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The Bay Study Group Department of Sanitary Sewers

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DOES THE TUNICATE *BOSTRICHOBANCHUS DIGONAS* (ABBOTT) CONTROL THE SEASONAL DISTRIBUTION OF PHYTOPLANKTON BIOMASS IN TAMPA BAY?

A REPORT SUBMITTED IN ACCORDANCE WITH CONSENT ORDER 96-3452

TO

THE FLORIDA DEPARTMENT OF ENVIRONMENTAL PROTECTION SOUTHWEST DISTRICT OFFICE

BY

THE BAY STUDY GROUP
DEPARTMENT OF SANITARY SEWERS
CITY OF TAMPA

MAY 31, 1998
EXECUTIVE SUMMARY

The City of Tampa Bay Study Group (BSG) has investigated water quality and biological indicators, including phytoplankton biomass in Tampa Bay since 1978. Results from these studies suggest that benthic filter feeding organisms strongly impact the Tampa Bay phytoplankton population seasonally. Specifically, the tunicate *Bostrichobranchus digonas*, which is often found in dense concentrations on the bottom of Hillsborough Bay and other subsections of Tampa Bay during the winter, may for several months control phytoplankton biomass through its feeding process. Therefore, the mechanism determining phytoplankton biomass (chlorophyll-a) in Tampa Bay may shift seasonally from the warm period, when the phytoplankton population is driven by the nutrient supply (bottom-up control), to the cold period when grazing (top-down control) dominates the phytoplankton population.

A study was initiated in 1987, and expanded in 1996, to investigate the temporal and spatial distribution of *B. digonas* in Tampa Bay and to attempt to link variations in winter season chlorophyll-a concentrations to the distribution and biomass of the tunicate. Statistical analyses of the data collected at specific monitoring stations suggest a strong positive association between *B. digonas* biomass and parameters that relate to water clarity, which include phytoplankton biomass (chlorophyll-a). Also, calculations that relate *B. digonas* feeding activities to impacts on the Tampa Bay phytoplankton population strongly imply that *B. digonas*, at least in areas with developed tunicate beds, has a controlling effect on chlorophyll-a concentrations. These results are supported by Tampa Bay field observations of extremely clear water in the vicinity of well developed *B. digonas* beds. Further, the results from this study agree with findings reported from other estuaries and fresh water systems with abundant populations of benthic filter feeders.
DOES THE TUNICATE *BOSTRICHOBRANCHUS DIGONAS* (ABBOTT) CONTROL THE SEASONAL DISTRIBUTION OF PHYTOPLANKTON BIOMASS IN TAMPA BAY?

INTRODUCTION

The City of Tampa Bay Study Group (BSG) has been investigating the Hillsborough Bay phytoplankton population since 1978 through measurements of phytoplankton composition, biomass and primary production. These studies were originally designed to evaluate the response of the phytoplankton population to anticipated nutrient pollution abatement actions, primarily the conversion of the City of Tampa’s wastewater treatment plant to state-of-the-art nitrogen removal. However, as the phytoplankton study has progressed, it has become apparent that benthic filter feeding organisms may strongly impact the phytoplankton population seasonally. Specifically, the tunicate *Bostrichobranchus digonas*, which is often found in dense concentrations on the bottom of Hillsborough Bay and other subsections of Tampa Bay during the winter, may for several months control phytoplankton biomass through its feeding process. Therefore, the mechanism determining the amount of phytoplankton biomass present (chlorophyll-a concentrations) in Tampa Bay may shift seasonally from the warm period, when the phytoplankton population is driven by the nutrient supply (bottom-up control), to the cold period when predation may impact the population (top-down control). The potential seasonal shift in the phytoplankton biomass control presents an opportunity to increase the understanding of pelagic and benthic interactions in Tampa Bay and other similar systems.

Numerous studies have shown that filter feeding organisms act as a natural control of eutrophication in both marine and freshwater systems. Bivalves dominate benthic populations in some shallow estuarine embayments such as San Francisco Bay (Cloern 1982 and Officer et al. 1982) and Chesapeake Bay (Nichols 1985) and the filtering activity of the animals often result in the removal of a large portion of the phytoplankton population. Hily (1991) concluded that suspension feeders in the Bay of Brest controlled phytoplankton populations by filtering one third of the bay on a daily basis. Zebra mussels in Lake Erie are capable of pumping between 39 and 96 percent of the water column daily and may be the primary contributor to recent improvements in water quality (Bunt et al. 1993 and Holland et al. 1995).

Tunicates sometimes dominate the benthic habitat and are generally very efficient filter feeders with some species capable of retaining particulate matter as small as one micron (Goldberg et al. 1951) and all particles larger than 5 microns (Randlov and Riisgard 1979). Fiala-Medioni (1979) reports that the sessile ascidian *Phallusia mammilita* has a retention efficiency of nearly eighty percent. In addition, tunicates have the capacity to process large volumes of water. Filtration rates in the solitary ascidian *Pyura stolonifera* have been estimated at over 100 liters per day (Klumpp 1984). Given the potential volume of water
filtered and the filtration efficiency documented in some tunicates, a significant portion of the seston and plankton in the water column may be impacted.

In January 1986, the BSG found dense beds of the tunicate, *Bostrichobranchus digonas*, covering large areas of the bottom of northeastern Hillsborough Bay. Extremely high water clarity was observed in the vicinity of the tunicate beds. This observation prompted the BSG to initiate a study to investigate the temporal and spatial distribution of *B. digonas*.

This report primarily examines relationships between the tunicate *B. digonas* and several water quality parameters, with emphasis on chlorophyll-a concentrations, for the period September 1996 through March 1998. This study period encompasses two complete September to March periods which, based on surveys in previous years by the BSG, has proven to be the time of year when hatched stages of the tunicate generally can be expected to be present on the bay bottom. However, the report also examines water quality and tunicate information gathered for several years prior to 1996. These data are used to explore potential relationships between the tunicate *B. digonas* and Tampa Bay chlorophyll-a concentrations prior to the primary study period for this report, September 1996 through March 1998. Water quality data from both the BSG and the Hillsborough County Environmental Protection Commission (EPC) are used for these analyses.

Further, tunicate filtration rates based on BSG laboratory experiments, and literature information, combined with tunicate biomass and distribution data, will be used to estimate the potential seasonal uptake of chlorophyll-a by *B. digonas* for several recent winter seasons during which Tampa Bay-wide distribution sampling of the tunicate has been conducted.

**METHODS**

**Water Quality and Benthic Sampling:**

Between 1983 and 1986, station COT4, was the sole BSG water quality station in Hillsborough Bay proper (HB). The BSG added stations COT17 and COT18 in 1987, and COT19, COT20, COT23 and COT40 in 1992 (Figure 1) in order to collect water quality and benthic data in areas seasonally populated by *B. digonas*. Stations COT4, COT17, COT18, COT19, and COT20 in Hillsborough Bay were sampled at least twice monthly. Benthic samples at stations COT17, COT18, COT19, and COT20 were retained for analysis when tunicates were present while samples from station COT4 were analyzed throughout the year. Water quality and benthic sampling at stations COT23 and COT40, in Middle Tampa Bay (MTB) and Old Tampa Bay (OTB), respectively, were conducted on a monthly basis and benthic samples were retained when tunicates were present.
For this study, water quality and benthic data were collected from COT4, COT17, COT18, COT19, COT20, COT23, and COT40 between September 1, 1996 and March 31, 1998. The sampling frequency for each station did not change. However, for quality assurance, water quality data collected from one station were duplicated for each sampling trip.

Sampling at each water quality station consisted of water column measurements for dissolved oxygen, pH, salinity, and temperature from the surface to bottom at one meter increments using a precalibrated Hydrolab Datasonde 3 water quality multiprobe interfaced with a Hydrolab Surveyor 3 datalogger. The Datasonde 3 was calibrated following the procedure suggested by Hydrolab. Water samples were collected using a 5l Niskin hydrocast bottle at the surface, one, two, and three meters at station COT4 and the surface and bottom for the remaining stations. Water samples for chlorophyll-a and turbidity analysis were stored in opaque Nalgene containers (either 500ml or 2l) and preserved on ice until analyzed. Water samples for NH$_3$-N analysis were stored in 250ml polyethylene containers on ice until analyzed. A 125ml aliquot was taken from the surface sample at stations COT4, COT23, and COT40 and preserved with Lugol’s solution for phytoplankton identification and enumeration. Water column light data was collected using two LiCor 4π 193SA radiation sensors with a 50cm separation from the top sensor to the bottom sensor and stored in a LiCor 1000 datalogger. Water column light extinction was determined at the surface and one meter increments (the top sensor placed at these depths) to a depth of three meters or the bottom, if the water column depth was less than three meters. Duplicate benthic collections were made using a petit ponar with a surface collection area of about 225cm$^2$. Benthic grabs were sieved in the field through a 500μm screen and the samples were preserved in a formaldehyde/Rose Bengal solution.

Mapping of B. digonas Distribution in Tampa Bay:

From November 1994 through March 1998, benthic trawls were conducted each winter in the major subsections of Tampa Bay to spatially map B. digonas. Trawl locations were selected in areas greater than two meters in depth, excluding shipping channels. At each trawl location, the dredge was lowered to the sediment surface while the boat was under power. The scope of the tow line was adjusted to insure that the dredge had continuous contact with the bay bottom. Each location was trawled for 1.5 minutes at slow speed. The content of the trawl was emptied on board and examined for the presence or absence of tunicates.

B. digonas presence or absence, determined from trawl samples, has been used to generate annual tunicate distribution maps for Tampa Bay. All trawl locations were plotted on a map and trawl locations which had tunicates present were designated as a tunicate site. Further, tunicate sites that were proximal to each other were grouped into areas. The boundaries of the tunicate areas were delineated by depth, sediment composition, and trawl locations with no tunicate presence. From these data, the annual areal coverage of B. digonas in Tampa Bay was calculated for each bay subsection.
For the 1997-98 winter season, a differentially corrected Global Positioning System (GPS) instrument, was added to to enhance the accuracy of trawl locations and to better delineate the extent of *B. digonas* distribution in Tampa Bay.

**Spectrophotometric Determination of Chlorophyll:**

Spectrophotometric chlorophyll-a concentrations were determined using a modification of the Strickland and Parsons (1972) trichromatic method. Seawater samples, generally 500ml, were filtered through GF/F filters in dim light and the resulting phytoplankton laden filters were folded, wrapped in tin foil, and placed in a freezer. Within three weeks, the filters were ground in approximately 15ml of a magnesium carbonate buffered 90% acetone/10% deionized water solution. The solution was chilled during the grinding. The solution was then decanted into graduated test tubes, which were placed in a refrigerator to steep for at least 2 hours. The samples were centrifuged for 30 minutes. The absorbance of the samples was read at 750nm, 665nm, 645nm, and 630nm wavelengths on a Perkin Elmer, Lambda 3B UV/Vis Spectrophotometer. Chlorophyll-a concentrations were calculated from the Parsons-Strickland equation (Strickland and Parsons 1972).

**Whole Water Fluorometric Determination of Chlorophyll:**

Chlorophyll-a concentrations were also determined using a fluorometric whole water method adapted from Phinney and Yentsch (1985). The whole water analytical procedure began immediately after samples were received in the laboratory. For each sample, 700μl of sample water was added to three screw cap test tubes containing 6.3 ml of 100% acetone buffered with MgCO$_3$. In addition, a deionized water blank was set up for each sample. The combination of the acetone and sample water produced a 90% acetone/10% sample solution which is the standard acetone concentration used for spectrophotometric chlorophyll extraction. The acetone/sample solution was stirred and left in the dark to steep for 5 to 10 days. After steeping, each sample was read in a Turner Filter Fluorometer model 10-AU which was configured with the same lamp and filters as suggested by Welschmeyer (1994). The fluorometer was calibrated against standard trichromatic chlorophyll-a samples which were analyzed in the spectrophotometer according to Strickland and Parsons (1972).

Results from the fluorometric whole water method and the standard trichromatic method were compared for at least four samples per sample date. A paired t-test determined that the two methods produced significantly different estimates of chlorophyll-a concentration. However, a regression analysis between chlorophyll-a concentrations estimated by the spectrophotometer and the fluorometer suggested a strong linear relationship ($r^2=0.97$; $p<0.01$). The whole water chlorophyll-a concentrations were corrected to approximate values from the standard trichromatic method using the following equation: corrected whole water
[μg/l] = 0.746(whole water [μg/l]) + 0.811. All chlorophyll-a concentrations reported in this study are corrected whole water values.

Phytoplankton Taxonomic Composition and Abundance Analyses:

Phytoplankton samples collected for taxonomic composition and abundance analyses were refrigerated until analyzed. Each sample was analyzed in duplicate using 0.1ml Palmer-Maloney chambers. Individual phytoplankton were identified and enumerated at 400x power using an inverted Zeiss microscope. Phytoplankton were identified to species when possible, however for the purpose of this report, reporting is limited to the four major groups, blue-green algae, diatoms, green algae, and phytoflagellates.

Determination of Ammonia Nitrogen:

Analysis of ammonia nitrogen was conducted on water quality samples collected from, surface and three meters depth on a weekly basis at station COT4, from the surface and bottom every two weeks at stations COT17, COT18, COT19, and COT20 and from the surface and bottom on a monthly schedule at stations COT23 and COT40. The procedure was modified after Koroleff (no reference available), where samples were treated in an alkaline citrate medium with sodium hypochlorite and phenol in the presence of sodium nitroprusside which acts as a catalyzer. The resulting blue indophenol color formed with ammonia was measured spectrophotometrically at 630nm and the results calculated using a standard curve generated on a monthly basis.

Benthic Faunal Identification and Enumeration:

Benthic samples collected by petit ponar were stored in 500ml glass jars until identification and enumeration of faunal content. Each sample was washed with running water for about two minutes to remove excess formaldehyde and fine particulates and then decanted into a 250μm sieve. The entire sample was washed to one side of the sieve and poured onto a sorting tray. From each sample, amphipods, bivalves, brachiopods (Glottidia pyramidata), and adult and juvenile B. digonas were identified, enumerated, and measured for size to the nearest 0.1mm. A mean size for each group was calculated by measuring the five largest and five smallest individuals with a calibrated whipple disc located in the microscope ocular. If the group population was less than ten, all individuals within the group were measured. Amphipods were measured from proximal end of the antennae to the proximal end of the telson. Bivalves and brachiopods were measured along the major axis of the shell (pedicle not included in brachiopods). Adult tunicates were measured on the major and minor axes, and the size was recorded as the mean of the two axes. Juvenile tunicates were measured
along the major axis only. Tunicates were segregated into adults and juveniles based on size. Tunicates larger than 1.9mm were considered adults. Samples were preserved and stored for future reference.

*B. digonas* Laboratory Pumping Rate and Filtration Experiments:

To study potential effects on phytoplankton biomass by *B. digonas* feeding activities, multiple experiments were performed to measure *B. digonas* chlorophyll uptake and pumping rates. For these examinations, tunicates were collected using the dredge or ponar grabs. Ambient seawater was collected at the same location and filtered in the field using a 64um mesh to remove large zooplankton. In the laboratory, a seawater subsample was further filtered through a GF/F Whatman glass fiber filter, resulting in “plankton free” seawater for holding and washing the tunicates. On return to the laboratory, near ambient temperature was maintained and the tunicates were washed in the filtered seawater and measured for size.

Chlorophyll-a uptake experiments were performed to determine the potential amount of phytoplankton biomass the ascidians could remove on a daily basis. Tunicates were collected in northwest Hillsborough Bay on November 15, 1996 and at station COT18 on January 15 and 16, 1997. For the experiments, a concentrated phytoplankton medium was prepared. Using the ambient seawater that had been filtered in the field to remove large zooplankton, the phytoplankton density was increased using a Dodson tube fitted with a 10um mesh. The chlorophyll-a concentration of the enhanced phytoplankton seawater was determined prior to the feeding experiments using the fluorometric whole water method. After the tunicates were washed and measured, ten individuals were delicately placed in 60ml test tubes that contained 25ml of the concentrated phytoplankton medium. Three controls, test tubes containing the concentrated phytoplankton medium without tunicates, and a blank containing “plankton free” seawater were also part of the experiments.

During the experiments, the individual tunicates were observed and rated according to their apparent health and filtration activity. Healthy activity was demonstrated by fully extended siphons and movement of the siphons. The tunicates were assigned a “1” rating if they appeared to be healthy and immediately started filtering when immersed in the phytoplankton medium. They were assigned a “2” rating if they appeared healthy and started filtering after 10 minutes. The tunicates that were not filtering and appeared to have compromised health were assigned a “3” rating.

The experiments were timed and chlorophyll-a readings were taken at 1 and 2 hours. Intermittently, the tunicates were carefully removed from the test tubes and held in the filtered “plankton free” seawater while the concentrated medium was stirred by swirling or a vortex mixer to resuspend potentially settled phytoplankton. At the completion of the experiments, the tunicates were evaluated for avoidance response to determine health. If the tunicates contracted their siphons when touched, a positive avoidance response was recorded.
showing good health, if the siphons did not contract when touched or were constantly contracted they were deemed in poor health or dead.

Utilizing the chlorophyll-a readings of the controls and blank as correction factors, the tunicate chlorophyll uptake rate was determined from the acquired 1 and 2 hour chlorophyll-a readings. A substantial reduction of chlorophyll concentration was evident for most of the tunicates (Figures 2 and 3). However, confidence in the calculated uptake rate was low. The primary weakness of the chlorophyll uptake experiments was the potential for phytoplankton settling. In addition, unreliable results may have been caused by excretion effects. Attempts were made to determine the chlorophyll content of the excreted material, however, these proved inconclusive. Results from the chlorophyll uptake experiments are reported below, however, as stated earlier, confidence in these results is low.

In contrast, a pumping rate experiment, performed to determine the volume of water an individual *B. digonas* can filter in a specific time period, resulted in filtration rates with high confidence. These rates will be used later to estimate the potential impact of *B. digonas* on Tampa Bay chlorophyll concentrations. Tunicates to be used in the pumping rate experiment were collected on February 1, 1994 from station COT18 in Hillsborough Bay. Ambient seawater was collected and filtered in the field as described above. In the laboratory, ten individual tunicates were measured for size and washed in filtered seawater and placed in a 2 gallon aquarium filled with “plankton free” seawater. Measurements were carefully taken to determine the length of the incurrent siphon and the inner diameter of the siphon once the tunicates started feeding and extended their siphons. These measurements were used to determine the volume of the incurrent siphon using the equation: \( V[\text{mls}] = (l[\text{mm}])(\pi r^2[\text{mm}]) \), where \( V \) is the volume of the siphon [mls], \( l \) is the length of the siphon [mm], and \( r \) is the inner radius of the siphon [mm].

Following these measurements, minute, near neutral density pellets of epiphytic microalgae, barely visible to the naked eye, were released just above the incurrent siphon, as shown in Figure 4. The tunicates readily ingested the microalgae pellets and the pellets could be observed as they traveled down the siphon and into the body cavity. The travel time of the food pellet was measured as it moved from the top of the siphon to the beginning of the body cavity. The experimental design is shown in Figure 5. Pumping rates were calculated by multiplying the volume of the incurrent siphon by the travel time through the siphon, \( (\text{Pumping Rate [ml/s]} = \text{Volume [ml]} \times \text{Time [s]}) \). The pumping rate experiment gave results with high confidence and rates that are comparable with the literature values reported by Goodbody (1974).

Additional laboratory experiments have been conducted to learn more about the potential impact of *B. digonas* on the Tampa Bay phytoplankton population. Attempts were made to determine filtration rates using flumes and dyes. However, due to poor health and/or premature death of the tunicates, these experiments yielded uncertain results. Also, *B. digonas* eggs have been collected in the field, brought to the laboratory and allowed to hatch. However, the hatched juveniles only survived a few days, never developing to adults.
Statistical Analyses:

Tampa Bay water quality information collected by the BSG was analyzed together with *B. digonas* biomass information to determine potential important water quality parameters that may influence the seasonality and abundance of the tunicate. Statistical routines included in SYSTAT v7.0 were used for these analyses.

First, scatter plots were generated for each of the seven monitoring stations for water quality and *B. digonas* data collected during the study period September 1996 through March 1998. Only data collected during the months of October through May, the season when *B. digonas* generally is present in Tampa Bay, were used in these analyses. The scatter plots were used to examine for correlations between *B. digonas* biomass (TUNWWT, g wet weight/m²), Secchi depth (SD, m), water column light attenuation (k, m⁻¹), bottom water temperature (TEMPB, °C), bottom water salinity (SALB, ppt), bottom water dissolved oxygen concentrations (DOB, mg/l), bottom water turbidity (NTUB), bottom water ammonia concentrations (NH₃B, uM), and bottom water chlorophyll-a concentrations (CHLM₃B, ug/l). Following examinations of the scatter plots, principal component analyses (PCA) were performed for each of the seven stations on the water quality parameters described above (excluding tunicate biomass) to summarize the variance on measured water quality parameters into a few water quality related components. The generated first two principal components (PC1 and PC2) were then regressed against *B. digonas* biomass to examine for associations between the tunicate and water quality related components.

Additional scatter plots were generated for Hillsborough Bay stations COT17 and COT18 for water quality and *B. digonas* information dating back to December 1987. The data were grouped for the two stations and only data collected when *B. digonas* was present were used in these analyses. The scatter plots were used to examine for correlations between *B. digonas* biomass and the water quality parameters listed above. Principal component analyses (PCA) were performed on the water quality parameters described above (excluding ammonia, water column light attenuation coefficient, and tunicate biomass) to summarize the variance on measured water quality parameters into a few water quality related components. The generated the first two principal components (PC1 and PC2) were then regressed against *B. digonas* biomass to examine for associations between the tunicate and water quality related components.

Further, scatter plots were generated for grouped data from stations COT4, COT23, and COT40 for the months of October through February for the study period September 1996 through March 1998. These scatter plots compared *B. digonas* biomass with phytoplankton abundance (PHYTOPL, cells/ml) and with the abundance of other types of benthic filter feeding organisms including, bivalves (BIV), amphipods (AMP), and the branchiopod *G. pyramidata* (GLO), all measured as individuals/m².

Finally, *B. digonas* biomass versus bottom water temperature was plotted for all stations sampled for the long-term record dating back to 1987.
RESULTS

Water Quality and *B. digonas* Abundance and Biomass:

Results from water quality and *B. digonas* abundance measurements from the seven monitoring stations for the study period September 1996 through March 1998 are illustrated below in Figures 6 through 16 (also see Appendix A through C).

Temperature (Figure 6):
There is very little variation between the surface and bottom temperature at each station. The expected seasonal variation is evident.

Salinity (Figure 7):
Generally, there is little variation in the surface and bottom salinity at each station. However, there is evidence of freshwater lensing at stations COT4, COT17, COT19, and COT20 as a result of the unusually high rainfall recorded in the fall and winter of 1997, and early spring of 1998. The reduced water column salinity as a result of the rainfall is evident at all stations.

Secchi Depth (Figure 8):
There is considerable temporal variation of Secchi depth at all stations. Generally, Secchi depths at stations COT23 and COT40 are greater than those reported at the Hillsborough Bay stations.

Dissolved Oxygen (Figure 9):
Generally, there is little difference between the surface and bottom dissolved oxygen (DO) at each station during the first nine months of the study. The surface DO began to increase in the summer of 1997 and this general trend continued through the end of the study in March 1998. However, the bottom DO at the Hillsborough Bay stations, except station COT18, began to diverge from the trends seen in the surface DO and were characterized by wide amplitude variations between sampling events. In spite of the variations seen in the bottom DO at these stations, a general trend of increasing bottom DO occurred in the fall and winter 1997, and early spring 1998. The surface and bottom DO at stations COT23 and COT40 were generally similar throughout the study. Both stations had increasing DO following the spring of 1997, similar to the Hillsborough Bay stations.

pH (Figure 10):
Substantial variations in pH were found at all seven monitoring stations over the study period. Generally, surface and bottom pH were very similar at all stations for the first nine months of the study, however, for the second half, surface and bottom pH occasionally diverged, particularly at station COT4 in Hillsborough Bay.
Ammonia Nitrogen (Figure 11):
Surface and bottom NH$_3$-N were similar at all stations throughout the study. There were periodic episodes of increased surface and bottom NH$_3$-N in the Hillsborough Bay stations, particularly in the second half of the study. In contrast, NH$_3$-N at stations COT23 and COT40 was relatively stable.

Water Column Light Extinction (Figure 12):
Water column light extinction (k) varied at all stations, however, the variability was most pronounced in Hillsborough Bay. In addition, there was a trend of increasing k during the study period at all stations except station COT40.

Surface and Bottom Chlorophyll-a (Figure 13):
Surface and bottom chlorophyll-a concentrations were similar at all stations. Chlorophyll-a varied temporally at all stations, however, the amplitude was greater at the Hillsborough Bay stations compared to stations COT23 and COT40. A period of low chlorophyll-a in the late fall to early winter of 1997 was followed by an increase in the late winter to early spring of 1998. This increase was most pronounced in Hillsborough Bay.

Total Water Column Chlorophyll-a (Figure 14):
Water column chlorophyll-a varied temporally at all stations. All stations had a period of low chlorophyll-a in the late fall to early winter of 1997 that was followed by an increase in the late winter to early spring of 1998.

*B. digonas* Abundance (Figure 15):
*B. digonas* abundance was seasonal with the tunicate present in the cooler months and absent in the warmer months. Juvenile *B. digonas* were present at all stations, except COT 20, for both winter seasons. Juveniles were only found in 1996 at COT20. The greatest density of juveniles found during the sampling period was nearly 12,000 individuals/m$^2$ at station COT17 during the 1996-97 winter season. Adult *B. digonas* were found at all stations except COT20, however, the tunicate was only found at stations COT17, COT18, and COT40 during both winter seasons. The highest density of adult tunicates was found at COT17 during the 1996-97 winter season (about 2,000 individuals/m$^2$).

*B. digonas* Biomass vs. Near Bottom Chlorophyll-a; September 1996-March 1998 (Figure 16):
Generally, low concentrations of near bottom chlorophyll-a were found when tunicates were present. However, the lowest chlorophyll-a concentrations measured during the study period at stations COT19, COT20, and COT23 occurred when tunicates were absent. Further, the highest chlorophyll concentration found at station COT19 (45μg/l
in the fall 1997) occurred when tunicates were present, although the biomass was very low.

Results from the the long-term *B. digonas* study, starting as early as 1987 for stations COT17 and COT18, are illustrated below in Figures 17 through 25.

*B. digonas* Biomass vs. Monthly Mean Bottom Temperature for all Stations; 1987-1998 (Figure 17): Generally, *B. digonas* is present during the cooler months of the year. Biomass increases when the water temperature decreases in the fall. Biomass reaches maximum during December and is followed by a decrease in subsequent months as water temperature increases. *B. digonas* has not been found in June, July, August, or September.

*B. digonas* Biomass vs. Bottom Temperature for all Stations; 1987-1998 (Figure 18): *B. digonas* was found when the bottom temperature ranged between 14°C to 28°C and the highest biomass was found in the 15°C to 25°C range.

*B. digonas* Biomass vs. Near Bottom Chlorophyll; Station COT4, 1989-1998 (Figure, 19): Near bottom chlorophyll-a varied temporally over the sampling period. *B. digonas* was present in the winter seasons of 1989-90 and 1997-98 during periods of low chlorophyll-a. However, *B. digonas* was absent during several periods of low chlorophyll-a.

*B. digonas* Biomass vs. Near Bottom Chlorophyll; Station COT17, 1989-1998 (Figure 20): *B. digonas* was present in the winter seasons of all years of the study period. The lowest annual chlorophyll-a concentrations were generally found when the tunicate was present.

*B. digonas* Biomass vs. Near Bottom Chlorophyll; Station COT18, 1989-1998 (Figure 21): *B. digonas* was present in the winter seasons of all years of the study period. The lowest annual chlorophyll-a concentrations were generally found when the tunicate was present.

*B. digonas* Biomass vs. Near Bottom Chlorophyll; Station COT19, 1992-1998 (Figure 22): *B. digonas* was present during the winter seasons of all years of the study period, often coinciding with periods of low chlorophyll. However, several periods of low chlorophyll-a occurred when *B. digonas* was absent.

*B. digonas* Biomass vs. Near Bottom Chlorophyll; Station COT20, 1992-1998 (Figure 23): *B. digonas* was present during the winter seasons 1992-93 through 1996-97, generally coinciding with periods of low chlorophyll. However, several periods of low chlorophyll-a occurred when *B. digonas* was absent.
**B. digonas** Biomass vs. Near Bottom Chlorophyll; Station COT23, 1995-1998 (Figure 24):

*B. digonas* was present during the winter seasons 1995-96 and 1997-98 coinciding with periods of low chlorophyll. However, several periods of low chlorophyll-a occurred when *B. digonas* was absent.

**B. digonas** Biomass vs. Near Bottom Chlorophyll, Station COT40, 1992-1998 (Figure 25):

*B. digonas* was present during the winter seasons 1992-93, 1996-97, and 1997-98 coinciding with periods of low chlorophyll. However, several periods of low chlorophyll-a occurred when *B. digonas* was absent.

Phytoplankton Abundance and Taxonomic Composition:

Phytoplankton abundance and taxonomic composition results for stations COT4, COT23, and COT40 are shown in Figures 26 through 31 (also see Appendix D). Taxonomic composition is limited to four major phytoplankton groups: blue-green algae, diatoms, phytoflagellates, and green algae.

Total Phytoplankton Abundance at Station COT4; September 1996 through March 1998 (Figure 26):

Diatoms were most common. Maximum diatom densities reached 40,000 cells/ml in February and July 1997. A seasonal trend was not apparent.

Total Phytoplankton Abundance at Station COT23; September 1996 through March 1998 (Figure 27):

Diatoms and phytoflagellates were most common. Maximum diatom densities reached 14,000 cells/ml in February 1997 and phytoflagellates reached about 7,000 cells/ml in March 1998. Total phytoplankton abundance was greatest in late winter.

Total Phytoplankton Abundance at Station COT40; September 1996 through March 1998 (Figure 28):

Diatoms and phytoflagellates were most common. Maximum diatom densities reached 7,000 cells/ml in November 1997 and phytoflagellates reached near 7,000 cells/ml in September 1996 and January 1998. No seasonal trend was apparent.

Percent Composition of Major Phytoplankton Groups at Station COT4; September 1996 through March 1998 (Figure 29):

Diatoms and phytoflagellates generally dominated the phytoplankton population. Blue-green algae contributed more than 10 percent of the total population in April and October of 1997.
Percent Composition of Major Phytoplankton Groups at Station COT23; September 1996 through March 1998 (Figure 30):
Phytoflagellates most often dominated the phytoplankton population. Blue-green algae contributed a large fraction of the total population in the fall of 1997.

Percent Composition of Major Phytoplankton Groups at Station COT40; September 1996 through March 1998 (Figure 31):
Phytoflagellates and diatoms dominated the phytoplankton population. Blue-green algae contributed a relatively small fraction of the total population.

Spatial Distribution of *B. digonas* in Tampa Bay:

The Tampa Bay-wide distribution of the tunicate *B. digonas* has been determined each winter season from 1994 through 1998. Results from approximately 543 benthic dredge samples (Tables 1 and 2) were used to construct the maps of annual tunicate distribution. In each year, *B. digonas* was found in three major subsections of Tampa Bay: Hillsborough Bay, Middle Tampa Bay, and Old Tampa Bay. In the 1994-95 winter season, *B. digonas* was found extensively in Hillsborough Bay, Middle Tampa Bay, and the northern half of Old Tampa Bay (Figure 32). However, in the 1995-96, 1996-97, and 1997-98 winter seasons (Figures 33, 34, and 35) the spatial distribution was more limited. Further, there was an apparent boundary for tunicate distribution established from these surveys. *B. digonas* was generally not found south of a line between Coquina Key in Pinellas County to Little Cockroach Bay in Hillsborough County.

Chlorophyll Uptake and Pumping Rate Experiments:

Results from the chlorophyll-a uptake experiments by *B. digonas* are presented in Table 3. In the initial experiment, conducted on November 15, 1996, chlorophyll-a uptake was estimated to be 7.05μg/l over a two hour period. Chlorophyll-a uptake results from additional experiments conducted on January 15 and 16, 1997 (Tables 4 and 5 and Figures 2, 3, 36, and 37) were 13.73μg/l/hr and 16.04μg/l/hr, respectively. As previously noted, the confidence of the chlorophyll-a uptake rates is low due experimental shortcomings.

Results from the pumping rate experiment, conducted on February 1, 1994, are shown in Table 6. The pumping rate was estimated to be 227ml/hr/g wet weight for the average size (20mm in diameter) *B. digonas* used in the experiment. However, the average sized *B. digonas* found in Tampa Bay was about 12mm in diameter and individuals of this size were estimated to pump approximately 48.9ml/hr/g wet weight. These pumping rates fall within the range reported for other ascidians (Goodbody 1974).
Statistical Analyses:

Scatter plots generated for each of the seven monitoring stations for data collected during the months October through May for the study period September 1996 through March 1998 are shown in Figures 38 through 44 (also see Appendix E Table 1). Each station figure contains eight separate scatter plots which examine the relationships between biomass of the tunicate *B. digonas* and measured water quality parameters (Secchi depth [SD], water column light attenuation [k], bottom water temperature [TEMPB], bottom water salinity [SALB], bottom water dissolved oxygen concentrations [DOB], bottom water turbidity [NTUB], bottom water ammonia concentrations [NH3B], and bottom water chlorophyll-a concentrations [CHLM3B]). Units of the water quality parameters are listed on Page 8.

Figure 38. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT4:

*B. digonas* biomass versus SD.
No significant correlation was found between these parameters.

*B. digonas* biomass versus TEMPB.
No significant correlation was found between these parameters. However, the highest tunicate biomass was recorded when the temperature was relatively low.

*B. digonas* biomass versus SALB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus DOB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus NTUB.
No significant correlation was found between these parameters. However, the lowest turbidities were generally measured when the tunicate had the greatest biomass.

*B. digonas* biomass versus NH3B.
A significant correlation (p<0.05) was found between these parameters. The tunicate had the greatest biomass when ammonia concentrations were the highest.

*B. digonas* biomass versus CHLM3B.
No significant correlation was found between these parameters. However, the lowest chlorophyll-a concentration was measured when the tunicate was most abundant.
B. digonas biomass versus k.
No significant correlation was found between these parameters. However, a relatively high water column attenuation coefficient (low water transparency) was measured when the tunicate had the greatest biomass.

Figure 39. Scatter plots of B. digonas biomass versus water quality parameters for station COT17:

B. digonas biomass versus SD.
No significant correlation was found between these parameters. However, the deepest Secchi depth was measured when the tunicate had the greatest biomass.

B. digonas biomass versus TEMPB.
No significant correlation was found between these parameters. Generally, the tunicate appears most abundant when temperatures are low.

B. digonas biomass versus SALB.
No significant correlation was found between these parameters. However, the highest salinity was measured when the tunicate had the greatest biomass.

B. digonas biomass versus DOB.
No significant correlation was found between these parameters.

B. digonas biomass versus NTUB.
No significant correlation was found between these parameters. However, the lowest turbidities were generally measured when the tunicate had the greatest biomass.

B. digonas biomass versus NH$_3$B.
No significant correlation was found between these parameters.

B. digonas biomass versus CHLM$^3$B.
No significant correlation was found between these parameters. However, the lowest chlorophyll-a concentrations were generally measured when the tunicate had the greatest biomass.

B. digonas biomass versus k.
A significant correlation (p<0.05) was found between these parameters. The lowest water column attenuation coefficient was measured when the tunicate had the greatest biomass.
Figure 40. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT18:

*B. digonas* biomass versus SD.
A significant correlation (p<0.05) was found between these parameters. The tunicate had the greatest biomass during periods when relatively deep SD were measured.

*B. digonas* biomass versus TEMPB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus SALB.
No significant correlation was found between these parameters. The tunicate was not found when the salinity was below 15ppt.

*B. digonas* biomass versus DOB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus NTUB.
No significant correlation was found between these parameters. However, low turbidities were generally measured when the tunicate had the greatest biomass.

*B. digonas* biomass versus NH$_3$B.
No significant correlation was found between these parameters.

*B. digonas* biomass versus CHL$_{M}$B.
No significant correlation was found between these parameters. However, the lowest chlorophyll-a concentrations were generally measured when the tunicate had the greatest biomass.

*B. digonas* biomass versus k.
A significant correlation (p<0.05) was found between these parameters. The lowest water column attenuation coefficient was measured when the tunicate had the greatest biomass.

Figure 41. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT19:

Extremely low biomass of the tunicate were recorded for this station for both the 1996-97 and 1997-98 winter seasons. No significant correlations were found between tunicate biomass and the water quality parameters measured. Potential relationships that may be suggested in Figure 41 are most probably fortuitous and will not be discussed further.
Figure 42. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT20:

Extremely low biomass of the tunicate were also recorded for this station for both the 1996-97 and 1997-98 winter seasons. Significant correlations were found both for Secchi depth (p<0.01) and the attenuation coefficient (p<0.05), suggesting increasing water clarity with increasing *B. digonas* biomass. However, due to the very low tunicate biomass these correlations are most probably fortuitous.

Figure 43. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT23:

*B. digonas* biomass versus SD.
No significant correlation was found between these parameters. However, the greatest tunicate biomass was found concurrent with the deepest SD.

*B. digonas* biomass versus TEMPB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus SALB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus DOB.
No significant correlation was found between these parameters.

*B. digonas* biomass versus NTUB.
No significant correlation was found between these parameters. However, the greatest tunicate biomass was found concurrent with relatively low turbidity.

*B. digonas* biomass versus NH$_3$B.
No significant correlation was found between these parameters.

*B. digonas* biomass versus CHLM$^3$B.
No significant correlation was found between these parameters. However, low chlorophyll-a concentrations were generally measured when the tunicate was present.

*B. digonas* biomass versus k.
No significant correlation was found between these parameters.

Figure 44. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT40:
*B. digonas* biomass versus SD.

A significant correlation (p<0.01) was found between these parameters. The greatest tunicate biomass was generally found concurrent with the deep SD readings.

*B. digonas* biomass versus TEMPB.

No significant correlation was found between these parameters. However, temperature was generally low when the tunicate was present.

*B. digonas* biomass versus SALB.

No significant correlation was found between these parameters. However, salinity was consistently above 20ppt when the tunicate was present.

*B. digonas* biomass versus DOB.

No significant correlation was found between these parameters.

*B. digonas* biomass versus NTUB.

No significant correlation was found between these parameters. However, the greatest tunicate biomass was found concurrent with the lowest turbidity.

*B. digonas* biomass versus NH$_3$.B.

No significant correlation was found between these parameters.

*B. digonas* biomass versus CHLM$^3$.B.

No significant correlation was found between these parameters. However, the lowest chlorophyll-a concentrations were measured when the tunicate was present.

*B. digonas* biomass versus k.

A significant correlation (p<0.05) was found between these parameters. The lowest water column attenuation coefficients (high water clarity) were measured when the tunicate had the greatest biomass.

Results from principal component analyses for each of the seven stations for the study period September 1996 through March 1998 are illustrated in Figures 45 through 51 (also see Appendix E Table 2). Each station figure contains two graphs in which the first two water quality principal components (PC1 or PC2) have been regressed against biomass of the tunicate *B. digonas*. The left graph shows the relationship between tunicate biomass and the water quality related principal component PC1 and the right graph the same relationship but for principal component PC2.
Figure 45. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT4:

The principal component PC1 is strongly affected by water quality parameters related to water clarity, including chlorophyll-a, water column light attenuation and Secchi depth. Water clarity increases with increasing values of PC1. Regression analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by salinity and turbidity and is difficult to interpret in terms of relationship to tunicate biomass. Regression analysis between biomass of the tunicate and PC2 did not yield a significant correlation.

Figure 46. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT17:

The principal component PC1 for station COT17 is also strongly affected by water quality parameters related to water clarity, including chlorophyll-a, water column light attenuation and Secchi depth. Water clarity increases with increasing values of PC1. Regression analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by salinity, temperature, and turbidity and is difficult to interpret ecologically. These parameters increase in value with decreasing PC2. The regression between biomass of the tunicate and PC2 did not yield a significant correlation.

Figure 47. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT18:

The principal component PC1 for station COT18 is also strongly affected by water quality parameters related to water clarity, including chlorophyll-a, water column light attenuation and Secchi depth. Water clarity increases with decreasing values of PC1. Regression analysis between the biomass of the tunicate *B. digonas* and PC1 yielded a significant correlation (p<0.05).

The principal component PC2 is most strongly affected by temperature and salinity and is difficult to interpret ecologically. These parameters increase in value with decreasing PC2. The regression between tunicate biomass and PC2 did not yield a significant correlation.

Figure 48. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT19:

The principal component PC1 for station COT19 is strongly affected by water quality parameters related to water clarity, including water column light attenuation and Secchi depth. Water clarity increases with decreasing values of PC1. The regression
analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by ammonia concentrations and turbidity and is difficult to interpret ecologically. These parameters increase in value with an increase in PC2. The regression between tunicate biomass and PC2 did not yield a significant correlation.

**Figure 49. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT20:**

The principal component PC1 for station COT20 is strongly affected by water quality parameters related to water clarity, including water column light attenuation and Secchi depth, but also to salinity. Water clarity increases and salinity decreases with decreasing values of PC1. The regression analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by turbidity. Turbidity increases in value with an increase in PC2. The regression between tunicate biomass and PC2 yielded a significant correlation (p<0.05).

**Figure 50. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT23:**

The principal component PC1 for station COT20 is strongly affected by salinity and dissolved oxygen concentration. Salinity increases and oxygen concentration decreases with increasing values of PC1. The regression analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by Secchi depth. Secchi depth increases in value with an increase in PC2. The regression between tunicate biomass and PC2 did not yield a significant correlation.

**Figure 51. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT40:**

The principal component PC1 for station COT40 is most strongly affected by temperature and oxygen concentration. Temperature increases and oxygen concentration decreases with increasing values of PC1. The regression analysis between biomass of the tunicate *B. digonas* and PC1 did not yield a significant correlation.

The principal component PC2 is most strongly affected by salinity. Salinity increases in value with a decrease in PC2. The regression between tunicate biomass and PC2 did not yield a significant correlation.
Scatter plots generated for the grouped data dating back to December 1987 for the Hillsborough Bay stations COT17 and COT18 are shown in Figure 52 (also see Appendix E Table 3). This figure contains eight separate scatter plots which illustrate the relationships between biomass of the tunicate *B. digonas* and measured water quality parameters (Secchi depth [SD], water column light attenuation [k], bottom water temperature [TEMPB], bottom water salinity [SALB], bottom water dissolved oxygen concentrations [DOB], bottom water turbidity [NTUB], bottom water ammonia concentrations [NH₃B], and bottom water chlorophyll-a concentrations [CHLM³B]). Units of the water quality parameters are listed on Page 8.

Figure 52. Scatter plots of grouped data from stations COT17 and COT18:

*B. digonas* biomass versus SD.
A significant positive correlation (p<0.01) exists between these parameters.

*B. digonas* biomass versus TEMPB.
No significant correlation was found between these parameters. However, the highest tunicate biomass was generally recorded when the temperature was relatively low.

*B. digonas* biomass versus SALB.
A significant positive correlation (p<0.01) exists between these parameters. The highest tunicate biomass was recorded during periods of high salinity.

*B. digonas* biomass versus DOB.
No significant correlation was found between these parameters. However, tunicate biomass was highest when dissolved oxygen concentrations near the bottom ranged from 6mg/l to 8mg/l.

*B. digonas* biomass versus NTUB.
A significant negative correlation (p<0.01) exists between these parameters. The tunicate had the greatest biomass when turbidity levels were low.

*B. digonas* biomass versus NH₃B.
No significant correlation was found between these parameters. However, the tunicate had the greatest biomass when ammonia concentrations were the low.

*B. digonas* biomass versus CHLM³B.
A significant negative correlation (p<0.01) exists between these parameters. The lowest chlorophyll-a concentrations were generally measured when the tunicate had the greatest biomass.
**B. digonas** biomass versus k.

A significant negative correlation (p<0.05) exists between these parameters. Relatively low water column attenuation coefficients (high water transparency) were recorded when the tunicate was at the greatest biomass.

Results from principal component analyses for the grouped data from Hillsborough Bay stations COT17 and COT18 dating back to 1987 are illustrated in Figure 53 (also see Appendix E Table 4). The figure contains two graphs in which the first two water quality principal components (PC1 or PC2) have been regressed against biomass of the tunicate **B. digonas**. The left graph shows the relationship between tunicate biomass and the water quality related principal component PC1 and the right graph the same relationship but for principal component PC2.

Figure 53. Grouped data from stations COT17 and COT18 showing **B. digonas** biomass versus PC1 and PC2:

The principal component PC1 is strongly affected by water quality parameters related to water clarity, including Secchi depth, turbidity, and chlorophyll-a concentrations. Regression analysis between **B. digonas** biomass and PC1 yielded a significant positive correlation (p<0.01).

The principal component PC2 is most strongly affected by dissolved oxygen concentrations and water temperature. Dissolved oxygen concentrations decrease and water temperature increases with increasing values of PC2. Regression analysis between biomass of the tunicate and PC2 did not yield a significant correlation.

The principal components scores for the grouped COT17 and COT18 data were also plotted against the measured **B. digonas** biomass values to examine for groupings of high tunicate biomass (Figure 54). The variance explained by each PC, expressed as percentage of total variance is given in parentheses. Figure 54 clearly shows that **B. digonas** biomass is greatest when PC1 scores are high, indicating a positive association between **B. digonas** biomass and water clarity.

Scatter plots generated for grouped data from stations COT4, COT23, and COT40 for the months of October through February for the study period September 1996 through March 1998 are shown in Figure 55 (also see Appendix E Table 5). The figure contains four separate scatter plots that illustrate the relationship between **B. digonas** biomass and the abundance of other organisms identified, including phytoplankton (PHYTOPL), bivalves (BIV), amphipods (AMP), and the branchiopod **G. pyramidata** (GLO). Abundance is reported as individuals/m².
Figure 55. Scatter plots of *B. digonas* biomass versus the abundance of other organisms identified for grouped data from station COT4, COT23, and COT40:

*B. digonas* biomass versus phytoplankton (PHYTOPL) abundance.
   No significant correlation was found between these parameters. However, the greatest tunicate biomass appears to coincide with low phytoplankton abundance.

*B. digonas* biomass versus bivalves (BIV) abundance.
   No significant correlation was found between these parameters. However, the greatest tunicate biomass appears to coincide with low bivalve abundance.

*B. digonas* biomass versus amphipod abundance.
   No significant correlation was found between these parameters. However, the greatest tunicate biomass appears to coincide with low amphipod abundance.

*B. digonas* biomass versus *Glottidia pyramidata* (GLO) abundance.
   No significant correlation was found between these parameters.

**DISCUSSION**

The City of Tampa Bay Study Group (BSG) has investigated water quality and biological indicators, including phytoplankton biomass in Tampa Bay since 1978. These studies were designed to evaluate the response of the measured parameters to nutrient pollution abatement, primarily caused by the upgrade of the City of Tampa’s wastewater treatment plant to state-of-the-art nitrogen removal in 1979.

Definite indications of improved water quality and reduced eutrophication were noted approximately two years after the wastewater plant conversion, including a large annual decrease in phytoplankton biomass (chlorophyll-a concentration) and increased water transparency (Johansson 1991). These improvements have primarily been attributed to the reduction in nitrogen discharges that resulted from the wastewater plant upgrade.

Seasonal examination of the water quality data collected prior to, and post to, the observed water quality improvements indicate that improvements mainly resulted from reduced phytoplankton biomass during the late summer and fall, the usual period of maximum phytoplankton biomass. The large reduction in chlorophyll-a concentrations that apparently occurred as a result of reduced nitrogen discharges suggests that Tampa Bay phytoplankton biomass during the warm period of the year primarily is driven by the nutrient supply (bottom-up control). In contrast, relatively small changes in winter season chlorophyll-a concentrations were noted following the nitrogen reductions, suggesting that grazing by pelagic and benthic secondary producers, or top-down control, may be the dominant factor.
controlling winter season phytoplankton biomass. Studies in other marine and freshwater systems have shown that filter feeding organisms often act as a natural control of eutrophication and may be linked to improvements in water quality (see introduction).

Extremely high water clarity was observed in the vicinity of dense beds (near 10,000 individuals/m²) of the benthic tunicate Bostrichobranchus digonas in Hillsborough Bay in January 1986. This field observation supported the hypothesis discussed above that grazing by secondary producers may control winter season chlorophyll-a concentrations in Tampa Bay. The observation prompted the BSG to initiate a study in 1987 to investigate the temporal and spatial distribution of B. digonas in Tampa Bay and to attempt to link variations in winter season chlorophyll-a concentrations to the distribution and biomass of the tunicate.

Results from this study suggest that a statistically significant link exists between B. digonas biomass and measured parameters that relate to water clarity, including chlorophyll-a concentrations and specific measurements of water transparency, at stations COT17 and COT18 in Hillsborough Bay. These stations have the longest monitoring record of the seven stations studied. Figures 53 and 54 summarize data collected at stations COT17 and COT18 since 1987, and show that high tunicate biomass generally concurs with high water clarity. These results strongly imply that B. digonas, at least locally, has a controlling effect on chlorophyll-a concentrations or phytoplankton biomass.

Data collected during the last two years from the seven Tampa Bay stations do not show the same strong relationship between B. digonas biomass and water clarity. Biomass was generally considerably lower during this period than during several previous years (see Figures 20 through 25). However, a positive trend exists between tunicate biomass and water clarity for the stations that had the greatest amounts of tunicates present during the two most recent winter seasons.

Comparisons between B. digonas information and the physical parameters, water temperature and salinity, suggest that these parameters are important in determining the temporal and spatial distribution of the tunicate in Tampa Bay. B. digonas has been found in the bay during the months of October through May. During this period, water temperatures generally range between 15°C to 25°C. Although the tunicate is present over a relatively wide temperature range, maximum biomass is generally found during early winter, most often in November and December, as the temperature decreases from relatively high late fall temperatures. Therefore, it appears that decreasing water temperatures in early winter “trigger” the hatching of B. digonas eggs located on the surface of bay sediments. As noted earlier in this report, hatching of B. digonas eggs have been accomplished in the laboratory by bringing eggs collected in the summer, at ambient temperatures of near 30°C, and placing them in water baths maintained at laboratory room temperatures of approximately 22°C to 24°C. These laboratory observations support the decreasing temperature “trigger” theory.
High *B. digonas* biomass is generally found in a relatively narrow salinity window (ranging between 23ppt to 29ppt), that is typical of upper Tampa Bay dry season conditions. Based on this salinity range and the long-term Tampa Bay salinity distribution, measured by the Hillsborough Environmental Protection Commission (EPC), *B. digonas* would not be expected to occur regularly south of a line drawn from Little Cockroach Bay in Hillsborough County to Coquina Key in Pinellas County. Winter season salinity in areas south of this line often exceeds 29ppt. The spatial distribution of *B. digonas* determined from benthic trawls in all major areas of Tampa Bay during the winter seasons (1994-95 through 1997-98; see Figures 32 through 35) confirms this line as an apparent limit of distribution. In contrast, there does not appear to be a similar definite spatial distribution limit associated with low salinity, because the tunicate is regularly found in the upper most reaches of both Hillsborough Bay and Old Tampa Bay. However, the low *B. digonas* biomass found during the 1997-98 winter season may be related to the unusually low salinity present in the Tampa Bay as a result of the heavy winter rains associated with the strong El Nino weather phenomena. Several areas in upper Tampa Bay had well developed tunicate beds (including areas in Hillsborough Bay, Old Tampa Bay and Middle Tampa Bay) prior to record rains, starting in mid December 1997 and lasting through mid March 1998, that drastically reduced salinity bay-wide. For example, bottom salinity at station COT23 in Middle Tampa Bay in January 1998 reached a low of 17.5ppt. The lowest bottom salinity the EPC has recorded in this area of Tampa Bay since 1974 is 17.2ppt, which was measured in 1979. Following the salinity reduction, a limited amount of tunicates persisted in a small area of Middle Tampa Bay until the end of January 1998. *B. digonas* has not been recorded at the seven monitoring stations or caught in benthic trawls since the beginning of February 1998.

Comparisons between *B. digonas* biomass and the abundance of phytoplankton and other benthic organisms, including bivalves, amphipods, and the branchiopod *Glottidia pyramidata* did not yield any statistically significant relationships. However, with the exception of *G. pyramidata*, there appears to be a trend suggesting that the abundance of phytoplankton, bivalves, and amphipods is low when the tunicate biomass is near maximum. The reason for low phytoplankton abundance when tunicate biomass is high has already been discussed and can be explained as a result of direct impacts on the phytoplankton population by tunicate feeding. An explanation why bivalves and amphipods appear to be less abundant when *B. digonas* biomass is high may be that the tunicate out-competes the other organisms for food and/or space. In areas of the northeastern United States that have been invaded by the zebra mussel *Dreissena polymorpha*, not only has phytoplankton biomass been reduced dramatically, but native benthic invertebrates have also declined as a result of direct competition with the zebra mussel for food (Findlay 1996).

Experimentally determined *B. digonas* pumping rates were used together with tunicate biomass and spatial distribution information to calculate the potential volume of bay water *B. digonas* may filter per day during the winter season in the upper three Tampa Bay subsections and also in specific areas within these subsections where tunicates were present.
Calculations were performed for the most recent four winter seasons which had extensive spatial coverage of benthic trawl samples. Results from these calculations can be used to estimate impacts to the phytoplankton community by assuming that the tunicate during feeding removes virtually all phytoplankton from the processed water (see introduction).

The greatest amount of water filtered per day, relative bay subsection volume, was estimated for Hillsborough Bay during the 1995-96 winter season (see Table 7). Approximately 5.5% of the volume in Hillsborough Bay could potentially be filtered by the tunicate each day. Considerably smaller volumes were filtered per day for other subsections and winter seasons. The estimated amount filtered in Hillsborough Bay during the 1995-96 season suggests that its volume could be completely filtered by *B. digonas* in 18 days. This water turn-over rate is relatively slow when compared to phytoplankton growth rates, which usually range between 0.3 to 1.0 doublings per day (Epply 1972). Therefore, based on these calculations and this period of study, it does not appear that bay-wide impacts to the phytoplankton population by *B. digonas* were substantial. On the other hand, local impacts to the phytoplankton community in the areas of tunicate beds may be considerable. For example, during the 1995-96 winter season approximately 62% of the water column above the tunicate beds could potentially be filtered in one day in both Hillsborough Bay and Old Tampa Bay. This filtration rate is similar to, or may possibly exceed, growth rates of the phytoplankton population. Of course, phytoplankton will be supplied to the tunicate areas from surrounding waters, resulting in a reduced overall impact to the phytoplankton above the tunicate beds. The rate of resupply is difficult to account for, nevertheless, the potentially large impacts to the phytoplankton population above the tunicate beds have been substantiated by numerous field observations of extremely clear water in the vicinity of well developed tunicate beds. Further, statistical results from the monitoring program suggest a strong positive association between *B. digonas* biomass and parameters that relate to water clarity, which include phytoplankton biomass (chlorophyll-a), at monitoring stations with an abundant tunicate biomass.

In summary, the data collected for this study strongly support the theory that the tunicate *B. digonas* control phytoplankton biomass in local areas of Tampa Bay during periods of developed tunicate beds. However, it does not appear that bay-wide impacts to the phytoplankton population by *B. digonas* feeding activities are substantial.
LITERATURE CITED


LITERATURE REVIEWED


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Table 1. Total number of benthic trawls and the number of trawls with *B. digonas* present from the major Tampa Bay subsections [Hillsborough Bay (HB), Old Tampa Bay (OTB), Middle Tampa Bay (MTB), and Lower Tampa Bay (LTB)] for the winter seasons of 1994-95 through 1997-98.

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<td>Total Trawls</td>
<td>52</td>
<td>25</td>
<td>28</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>Trawls with <em>B. digonas</em></td>
<td>33</td>
<td>13</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>LTB</td>
<td>Total Trawls</td>
<td>14</td>
<td>1</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Trawls with <em>B. digonas</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 2. Areal coverage (m²) of *B. digonas* in the major Tampa Bay subsections, Hillsborough Bay (HB), Old Tampa Bay (OTB), Middle Tampa Bay (MTB) and Lower Tampa Bay (LTB), for the winter seasons 1994-95 through 1997-98.

<table>
<thead>
<tr>
<th>Bay Subsection</th>
<th>Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>HB</td>
<td>18.61 x 10⁶</td>
</tr>
<tr>
<td>OTB</td>
<td>31.40 x 10⁶</td>
</tr>
<tr>
<td>MTB</td>
<td>51.84 x 10⁶</td>
</tr>
<tr>
<td>LTB</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>101.85 x 10⁶</td>
</tr>
</tbody>
</table>
Table 3. *B. digonas* chlorophyll-a uptake on November 15, 1996. Chlorophyll-a concentration was taken at the beginning and end of the 2hr experiment, and was corrected for the uptake of the controls.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Start ug/l</th>
<th>2hrs ug/l</th>
<th>Uptake ug/l</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tunicate #1</td>
<td>21.82</td>
<td>17.22</td>
<td>4.60</td>
</tr>
<tr>
<td>Tunicate #2</td>
<td>21.82</td>
<td>7.67</td>
<td>14.15</td>
</tr>
<tr>
<td>Tunicate #3</td>
<td>21.82</td>
<td>9.60</td>
<td>12.22</td>
</tr>
<tr>
<td>Tunicate #4</td>
<td>21.82</td>
<td>10.60</td>
<td>11.22</td>
</tr>
<tr>
<td>Tunicate #7</td>
<td>21.82</td>
<td>16.01</td>
<td>5.81</td>
</tr>
<tr>
<td>Tunicate #9</td>
<td>21.82</td>
<td>20.73</td>
<td>1.09</td>
</tr>
<tr>
<td>Tunicate #10</td>
<td>21.82</td>
<td>21.57</td>
<td>0.25</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>21.82</strong></td>
<td><strong>14.77</strong></td>
<td><strong>7.05</strong></td>
</tr>
</tbody>
</table>

Table 4. *B. digonas* chlorophyll-a uptake on January 15, 1997. Chlorophyll-a concentration was taken at the beginning, 1hr, and 2hr periods of the experiment and was corrected for the uptake of the controls.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Start ug/l</th>
<th>1hr ug/l</th>
<th>2hr ug/l</th>
<th>1hr Uptake</th>
<th>2hr Uptake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tunicate #1</td>
<td>31.06</td>
<td>30.89</td>
<td>16.77</td>
<td>0.17</td>
<td>14.29</td>
</tr>
<tr>
<td>Tunicate #2</td>
<td>31.06</td>
<td>21.24</td>
<td>25.86</td>
<td>9.82</td>
<td>5.20</td>
</tr>
<tr>
<td>Tunicate #3</td>
<td>31.06</td>
<td>16.91</td>
<td>10.38</td>
<td>14.15</td>
<td>20.68</td>
</tr>
<tr>
<td>Tunicate #4</td>
<td>31.06</td>
<td>19.33</td>
<td>14.34</td>
<td>11.73</td>
<td>16.72</td>
</tr>
<tr>
<td>Tunicate #5</td>
<td>31.06</td>
<td>18.48</td>
<td>16.49</td>
<td>12.58</td>
<td>14.57</td>
</tr>
<tr>
<td>Tunicate #6</td>
<td>31.06</td>
<td>13.24</td>
<td>7.24</td>
<td>17.82</td>
<td>23.82</td>
</tr>
<tr>
<td>Tunicate #7</td>
<td>31.06</td>
<td>19.09</td>
<td>10.49</td>
<td>11.97</td>
<td>20.57</td>
</tr>
<tr>
<td>Tunicate #8</td>
<td>31.06</td>
<td>13.70</td>
<td>14.25</td>
<td>17.36</td>
<td>16.81</td>
</tr>
<tr>
<td>Tunicate #9</td>
<td>31.06</td>
<td>14.30</td>
<td>11.79</td>
<td>16.76</td>
<td>19.27</td>
</tr>
<tr>
<td>Tunicate #10</td>
<td>31.06</td>
<td>6.12</td>
<td>5.67</td>
<td>24.94</td>
<td>25.39</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>31.06</strong></td>
<td><strong>17.3</strong></td>
<td><strong>13.3</strong></td>
<td><strong>13.73</strong></td>
<td><strong>17.73</strong></td>
</tr>
</tbody>
</table>
Table 5. *B. digonas* chlorophyll-a uptake on January 16, 1997. Chlorophyll-a was taken at the beginning, 30 min, 1 hr, and 2 hr 15 min periods of the experiment. The uptake values were corrected for the uptake of the controls.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Start ug/l</th>
<th>30min ug/l</th>
<th>1 hr ug/l</th>
<th>2 hr ug/l</th>
<th>Uptake 30min ug/l</th>
<th>Uptake 1 hr ug/l</th>
<th>Uptake 2 hr 15min ug/l</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tunicate #1</td>
<td>57.93</td>
<td>55.18</td>
<td>43.07</td>
<td>43.72</td>
<td>2.75</td>
<td>14.86</td>
<td>14.21</td>
</tr>
<tr>
<td>Tunicate #2</td>
<td>57.93</td>
<td>50.74</td>
<td>58.28</td>
<td>38.21</td>
<td>7.19</td>
<td>-0.35</td>
<td>19.72</td>
</tr>
<tr>
<td>Tunicate #5</td>
<td>57.93</td>
<td>50.79</td>
<td>55.18</td>
<td>47.04</td>
<td>7.14</td>
<td>2.75</td>
<td>10.89</td>
</tr>
<tr>
<td>Tunicate #6</td>
<td>57.93</td>
<td>42.28</td>
<td>33.24</td>
<td>24.16</td>
<td>15.65</td>
<td>24.69</td>
<td>33.77</td>
</tr>
<tr>
<td>Tunicate #7</td>
<td>57.93</td>
<td>32.76</td>
<td>33.47</td>
<td>25.08</td>
<td>25.17</td>
<td>24.46</td>
<td>32.85</td>
</tr>
<tr>
<td>Tunicate #8</td>
<td>57.93</td>
<td>36.60</td>
<td>35.85</td>
<td>28.24</td>
<td>21.33</td>
<td>22.08</td>
<td>29.69</td>
</tr>
<tr>
<td>Tunicate #9</td>
<td>57.93</td>
<td>50.62</td>
<td>32.38</td>
<td>20.37</td>
<td>7.31</td>
<td>25.55</td>
<td>37.56</td>
</tr>
<tr>
<td>Tunicate #10</td>
<td>57.93</td>
<td>48.51</td>
<td>43.62</td>
<td>37.83</td>
<td>9.42</td>
<td>14.31</td>
<td>20.10</td>
</tr>
<tr>
<td>Average</td>
<td>57.93</td>
<td>42.62</td>
<td>37.16</td>
<td>29.78</td>
<td>12.00</td>
<td>16.04</td>
<td>24.80</td>
</tr>
</tbody>
</table>

Table 6. Results from the *B. digonas* pumping rate experiment conducted on February 1, 1994. The incurrent siphons of the tunicates were measured for length and diameter. The volume of the siphon was determined by \( V[\text{mls}] = (l[\text{mm}]) \pi r^2[\text{mm}] \). The average time for a food pellet to pass through the incurrent siphon into the body cavity was used to determine the pumping rate by \( \text{Pumping Rate} = (V[\text{ml}])/(T[\text{s}]) \).

<table>
<thead>
<tr>
<th>Tunicate Id #</th>
<th>Incurrent siphon</th>
<th>Volume (ml)</th>
<th>Average Time (s)</th>
<th>Pumping Rate (ml/s)</th>
<th>Pumping Rate (l/24h)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length (mm)</td>
<td>Diameter (mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>16</td>
<td>4.0</td>
<td>0.20</td>
<td>0.87</td>
<td>0.23</td>
</tr>
<tr>
<td>2</td>
<td>17</td>
<td>4.0</td>
<td>0.21</td>
<td>0.62</td>
<td>0.34</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>3.5</td>
<td>0.14</td>
<td>0.83</td>
<td>0.17</td>
</tr>
<tr>
<td>9</td>
<td>21</td>
<td>4.0</td>
<td>0.26</td>
<td>0.78</td>
<td>0.34</td>
</tr>
<tr>
<td>Average</td>
<td>18</td>
<td>3.9</td>
<td>0.21</td>
<td>0.78</td>
<td>0.27</td>
</tr>
</tbody>
</table>
Table 7. The potential volume of bay water (m³) filtered by *B. digonias* for the winter seasons of 1994-95 through 1997-98. Values were based on 12mm diameter tunicates and estimated average biomass (gww/m²) of the tunicate beds for each season. The volume of each bay subsection was determined as 323 x 10⁶ m³ for Hillsborough Bay (HB), 608 x 10⁶ m³ for Old Tampa Bay (OTB), and 1161 x 10⁶ m³ for Middle Tampa Bay (MTB).

<table>
<thead>
<tr>
<th>Season</th>
<th>Bay Subsection</th>
<th>HB</th>
<th>OTB</th>
<th>MTB</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994-95</td>
<td>Area of tunicate beds (m³)</td>
<td>18.61 x 10⁶</td>
<td>31.40 x 10⁶</td>
<td>51.84 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Biomass (gww/m²)</td>
<td>110</td>
<td>110</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>Volume filtered per day (m³/day)</td>
<td>2.35 x 10⁴</td>
<td>3.96 x 10⁴</td>
<td>6.54 x 10⁴</td>
</tr>
<tr>
<td></td>
<td>Days to filter bay</td>
<td>138</td>
<td>154</td>
<td>247</td>
</tr>
<tr>
<td></td>
<td>Days to filter water column over tunicates</td>
<td>25</td>
<td>25</td>
<td>44</td>
</tr>
<tr>
<td>1995-96</td>
<td>Area of tunicates (m³)</td>
<td>8.96 x 10⁴</td>
<td>0.50 x 10⁶</td>
<td>10.47 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Biomass (gww/m²)</td>
<td>1700</td>
<td>1700</td>
<td>1700</td>
</tr>
<tr>
<td></td>
<td>Volume filtered per day (m³/day)</td>
<td>17.7 x 10⁴</td>
<td>0.99 x 10⁶</td>
<td>20.7 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Days to filter bay</td>
<td>18</td>
<td>616</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Days to filter water column over tunicates</td>
<td>1.6</td>
<td>1.6</td>
<td>2.8</td>
</tr>
<tr>
<td>1996-97</td>
<td>Area of tunicates (m³)</td>
<td>5.07 x 10⁴</td>
<td>14.27 x 10⁶</td>
<td>1.00 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Biomass (gww/m²)</td>
<td>87</td>
<td>87</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td>Volume filtered per day (m³/day)</td>
<td>0.52 x 10⁶</td>
<td>1.46 x 10⁶</td>
<td>0.10 x 10⁶</td>
</tr>
<tr>
<td></td>
<td>Days to filter bay</td>
<td>623</td>
<td>417</td>
<td>15772</td>
</tr>
<tr>
<td></td>
<td>Days to filter water column over tunicates</td>
<td>31</td>
<td>31</td>
<td>54</td>
</tr>
<tr>
<td>1997-98</td>
<td>Area of tunicates (m³)</td>
<td>3.32 x 10⁴</td>
<td>3.32 x 10⁴</td>
<td>3.93 x 10⁴</td>
</tr>
<tr>
<td></td>
<td>Biomass (gww/m²)</td>
<td>250</td>
<td>250</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>Volume filtered per day (m³/day)</td>
<td>0.96 x 10⁴</td>
<td>0.96 x 10⁴</td>
<td>1.13 x 10⁴</td>
</tr>
<tr>
<td></td>
<td>Days to filter bay</td>
<td>338</td>
<td>635</td>
<td>1422</td>
</tr>
<tr>
<td></td>
<td>Days to filter water column over tunicates</td>
<td>11</td>
<td>11</td>
<td>19</td>
</tr>
</tbody>
</table>
Figure 1. Location of *Bostrichobranchus digonas* sampling stations in Tampa Bay.
Figure 2. *B. digonas* experimental chlorophyll-a uptake on January 15, 1997. The chlorophyll-a concentrations were taken at the beginning, 1hr, and 2hr periods during the experiment.

Figure 3. *B. digonas* experimental chlorophyll-a uptake on January 16, 1997. Chlorophyll-a concentrations were taken at the beginning, 30min, 1hr, and 2hr15min periods during the experiment.
Figure 4. Photograph of *B. digonas* at the time of a food pellet release near the incurrent siphon during the pumping rate experiment on February 1, 1994.
Figure 5. *B. digonos* pumping rate experimental design. The diameter (d) and the length (l) of the incumbent siphon was measured, as well as, the travel time (t_f-t_i) of the food pellet through the incumbent siphon.
Figure 6. Surface and bottom temperature at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 7. Surface and bottom salinity at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 8. Secchi depth at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 9. Surface and bottom dissolved oxygen concentrations at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 10. Surface and bottom pH values at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 11. Surface and bottom ammonia nitrogen (NH$_3$-N, µmoles) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 12. Water column light extinction (k; m$^{-1}$) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 13. Surface and bottom chlorophyll-a (μg/l) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 14. Water column chlorophyll-a concentrations (mg/m$^3$) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 15. *B. digonas* abundance (individuals/m²) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 16. *B. digonas* biomass (grams wet weight/m²) versus bottom chlorophyll (µg/l) at stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40 from September 1996 through March 1998.
Figure 17. *B. digonas* biomass (grams wet weight/m²) versus the bottom temperature between 1987 through 1998. Values are monthly averages of data from stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40.
Figure 18. *B. digonias* biomass (gram wet weight/m²) versus bottom temperature between 1987 and 1998. Values are from stations COT4, COT17, COT18, COT19, COT20, COT23, and COT40.
Figure 19. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (μg/l) at station COT4 from 1989 through 1998.

Figure 20. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (μg/l) at station COT17 from 1989 through 1998.
Figure 21. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (µg/l) at station COT18 from 1989 through 1998.

Figure 22. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration at station COT19 from 1992 through 1998.
Figure 23. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (µg/l) at station COT20 from 1992 through 1998.

Figure 24. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (µg/l) at station COT 23 from 1995 through 1998.
Figure 25. *B. digonas* biomass (grams wet weight/m²) versus the bottom chlorophyll-a concentration (µg/l) at station COT40 from 1992 through 1998.
Figure 26. Total abundance of major phytoplankton groups at station COT4 from September 1996 through March 1998.

Figure 27. Total abundance of major phytoplankton groups at station COT23 from September 1996 through March 1998.
Figure 28. Total abundance of major groups of phytoplankton at station COT40 from September 1996 through March 1998.

Figure 29. Percent abundance of major phytoplankton groups at station COT4 from September 1996 through March 1998.
Figure 30. Percent abundance of major groups of phytoplankton at station COT23 from September 1996 through March 1998.

Figure 31. Percent abundance of major groups of phytoplankton at station COT40 from September 1996 through March 1998.
Figure 32. Trawl map for the 1994-95 winter season. The X represent the trawl locations and the encircled locations are areas with *B. digonas*. 

Scale 1:300,000

<table>
<thead>
<tr>
<th>Meters</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>10000</td>
</tr>
</tbody>
</table>
Figure 33. Trawl map for the 1995-96 winter season. The X represent the trawl locations and the encircled locations are areas with *B. digonas*.
Figure 34. Trawl map for the 1996-97 winter season. The X represent the trawl locations and the encircled locations are areas with *B. digonos*. 

Scale 1:300000 

N 
0 10000 
Meters
Figure 35. Trawl map for the 1997-98 winter season. The X represent the trawl locations and the encircled locations are areas with *B. digonias*.
Figure 36. Laboratory measurements of *B. digonas* chlorophyll-a uptake on January 15, 1997.

Figure 37. Laboratory measurements of *B. digonas* chlorophyll-a uptake on January 16, 1997.
Figure 38. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT4 from 1996-1998.
Figure 39. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT17 from 1996-1998.
Figure 40. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT18 from 1996-1998.
Figure 41. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT19 from 1996-1998.
Figure 42. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT20 from 1996-1998.
Figure 43. Scatter plots of *B. digonas* biomass versus water quality parameters for station COT23 from 1996-1998.
Figure 44. Scatter plots of *B. digonas* versus water quality parameters for station COT40 from 1996-1998.
Figure 45. Scatter plots of *B. digonias* biomass versus PC1 and PC2 for station COT4 from 1996-1998.

Figure 46. Scatter plots of *B. digonias* biomass versus PC1 and PC2 for station COT17 from 1996-1998.
Figure 47. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT18 from 1996-1998.

Figure 48. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT19 from 1996-1998.
Figure 49. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT20 from 1996-1998.

Figure 50. Scatter plot of *B. digonas* biomass versus PC1 and PC2 for station COT23 from 1996-1998.
Figure 51. Scatter plots of *B. digonas* biomass versus PC1 and PC2 for station COT40 from 1996-1998.
Figure 52. Scatter plots of grouped data from 1987-1998 for stations COT17 and COT18.
Figure 53. Grouped data for stations COT17 and COT18 from 1987-1998 showing *B. digonias* biomass versus PC1 and PC2.
Figure 54. PC1 and PC2 scores plotted against measured *B. digonas* biomass values of grouped data for stations COT17 and COT 18 from 1987 through 1998. The variance explained by each PC, expressed as a percentage of total variance, is given in parentheses.
Figure 55. Scatter plots of *B. digonias* biomass versus the abundance of phytoplankton, bivalves, amphipods, and the brachiopod, *Glottida pyramidata*, of grouped data for stations COT4, COT23, and COT40 from 1996-1998.