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COMMUNITY METABOLISM AND NUTRIENT FLUXES AT GRAYS REEF NATIONAL MARINE SANCTUARY

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THE UNIVERSITY OF GEORGIA
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U.S DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
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During 1984 and 1985 metabolic and current meter measurements were made at Gray's Reef National Marine Sanctuary (GRNMS). Current meters (top and bottom) were positioned at Gray's Reef and F reef from June 1984 through December 1985. The most energetic fluctuations in ocean current speeds were generated by the astronomical tide at 0.5 day periods. There was a rather low correlation between winds and currents, suggesting that forces other than winds help drive the observed currents in the GRNMS region. Nutrient fluxes and metabolism at GRNMS were measured from 6-11 July 1985. The hard bottom community with medium epifaunal density had an areal respiration rate of 3.2 gC $m^{-2}d^{-1}$, about 10 fold higher than a low density region of the live bottom and similar to rates observed in organically rich coastal and coral reef habitats. Production/respiration estimates show that the low density areas are autotrophically and heterotrophically balanced with a P/R ratio of 1. Medium density areas had a P/R ratio of 0.63, indicating that they were heterotrophic. In agreement with the metabolic measurements, nutrient fluxes in the benthic domes showed a release of inorganic nutrients from benthos to the overlying water column. Rates of pelagic metabolism and ammonia regeneration were higher than expected for the season and distance from shore. These observations may have important implications for fisheries in the southeastern U.S. and for ecological theories regarding reef ecosystems.

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ABSTRACT

During 1984 and 1985 metabolic and current meter measurements were made at Gray's Reef National Marine Sanctuary (GRNMS). Current meters (top and bottom) were positioned at Gray's Reef and F reef from June 1984 through December 1985. The most energetic fluctuations in ocean current speeds were generated by the astronomical tide at 0.5 day periods. There was a rather low correlation between winds and currents, suggesting that forces other than winds help drive the observed currents in the GRNMS region. Nutrient fluxes and metabolism at GRNMS were measured from 6-11 July 1985. The hard bottom community with medium epifaunal density had an areal respiration rate of 3.2 gC m^{-2} d^{-1}, about 10 fold higher than a low density region of the live bottom and similar to rates observed in organically rich coastal and coral reef habitats. Production/respiration estimates show that the low density areas are autotrophically and heterotrophically balanced with a P/R ratio of 1. Medium density areas had a P/R ratio of 0.63, indicating that they were heterotrophic. In agreement with the metabolic measurements, nutrient fluxes in the benthic domes showed a release of inorganic nutrients from benthos to the overlying water column. Rates of pelagic metabolism and ammonia regeneration were higher than expected for the season and distance from shore. These observations may have important implications for fisheries in the southeastern U.S. and for ecological theories regarding reef ecosystems.

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PREFACE

The work described was carried out from May 1984 through December 1985. Biological and chemical sampling on Gray's Reef occurred during July 6-11, 1985. The assistance of Nick Nicholson (Coastal Resorces Division, Georgia Department of Natural Resources, Brunswick, GA.) with current meter set-up, choice of sampling location, and specimen identification is greatly appreciated. The Coastal Resources Division also assisted, through the cooperation of Mr. Duane Harris, by loaning us a variety of equipment for the work at Gray's Reef. General Oceanics, Inc. (Miami, Florida) served as sub-contractor for current meter set-up, maintenance, and data collection and analysis. General Oceanics employees Robert Calvert, Greg Hahn, and Chris Casagrande are acknowledged for their cooperation and assistance during this project. Drs. David Gillespie and James Harding (University of Georgia Marine Science Program, Marine Extension Dvision, Skidaway Institute of Oceanography, Savannah, GA.) supplied charts describing the location of various bottom features at GRNMS.

We gratefully acknowledge the ship, diving and laboratory assistance of personnel at the University of Georgia Marine Institute, especially Janet Fallon, Johnny Harris, Rick Hoffman, Bengt-Owe Jansson, Pelle Jansson, Steve Kipp, Joe Shubauer, and George Walker.

INTRODUCTION

Description of the Area

Gray's Reef is representative of live bottom areas common to the South Atlantic Bight. As with most live bottoms in the Georgia Bight, the Gray's Reef live bottom developed on a rock outcrop (sandy limestone) which formed during previous sea level declines during or after the Miocene epoch (25 M yr B.P.) (Hunt, 1974; MacIntyre and Pilkey, 1969; Powles and Barans, 1980). Past subaerial exposure and greater nearshore sediment thickness generally result in a tendency for greater relief with increasing distance offshore (Henry and Giles, 1980). Gray's Reef, however, is unusual for inner shelf live bottoms because of the high frequency (~10% of area) of greater relief, rock ledges present (Hunt, 1974; Henry and Van Sant, 1982). This feature is reflected in a biological community structure which is in some ways more similar to mid-shelf live bottoms than to other inner shelf sites (BLM, 1981).

Hydrographic observations show that because of its inner shelf location, Gray's Reef is subject to terrestrial influence. This is reflected in the wide temperature range in the overlying water, 12-18°C (Hunt, 1974). Also, data from Blanton (1981) and Atkinson et al. (1978) show that Gray's Reef can be strongly influenced by freshwater runoff. It is at the outer edge of the frontal zone described by Blanton (1981) and thus may be influenced by particulate organic carbon loads often associated with frontal regions (Pingree et al., 1974) and estuarine plumes (Hopkinson, 1985).

On a finer scale, the community of Gray's Reef is influenced by bottom topography and composition. Hunt's (1974) data shows that the dominant bottom type of Gray's Reef is rock thinly covered by sand. These areas contain moderate to sparse growth and are dominated by megafauna such as octocorals (Leptogorgia and Titanideum) and sponges (Cliona and Haliclona) with echinoderms, molluscs and ascidians dominating the macrofauna (BLM, 1981). Macrofaunal abundance generally increases with decreasing sand thickness and distance from rock ledges.

History and Current State of Research

Gray's reef was nominated for sanctuary status in 1978 and was officially designated as such in July 1981. First discovered and sampled by Gray (1961), the reef area has been the subject of a number of more recent studies. Hunt (1974) described the geological make-up and origin of the reef's rock substratum. Further descriptions of reef fauna were made by a number of investigators (Ansley and Harris, 1981; BLM, 1981; Harris 1978 a,b). Searles (1981) made limited seaweed collections from Gray's Reef. As part of the research program at Gray's Reef National Marine Sanctuary (GRNMS), a variety of new studies directed toward a better understanding of geological and biological phenomenon at GRNMS have been undertaken. Some of these are still ongoing. Included are mapping studies (Henry and Van Sant, 1982) and studies designed to enumerate and describe reef species and the potential impact of human activities on these species (NOAA, 1985). Previous biological studies have been primarily devoted to species enumeration and community

structure studies (e.g., BLM, 1981; NOAA, 1985; Searles, 1981). Prior to the present work, functional studies of the GRNMS system had not been done. However, functional studies were identified as priority studies in the Phase 1 research plan (NOAA, 1983). Also, recognizing that current understanding of reef system function is based primarily upon descriptions of coral reefs (Goldfelter and Kinsey, 1985), information gained by functional studies of temperate reef systems allows us to formulate better models of reef function in general and to better predict the susceptibility of temperate reef systems to environmental perturbations.

Objectives

The primary objective of this pilot study was to determine the major features of community production and respiration, and of nutrient dynamics of the live bottom community at GRNMS. Our plan was to test the utility of benthic domes as a technique to measure benthic metabolism and nutrient fluxes at sites with low and medium epifaunal densities. Because the low density sites are generally covered by a thin veneer of sand, skirted domes of the type used in bare sand bottoms by Hopkinson (1985) could be used to seal off a parcel of benthos and bottom water for metabolic measurements. However, in the medium and high density areas, the hard, rough substratum prevents a proper seal with the skirted dome. Therefore, an additional objective of this study was to design a system that would allow a suitable seal to be made for dome use in the hard substratum areas. Finally, the Santuary Programs Office desired better physical information

about the reef environment. Therefore, two current meter arrays were established by a sub-contractor, General Oceanics (one- 2-meter array each at F reef and GRNMS, see Figure 1). Current speed and direction and water temperature data were collected for approximately 18 months. Three major hypotheses were tested in this project:

1) GRNMS live bottom is a net heterotrophic system requiring input of allochthonous organic matter to sustain metabolism,

2) in situ mineralization is a primary source of nutrients sustaining community production at GRNMS, and

3) horizontal fluxes driven by water current represent an important source of "new" nutrients to the GRNMS system.

These hypotheses were directed toward uncertainties regarding functional aspects of the GRNMS system.

Significance of the Study

The need to address questions regarding system function was recognized early on in formulating research plans for GRNMS (NOAA, 1983). In the final plan (NOAA 1985), item OCY 3, component 2 states that " a study to analyze community metabolism and nutrient flux in the live bottom system" is desirable. Our study has precisely addressed this priority. In addition, the study has provided data regarding water circulation (OCY-2:NOAA,1985) and phtyoplankton activity (ECO-6:NOAA,1985). Finally, these data can contribute to baseline information for establishing a conceptual ecosystem model of the dynamics and variability of live bottom ecosystems (ECO-8:NOAA, 1985). The present study provides the framework for a functional integration

of previous descriptive studies, allowing us to better predict the sensitivity of this important economic and recreational resource to environmental perturbations. In additon, our approaches and methods have similarities to those used in previous studies of the Key Largo National Marine Sanctuary, which will facilitate comparisons between these two reef systems, which are subject to radically different physical and geological environments. This can provide a unique opportunity to develop generally apllicable theories about reef ecosystem function. As a fishery resource, GRNMS is economically important. The present study will contribute significantly to the information framework required to define long-term policy for live bottom fishery harvests in the South Atlantic Bight.

METHODS

Sites Selection

A region with both medium to high density uncovered hard bottom and low density sand covered hard bottom in close proximity was chosen. Based on observations by the Coastal Resources Division, Georgia Dept. of Natural Resources (Nick Nicholson, pers. comm.) an area at the northeastern corner of the moderate relief hard bottom region appeared optimal (Fig. 1 and 2). A current meter mooring was located approximately 50 m to the southeast of sites where benthic respiration measurements were conducted (see Appendix II). Low and medium density sites were chosen by correlating epifaunal density with previous photographic surveys where these bottom types were described.

Community Description

Epibiota were sampled from both the low and medium density areas. At the low density sites, all large organisms (i.e. >2-5cm) were collected from within domes used for measuring metabolism (0.28 m^2) at the conclusion of metabolic measurements. In the medium density region, four 0.25 m^2 triangular quadrats were dropped ramdomly by diver. All large organisms within the quadrat were collected. These organisms were refrigerated until return to the lab and then frozen at -14 ^oC. Prior to drying organisms were divided into 4 catagories: a) sponge, b) plant, c) coral, and d) miscellaneous. Dry (60 ^oC until constant weight) and ash-free dry weights (450 ^oC overnight) were determined gravimetrically.

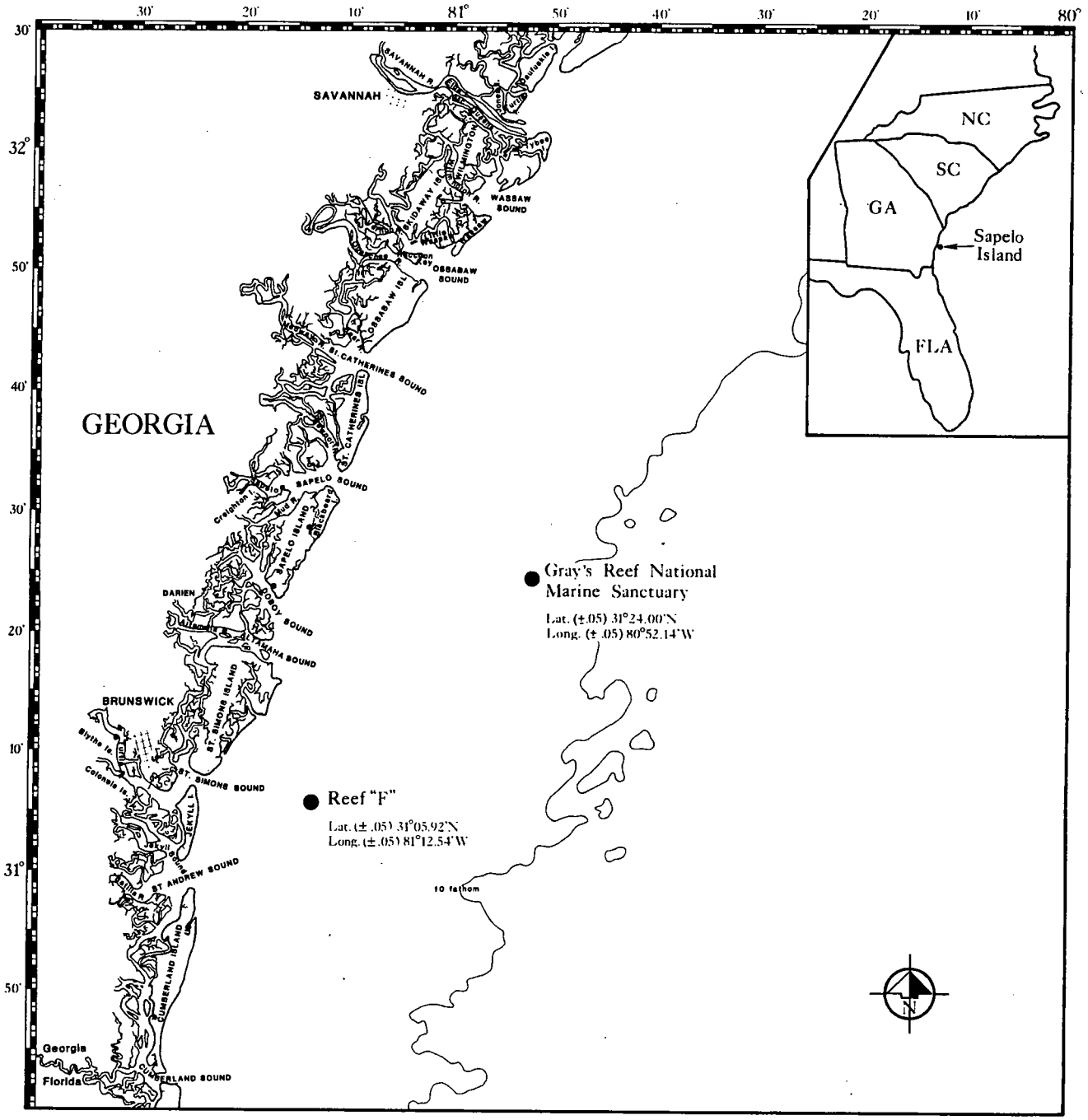

Figure 1. Location of Gray's Reef National Marine Sanctuary on the continental shelf of the Georgia Bight.

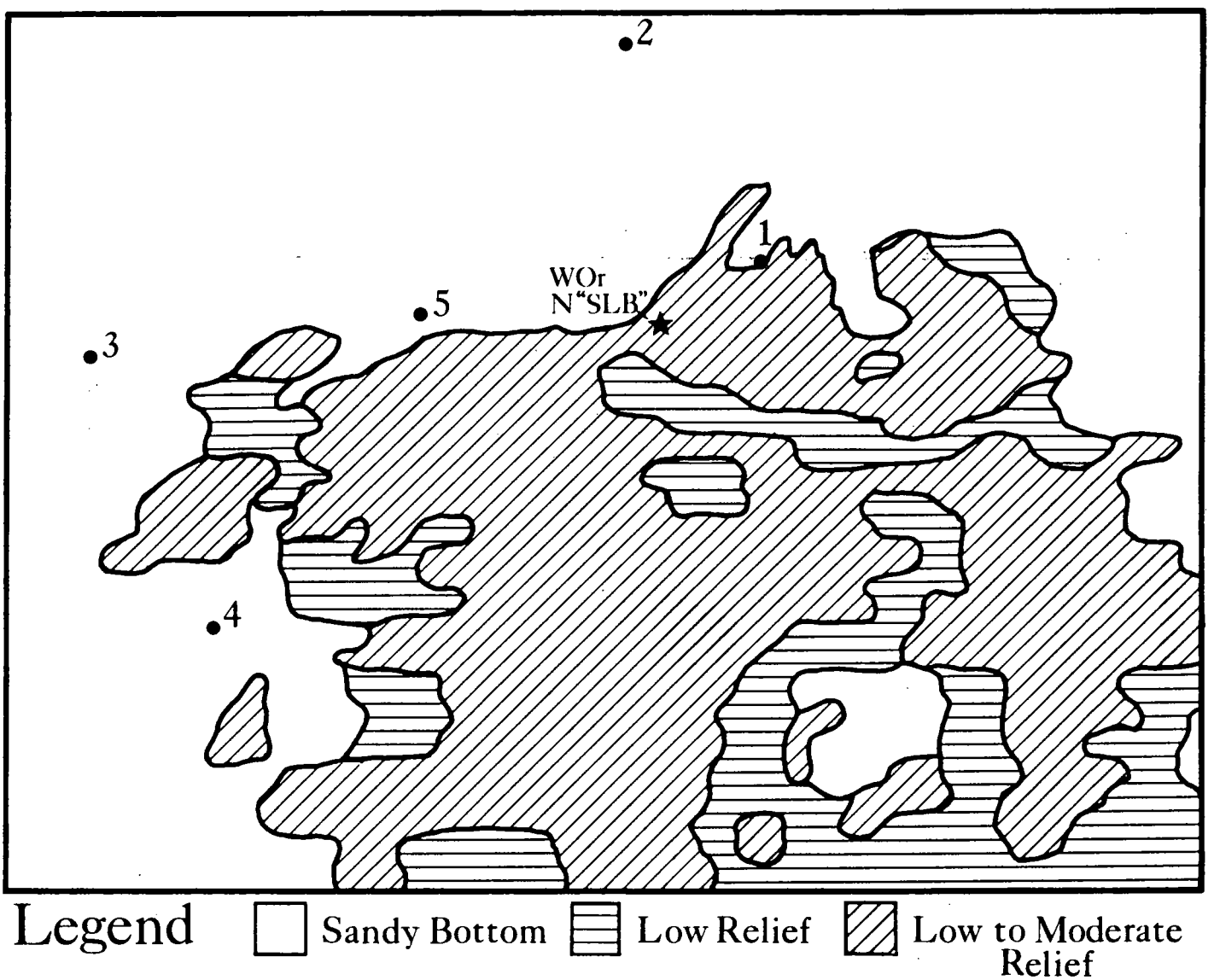

Figure 2. Map of Gray's Reef indicating the station where benthic work was conducted (Station 1). Current meters were sited 50 m southeast of Station 1. Water was collected for Eulerian measurements at Stations 1 through 5.

Benthos

Standing stocks

Sediment cores were collected from the low density region using cut-off plastic syringes, 2.65-cm diameter. After recovery of the sediment sample, black rubber stoppers were used to close the syringe. These cores were frozen (-14 °C) upon return to the surface. For analysis, the cores were unfrozen and cut, as extruded, into 1 cm deep sections. Water content, dry weight, and percent ash-free dry weight (450 °C overnight) were determined gravimetrically. Dissolved nitrite-nitrate, dissolved reactive phosphorous and exchangeable ammonium were determined in pore water from 1 cm sections (see Analytical Techniques).

To determine the composition of the bulk hard bottom material, a small section of consolidated reef material was recovered (ca. 25 kg dry weight). Ash-free dry weight (450 °C overnight) was determined for: a) homogenized bulk material, b) outer layer (0-2.5 cm deep, contains high percentage of encrusting organisms), c) mid-layer (2.5-10 cm deep, contains mostly consolidated rock with some animal contamination, and d) core layer (center of recovered piece). No dissolved nutrient analyses were done.

Sediment metabolism

Benthic metabolism was determined following the technique described by Hopkinson (1985) with *in situ* measurements of benthic oxygen production and uptake using 3 or 4 belljars in two different portions of the hard bottom at Gray's Reef: a sandy substrate,low faunal density area and an area of medium faunal

density with very little bare sand substrate. In the low density area, 3 acrylic hemispheres (domes) covering 0.28 m^2 of bottom surface were carefully placed by SCUBA divers ensuring a minimum of sediment disturbance (Figure 3). Due to the thinness of the sandy substrate overlying the hard bottom, the 6-cm long vertical aluminum skirts of the domes did not fully penetrate into the sand. Dome volume was therefore determined by measuring the dilution of a known volume of rhodamine dye injected into the water enclosed within the dome.

In the topographically rough, medium density area, 2 flexible, mylar plastic-sided domes were placed by SCUBA divers onto level, concrete rings which had been attached to the hard bottom 1 month prior. Concrete rings (Figure 4) were constructed by pouring concrete (a mixture of seawater, Type II cement and plaster) into a 6.4-cm high by 92-cm diameter, circular PVC frame with an internal frame width of 7.6 cm. The concrete was completely and permanently attached to the hard bottom. Domes consisted of an approximately 30-cm high mylar plastic cylinder attached to a 10-cm high by 96-cm diameter PVC ring on the bottom and a circular sheet of clear 0.32-cm thick by 100-cm diameter acrylic plastic on the top (Figure 5). A gasket of seawater-aged foam rubber was placed between the concrete ring and the PVC base of the dome. Portals within the acrylic top sheet enabled access to internal water. The acrylic sheet was suspended above the bottom by a small 1- to 2-l volume styrofoam float. Water currents caused the dome to sway back and forth, ensuring that the dome was well mixed. As with the low density domes, dome volume was determined as the dilution of a known injection of

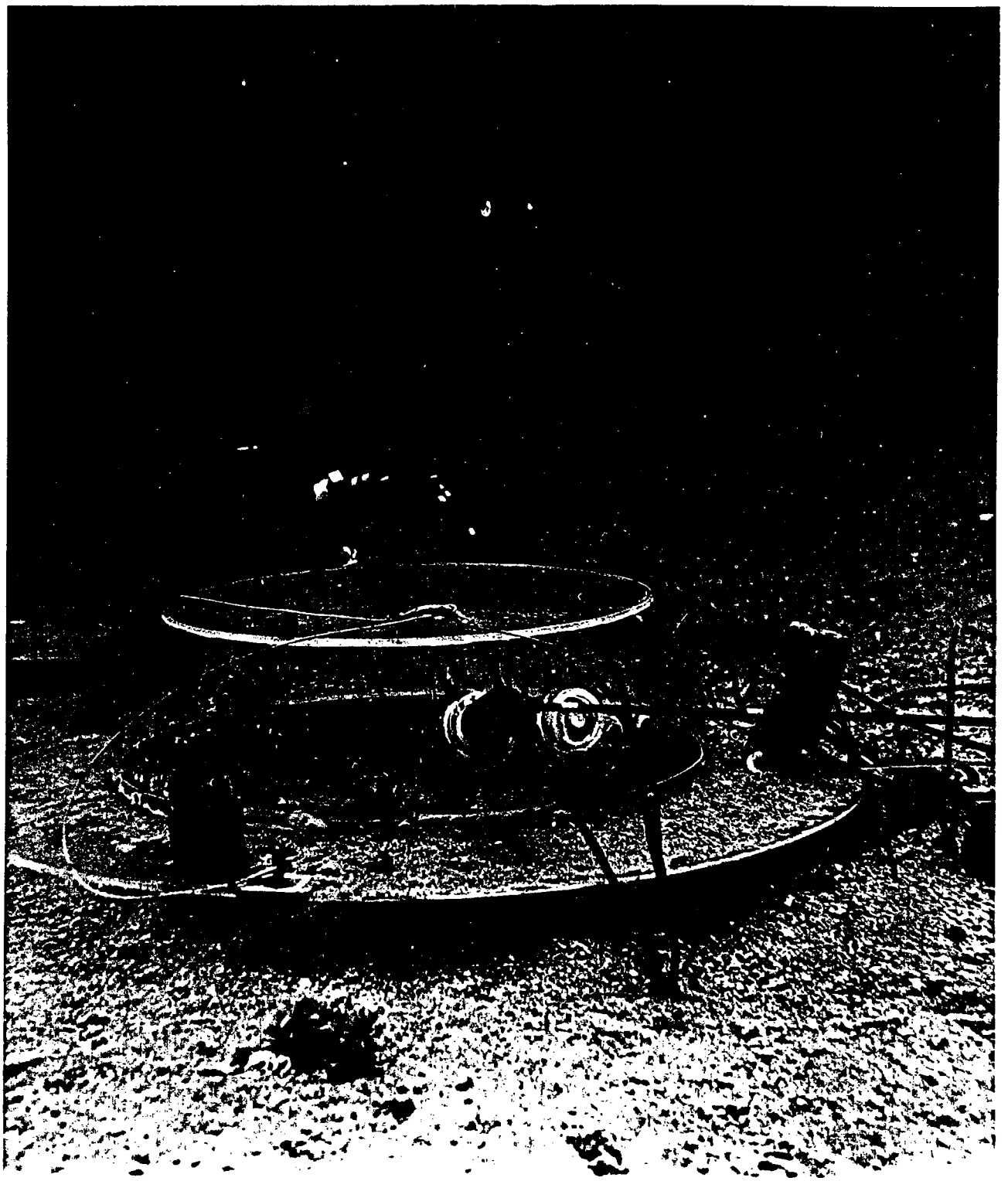

Figure 3. Low density site at Gray's Reef with domes in place for measuring benthic nutrient fluxes.

Figure 4. Concrete rings which were poured in place over the medium density portions of the hard bottom substratum at Gray's Reef. Rings allowed benthic chambers to be positively sealed with the substratum, thereby preventing exchange with the overlying water.

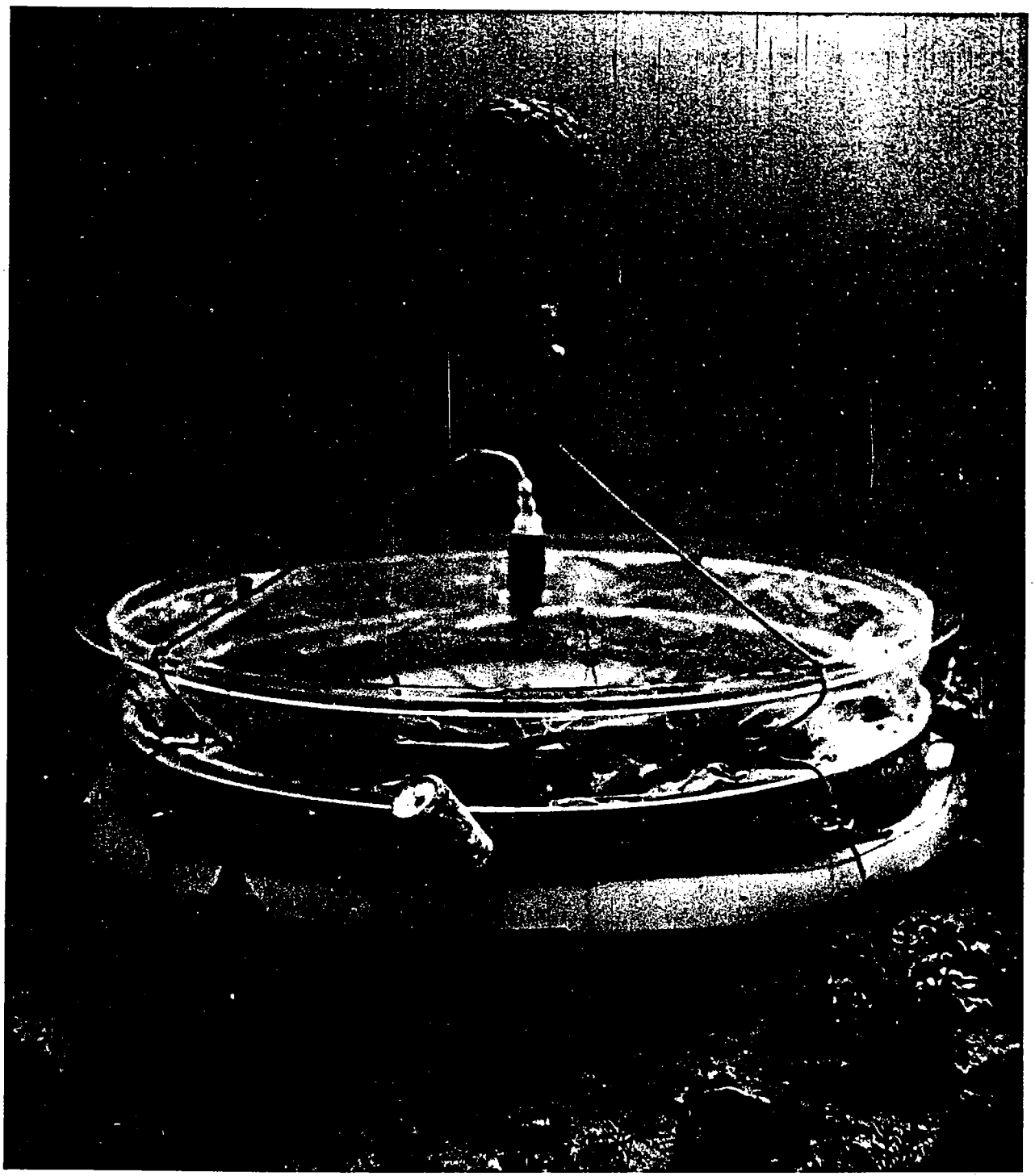

Figure 5. Flexible chamber for measuring benthic metabolism and nutrient regeneration at the medium-density site at Gray's Reef. Flexible nature allows wave and current induced turbulence to be transmitted into the chamber.

rhodamine dye.

Dissolved oxygen concentration was monitored with self-stirring oxygen electrodes in the low density domes and by the Winkler technique in the medium density domes. In the former, dissolved oxygen was measured continuously for about 36 h beginning at about 1800 h. Dissolved oxygen was measured discontinuously during one night and two day periods in the medium density domes. BOD bottles were filled contemporaneously with dome placement to provide a correction for oxygen changes due to metabolism in the water enclosed in each dome.

After correcting for water-column metabolism, benthic community primary production and respiration were estimated by regressing dissolved oxygen concentration against time and then converted to an areal basis by multiplying by dome volume to area ratios. Community respiration was determined only in the dark at night. Net daytime community production was the net change in dissolved oxygen during daylight hours. Gross community primary production was the time-weighted sum of net daytime production and nighttime respiration. Net community production was the balance of gross production and respiration over a 24 h period.

Nutrient flux across sediment/water interface

Net fluxes of dissolved organic and inorganic nitrogen and phosphorus between the sediment and overlying water were measured in the domes contemporaneously with metabolic measurements (Hopkinson, 1986). Water samples (<60 ml) were pumped from the surface through narrow bore tubing with the low density domes (see Figure 3) and collected by divers with 60-ml syringes from

the medium density domes. Intervals ranged from 2 to 6 h. Replacement water entered through small dome-top ports during sample withdrawal to avoid interstitial water exchange. All samples for nutrient analysis were filtered through precombusted, prerinsed glass-fiber filters (Gelman A/E) immediately after collection and transported frozen to the laboratory. Samples for ammonium analysis were fixed with reagents in the field (see Analytical Techniques). Nutrient flux was determined by regression of nutrient concentration against time after correction for water column activity measured in BOD bottles. Rates were put on an areal basis by taking into consideration the volume/surface area ratios of the two types of domes.

Water Column

Concentrations and fluxes of nutrients across Gray's Reef

In order to evaluate changes in the chemical makeup of water passing over GRNMS, a box model calculation was made using data collected on dissolved and particulate matter. Five stations were monitored over a 12 h tidal cycle (Fig. 2). The faces of the box were: along shore (positive curents to the northeast): 3,4 - 2,1; cross shore (positive currents to the northwest):4,1 - 3,2. Current vectors were rotated to be perpendicular to the respective faces. Fluxes were then calculated for a top (0-10 m) and bottom (10-20 m) box as:

along shore: current vector x (([3]+[4])/2)-([2]+[1]/2))

cross shore: current vector x (([4]+[1])/2)-([3]+[2]/2))

where [#] is the concentration at station #. With this convention a positive flux indicates a loss from the water column

and a negative flux indicates a gain by the water column. Total water column pools were calculated by multiplying the average concentration over twelve hours by the estimated total volume of water over the monitored section at GRNMS. Potential availability was calculated as the material available on average to one square meter of benthos per hour from a 2 or 20 m deep water column flowing over the bottom with an average concentration based on the mean from all five stations.

Pelagic primary production

Pelagic primary production was estimated by $^{14}CO_2$ incorporation during 4 hour onboard incubations at 5 light levels (100%, 61%, 48%, 23%, and 5% of surface light) and in situ temperature (28 ^{o}C) (Strickland and Parsons, 1972). Particulate 14-carbon was collected on a 47-mm, 0.45-um Millepore HA filters. Dissolved 14-carbon was determined in the filtrate after acidification and 45 min. bubbling to remove inorganic 14-carbon (Peterson, 1978). Radioactivity was determined by liquid scintillation counting with H-number (Beckman) quench correction. Primary production was measured on two separate days and depth integrated results were averaged to obtain a single primary production estimate for the water column.

Pelagic respiration

Pelagic metabolism was measured in vitro by monitoring dissolved oxygen uptake in three opaque, 20-l polyethylene carboys incubated in the laboratory within 1 ^{o}C of ambient temperatures. Water was collected in late afternoon by pumping water from throughout the water column through a 2-cm diameter

plastic hose with an 8-l min^{-1} diaphragm pump. Water was allowed to overflow each carboy until air bubbles stopped rising to the surface. Incubations were initiated within 4 h of water collection. Dissolved oxygen was measured periodically for 17 h with an oxygen probe (YSI- clark electrode). Pelagic community metabolism was calculated by regressing dissolved oxygen concentration against time. Rates were expressed on an areal basis by accounting for water column depth. No attempt was made to examine possible diel patterms in community respiration.

Pelagic NH_4^+ turnover

Pelagic ammonium remineralization was investigated using the isotope dilution technique (Caperon et al., 1979; Blackburn, 1979). Water was collected during mid-morning in a 20-l carboy with a diaphragm pump from throughout the water column. Within 30 minutes of collection, water was gently siphoned through 208 micron screening to four 2.5-l glass reagent bottles. In sequential order, each bottle was amended with ^{15}N tracer, initially sampled and incubated. Sufficient ^{15}N-$(NH_4)_2SO_4$ (99%) was added to each bottle to make a final concentration of 0.2 uM ^{15}N. Immediately after tracer addition, bottles were swirled, a 600 ml sample withdrawn, and placed in an on-deck flowing seawater incubator covered with neutral density screening allowing 25% light transmission. 75 ml of the sample withdrawn was used to rinse filtering apparatus (including Gelman glass fiber GF/F) and polyethylene storage bottles and then discarded. After withdrawing 25 ml for ammonium analysis, the remainder of the filtrate was frozen until further processing on shore.

Bottles were resampled 0.5, 2 and 3.5 hr after tracer addition.

Ammonium concentration was redetermined (Grasshoff, 1976) following thawing and ammonium stripped from stored samples within 1 week of collection at the onshore laboratory. Prior to stripping, 2.0 umols ^{14}N-$(NH_4)_2SO_4$ carrier was added to the 400 ml sample. The solvent extraction procedure described by Dudek et al. (1986) was used to strip ammonium nitrogen for the determination of relative ^{15}N abundance. In this procedure ammonium is converted to indophenol using a modification of the phenol-hypochlorite reaction for seawater ammonium analysis. The indophenol is extracted into methylene chloride, concentrated by partial evaporation of the solvent and dried on a glass fiber filter (Whatman 934 AH). Filters were dried at 80^0 C and stored in plastic scintillation vials. ^{15}N content was analyzed by emission spectrometry following a modification of the micro-Dumas procedure (Dudek et al., 1986). Filters were ground with 0.5 g precombusted (500 ^oC) Cuprox and stored in evacuated vucatainers until placement into a 5 mm OD pyrex discharge tube containing about 2 cm precombusted (900 ^oC) CaO. The tubes were evacuated to $<10^{-5}$ torr, sealed, combusted for 8 hr at 500 ^oC and analyzed on a Jasco emission spectrometer.

Ammonium regeneration rates were calculated from measurements of ammonium concentration and isotope ratio according to the Blackburn (1979) equations (see Laws, 1984). Corrections to the measured isotope ratio were made for isotope contamination during sample freezing, ammonium extraction, and micro-Dumas combustion.

Analytical Techniques

Inorganic nutrients were analyzed using the colorimetric techniques outlined in Grasshoff (1976): phenol-hypochorite for ammonium, cadmium reduction followed by sulfanilimide for nitrite and nitrate, ascorbic acid and molybdate for phosphate, and oxidation to nitrate and phosphate for dissolved organic N and P. A Perkin-Elmer Model 240C was used for carbon analyses of particulate samples. Inorganic carbon was removed with weak hydrochloric acid following the technique of Hedges and Stern (1984). Dissolved oxygen, when measured by the Winkler technique, followed that outlined in Strickland and Parsons (1968). Chlorophyll was determined by fluorometry (Strickland and Parsons, 1972) on a Turner fluorometer. Pelagic chlorophyll samples were obtained by filtering 900-1200 ml onto a Millipore 0.45um, 47mm HA filter and dissolving the filter and extracting (4 ^{o}C overnight) particulates in dimethyl sulfoxide-90% acetone (DMSO-acetone) (Shoaf and Lium, 1976). Benthic chlorophyll samples were also collected from the sand and hard bottom areas. Samples averaging 28 g dry weight were extracted overnight (4 ^{o}C) in 150 ml DMSO-acetone. The extract was cleansed by centrifugation and chlorophyll measured fluorometrically.

RESULTS

Benthic Community Description and Standing Stocks

The sites used for the respiration studies contained a variety of epibiota (Table 1). All three of the faunal catagories showed a variety of species present. Macroalgal material was also collected, but was not characterized taxonomically beyond the observation that red algae appeared to dominate. Macroalgal biomass was a minor component at both the medium and low density sites (Table 2). The hard coral Oculina was found only at the medium density site. Bryozoans appeared to be much more important at the medium density site also. Examining the biomass carbon distribution (Table 2) one notes that the miscellaneous catagory was more important at the medium density location. Also there appeared to be a strong shift in the relative biomass of sponge versus coral in moving from the low to medium density site. This trend was complicated by the high variance in the sponge distribution at the low density site. As noted in Table 2, Halichondria bowerbanki, was found in only one of the three samples from the low density site. Yet, it dominated the sponge catagory on a volume basis. This may have caused an overestimate of the mean sponge carbon biomass for low density locations at the reef. By removing this sample from the calculation for the mean, we reduced the contribution of sponge biomass from 32% to 3% at the low density site. If this is a more representative picture of the average low density site at the reef, then the biomass distribution going from low density to medium density areas would show a distinctive shift in the

Table 1. Predominant species observed at the benthic dome respiration sites.

LOW DENSITY SITES	
SPONGES:	Homaxinella waltonsmithi, Homaxinella sp., Phakellia lobata, Halichrondria bowerbanki, Ciocalapata gibbsi, Anthosigmella varians
SOFT CORAL:	Titanideum frauenfeldii, Lophogorgia hebes, Telesto fruticlosus
PLANTS:	various red macro algae
MISCELLANEOUS:	Arca zebra, Arca imbricata (encrusted with Balanus sp. and Astrangia astreiformis), various bryozoans, encrusting Ascidiacea (e.g. Diplosoma macdonaldi & Ascidia curvata), various small decapods, various hydroids, Astrophyton muricatum, Conus sp., Vermicularia knorrii, Botrylloides nigrum, Filograna implexa
MEDIUM DENSITY SITE	
SPONGES:	Ircinia ramosa, Neofibularia nolitangere, Homaxinella waltonsmithi, Homaxinella rudis, Phakellia lobata, Ircinia strobelina, Aplysina fistularis, Ircina campana
CORAL:	Lophogorgia sp., Titanedeum sp., Astrangia sp., Oculina sp., Astrea sp.
PLANTS:	various red macroalgae and brown macroalgae
MISCELLANEOUS:	various Bryozoans, various Ascidiacea (e.g. Diplosoma macdonaldi, Styela plicata, Diplosoma sp., Ascidia curvata, Botrylloides nigrum), various hydroids, Arca sp., Astrea sp., Chama congregata, various decapods, Batroides sp., Ocnus pygmaeus, various crinoids, Ostrea permolis, Filograna implexa

Table 2. Benthic pools for the various chemical components.

COMPONENT	STANDING STOCK
LOW DENSITY SITE	
Organic Carbon	
Sand (to 6 cm deep)	570 $gC \cdot m^{-2}$
Epibiota	38.9 $gC \cdot m^{-2}$ a
Chlorophyll	
Sand (to 3.9 cm deep)	869 mg chl a $\cdot m^{-2}$
Dissolved Nutrients	
NH_4^+	57 $mgNH_4^+-N \cdot m^{-2}$
NO_{2+3}^-	27.7 $mgNO_3^--N \cdot m^{-2}$
PO_4^{3-}	107.9 $mgPO_4^{3-}-P \cdot m^{-2}$
MEDIUM DENSITY SITE	
Organic Carbon	
Reef face (to 3 cm deep)	673 $gC \cdot m^{-2}$
Epibiota	77.2 $gC \cdot m^{-2}$ a
Chlorophyll	
Reef face (to 2 cm deep)	197 $gC \cdot m^{-2}$

a - For the categories distinguished in sorting the epibiota, carbon distributions were as follows:

Low Density - Misc., 32%; Sponge, 32%; Coral, 36%; Plant, trace. However, in the sponge category, the main contributor was a mass of the pancake sponge, Halichondria bowerbanki, which was found in only one of the three samples. Thus the category and the total carbon value may be overestimated. With this material removed, average carbon in the epibiota was approximately 27.2 gC per square meter, and the distribution was: Misc., 45%; Sponge, 3%; Coral, 52%; Plants, trace.

Medium Density - Misc., 58%; Sponge, 35%; Coral, 6%; Plant, 1%.

sponge/coral ratio: 3% : 36% (low density) to 35% : 6% (medium density).

On an areal basis the bulk substratum at both sites dominated the organic carbon distribution (Table 2). Organic carbon in the sand at the low density site (integrated over the depth down to hard bottom, ca. 6 cm) represented a carbon pool (570 gC m^{-2}) almost 15 fold higher than the carbon contributed by the epibiota (38.9 gC m^{-2}) (Table 2). A similar situation occurred at the medium density site where the substratum (to 3 cm) (673 gC m^{-2}) contributed almost 9 times as much organic carbon as the epibiota (77.2 gC m^{-2}) (Table 2). On an areal basis the organic carbon contribution by epibiota was 2 to 3 fold higher (Table 2) at the medium density location than at the low density location. Chlorophyll concentrations (Table 2) showed that there may be a substantial microalgal biomass associated with both substratra.

Benthic Metabolism

Low Macrofaunal Density Site- Community metabolism was quite low in regions of low macrofaunal density on Gray's Reef. Net daytime production was measured during one entire daytime period, while respiration was measured during consecutive nights proximate to daytime measurements. As seen in Table 3 there were substantial temporal and spatial differences in rate of oxygen consumption and production with rates varying from 31% to 158% between sites and about 40% from one night to the next. Oxygen concentrations during incubations deviated less than 30% from saturation levels.

Although there was some primary production occurring in the low density region (mean: 303 mg C m^{-2} d^{-1}), it was approximately balanced by community respiratory demands (mean: 313 mgC m^{-2} d^{-1}) resulting in a rate of net community production that was not significantly different from zero (mean: -10 mg C m^{-2} d^{-1}, Table 4).

Medium Macrofaunal Density Site- Our primary objective at the medium density region was to design and test a chamber for conducting metabolic measurements in topographically rough portions of Gray's Reef. In that sense we were quite successful. We succeeded in attaching a collar to the hard bottom surface which enabled us to use a dome to isolate a small volume of water over a portion of the benthic community. Our prototype dome design with thin mylar sides worked quite favorably. By flexing in response to underwater currents, it enabled us to maintain water movement within the dome. Future domes should be constructed with a heavier gauge mylar or tedlar plastic however, as the thin 1 mil mylar used on these prototype domes had a tendency to rip when current velocities were high.

Community metabolism was exceptionally high in the medium density site (Table 5). Respiration averaged 3.2 gC m^{-2} d^{-1} (range 2.1 to 4.3) while net daytime production averaged -0.7 gC m^{-2} d^{-1} (range -0.33 to -1.0). Gross primary production was thus lower than community respiration and ranged from 1.5 to 2.5 gC m^{-2} d^{-1}. Over a 24 hr period, the medium density region was heterotrophic with net community production averaging -1.74 gC m^{-2} d^{-1}.

Table 3. Rate of oxygen change in domes overlying regions of low macrofaunal density on Gray's Reef. Experiments initiated at 18:00 hrs on day 1. Units- mg O_2 l^{-1} d^{-1}.

TIME	RESPIRATION		NET DAYTIME PRODUCTION		GROSS PRODUCTION	
			DOME			
	A	B	A	B	A	B
Night 1	-2.83	-3.72				
Day 2			+0.81	+2.09	+2.46	+4.26
Night 2	-2.04	-5.29				

Table 4. Community metabolism of low density portions of Gray's Reef. Units- mgC m^{-2} d^{-1} assuming RQ and PQ of 1.00.

	DOME A	DOME B	MEAN
RESPIRATION	-219	-406	-313
NET DAYTIME PRODUCTION	+73	+188	+131
GROSS PRODUCTION	+222	+384	+303
NET COMMUNITY PRODUCTION	+3	-23	-10

Table 5. Community metabolism of medium density regions of Gray's reef. Units- gC m^{-2} d^{-1}. Values separated by a "/" represent estimates from separate days. NA - not available.

	DOME A	DOME B	MEAN
RESPIRATION	-4.28	-2.1	-3.2
NET DAYTIME PRODUCTION	-0.33/-1.0	NA	-0.67
GROSS PRODUCTION	+2.53/+1.48	NA	+2.01
NET COMMUNITY PRODUCTION	-1.75/-2.8*	NA	-1.74
	-0.67/-1.72		

Note- (*) top values based on separate estimates of gross production and respiration from dome A only. Bottom values are calculated similarly except for using a mean value for respiration.

Benthic Nutrient Flux

Low Density Region- Sediments and benthos were a source of inorganic nutrients for the overlying water column during both light and dark periods of the day (Table 6). Ammonium dominated the flux of nitrogenous compounds averaging 526 ug N m^{-2} d^{-1}. Fluxes of $NO_{2\&3}^-$ represented about 32% of the total inorganic nitrogen flux. Phosphate fluxes were comparable in magnitude to the flux of nitrite-nitrate. The ratio of inorganic nitrogen to phosphorous flux ranged from about 2 to 11:1 and averaged 3.6:1 over a 24 hr period. The magnitude of some nutrient fluxes varied considerably between light and dark periods. However, there was no consistent pattern for all nutrient fluxes being higher or lower during light or dark periods. Although fluxes of dissolved organic nitrogen and phosphorous were relatively large, their directions reversed from light to dark periods so that averaged over the entire day fluxes of both compounds were minor.

There were substantial small scale horizontal heterogeneities as evidenced by rather large coefficients of variation for replicated (n=3) flux measurements. Coefficients of variation were generally close to 100% but for DON they exceeded 600%. Analytical variability contributed only slightly to the overall level of variation (c.v. less than 10% for all chemical species). Horizontal variability is more than likely attributable to patchiness in sediment macrofauna which are important agents in sediment irrigation and pore water movement and to patchiness in benthic filter feeders (Tables 1 & 2) which appear to dominate hard bottom metabolism.

Medium Density Region- Nutrient fluxes from medium density portions of the hard bottom community on Gray's Reef were high and always in the direction of bottom to overlying water column (Table 7). DON dominated the flux of nutrients followed by ammonium, nitrite-nitrate, phosphate and DOP. Flux levels varied irregularly from one day to the next (ie. some levels up, some down), suggesting nonsystematic random variation. In general, fluxes were greater at night than during the day. The ratio of inorganic nitrogen to phosphorous fluxes varied from about 8 to 17.3:1 and averaged 14:1.

Standing Stocks of C and N in the Water Column

Particulate carbon in the water column was estimated to be 9.6 gC m^{-2} (Table 8). Chlorophyll in the water column, 12.8 mg chl a m^{-2}, was substantially lower than the benthic chlorophyll (Table 2 & 8). Pelagic nitrogen concentrations were dominated by the DON pool, 3.2 g N m^{-2}. On an areal basis the inorganic nitrogen and phosphorous pools in the water column were similar to those estimated for the interstitial waters at the low density site (Table 2 & 8).

Pelagic Primary Production

Light attenuation, k (meters), in the water column was -0.0705. Both days when photosynthesis was measured were clear with maximum PAR (photosynthetically available radiation) of >2000 uE m^{-2} sec^{-1}. As measured by 14-carbon dioxide incorporation, pelagic photosynthesis was maximal at light levels equivalent to 2-4 m deep in the water column. This indicates

Table 6. Benthic nutrient flux in low density portions of Grays' Reef. Numbers in parentheses represent 1 standard deviation. Units are ug-at N or P * m^{-2} * d^{-1}.

CONSTITUENT	FLUX DAY	NIGHT	MEAN
NH_4^+	522 (595)	529 (451)	526
$NO_{2\&3}^-$	319 (308)	161 (148)	240
PO_4^{3-}	77 (57)	353 (309)	215
DON	-1123 (7259)	1080 (2671)	-21
DOP	269 (338)	-143 (158)	63
TIN	841	690	766
TIN/PO_4^-	10.9:1	2.0:1	3.6:1

Table 7. Benthic nutrient flux from medium density portions of the hard bottom at Gray's Reef. Units are mg-at N or P * m^{-2} * d^{-1}.

CONSTITUENT	FLUX DAY 1	DAY 2	MEAN DAY	NIGHT
NH_4^+	8.5	18.9	13.7	21.5
$NO_{2\&3}^{-1}$	6.9	2.7	4.8	6.4
PO_4^{3-}	1.98	1.25	1.62	2.0
DON	0	28.6	14.3	34.0
DOP	0	-0.68	-0.34	+1.22
TIN	15.4	21.6	18.5	27.9
TIN/PO_4^{3-}	7.8:1	17.3:1	12.6:1	14.0:1

Table 8. Pools of particulate and dissolved components in the water column at Gray's Reef.

COMPONENT	STANDING STOCK
Particulates	
Chlorophyll	12.8 mg chl *a* $\cdot m^{-2}$
Particulate Organic Carbon*	9.6 gC $\cdot m^{-2}$
Particulate Nitrogen*	850 mgN $\cdot m^{-2}$
Dissolved	
DON-N	3248 mgN $\cdot m^{-2}$
DOP-P	59.5 mgP $\cdot m^{-2}$
NH_4^+-N	109 mgN $\cdot m^{-2}$
NO_{2+3}^--N	39.2 mgN $\cdot m^{-2}$
PO_4^{3-}-P	248 mgP $\cdot m^{-2}$

* - Particulate organic carbon and particulate nitrogen are based on chlorophyll measurements assuming a chl *a*/particulate organic carbon ratio of 1:750 and a particulate carbon/particulate nitrogen ratio of 11.3:1 for coastal Georgia waters at this distance from shore (Haines and Dunstan, 1975; Oertel and Dunstan, 1981).

that surface light levels were inhibitory to photosynthesis. The maximum volumetric rate observed for both days on which measurements were made was 35.1 ugC l^{-1} h^{-1}, which occurred at a light level equivalen to 2.1 m deep during the first experiment. Three days later the maximum rate, 17 ugC l^{-1} h^{-1}, occurred at a light level equivalent to 3.6 m. Integrating over the water column, primary production was 2.0 gC m^{-2} d^{-1} for Experiment 1 and 2.3 gC m^{-2} d^{-1} for Experiment 2, which yields an average estimate of 2.15 gC m^{-2} d^{-1} for the water column.

Pelagic Respiration

Oxygen consumption in the water column ranged from 0.0159 to 0.0194 g O_2 m^{-3} h^{-1} and averaged 0.0172 g O_2 m^{-3} h^{-1}. The rate of oxygen consumption was linear over time indicating that bacterial populations remained relatively constant and that there was sufficient organic matter to sustain metabolism during the 17h interval. Integrated over the water column and assuming a respiratory coefficient of 1.0 (Hopkinson, 1985), pelagic respiration averaged 2.84 gC m^{-2} d^{-1}.

Pelagic ammonium recycling

Time course information on ammonium concentration, ^{15}N atom percent excess, and rate of ammonium regeneration in the water column is summarized for replicate bottles in Table 9. Variation between replicate bottles was less than 15% for all parameters measured or calculated. Although data indicated a slight drop in NH_4^+ concentration during the final 1.5 hr of incubation, there was no statistically significant ($P<0.05$) drop during the entire 3.5 hr incubation. NH_4^+ recycling ranged from 0.048 to 0.089

Table 9. Time course history of incubations for measuring ammonium regeneration.

TIME (hrs)	NH_4^+ CONCENTRATION (uM)	ISOTOPE RATIO (atom percent excess)	REGENERATION (ug at N l^{-1} hr^{-1})
0	0.54	37.60	
0.5	0.54	35.96	0.048
2.0	0.54	31.22	0.051
3.5	0.50	24.09	0.089

during the 3.5 hr incubation. The mean rate of regeneration was 0.067 ug at NH_4^+-N l^{-1} hr^{-1}. Assuming a constant rate of regeneration throughout a 24 hr period, ammonium regeneration amounts to 1.5 mg at N m^{-3} d^{-1}. With an average pool size of 0.5 mg at/m^3, the NH_4^+ turnover time is 7.9 hrs; the turnover rate is 3.02 d^{-1}.

Advective Flux of Nutrients Across Gray's Reef

Nutrient fluxes for the water passing over the reef were dominated by the transfers of DON-N, +7862 mMoles sec^{-1} (Table 10). This indicates a net loss of DON from the water column. $NO_{2\&3}^{-1}$ and PO_4^{3-} also showed positive fluxes indicating that material was lost from the water column as it passed over the bottom in the monitored area (Table 10). There was a net gain of NH_4^+ and DOP by the water column over the one monitored tidal cycle. Although these fluxes appear substantial, comparisons to the total pools in the water column at any time (Table 11) show that these flux rates represent a change of 0.002% or less in the average standing stocks of the measured components (Table 10). In addition the inorganic material available in the water flowing past the bottom is far in excess of the potential demands of benthic primary production, even if one assumes that only material in the bottom 2 meters is accessible (Table 12).

Table 10. Average fluxes* of dissolved components over one tidal cycle.

COMPONENT	FLUX (mMoles · sec^{-1})	AREAL FLUX (mMoles · day^{-1} · m^{-2})
DON-N	+7862	+79.3
DOP-P	-617	-6.2
NH_4^+-N	-147	-1.5
NO_{2+3}^--N	+361	+3.6
PO_4^{3-}-P	+1055	+10.6

* - Calculated from the box model equation as described in the Methods. A positive flux indicates a loss from the water column, and a negative flux indicates a gain by the water column as it passed through the monitored area. Areal fluxes are calculated from the average flux by dividing by 8.56×10^6 square meters and multiplying by 8.64×10^4 sec/day.

Table 11. Average pools* of dissolved chemical components in monitored reef section.

COMPONENT	STANDING STOCK (mMoles)
DON-N	2.0×10^9
DOP-P	164×10^5
NH_4^+-N	671×10^5
NO_{2+3}^--N	234×10^5
PO_4^{3-}-P	686×10^5

* - Calculated as the average concentration over the tidal cycles times the total volume of the monitored water column.

Table 12. Potential availability* of dissolved chemical components for one square meter of bottom.

COMPONENT	AVAILABILITY (mMoles · h^{-1})	
	Water Column Height (m)	
	2	20
DON-N	8919	150159
DOP-P	73.9	979
NH_4^+-N	303	5224
NO_{2+3}^--N	127	1668
PO_4^{3-}-P	329	5349

* - Calculated as the average of concentration times the volume in a 1 x 1 meter square 2 or 10 m high times the current speed for each hourly interval over one tidal cycle.

DISCUSSION

Intra- and Inter-Site Comparisons

Standing Stocks- Grays reef is located at the edge of the boundary zone between turbid, nutrient rich coastal zone waters and transparent, oligotrophic shelf waters (Oertel and Dunstan, 1981). Therefore, material in the water column is somewhat variable, dependent on the local behavior of the nearshore fronts. The average concentrations of chlorophyll A and dissolved inorganic and organic nitrogen seen in the present study are similar to those from previous studies at this season and distance from shore (Atkinson, 1985; Oertel and Dunstan, 1981; Yoder, 1985). However, reactive phosphorous concentrations were about 50% higher than levels generally observed in previous studies (Oertel and Dunstan, 1981). No explanation for such high values was apparent.

The shelf benthos is also dependent on nutrient inputs from inner and outer edges of the continental shelf (Hanson et al., 1981; Tenore, 1978). In addition, faunal biomass may fluctuate over a wide range because of seasonal recruitment. Benthic chlorophyll can also vary with light availability. Few data are available for the predominant sand bottom type present on the Georgia continental shelf. Therefore, comparisons between data from our study of Gray's Reef and sand bottom data must be considered as preliminary. We saw mean (maximum values in parentheses) chlorophyll A values of 7.3(8.7) and 14.2(31.4) ug g^{-1} dry weight for the low (sand) and medium (reef) density sites, respectively. In comparison, reports from inner and mid-

shelf stations in surrounding sandy areas show mean values of 2.4 - 2.6 (maximum: 5.98) ug chl A g^{-1} dry weight (Hanson et al., 1981; Tenore et al., 1978). Mean macro-infaunal density was 1.6 gC m^{-2} (assuming C = 50% of ash free dry weight) at the same stations (Hanson et al., 1981). In contrast, macro-epifauna; densities were 38.9 gC m^{-2} and 77.2 gC m^{-2} for our low and medium density sites, respectively (Table 2). Also, in the sands from the low density site in the present study we estimated a bulk organic carbon value of 0.63 mgC g^{-1} dry weight (C = 37% of ash free dry weight; Hopkinson, 1985) while Hanson et al. (1981) reported a mean value of 0.33 mgC g^{-1} dry weight for inner and mid-shelf stations. If future sampling supports these trends, it appears that Gray's Reef, even in regions of low epifaunal density, is greatly enriched in a variety of biotic components in comparison to the surrounding open sand areas, which predominate on the Georgia continental shelf.

Comparisons of biota and respiratory activity between the low and medium density sites at Gray's Reef also yield some interesting patterns. We noted that organic carbon in fauna and substratum differed little between low and medium density sites (Table 2). However, areal respiration rates were approximately 10 fold higher on the medium density (reef) substrate (see discussion below). Even if we eliminate the contribution made to the mean organic carbon estimate for epifanuna by Halichondria bowerbanki at the low density site (see footnote, Table 2), the epifaunal carbon biomass is still only about 3 fold less at the low density site. Substrate bulk organic carbon is only about

20% less at the low density site. Therefore, on a per organic carbon basis, respiratory activity at the medium density site is about 9 fold higher than at the low density site ($4.3 * 10^{-3}$ vs. $4.9 * 10^{-4}$ gC m^{-2} d^{-1} gC^{-1}). One should also note that this serves only as a rough comparison because Hanson et al. (1981), based on ATP measurements, reported that only about 2% of the bulk sediment carbon in sandy sediments represented living biomass. In fact, this observation may partially explain the difference. Bulk substrate carbon for the medium density (reef) site includes organisms which are difficult to separate from the rock substrate (e.g. Arca sp. and small invertebrates). Thus, the bulk substrate carbon estimate for the reef site may include a greater contribution by such cryptic, living biomass than does the carbon estimate for the sand site. A more accurate comparison would then require that actual living carbon be analysed for both sites. Alternatively, species composition changes significantly between the low and medium desnsity sites with the sponge/coral ratio much higher on the reef (Table 2). If the organic carbon specific metabolic activity is higher for sponges than for coral, the change in community composition could also contribute to the higher organic carbon specific repiration rate at the medium density site.

Pelagic Metabolism- Pelagic primary production in the Georgia Bight region is strongly dependent on nitrogen availability (Haines and Dunstan, 1975; Yoder, 1985). Outwelling from the marsh/estuarine system along the coast and advection of upwelled water from Gulf Stream waters are the main supplies of "new"

nitrogen resulting in higher production along the inner and outer edges of the shelf with often lower production in the mid-shelf region (Yoder, 1985). GRNMS is at the edge of the inner and mid-shelf regions. Thus, coastal outwelling is likely to be the major "new" nutrient source to the region (Yoder, 1985). Average primary production observed in the present study, 2.15 gC m^{-2} d^{-1}, is 6-7 fold higher than rates previously reported at this distance from the shore during summer (Haines and Dunstan, 1975; Thomas, 1970; Turner et al., 1979; Yoder, 1985). We are uncertain as to the explanation of this unusually high value. Increased outwelling of nutrients due to coastal thunderstorms that occurred during the early part of the week may have allowed a pulse of production at GRNMS. This might also explain the high reactive phosphorous values noted above. Previous reports put the expected rate of primary production at about 300 mgC m^{-2} d^{-1}. However, during our study, such a rate would have meant that the water column was respiring far more than it was producing (see Table 13). Such a situation is very unlikely. Thus, the high respiration rate observed suggests that the high average production observed was not an artifact.

On a volumetric basis the rate of respiration in the water column at Grays Reef was high relative to most coastal regions but less than that observed by Hopkinson (1985) in the estuarine plume region of the nearshore Georgia Bight. The respiration was similar to that observed in many highly productive estuarine regions. On an areal basis the rate of respiration exceeded by about 20 percent that measured even in the highly heterotrophic nearshore region at a comparable time of year.

Pelagic Ammonium Regeneration- Estimates of pelagic ammonium regeneration at Gray's Reef were among the highest reported in the literature. Ammonium regeneration was about an order of magnitude higher than that observed in the nearshore region of the Georgia Bight during April (Hanson and Robertson, submitted manuscript) but comparable to rates observed in Chesapeake Bay during summer (Glibert et al., 1982).

Benthic Metabolism- Rates of benthic metabolism in low density portions of Gray's Reef are similar to rates measured by Fallon and Hopkinson (unpublished data) in bare sand regions adjacent to to the reef. However, metabolic rates are several orders of magnitude lower than Hopkinson (1985) measured 28 km inshore in the organically richer estuarine plume portion of the nearshore continental shelf. Presumably the difference between sites reflects the low organic content of the sands at Gray's Reef and the relatively low biomass of filter feeding macrofauna in low density portions of Gray's Reef.

The estimates of community respiration for medium density portions of Gray's Reef are similar to the highest reported measurements from estuarine areas. They are slightly higher than rates measured by Hopkinson (1985) in the estuarine plume region of the nearshore zone during summer. Although these rates are relatively high in comparison to bare sediment systems, they are only 1/4 to 1/2 as high as rates observed in many coral reef hard bottom systems (Gladfelter and Kinsey, 1985).

Benthic Nutrient Regeneration- Cross site comparisons must be evaluated cautiously due to the low relicability and high sample variability we found at Gray's Reef. With this in mind however, we noted that in general, nutrient fluxes were over an order of magnitude higher at the medium density site than at the low density site; an observation in agreement with the pattern noted for metabolism at the two sites. Apparent diurnal patterns in nutrient flux at the medium density site were not seen in the low density area, perhaps because high variability masked any real patterns. While DOP fluxes were relatively unimportant at both sites, DON was a major component of overall nutrient flux.

Nutrient flux levels at the low density site are typical of oligotrophic, deeper shelf, sandy sediments while those at the medium density site are very high and comparable to levels found in highly productive estuarine systems (see Hopkinson, 1987). The difference in nutrient flux between the two sites (factor of about 10) only partially reflects the difference in biomass of macrofauna (factor of about 3) found between the two areas on Gary's Reef. Perhaps filter feeding is less important relative to deposit and nonselective detrital feeding within the sediments in low density regions. This would render the low density community to be relatviely more dependent on organic matter settling from the water column as opposed to filtering high loads of suspended material from the water column. Sedimentation at Gray's Reef is probably less than would be expected on the basis of the level of primary production and the depth of the water column (Hargrave, 1973) because high current velocities tend to increase the residence time and hence the degree to which organic

particles are decomposed in the water column (Hopkinson, 1985).

Material Fluxes Through and From the Marine Sanctuary - Observations from Direct Eulerian Measures

Approximately 26% of the benthos within the area used to make water column flux estimates (i.e. box model calculations) consisted of moderate relief bottom (Figure 2). Moderate relief areas are likely to have medium to high epifaunal densities. Thus, we would expect these regions to dominate the benthic flux in the box area used for the Eulerian flux estimates during one daylight tidal cycle. We note, however, in comparing the areal fluxes estimated from the box model (Table 10) to those estimated from the medium density benthic domes during the daylight period (Table 7) that in only one case (nitrite + nitrate) do the magnitudes agree and in only one case (NH_4^+) do the directions agree. There are a number of possible explanations for the poor agreement between these two flux estimators. Firstly, we do not have a complete balance for the combined benthic-pelagic system. Although exchanges between the benthos and the water column might be expected to dominate inorganic nutrient transfers, exchanges that occur in the water column during the time that the water mass moves across the reef (e.g. nutrient uptake by patches of phytoplankton) will also influence the changes in nutrient concentrations observed between the upstream and downstream sides of the box. Such exchanges could not be accounted for. Secondly, variability in both pelagic and benthic components can contribute to poor agreement. In the hourly flux estimates there was never a consistent upstream-downstream pattern as would be

expected if there was steady benthic-pelagic exchange. Rather, the average flux is a net value derived from hourly estimates that fluctuated in both positive and negative directions over the one measured tidal cycle. Thus, the Eulerian flux estimates may be dominated by noise which results when we try to derive terms of small magnitude from a series of large numbers. Spatial variability also strongly influences the flux estimates made from the benthic dome observations. However, the directions of the fluxes (which generally indicated a net release of inorganic nutrients from the benthos) is in agreement with what would be expected for a net respiring system. Thus, in contrast to the box model calculations, the nutrient fluxes estimated from the domes present a picture consistent with other measured parameters. Overall, both flux estimators are based on relatively small data sets for parameters with such high variability. Therefore, this disagreement does not necessarily mean that only one method is correct, but rather that more replication is needed in order to improve the precision of the estimates.

Community Metabolism of Hard Bottom Habitats - Evidence for System Heterotrophy

During summer primary production in the water column amounted to about 2.15 gC * m^{-2} * d^{-1} which was just slightly insufficient to meet pelagic respiratory demands which were 2.84 gC * m^{-2} * d^{-1}. Thus during summer the water column was heterotrophic (P/R=0.74) and dependent on organic matter brought in from outside the system or on organic matter accumulated during an earlier period of autotrophy. Hopkinson (1985) noted

that the water column of the estuarine plume portion of the nearshore zone of the Georgia Bight was autotrophic during late spring/early summer; perhaps a similar timing of autotrophy extends further across the shelf thereby permitting summer periods of heterotrophy.

There was a substantial difference in the level of metabolism between the low and medium density hard bottom sites on Gray's Reef (Tables 4 & 5). In low density areas, gross primary production and community metabolism were relatively low (about 0.3 $gC * m^{-2} * d^{-1}$) and statistically balanced (P/R=1). Metabolism was considerably higher in the medium density portions of the reef. Mean community respiration (-3.2 $gC * m^{-2} * d^{-1}$) exceeded gross primary production (+2.01 $gC * m^{-2} * d^{-1}$) by about 1.2 $gC * m^{-2} * d^{-1}$, indicating a high degree of system heterotrophy (P/R=0.63).

Assessment of the autotrophic/heterotrophic nature of the entire Gray's Reef Sanctuary must take into consideration the relative areas of the three different types of bottom habitat within the sanctuary. Bare sand, low density and medium density hard bottom habitats cover approximately 53%, 13% and 34% of the total sanctuary bottom area, respectively (Figure 2). Areal-weighted estimates of metabolism for the entire sanctuary are shown in Table 13.

Examined at the level of the entire ecological system enclosed within the Marine Sanctuary, Gray's Reef is an heterotrophic system dependent on allochthonous organic carbon for support of 1/4 of its total respiratory requirements

Table 13. Whole and subsystem estimates of community metabolism for Gray's Reef National Marine Sanctuary. Whole system estimates take into consideration water column depth and relative areas of bare sand, and low density and medium density hard bottom regions within the sanctuary.

	METABOLISM ($gC * m^{-2} * d^{-1}$)
WATER COLUMN	
Primary Production	2.15
Community Respiration	-2.84
Net Community Production	-0.69
P/R	0.76
BENTHOS	
Primary Production	0.88
Community Respiration	-1.29
Net Community Production	-0.41
P/R	0.68
GRAY'S REEF SYSTEM	
Primary Production	3.03
Community Respiration	-4.13
Net Community Production	-1.10
P/R	0.73

(P/R=0.73). Primary production is quite high (3.03 gC * m^{-2} * d^{-1}) but about 1.1 gC lower than that required to sustain total community respiration which is -4.13 gC * m^{-2} * d^{-1}. Although the water column is slightly less heterotrophic than the benthos, its overall level of metabolism is almost twice as high and thus more dependent, in an absolute sense, on allochthonous material than the benthos.

Importance of Pelagic Ammonium Regeneration and Benthic/Sediment Nutrient Flux in Nutrient Balances of Gray's Reef

The quantitative importance of nutrient fluxes within the water column and from the sediments can be assessed by calculating the proportion of primary producer's nutrient demand that is potentially supplied from sediment and pelagic release. Pelagic ammonium regeneration (27.45 mg-at N * m^{-2} * d^{-1}) is of sufficient magnitude to fully meet autotrophic uptake requirements within the water column (27.04 mg-at N * m^{-2} * d^{-1}), which were estimated assuming a Redfield et al. (1963) stoichiometry for N uptake and C fixation (106 C: 16 N). The estimated benthic algal uptake of N, again assuming Redfield stoichiometry for C and N, is 3.77 and 25.3 mg-at N * m^{-2} * $^{-1}$ for low and medium density portions of the hard bottom, respectively. Benthic uptake requirements are fully met by benthic nutrient regeneration as measures of net nutrient release from the benthos/sediments indicates that release was in excess of benthic uptake requirements. Thus the release of nutrients from the benthic community represents an additional input to the pelagic community. As pelagic phytoplankton receive sufficient N from regeneration within the water column alone, the additional

release from the bottom represents a surplus of nutrients which can be exported to adjacent systems. The net exchanges of inorganic nitrogen from benthos/sediments to the overlying water column were +0.76 and +23.2 mg-at N * m^{-2} * $^{-1}$ for low and medium sites, respectively. Taking into consideration the relative areas of sand, and low and medium density sites within Gray's Reef, the total N balance for the Marine Sanctuary is +8.39 mg-at N * m^{-2} * d^{-1}. It is unfortunate that high spatial variability in nutrient concentrations in the overlying water column prevented our detection of net nutrient export from the Marine Sanctuary in the Eulerian analysis of system fluxes.

Synthesis of these several independent measures of specific metabolic and nutrient cycling processes at Gray's Reef indicates that during a one week period in July 1985, the National Marine Sanctuary as a whole was an heterotrophic system that exported inorganic nutrients. The ultimate source of organic matter degraded in excess of current local production is unclear. The organic material could be that which was stored at an earlier time when production exceeded consumption or it could be allochthonous carbon input from adjacent regions.

Hard Bottoms and Coral Reefs - System Similarities?

Coral reefs are widely distributed hard bottom ecosystems in shallow waters of warm seas that superficially may appear to functionally resemble hard bottoms in the Georgia Bight such as Gray's Reef. Coral reefs are among the most biologically productive, diverse and esthetically beautiful of all ecosystems of the world. They are generally considered to be energetically

self-sustaining systems that accumulate and tightly recycle essential nutrients (Odum, 1971). Although specific reef organisms exhibit clear latitudinal trends in metabolic activity, as ecosystems, they seem to exhibit little functional difference over a wide range of latitude (Gladfelter and Kinsey, 1985). Metabolism in coral reef systems is dominated by benthic processes. While total primary production generally ranges between 1-14 gC m^{-2} d^{-1} (Lewis, 1977), phytoplankton production is relatively trivial and certainly equivalent to less than 10% of total system production (Lewis, 1977; Gladfelter and Kinsey, 1985). Of the total carbon fixation on coral reefs generally 10-30% goes into carbonate production.

Most, if not all, coral reef systems exhibit a virtual balance between P and R over extended periods of time (Gladfelter and Kinsey, 1985). Although recent research has demonstrated that some direct organic feeding is necessary to sustain growth in reef corals, there is little evidence to suggest any great importance of a similar kind for the reef as a whole. Nevertheless, there are zones within the reefal system acting as sources and sinks with respect to each other. Some of the surplus or deficit may represent build-up or decline in standing stocks over relatively short time periods (seasonal).

Although changes in concentrations of dissolved and particulate materials crossing a coral reef are often appreciable, material fluxes entering and leaving reefs have been very inadequately studied (Gladfelter and Kinsey, 1985). Net exchange of organic carbon is perhaps appreciable within the reef system but more than likely negligible between reef and ocean.

Kinsey and Davies (1979) generalized that complete reef systems exhibit a very small net loss of organics to the ocean at a rate equivalent to less than 0.5% of the total in situ photosynthetic turnover.

The general conclusion reached for coral reefs is that net ecosystem production (P-R) "tends towards zero" and there are no potential renewable resources such as fish which can support sustainable harvests (Smith, 1983). To a large extent, net ecosystem production of coral reefs is limited by their inability to accumulate "new" sources of inorganic nutrients, especially phosphorous (Smith, 1984). Pomeroy et al. (1974) showed that coral reefs had little effect on the phosphorus content of water flowing across them and concluded that nutrient recycling was the dominant phenomenon in coral reef nutrient dynamics. High rates of nutrient recycling promote high rates of gross primary production.

The general impression one develops of Gray's Reef is that it has little direct similarity with "classical" coral reefs. Gray's Reef is a superficial, apparently neglibly accumulating community on a relict hard surface. Coral reefs on the other hand involve real growth in time and space. Although Gray's Reef has a level of total primary production within the range noted for coral reefs, the most substantial portion (about 71%) is attributable to non-benthic phytoplankton in the water column. Whereas coral reefs generally have balanced levels of community production and respiration, Gray's Reef is highly heterotrophic and hence strongly dependent on allochthonous sources of organic

matter. Further, biotic storages of nutrients are relatively low at Gray's Reef. There does not appear to be tight internal recycling of nutrients at Gray's Reef, and in fact the reef exports substantial quantities of inorganic nutrients to adjacent pelagic systems. With such a high level of nutrient availability at Gray's Reef, control of primary production probably rests on light availability. Similarity between Gray's Reef and most coral reefs primarily extends only to the presence and importance of benthic filter feeding megafauna such as sponges and corals.

Fisheries Implications of Heterotrophic Hard Bottom Communities in the Georgia Bight

Regions of the continental shelf in the Georgia Bight with hard bottoms are generally characterized by large numbers, biomasses and diversity of fishes (BLM, 1981). That up to 30% of the shelf surface area is comprised of such bottoms would suggest from first considerations that total commercial fishery harvest in the Georgia Bight should be high. Our analysis of community structure and metabolism on Gray's Reef however, indicates that from the perspective of the overall Georgia Bight region, fishery production is probably substantially reduced from that which is theoretically possible because of the presence of hard bottoms.

Commercial landings (edible and industrial) by U.S. fishermen at ports in the 4 states between Cape Hatteras, North Carolina and Key West, Florida have historically been substantially lower than landings at ports in any other region of the United States (NMFS, 1986). As shown in Figure 6a, there is a positive relationship between fish landings in various states and the tidal shoreline length of each state. Only three coastal

states in the U.S. have landings lower than Georgia or South Carolina. By grouping landings into fishery regions along the Atlantic and Gulf of Mexico coasts, we find that for three of the four eastern and southeastern coastal regions of the U.S., there is a strong positive curvilinear relationship between commercial landings and regional tidal shoreline length (Figure 6b). Landings increase substantially in the direction of north to south. The factors leading to this curvilinear relationship are unknown but may reflect increased pelagic productivity in the warmer southern waters and increased organic matter outwelling from Gulf of Mexico estuaries. Of particular interest in Figure 6b, however, is the fact that landings from the south Atlantic fishery region are substantially removed from the curvilinear relationship that exists for the other fishery regions. There is an apparent underproduction of the southeastern fishery.

High levels of system heterotrophy for hard bottom communities across the southeastern continental shelf which are functionally similar to Gray's Reef may lead to under production of commercially important fishes. Gray's Reef live bottom was found to be substantially heterotrophic (P/R=0.73), consuming 1.1 gC m^{-2} d^{-1} more than was produced by pelagic and benthic primary producers (Table 13). A very large percentage of system biomass and respiration was attributable to filter feeding organisms which are largely ungrazed, including corals, sponges and mussels. Consequently it appears as if a net effect of hard bottom communities such as that found on Gray's Reef is the capture and removal of organic matter produced in the water

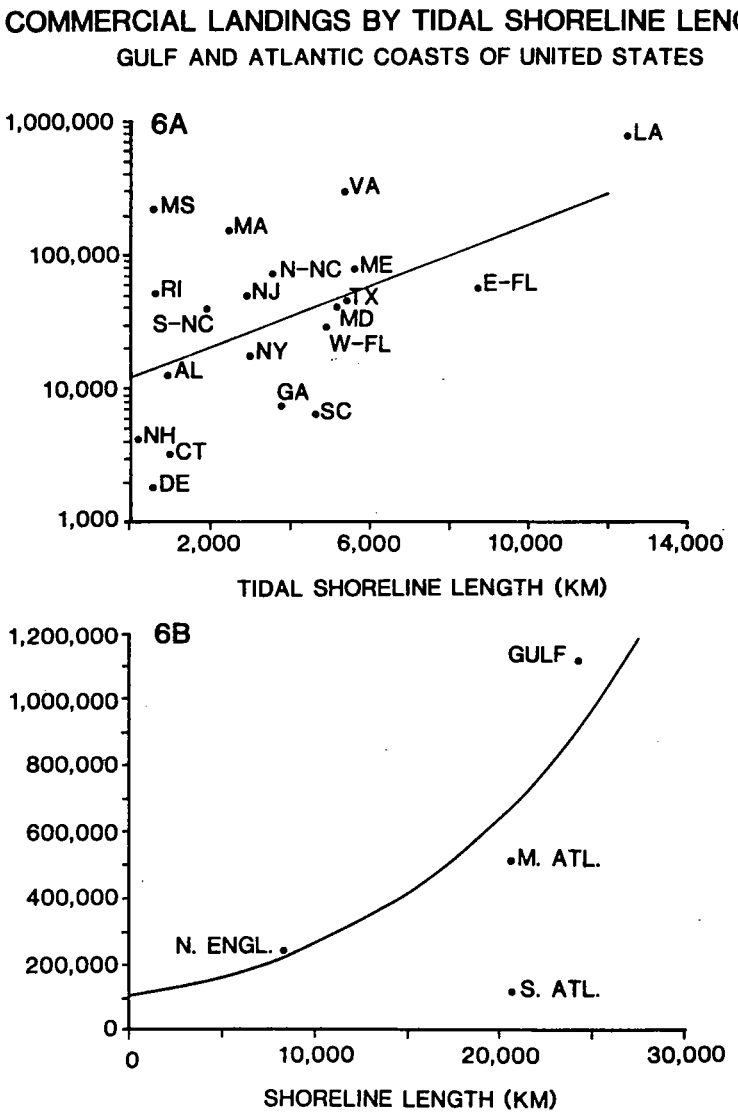

Figure 6a and 6b. Relationships between tidal shoreline length in various states/regions and the commercial landings (edible and industrial) of fish and shellfish by U.S. fishermen in particular states or regions. (6a)- landings by state. (6b)- landings by geographic region. New England region (N.ENGL) is from Massachusetts through Maine. Middle Atlantic (M.ATL) is from Cape Hatteras, North Carolina (N-NC) through Rhode Island. South Atlantic (S.ATL) is from Key West, Florida (E-FL) to Cape Hatteras, North Carolina (S-NC). Gulf of Mexico (GULF) is the entire U.S. shoreline along the Gulf of Mexico including western Florida (W-FL). Curve in 6a from linear regression of $\log_{(10)}$landings against tidal shoreline length (R^2=0.41). Curve in 6b from linear regression of $\log_{(10)}$regional landings against tidal shoreline length excluding the south Atlantic region (R^2=0.93). Landings from 1984 and 1985.

column. As a result of being respired by ungrazed macrofauna, this organic matter becomes unavailable for support of the planktonic food chain leading to the production of commercially important fishes.

As up to 30% of the bottom area of the southeastern continental shelf is hard bottom, the gross removal of organic matter from the water column is potentially substantial (1.1 gC m^{-2} hard bottom * 30% of shelf bottom area is equivalent to an average consumption of 0.33 gC m^{-2} (of total shelf bottom area) d^{-1}). As average pelagic primary production across the Georgia Bight is less than 1 gC m^{-2} d^{-1} (Haines and Dunstan, 1975; Yoder, 1985), hard bottom communities may be responsible for consuming up to 1/3 of the total primary production in the water column. Thus the organic matter resource base upon which commercial fisheries in the southeastern portion of the U.S. must develop is 1/3 smaller than that which would be available in the absence of hard bottom communities.

The apparent paradox between the high fish densities on hard bottoms and low commercial fish landings in the southeastern Atlantic fishery region may be explained by the presence of an independent benthic grazing food chain on hard bottoms which leads to the production of reef fish at the expense of pelagic fish species which develop from a planktonic food chain. The base of such a benthic food web presumably rests on the production of benthic algae which we found to be substantial (Table 13: 0.88 gC m^{-2} d^{-1}).

CONCLUSIONS AND RECOMMENDATIONS

1. A methodology was developed for measuring community metabolism and nutrient regeneration of medium to high density portions of the live bottom at Gray's Reef. The new methodology will enable the vitality of the live bottom community to be routinely assessed and monitored over time.

2. The pelagic community above the hard bottom at GRNMS was highly active metabolically. Levels of primary production, community metabolism and nutrient regeneration were substantially higher than in the adjacent mid-shelf region in general. Such high levels of activity may reflect a stimulatory role (through nutrient regeneration) of hard bottom benthic communities in the Georgia Bight.

3. Low density regions of the hard bottom at Gray's Reef were metabolically similar to adjacent sandy bottom areas within Gray's Reef. These regions were substantially less active with respect to metabolism and nutrient cycling than sandy sediment systems within the estuarine plume portion of the nearshore continental shelf. Relatively low levels of metabolism may reflect low levels of allochthonous organic material inputs relative to the nearshore region (which is immediately adjacent to productive coastal marshes and estuaries) and the low density of filter feeding epifauna relative to higher density regions of Gray's Reef.

4. The benthic community in medium (and presumably high) density portions of Gray's Reef had the highest level of metabolism and nutrient regeneration within the GRNMS. Rates of benthic primary production were only slightly lower than rates in the water column while benthic respiration exceeded pelagic respiration. These levels of metabolism were comparable to those observed in highly productive coastal marshes and estuaries. Nutrient release from the benthos to the overlying water column was substantial; benthic fertilzation of the water column may stimulate primary production of pelagic systems adjacent to the GRNMS.

5. The entire benthic and pelagic system within the Gray's Reef National Marine Sanctuary was net heterotrophic. The presence of relatively ungrazed, heterotrophic live bottom communities on the south Atlantic continental shelf may be a factor leading to the unusually low commercial fishery landings in this region.

6. Gray's Reef is a unique highly active system that exists at the boundary between the turbid nearshore region and the barren mid-shelf region. At such a location, it may be highly susceptible to effects of outside activities and influences. This study and others (see Gladfelter and Kinsey, 1985) have established that community metabolism studies integrate a great number of population and community level processes. A management plan for GRNMS should include routine monitoring of community metabolism which can provide valuable early warnings of system stress induced by outside activities.

7. We found substantial metabolic and nutrient recycling differences between low and medium density regions of Gray's Reef. Metabolism was an order of magnitude higher in medium density regions. To properly assess the importance of live bottom communities on the continental shelf in the Georgia Bight, we need to know the absolute and relative areas of low, medium and high density communities.

8. The majority of the biomass in medium density portions of Gray's Reef consisted of apparently ungrazed epifauna such as corals, sponges and bryozoans. To determine whether these species represent a significant shunt or dead end in the food chain leading to the production of commercial fish in the Georgia Bight, we must determine the contribution of these organisms to total system metabolism. We suggest that this be accomplished with a variety of techniques including whole community measures of metabolism following the removal of sponges, corals and bryozoans and by measuring the metabolism of isolated individual species of each of the ungrazed organisms.

9. The balance between benthic autotrophy and heterotrophy is partially governed by light levels reaching the bottom. Activities within the coastal zone that alter turbidity and hence light penetration within the water column could adversely affect the health of the live bottom community. Similarly, increased sediment loads in the water column could interfere with feeding of benthic filter feeders. We recommend that future studies should determine the effect of light and turbidity on live bottom metabolism.

10. Community development at Gray's Reef is arrested in comparison to most "classical" coral reefs. To some extent this may be due to cold water temperatures during winter, but it may also be due to occassional burial and destruction of the benthic community by migration of sand waves (V. J. Henry, personal communication). To evaluate this hypothesis, we recommend that a series of concrete rings, which can also be used to monitor community metabolism, be established across Gray's Reef to determine the degree and frequency to which sand waves do propagate across Gray's Reef and bury benthic communities.

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APPENDIX I

Nutrient concentrations, current velocities and nutrient flux through Gray's Reef during one daylight period in midsummer 1985.

JULY 8, 1985 EULERIAN SAMPLES
DISSOLVED ORGANIC N - PAGE 1

TIME	TOP METER: SPEED	VELOCITIES ALONG(Y)	CROSS(X)	BOTTOM METER: SPEED	VELOCITIES ALONG	CROSS	TOP DON T-DON STA-1	CONCENTRATIONS T-DON STA-2	T-DON 3	T-DON 4	T-DON 5
0	29.55	-1.35	-29.52	7.44	1.79	-7.22					
1	22.19	11.98	-18.68	1.98	1.89	-0.59					
2	26.20	26.05	2.85	7.84	7.82	-0.59					
3	37.51	30.06	22.44	10.22	8.74	5.30					
4	41.89	27.73	31.40	13.55	9.46	9.70					
5	35.56	19.79	29.54	20.48	14.44	14.52					
6	27.11	18.69	19.64	13.72	8.64	10.66					
7	13.58	12.90	4.22	0.51	-0.18	-0.48					
8	16.34	-6.83	-14.84	8.39	-0.21	-8.39	NA	10.26	NA	NA	NA
9	33.76	-17.42	-28.92	18.28	-4.27	-17.77	10.44	11.14	16.07	9.5	NA
10	34.81	-18.73	-29.35	25.37	-7.61	-24.20	10.05666666	12.02	14.41	14.26	8.96
11	30.82	-12.48	-28.18	19.71	-4.06	-19.29	9.673333333	12.9	12.75	19.02	9.69
12	25.42	1.23	-25.39	7.99	0.17	-7.99	9.29	13.41333	11.09	23.78	10.42
13	14.80	7.44	-12.79	5.62	4.12	-3.82	9.386666666	13.92666	11.88333	21.23	11.98666
14	19.82	19.11	5.28	10.40	10.07	2.59	9.483333333	14.44	12.67666	18.68	13.55333
15	30.90	27.24	14.60	19.01	16.02	10.24	9.58	13.56	13.47	16.13	15.12
16	29.20	20.46	20.83	12.62	9.99	7.72	9.82	12.68	12.97666	14.23	13.36333
17	31.57	14.42	28.08	7.37	4.95	5.45	10.06	11.8	12.48333	12.33	11.60666
18	28.47	8.31	27.23	3.68	2.79	2.40	10.3	10.82	11.99	10.43	9.85
19	12.88	3.31	12.44	0.18	0.12	0.13	10.91	9.84	10.57	10.64	9.726666
20	0.13	0.12	0.05	4.39	-1.05	-4.27	11.52	8.86	9.15	10.85	9.603333
21	14.24	-8.95	-11.08	14.11	-2.27	-13.93	NA	NA	NA	11.06	9.48
22	29.93	-18.73	-23.34	20.34	-2.16	-20.23					
23	32.89	-17.89	-27.59	17.72	-1.14	-17.69					
							means				
							10.04333333	11.97384	12.46	14.78	11.11333

grand mean
11.66090705 mM/m3

x volume(171.1E6m3)

= 2.0E+09 mMoles per total volume

= 233.7131 mMoles per square meter

JULY 8, 1985 EULERIAN SAMPLES
DISSOLVED ORGANIC N - PAGE 2

TIME	BOTTOM DON CONCENTRATIONS B-DON 1	B-DON 2	B-DON 3	B-DON 4	B-DON 5	TOP ALONG	TOP CROSS mM/SEC	BOTTOM ALONG	BOTTOM CROSS		NUTRIENT AVAILABILITY/HR mM/M3/HR PER 1 M WIDE DOOR	
0												DEEP
1						0	0	0	0		20 OR	2 M ~~WIDE~~
2						0	0	0	0			
3						0	0	0	0			
4						0	0	0	0			
5						0	0	0	0			
6						0	0	0	0			
7						0	0	0	0	ROW		
8	NA	13.19	NA	NA	NA	NA	NA	NA	NA	SUM	NA	NA
9	9.08	12.9	12.19	9.67	NA	-6427.53	48676.22	47.42750	26082.97	68379.09	NA	NA
10	9.15	12.61	14.58	10.26333	9.51	-11420.9	14358.72	-2169.55	43572.15	44340.34	252162.9	20499.78
11	9.22	12.32	16.97	10.85666	9.96	-10612.8	-19857.1	-2358.10	41133.46	8305.347	226283.1	16835.82
12	9.29	12.89	19.36	11.45	10.41	1381.451	-50350.8	138.8186	21293.65	-27536.9	160924.9	7297.572
13	9.386666	13.46	17.70666	11.82	11.07333	6741.224	-14235.4	2541.220	8809.153	3859.107	98548.34	5131.855
14	9.483333	14.03	16.05333	12.19	11.73666	13137.69	1200.468	4406.993	-5046.14	13779.01	145796.5	9509.381
15	9.58	13.06666	14.4	12.56	12.4	16274.73	-4461.04	6391.299	-12625.4	5579.560	235858.8	16975.25
16	9.82	12.10333	12.96	11.75333	11.00333	8906.789	-2749.06	2577.197	-6234.20	-2499.28	184968.6	10474.82
17	10.06	11.14	11.52	10.94666	9.606666	3937.948	-12309.7	580.3348	-2036.61	-9878.07	160717.5	5650.502
18	10.3	10.56	10.08	10.14	8.21	998.9538	-13112.2	-164.888	-111.189	-12339.4	122492.3	2610.297
19	10.91	9.98	9.705	9.353333	8.436666	140.9385	3283.488	-20.9011	17.60042	3421.126	48541.80	125.6073
20	11.52	9.4	9.33	8.566666	8.663333	-4.10092	46.12441	292.6507	-1339.57	-1004.89	15464.28	3002.671
21	NA	NA	NA	7.79	8.89	NA	NA	NA	NA			
22						0	0	0	0			
23						NA	NA	0	0			
	9.816666	12.12692	13.23791	10.56533	9.991666	COLUMN SUM:				* AVG (N=12)		
						23054.22	-5430.5	12265.48	113465.8	7862.917		
						TOP SUM		BOT SUM		24551.03	AVERAGE	AVERAGE
						-31376.3		125731.3			150159.9	8919.416
						TOTAL SUM						
						94355.00						

AREA = 8565500 M2 AREAL FLUX mMOLES/M2/DAY
29.31306

TIME = 86400 SEC/DAY

* = AVERAGE FLUX RATE IN mMOLES/SEC ± STD. DEVIATION

JULY 8, 1985 EULERIAN SAMPLES
DISSOLVED ORGANIC P - PAGE 1

TIME	TOP METER: SPEED	VELOCITIES ALONG(Y)	CROSS(X)	BOTTOM METER: SPEED	VELOCITIES ALONG	CROSS	TOP DOP T-DOP STA-1	CONCENTRATIONS T-DOP STA-2	T-DOP 3	T-DOP 4	T-DOP 5
0	29.55	-1.35	-29.52	7.44	1.79	-7.22					
1	22.19	11.98	-18.68	1.98	1.89	-0.59					
2	26.20	26.05	2.85	7.84	7.82	-0.59					
3	37.51	30.06	22.44	10.22	8.74	5.30					
4	41.89	27.73	31.40	13.55	9.46	9.70					
5	35.56	19.79	29.54	20.48	14.44	14.52					
6	27.11	18.69	19.64	13.72	8.64	10.66					
7	13.58	12.90	4.22	0.51	-0.18	-0.48					
8	16.34	-6.83	-14.84	8.39	-0.21	-8.39	NA	0.21	NA	NA	NA
9	33.76	-17.42	-28.92	18.28	-4.27	-17.77	0.03	0.14	0.03	0.07	NA
10	34.81	-18.73	-29.35	25.37	-7.61	-24.20	0.116666666	0.07	0.02	0.046666	0.3
11	30.82	-12.48	-28.18	19.71	-4.06	-19.29	0.153333333	0	0.01	0.023333	0.15
12	25.42	1.23	-25.39	7.99	0.17	-7.99	0.19	0	0	0	0
13	14.80	7.44	-12.79	5.62	4.12	-3.82	0.126666666	0	0.03	0.06	0
14	19.82	19.11	5.28	10.40	10.07	2.59	0.063333333	0	0.06	0.12	0
15	30.90	27.24	14.60	19.01	16.02	10.24	0	0	0.09	0.18	0
16	29.20	20.46	20.83	12.62	9.99	7.72	0.006666666	0	0.13	0.15	0.053333
17	31.57	14.42	28.08	7.37	4.95	5.45	0.013333333	0	0.17	0.12	0.106666
18	28.47	8.31	27.23	3.68	2.79	2.40	0.02	0	0.21	0.09	0.16
19	12.88	3.31	12.44	0.18	0.12	0.13	0.125	0	0.105	0.06	0.156666
20	0.13	0.12	0.05	4.39	-1.05	-4.27	0.23	0	0	0.03	0.153333
21	14.24	-8.95	-11.08	14.11	-2.27	-13.93	NA	NA	NA	0	0.15
22	29.93	-18.73	-23.34	20.34	-2.16	-20.23	means				
23	32.89	-17.89	-27.59	17.72	-1.14	-17.69	0.09375	0.032307	0.07125	0.073076	0.1025

grand mean
0.095516025 mM

x volume (171.1E6 m3)

= 16425600 mMoles

JULY 8, 1985 EULERIAN SAMPLES
DISSOLVED ORGANIC P - PAGE 2

TIME	BOTTOM DOP CONCENTRATIONS B-DOP 1	B-DOP 2	B-DOP 3	B-DOP 4	B-DOP 5	TOP ALONG	TOP CROSS mM/SEC	BOTTOM ALONG	BOTTOM CROSS		NUTRIENT AVAILABILITY/HR mM/M3/HR PER 1 M2 HIDE DOOR	
0												
1						0	0	0	0			
2						0	0	0	0			
3						0	0	0	0		20 OR 2 M DEEP	
4						0	0	0	0			
5						0	0	0	0			
6						0	0	0	0			
7						0	0	0	0	ROW		
8	NA	0.23	NA	NA	NA	NA	NA	NA	NA	SUM		
9	0.56	0.153333	0	0	NA	193.3091	133.9098	281.9301	-1673.04	-1063.89	NA	NA
10	0.136666	0.026666	0	0.023333	0.25	207.8643	-498.252	344.7831	-2147.29	-2093.39	2823.974	287.3915
11	0.313333	0	0	0.046666	0.235	138.4792	-1087.46	100.0258	-1607.24	-2456.20	1591.387	168.8501
12	0.19	0.013333	0	0.07	0.22	-21.5733	-1116.73	-2.14474	-456.336	-1596.78	631.6482	56.78447
13	0.126666	0.026666	0	0.046666	0.146666	-25.2222	-463.986	-40.6262	-129.719	-659.554	371.0413	28.03998
14	0.063333	0.01	0	0.023333	0.073333	206.1970	150.0832	-74.5368	28.00001	310.5441	497.0931	29.95395
15	0	0.006666	0	0	0	680.2133	304.1619	-143.236	-229.122	612.0167	733.0461	26.16395
16	0.006666	0.153333	0.083333	0.036666	0.046666	517.2498	120.6151	-36.9490	-345.352	263.5633	1011.618	59.36459
17	0.013333	0.21	0.166666	0.073333	0.093333	368.9048	-238.393	7.635984	-365.998	-227.850	1227.109	59.01354
18	0.02	0.23	0.25	0.11	0.14	215.1592	-630.398	28.34028	-194.581	-581.479	1182.514	39.71045
19	0.125	0.25	0.125	0.163333	0.146666	12.25552	230.4202	-0.98395	-2.63752	239.0492	424.5757	2.102757
20	0.23	0.22	0	0.216666	0.153333	-2.15838	2.750538	27.42592	-174.440	-146.422	278.8262	55.01946
21	NA	NA	NA	0.27	0.16	NA	NA	NA	NA			
22						NA	NA	0	0			
23	0.17375	0.134615	0.052683	0.083076	0.13875							
						COLUMN SUM:				* AVG		
						2190.678	-3084.48	491.6591	-7298.26	-616.700		
						TOP SUM		BOT SUM		956.4292	AVERAGE	AVERAGE
						-593.805		-6806.60			979.3486	73.88480
						TOTAL SUM						
						-7400.40						

AREA = 8565500 M2 AREAL FLUX mMOLES/M2/DAY
-6.22064

TIME = 86400 SEC/DAY

* = AVERAGE FLUX RATE IN mMOLES/SEC ± STD. DEVIATION

JULY 8, 1985 EULERIAN SAMPLES
NH4+ - PAGE 1

TIME	TOP METER: SPEED	VELOCITIES ALONG(Y)	CROSS(X)	BOTTOM METER: SPEED	VELOCITIES ALONG	CROSS	TOP NH4 T-NH4 STA-1	CONCENTRATIONS T-NH4 STA-2	T-NH4 3	T-NH4 4	BOTTOM NH T-NH4 5
0	29.55	-1.35	-29.52	7.44	1.79	-7.22					
1	22.19	11.98	-18.68	1.98	1.89	-0.59					
2	26.20	26.05	2.85	7.84	7.82	-0.59					
3	37.51	30.06	22.44	10.22	8.74	5.30					
4	41.89	27.73	31.40	13.55	9.46	9.70					
5	35.56	19.79	29.54	20.48	14.44	14.52					
6	27.11	18.69	19.64	13.72	8.64	10.66					
7	13.58	12.90	4.22	0.51	-0.18	-0.48					
8	16.34	-6.83	-14.84	8.39	-0.21	-8.39	NA	0.4	NA	NA	NA
9	33.76	-17.42	-28.92	18.28	-4.27	-17.77	0.64	0.453333	0.58	0.4	NA
10	34.81	-18.73	-29.35	25.37	-7.61	-24.20	0.536666666	0.506666	0.546666	0.47	0.29
11	30.82	-12.40	-28.18	19.71	-4.06	-19.29	0.433333333	0.56	0.513333	0.54	0.435
12	25.42	1.23	-25.39	7.99	0.17	-7.99	0.33	0.64	0.48	0.61	0.58
13	14.80	7.44	-12.79	5.62	4.12	-3.82	0.296666666	0.72	0.523333	0.54	0.536666
14	19.82	19.11	5.28	10.40	10.07	2.59	0.263333333	0.8	0.566666	0.47	0.493333
15	30.90	27.24	14.60	19.01	16.02	10.24	0.23	0.64	0.61	0.4	0.45
16	29.20	20.46	20.83	12.62	9.99	7.72	0.33	0.48	0.523333	0.326666	0.343333
17	31.57	14.42	28.08	7.37	4.95	5.45	0.43	0.32	0.536666	0.253333	0.236666
18	28.47	8.31	27.23	3.68	2.79	2.40	0.53	0.266666	0.5	0.18	0.13
19	12.88	3.31	12.44	0.18	0.12	0.13	0.605	0.213333	0.29	0.136666	0.113333
20	0.13	0.12	0.05	4.39	-1.05	-4.27	0.68	0.16	0.08	0.093333	0.096666
21	14.24	-8.95	-11.08	14.11	-2.27	-13.93	NA	NA	NA	0.05	0.08
22	29.93	-18.73	-23.34	20.34	-2.16	-20.23	means				
23	32.89	-17.89	-27.59	17.72	-1.14	-17.69	0.442083333	0.473846	0.483333	0.343846	0.315416

grand mean
0.391506410 mM/M3

x volume (171.1E6 m3)

= 67021200 mMoles

JULY 8, 1985 EULERIAN SAMPLES
NH4+ - PAGE 2

BOTTOM NH4 CONCENTRATIONS

TIME	B-NH4 1	B-NH4 2	B-NH4 3	B-NH4 4	B-NH4 5	TOP ALONG	TOP CROSS mM/SEC	BOTTOM ALONG	BOTTOM CROSS		NUTRIENT AVAILABILITY/HR mM/M3/HR PER 1 M2 WIDE DOOR	
0												
1						0	0	0	0			
2						0	0	0	0			
3						0	0	0	0		20 OR 2 M DEEP	
4						0	0	0	0			
5						0	0	0	0			
6						0	0	0	0			
7						0	0	0	0	ROW		
8	NA	0.72	NA	NA	NA	NA	NA	NA	NA	SUM	NA	NA
9	0.53	0.613333	0.29	0.21	NA	182.5697	-44.6366	254.2641	671.9588	1064.156	NA	NA
10	0.463333	0.506666	0.316666	0.23	0.27	46.19207	317.0697	297.8738	728.3815	1389.517	9154.240	652.7198
11	0.396666	0.4	0.343333	0.25	0.335	-69.2396	652.4789	76.26970	431.5739	1091.082	7954.979	489.5235
12	0.33	0.54	0.37	0.27	0.4	13.62527	1057.955	-3.69968	573.5041	1641.385	5930.799	219.8479
13	0.296666	0.68	0.503333	0.33	0.406666	32.10106	1204.389	-54.5915	492.3456	1674.244	3684.324	179.2941
14	0.263333	0.82	0.636666	0.39	0.413333	-47.1307	-774.805	-52.7969	-482.013	-1356.74	5591.205	377.9190
15	0.23	0.67	0.77	0.45	0.42	352.7032	-2095.33	474.1613	-1801.37	-3069.84	8660.862	695.3632
16	0.33	0.52	0.603333	0.343333	0.323333	170.3139	-1913.15	99.29356	-903.837	-2457.38	6243.123	385.2640
17	0.43	0.37	0.436666	0.236666	0.226666	53.33564	-1126.94	-58.0334	-176.688	-1308.33	4939.761	180.3126
18	0.53	0.263333	0.27	0.13	0.13	-89.6497	-357.225	-101.337	70.41986	-477.793	3643.812	70.08101
19	0.605	0.156666	0.19	0.103333	0.193333	-120.002	686.4602	-5.34415	11.00660	572.1207	1275.384	3.240669
20	0.68	0.05	0.11	0.076666	0.256666	-7.19460	5.642130	52.59324	-589.148	-538.107	381.0264	74.20249
21	NA	NA	NA	0.05	0.32	NA	NA	NA	NA			
22						NA	NA	0	0			
23	0.42375	0.485384	0.403333	0.236153	0.307916							
						COLUMN SUM:				* AVG		
						517.6243	-2383.10	968.6519	-873.874	-147.975		
						TOP SUM		BOT SUM		1563.825	AVERAGE	AVERAGE
						-1870.48		94.77793			5223.592	302.5241
						TOTAL SUM						
						-1775.70						

AREA = 8565500 M2 AREAL FLUX mMOLES/M2/DAY
TIME= 86400 SEC/DAY -1.49262

* = AVERAGE FLUX IN mMOLES/SEC + STD. DEVIATION

JULY 8, 1985 EULERIAN SAMPLES
NO3 - PAGE 1

TIME	TOP METER: SPEED	VELOCITIES ALONG(Y)	CROSS(X)	BOTTOM METER: SPEED	VELOCITIES ALONG	CROSS	TOP NO3 CONCENTRATIONS T-NO3 STA-1	T-NO3 STA-2	T-NO3 3	T-NO3 4	T-NO3 5
0	29.55	-1.35	-29.52	7.44	1.79	-7.22					
1	22.19	11.98	-18.68	1.98	1.89	-0.59					
2	26.20	26.05	2.85	7.84	7.82	-0.59					
3	37.51	30.06	22.44	10.22	8.24	5.30					
4	41.89	27.23	31.40	13.55	9.46	9.70					
5	35.56	19.79	29.54	20.48	14.44	14.52					
6	27.11	18.69	19.64	13.72	8.64	10.66					
7	13.58	12.90	4.22	0.51	-0.18	-0.48					
8	16.34	-6.83	-14.84	8.39	-0.21	-8.39	NA	0.166	NA	NA	NA
9	33.76	-17.42	-28.92	18.28	-4.27	-17.27	0.1	0.162333	0.107	0.067	NA
10	34.81	-18.23	-29.35	25.37	-7.61	-24.20	0.100666666	0.158666	0.102666	0.075666	0.064
11	30.82	-12.48	-28.18	19.71	-4.06	-19.29	0.101333333	0.155	0.098333	0.084333	0.071
12	25.42	1.23	-25.39	7.99	0.17	-7.99	0.102	0.131	0.094	0.093	0.078
13	14.80	7.44	-12.79	5.62	4.12	-3.82	0.117333333	0.107	0.068	0.115333	0.090666
14	19.82	19.11	5.28	10.40	10.07	2.59	0.132666666	0.083	0.042	0.137666	0.103333
15	30.90	27.24	14.60	19.01	16.02	10.24	0.148	0.112	0.016	0.16	0.116
16	29.20	20.46	20.83	12.62	9.99	7.72	0.152	0.141	0.061666	0.159333	0.139333
17	31.57	14.42	28.08	7.37	4.95	5.15	0.156	0.17	0.107333	0.158666	0.162666
18	28.47	8.31	27.23	3.68	2.79	2.40	0.16	0.185333	0.153	0.158	0.186
19	12.88	3.31	12.44	0.18	0.12	0.13	0.145	0.200666	0.1445	0.164666	0.158333
20	0.13	0.12	0.05	4.39	-1.05	-4.27	0.13	0.216	0.136	0.171333	0.130666
21	14.24	-8.95	-11.08	14.11	-2.27	-13.93	NA	NA	NA	0.178	0.103
22	29.93	-18.73	-23.34	20.34	-2.16	-20.23	means				
23	32.89	-17.89	-27.59	17.72	-1.14	-17.69	0.12875	0.152923	0.094208	0.132538	0.116916

grand mean
0.132152243

x volume (171.1E6 m3)

= 23440700 mMoles

JULY 8, 1985 EULERIAN SAMPLES
NO3 - PAGE 2

TIME	BOTTOM NO3 CONCENTRATIONS B-NO3 1	B-NO3 2	B-NO3 3	B-NO3 4	B-NO3 5	TOP ALONG	TOP CROSS mM/SEC	BOTTOM ALONG	BOTTOM CROSS		NUTRIENT AVAILABILITY/HR mM/M3/HR PER 1 M2 WIDE DOOR	
0												
1						0	0	0	0			
2						0	0	0	0			
3						0	0	0	0		20 OR 2 M DEEP	
4						0	0	0	0			
5						0	0	0	0			
6						0	0	0	0			
7						0	0	0	0	ROW		
8	NA	0.222	NA	NA	NA	NA	NA	NA	NA	SUM	NA	NA
9	0.178	0.217	0.209	0.212	NA	142.2970	685.1720	-10.2759	148.1052	965.2983	NA	NA
10	0.152666	0.212	0.218666	0.230666	0.184	140.3084	577.5198	-59.5747	265.2055	923.4590	3080.493	364.5975
11	0.127333	0.207	0.228333	0.249333	0.1245	85.01087	441.5107	-53.7638	261.9207	734.6784	2460.609	265.7616
12	0.102	0.204	0.238	0.268	0.065	-5.22302	176.3259	3.217118	133.2009	307.5209	1416.137	100.9459
13	0.117333	0.201	0.203	0.26	0.076333	-28.2030	-170.786	55.09938	23.58541	-120.304	877.7952	69.32198
14	0.132666	0.198	0.168	0.252	0.087666	-63.6265	177.7975	33.23286	11.20032	203.6041	1339.559	125.5569
15	0.148	0.170666	0.133	0.244	0.099	-211.621	608.3238	86.43565	209.3704	692.5080	2315.911	217.5519
16	0.152333	0.143333	0.116333	0.216	0.091666	-136.251	524.1068	33.86997	134.1119	615.8376	2027.417	130.7838
17	0.156666	0.116	0.099666	0.188	0.084333	-80.8034	242.7274	6.872386	162.8061	332.4025	2057.174	68.37736
18	0.161	0.096	0.083	0.16	0.077	-26.3826	-128.180	-3.60694	78.94437	-79.2261	1879.430	30.55673
19	0.146	0.076	0.0525	0.126333	0.083666	-11.1831	-102.248	-0.49257	4.377281	-109.547	760.0978	1.257760
20	0.131	0.056	0.022	0.092666	0.090333	-0.41728	-0.53600	2.001677	-143.831	-137.782	131.0248	24.79037
21	NA	NA	NA	0.059	0.097	NA	NA	NA	NA		NA	
22											NA	
23	0.142083	0.163	0.147625	0.196769	0.096708							

COLUMN SUM:				* AVG		
-195.295	3031.731	148.0149	1348.997	361.1206		
TOP SUM		BOT SUM		399.8506	AVERAGE	AVERAGE
2836.435		1497.012			1667.789	127.2320
TOTAL SUM						
4333.448						

AREA = 8565500 M2 AREAL FLUX mMOLES/M2/DAY
TIME 86400 SEC/DAY 3.642615

* = AVERAGE FLUX IN mMOLES/SEC ± STD. DEVIATION

JULY 8, 1985 EULERIAN SAMPLES
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TIME	TOP METER: SPEED	VELOCITIES ALONG (Y)	CROSS (X)	BOTTOM METER: SPEED	VELOCITIES ALONG	CROSS	TOP P04 CONCENTRATIONS T-P04 STA-1	T-P04 STA-2	T-P04 3	T-P04 4	T-P04 5
0	29.55	-1.35	-29.52	7.44	1.79	-7.22					
1	22.19	11.98	-18.68	1.98	1.89	-0.59					
2	26.20	26.05	2.85	7.84	7.82	-0.59					
3	37.51	30.06	22.44	10.22	8.74	5.30					
4	41.89	27.73	31.40	13.55	9.46	9.70					
5	35.56	19.79	29.54	20.48	14.44	14.52					
6	27.11	18.69	19.64	13.72	8.64	10.66					
7	13.58	12.90	4.22	0.51	-0.18	-0.48					
8	16.34	-6.83	-14.84	8.39	-0.21	-8.39	NA	0.19	NA	NA	NA
9	33.76	-17.42	-28.92	18.28	-4.27	-17.27	0.12	0.37	0.12	0.14	NA
10	34.81	-18.73	-29.35	25.37	-7.61	-24.20	0.166666666	0.55	0.316666	0.32	0.15
11	30.82	-12.48	-28.18	19.71	-4.06	-19.29	0.213333333	0.73	0.513333	0.5	0.29
12	25.42	1.23	-25.39	7.99	0.17	-7.99	0.26	0.606666	0.71	0.68	0.41
13	14.80	7.44	-12.79	5.62	4.12	-3.82	0.723333333	0.483333	0.556666	0.506666	0.38
14	19.82	19.11	5.28	10.40	10.07	2.59	1.186666666	0.36	0.403333	0.333333	0.35
15	30.90	27.24	14.60	19.01	16.02	10.24	1.65	0.366666	0.25	0.16	0.32
16	29.20	20.46	20.83	12.62	9.99	7.72	1.193333333	0.323333	0.256666	0.25	0.296666
17	31.57	14.42	28.08	7.37	4.95	5.45	0.736666666	0.38	0.263333	0.34	0.273333
18	28.47	8.31	27.23	3.68	2.79	2.40	0.28	0.396666	0.27	0.43	0.25
19	12.08	3.31	12.44	0.18	0.12	0.13	0.255	0.413333	0.385	0.416666	0.233333
20	0.13	0.12	0.05	4.39	-1.05	-4.27	0.23	0.43	0.5	0.403333	0.216666
21	14.24	-8.95	-11.08	14.11	-2.27	-13.93	NA	NA	NA	0.39	0.2
22	29.93	-18.73	-23.34	20.34	-2.16	-20.23	means				
23	32.89	-17.89	-27.59	17.72	-1.14	-17.69	0.584583333	0.434615	0.37875	0.374615	0.28

grand mean concentration mM/m3
0.401480769

x volume(171.1 x 10E6 m3)

= 68611100 mM

JULY 8, 1985 EULERIAN SAMPLES
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TIME	BOTTOM P04 CONCENTRATIONS B-P04 1	B-P04 2	B-P04 3	B-P04 4	B-P04 5	TOP ALONG	TOP CROSS mM/SEC	BOTTOM ALONG	BOTTOM CROSS		NUTRIENT AVAILABILITY/HR mM/M3/HR PER 1 M2 WIDE DOOR	
0												
1						0	0	0	0			
2						0	0	0	0			
3						0	0	0	0		20 OR 2 M DEEP	
4						0	0	0	0			
5						0	0	0	0			
6						0	0	0	0			
7						0	0	0	0	ROW		
8	NA	0.14	NA	NA	NA	NA	NA	NA	NA	SUM		
9	0.21	0.22	0.3	0.09	NA	370.5092	1539.963	-339.397	-2297.54	-1226.96	NA	NA
10	0.226666	0.3	0.306666	0.736666	0.19	138.5762	2501.853	-419.837	-1550.14	750.4463	7129.389	672.2039
11	0.243333	0.38	0.473333	0.483333	0.165	-80.7795	3458.138	-125.032	565.5106	3817.837	7439.649	495.1991
12	0.26	0.356666	0.56	0.23	0.14	59.42135	2213.870	2.788169	789.3339	3065.413	5770.498	178.0269
13	0.223333	0.333333	0.51	0.326666	0.2	-98.5961	-562.706	-83.7916	-182.786	-927.881	3669.959	169.3183
14	1.166666	0.31	0.46	0.423333	0.26	-1431.59	925.6888	-571.119	504.0146	-573.342	5735.665	395.3921
15	1.05	0.303333	0.41	0.52	0.32	-4042.68	4032.962	-1516.32	3452.636	1921.580	10495.89	876.3607
16	1.143333	0.296666	0.363333	0.46	0.283333	-2005.92	3922.262	-615.817	1774.397	3075.422	7341.983	471.8829
17	0.736666	0.29	0.316666	0.4	0.246666	-681.474	2817.321	-142.029	668.0935	2659.762	5586.020	211.0718
18	0.28	0.23	0.27	0.34	0.21	17.92994	273.1724	25.76389	66.71355	383.5798	3686.574	70.43406
19	0.255	0.17	0.34	0.28	0.206666	10.35175	-364.832	2.225146	0.760825	-320.994	1595.244	3.249322
20	0.23	0.11	0.41	0.22	0.203333	2.626031	-3.13845	-28.0712	69.11793	40.53423	387.0708	74.20249
21	NA	NA	NA	0.16	0.2	NA	NA	NA	NA		NA	
22												
23	0.599583	0.264615	0.450833	0.420461	0.21875							

surface mean
0.366995

sta 1 was integrated - not included

bottom mean
0.340665

COLUMN SUM:				* AVG		
-7719.14	20835.10	-3811.47	3360.909	1055.449		
TOP SUM		BOT SUM		1691.649	AVERAGE	AVERAGE
13115.96		-450.568			5348.901	328.9042
TOTAL SUM						
12665.39						

AREA = 8565500 M2 AREAL FLUX mMOLES/M2/DAY
TIME = 86400 SEC/DAY 10.64629

* = AVERAGE FLUX IN mMOLES/SEC ± STD. DEVIATION

APPENDIX II

Report by subcontractor, General Oceanics, on surface and bottom currents at Gray's Reef during 1984-1985. See separate enclosed report.