L.A., 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): A mesocosm study. *Biol. Bull.* 171, 143–160.
- Levin, L., Caswell, H., Bridges, T., DiBacco, C., Cabrera, D., Plaia, G., 1996. Demographic responses of estuarine polychaetes to pollutants: Life table response experiments. *Ecol. Appl.* 6, 1295–1313.
- Levin, L.A., Huggett, D.V., 1990. Implications of alternative reproductive modes for seasonality and demography in an estuarine polychaete. *Ecology* 71, 2191–2208.
- Montagna, P.A., Stockwell, D.A., Kalke, R.D., 1993. Dwarf surfclam *Mulinia lateralis* (Say, 1822) populations and feeding during the Texas brown tide event. *J. Shellfish Res.* 12, 433–442.
- Stockwell, D.A., Buskey, E.J., Whitley, T.E., 1993. Studies on conditions conducive to the development and maintenance of a persistent 'brown tide' in Laguna Madre, Texas. In: Smayda, T.J., Shimizu, Y. (Eds.), *Toxic Phytoplankton Blooms in the Sea*, Elsevier, New York, pp. 693–698.
- Street, G.T., Montagna, P.A., Parker, P.L., 1997. Incorporation of brown tide into an estuarine food web. *Mar. Ecol. Prog. Ser.* 152, 67–78.
- Sullivan, B.K., Buskey, E., Miller, D.C., Ritacco, P.J., 1983. Effects of copper and cadmium on growth, swimming and predator avoidance in *Eurytemora affinis* (Copepoda). *Mar. Biol.* 77, 299–306.