Short title:

The occurrence and biology of *Trichodesmium* at Barbados.

SOME ASPECTS OF THE OCCURRENCE AND BIOLOGY OF *TRICHODESMIUM* (CYANOPHYTA) IN THE WESTERN TROPICAL ATLANTIC NEAR BARBADOS, WEST INDIES.

GARY A. BORSTAD

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Marine Sciences Centre
McGill University
Montreal, Quebec
Canada.

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Abstract

Previously reported cyclical fluctuations of surface Trichodesmium (Oscillatoria) standing stock off Barbados have been shown to occur regularly over periods of several years. Large numbers of Trichodesmium and diatoms appear simultaneously at Barbados in surface waters of slightly lowered salinity, and these patches (which may be up to 1000 km in diameter) alternate temporally with more saline plankton-poor water dominated by dinoflagellates and coccolithophorids. Physical and hydrological data from a variety of sources indicate that the poorly known wave-like nature of the Guiana Current and the westward movement of these meanders as waves may be responsible for the periodicity of events at Barbados. Cyclical fluctuations with similar period can be observed in the data from six independent plankton studies and it appears that the phenomenon is one of the most important mechanisms determining plankton species composition and abundance in this area.

In separate studies of the biology of Trichodesmium, some aspects of the photosynthetic character of the alga were investigated. Trichodesmium comprises about half of the phytoplankton biomass in the near surface layer off Barbados, and contributes nearly the same fraction of the primary production in this layer. As Trichodesmium colonies age, individual cells die and lyse, but do not sink out of the mixed layer like unicellular plankton. Cellular debris and other organic material accumulate among the living filaments of the colony and become infested with bacteria, fungi and protozoa. Much remineralization of Trichodesmium appears to take place in living colonies in the mixed layer. Seventeen species of diatoms, three species of dinoflagellates, a previously undescribed hydrozoan, and a naupliar copepod utilize the Trichodesmium colonies as floating substrates and may benefit from the local supply of recycled nutrients.

Résumé

Des fluctuations cycliques des populations du cyanophyte planctonique Trichodesmium (= Oscillatoria) au large de la Barbade se sont manifestées régulièrement sur des périodes de plusieures années. De larges populations de Trichodesmium et de diatomeés apparaissent simultanement à la Barbade, dans les eaux de surface dont la salinité est légèrement abaissée. Ces régions (qui peuvent atteindre un diametre de 1000 km) alternent temporellement avec des eaux plus salines et moins riches en plancton (dont les especes dominantes sont les dinoflagellées et les coccolithophoreés). Les donneés physiques et hydrologiques - de sources varieés - indiquent que ce sont la nature ondulueuse, encore mal connue, du courant de Guyane et le mouvement vers l'ouest de cette vague qui peuvent être la cause de la périodicité des phènomènes de la Barbade.

On peut remarquer, d'après les donneés de six études indépendentes sur le plancton, des fluctuations cycliques de période similaire; il semble que le phènomène est un des mècanismes les plus importants qui règlent la composition et l'abondance des espèces dans cette region.

Dans differentes études sur la biologie du Trichodesmium, on s'est penchè plus particulièrement sur certains aspects du caractère photosynthètique de cette algue. Au large de la Barbade, dans la couche près de la surface, la biomasse est composeé, pour moitie, par le Trichodesmium, qui contribue egalement à pres de 50% de la production primaire. Quand les colonies du Trichodesmium vieillissent, les cellules meurent et se lysent, mais ne tombent pas de là zone de mélange comme le phytoplancton unicellulaire. Les débris cellulaires et les autres matières organiques s'accumulent entre les filaments vivants de la colonie et sont envahis par des bactéries, des champignons

et des protozoaires.

La reminéralisation du Trichodesmium se fait en majorité dans les colonies vivantes de la zone de mélange.

Dix-sept espèces de diatomées, trois espèces de dino-flagellées, un hydrozoaire inconnu auparavant et un copépode au stade nauplius utilisent tous les colonies de Trichodesmium comme substrat flottant et peuvent s'en servir comme source de nutriments.

CONTENTS

List of Figures

List of Plates

List of Tables

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This work is dedicated to the memory of my original supervisor, Dr. David Steven, who died shortly after the field work began. He was a kind and generous man.

Statement of originality

This thesis represents the first recognition of the fact that the 'oscillatory variations' of Trichodesmium standing stocks off Barbados, originally described by Steven et al. (1970), are actually part of a much more general phenomenon, in which the coincident fluctuation of many other components of the planktonic regime is related to the spreading of low salinity waters from South America. The observation that the alternate passage of plankton-rich neritic waters of low salinity and plankton-poor oceanic waters is in some way related to the wave-like nature of the Guiana Current is also original. This phenomenon is of major importance in determining the species composition and abundance of the phytoplankton, some of the zooplankton, and possibly some of the nekton off Barbados.

Section 3 reports on several aspects of the little known photosynthetic character of Trichodesmium and indicates its importance in Barbados waters. The observation that much of the remineralization of the algal biomass appears to take place in the mixed layer is of importance in the consideration of the nutrient economy of that zone.

The description of the Trichodesmium periphyton is also new, as is the recognition that these organisms may affect whole colony physiological measurements conducted on the alga. This is the first record of a new genus of hydrozoan, and of a description of its life history. This is also the first note of the association between Trichodesmium and diatoms and dinoflagellates.

1 INTRODUCTION

Primary production in most tropical oceanic areas is low and limited by the availability of plant nutrients (Sverdrup et al., 1942). Vertical mixing between the surface and deep layers is almost completely lacking in these regions because of the intense permanent stratification resulting from continuous heating of the surface layers; without horizontal transport of nutrients, these water masses may become almost completely stripped of nitrate and phosphate. As a result, phytoplankton standing crops are much less than those in waters at higher latitudes, and appear to depend upon nutrients recycled within the euphotic zone for growth (Wangersky, in press). Seasonal fluctuations, which in temperate regions are often the ultimate factor responsible for fluctuations in phytoplankton standing crops, are weak and of less importance in tropical regions. The small increases and decreases in phytoplankton and zooplankton standing stocks appear to be determined primarily by local weather conditions or movement of water masses (Sournia, 1969; Blackburn et al., 1970).

It is in such impoverished tropical seas that the planktonic cyanophyte Trichodesmium abounds. The genus includes a number of filamentous and colonial species which closely resemble the freshwater Oscillatoria - in fact some authors consider them members of the latter genus (Drouet, 1968; Sournia, 1968). The taxonomy of the algae, which is complicated and at present based solely on morphological characters, is discussed in Appendix A.1 in the light of experience at Barbados.

The hydrographic conditions favouring growth of Trichodesmium blooms are not clearly understood. Reports commonly mention calm, sunny weather (Brongersma-Sanders, 1957; Bowman and Lancaster, 1965; Qasim, 1970; and others), conditions which will lead to stratification of the water mass and reduction of vertical mixing. Wyatt and Horwood

(1973) consider such conditions favourable for blooming of motile phytoplankton such as dinoflagellates and Trichodesmium. (The latter is also motile in the sense that it possesses gas vacuoles which enable it to rise in the water column.) Many species of freshwater blue-greens can position themselves at the depth most favourable for their growth through regulation of their buoyancy (Walsby, 1972). Since Trichodesmium is well supplied with gas vacuoles (Van Baalen and Brown, 1969), it seems logical to assume this is the case with this alga also.

Trichodesmium has been considered characteristic of oligotrophic oceanic water (Dugdale et al., 1964; Qasim, 1970; Fogg et al., 1973; and others) and no small part of the alga's success in these regions is now considered by many to be due to its apparent ability to fix molecular nitrogen. Nitrogen fixation by Trichodesmium colonies has been demonstrated by a number of authors (Dugdale et al., 1961, 1964; Goering et al., 1966; Taylor et al., 1973; Carpenter, 1973; Carpenter and McCarthy, 1975; Carpenter and Price, 1977; Mague et al., 1974, 1977) and, while nitrogenase activity has not been demonstrated in axenic cultures, the evidence from field studies indicates that the alga is probably responsible. Nitrogen fixation in Trichodesmium is interesting because this genus is one of the few blue-greens for which nitrogen fixation has been demonstrated that does not possess heterocysts. In heterocystous cyanophytes, the nitrogenase enzyme is protected from oxygen deactivation in these thick-walled cells, and in other nonheterocystous nitrogen-fixing types (e.g. Plectonema boryanum) the enzyme is only active under microaerobic conditions (Stewart and Lex, 1970). The question as to how Trichodesmium can fix nitrogen in the oxygen saturated waters of the sea therefore arises.

The earliest reports of nitrogen fixation by natural Trichodesmium populations were therefore seriously questioned, and fixation was assumed to be due to bacteria associated with the colonies

(Stewart, 1971). Bacteria which grow in nitrogen-free media have in fact been isolated from Trichodesmium gathered from the Kuroshio by Maruyama et al. (1970), and other workers (Carpenter and McCarthy, 1975; L. Borstad, pers. comm.*), but such isolates are apparently scavenging contaminating nitrogen, since they do not reduce acetylene.

Much of the still scanty knowledge of the biology of Trichodesmium has come from observations of the alga on short cruises to oligotrophic seas, where experiments were conducted on algal colonies drawn from the sea. Such experiments suffer from the fact that previous history of the alga is not known, and from the fact that many colonies may be heavily infested with bacteria (this study, see Section 4). To date, attempts at obtaining cultures of the alga have been unsuccessful (Van Baalan and Brown, 1969; Taylor et al., 1973; Carpenter and McCarthy, 1975; J. Sharp, pers. comm.†). The report of an axenic culture by Ramamurthy (1970) has been severely questioned, (Stewart, 1971; Fogg et al., 1973; J. Sharp, pers. comm.).

Trichodesmium has been recognized as the dominant phytoplankton in much of the western tropical Atlantic, the Caribbean Sea and the Florida Current (Margalef et al., 1971; Björnberg, 1971; Carpenter and Price, 1977), often contributing over 50% of the total phytoplankton biomass. Beers et al. (1965) likewise recorded Trichodesmium as contributing 20 to 40% of the phytoplankton standing stocks near Barbados.

During a subsequent study off Barbados, Steven et al. (1970) also encountered Trichodesmium in abundance and noted regular numerical

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* Lorraine Borstad, Microbiology Department, Macdonald College of McGill University, Ste. Anne de Bellevue, Quebec.

† Dr. Jon Sharp, Scripps Institute of Oceanography, La Jolla, California.

fluctuations of the alga in the surface layer which corresponded well with variations of chlorophyll concentration at the same depths. Examination of other data indicated to them that the numbers of phytoplankton excluding Trichodesmium were rather stable, and the agreement between variations of Trichodesmium numbers and those of chlorophyll led them to conclude that the blue-green was largely responsible for variations of chlorophyll.

In 1972, Steven and Glombitza (1972) re-examined these chlorophyll and Trichodesmium data. Mathematical analysis confirmed that both parameters fluctuated with a period of between 93 and 120 days, quite unlike any other biological system. The oscillations could not be related to the annual solar cycle or annual variations in the hydrographic conditions. Variations of day length, surface water temperature and salinity are all small in this part of the ocean. The water column is permanently stratified and the concentrations of nutrients in the mixed layer are low at all times. Steven and Glombitza (1972) regarded the oscillations as a growth and decay cycle of Trichodesmium, and put forward a tentative hypothesis based on the presence of a relatively small 'seed' population of healthy Trichodesmium filaments near the base of the euphotic zone, from which the surface 'blooms'* were generated at regular intervals. This suggested to them that the alga had "access to essential nutrients in deeper water, in sufficient quantities to sustain its growth in the impoverished surface water for a

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* What Steven et al. (1970) and others have referred to as Trichodesmium 'blooms' off Barbados cannot be compared to red tides caused by this alga elsewhere (Ramamurthy et al., 1972; Qasim, 1970; Wood, 1965; and others) or even the spring blooms in temperate latitudes. The relatively small increases of the alga are nevertheless striking compared to the paucity of phytoplankton off Barbados, and the term 'bloom' will be used here in quotes to indicate that it is used only as a relative term indicating an abundance of the alga.

limited period and that the population collapses when this reserve is exhausted". They tentatively regarded the oscillations of Trichodesmium numbers as an example of a free-running cycle.

In this respect, the oscillations of the Trichodesmium populations at Barbados seemed to present an excellent opportunity to study the biology of the alga. When this study began, little was known concerning the genus as it had been studied very rarely and seldom recorded in the nonbloom phase. Its continuous abundance at Barbados and the regularity with which it 'bloomed' suggested that information regarding the causes of the blooms elsewhere might be available at Barbados.

The studies on which this thesis reports arose from Steven's work and questions posed by it. The primary focus of the research was on the apparent cyclical 'blooming' of Trichodesmium off Barbados and on the biology of the alga in its nonbloom phase.

In the initial stages of the field work, several questions relating to the numerical fluctuations of the alga were addressed. A program to closely monitor the temporal variations of the vertical distribution in relation to hydrological variables was established so that long term synchrony, periodicity, and amplitude of the variations could be examined. This original program was structured to provide intensive data on the vertical and seasonal distribution of the two colony types, trichome diameters and filament length, since little was known of the vertical distribution of Trichodesmium.

Coincident with this enumeration phase which lasted about eighteen months, extensive microscopic observations were conducted on Trichodesmium collected from various depths and in different phases of the cycle, in order to monitor changes in species abundance and/or morphology of the filaments and colonies. These observations drew

attention to the fact that some, but not all, of the algal colonies encountered harboured other microorganisms. In colonies not drawn from 'blooms', large numbers of bacteria and fungi could usually be found embedded in a mucilaginous material accumulating at the center of the colony. A number of other organisms including dinoflagellates, diatoms and a previously undescribed hydrozoan (Borstad and Voss, in preparation) were also frequently observed in the Trichodesmium colonies, and microscopic observations have allowed description of the relationship between the alga and several other organisms.

The presence of large numbers of heterotrophs in the algal colonies suggested that many of the Trichodesmium colonies encountered were senescent, either slowly dying and providing mineralizable material to the associated microbes, or leaking large amounts of dissolved organic compounds. Studies of the photosynthetic capabilities of the alga included some investigations of the loss of newly fixed carbon as well as the photosynthesis vs. irradiance response of the surface nearshore Trichodesmium population. Rough estimation of the percent contribution to total photosynthesis was also possible using data gathered during the enumeration phase and other published data.

In view of the obvious potential for fertilizing the euphotic zone which the Trichodesmium 'blooms' represent, experiments were also conducted to investigate the rate and amount of decomposition of dying Trichodesmium by bacteria and fungi.

2 DISTRIBUTION OF TRICHODESMIUM AT BARBADOS IN SPACE AND TIME

2.1 Introduction

As described above, the work of Steven and others indicated the existence of regularly occurring 'blooms' of Trichodesmium off Barbados. The following includes a partial description of the physical environment of the alga and a consideration of the factors controlling the temporal fluctuations in Trichodesmium standing stock. Also included is a re-examination of published time-series studies concerning plankton (especially phytoplankton) at Barbados, and an extensive review of published and unpublished hydrographic data from a variety of sources.

2.2 Methods

2.2.1 Description of stations and physical measurements

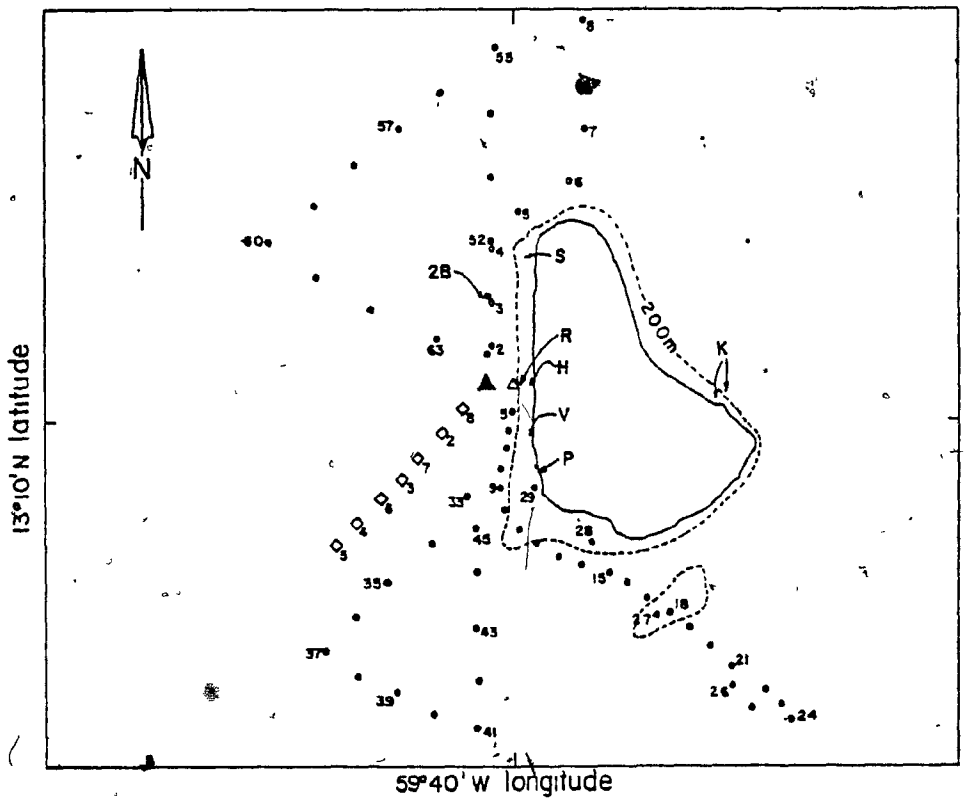
Two stations were established off the west coast of Barbados, at approximately 13°12'N, 59°42'W and 1 °12'N, 59°40'W. As indicated in Figure 2.1, these were 8 km and 4 km directly west of Bellairs Research Institute, in 400 and 200 m of water respectively. Stations were located on each cruise by depth soundings and line of sight bearings.

Beginning in July 1974, the 8 km station was visited regularly at about 15 day intervals until August 1975, and at monthly intervals thereafter on the R.V. Martlet, operated by Bellairs Research Institute. At each station a bathythermograph cast was made to 250 m using a Mark IV Thermoline Recorder, and water samples were collected in 7 l opaque Van Dorn bottles for analysis of chlorophyll a and phaeopigment concentrations, Trichodesmium cell counts, and salinity analysis. Depths sampled were 0, 5, 10, 15, 25, 35, 50, 75, 100, 150 and 175 m. Samples at 0 and 10 m were not taken after November 1974. Sea surface

Figure 2.1 Location of stations and occasional samples mentioned in the text.

This study: 8 km station (▲); 4 km station (Δ); May 21, 1975 (o); July 21-23, 1975 ASTP (●); January 21, 1976 (◇); Steven et al., 1970 (2B); Sander, 1971 (S, H); Vezina, 1974 (V, P); Partlo, 1975 (P); Sander, 1977 (H); R. Kidd, unpubl. (R, K, H); C. Hawkins, unpubl. (H).

Small numbers identify consecutive stations visited the same day (see data listing).


N
S
R
H
V
P
K
200m
2B
13°10'N latitude
59°40'W longitude

temperature, air temperature, windspeed, sea state, Secchi disc transparency, and general meteorological observations were made. After July 1975, observations of sea colour were also made using a Forel comparator. Qualitative plankton tows were taken regularly at the surface and irregularly at various depths to 50 m.

The 4 km station was visited at weekly intervals, alternately from the Martlet on return from the 8 km station, and from a small open boat. A similar routine was followed except the bathythermograph cast was made to 150 m and the hydrocast to 50 m. This station was visited regularly for 35 weeks to provide comparative data on the distribution and patchiness of the parametefs measured.

On three occasions, other locations were visited as illustrated in Figure 2.1, to provide nearly synoptic data on the small scale (30 km) distribution of temperature, salinity, chlorophyll a, phaeopigment concentration and Trichodesmium numbers around the island. On May 21, 1975, a series of 6 surface samples and two 'short' stations (3 depths) were conducted along the northwest coast and north of the island, in an attempt to establish the distribution of the parameters in and out of the land lee, and to investigate the horizontal extent of a Trichodesmium 'bloom' occurring at the regular 8 km station at that time.

On July 21, 22 and 23, 1975, three cruises were made to the southeast, southwest and northwest of the island for similar purposes, but also timed to provide ground 'truth' data for observations of the sea surface made by American astronauts in space during the Apollo Soyuz Test Project (ASTP). Similar parameters were measured as during previous cruises for 64 surface samples as illustrated in Figure 2.1. Bathythermograph casts to 75 m, and measurements of Secchi transparency and Forel colour were made at alternate stations. Drift bottles were

released at approximately 1 km intervals over the entire cruise track.

A third line of surface samples and two abbreviated stations (BT and 0, 5, 25 and 50 m samples only) were conducted on January 19, 1976 to the southwest of the island to investigate horizontal distribution of various parameters at that time of year, and to search for a Trichodesmium 'bloom' which historical data suggested should have been occurring at the 8 km station at that time. Drift bottles were released to give an indication of the speed and direction of surface drift in winter.

At most of the routine 4 and 8 km stations, the entire 7 l contents of the Van Dorns were transferred to large nalgene bottles which were then stowed in wooden boxes to protect them from bright sunlight during transit to the laboratory. Immediately upon return to shore (usually about 1-2 hrs after the hydrocast), the samples were subsampled for salinity, chlorophyll a and Trichodesmium analysis. The sample bottles were slowly inverted several times immediately before withdrawing each sample to reduce errors due to settling or floating. Salinity bottles were filled and rinsed several times, capped tightly and stored for later analysis using an inductively coupled Autolab Industries Model 601, Mark III salinometer. Temperature and salinity data from the standard depths were used to calculate sigma-T, rho and stability, using a computer program provided by Dr. R.G. Ingram.

Measurements of descending irradiance were conducted on several occasions, using a G.M. Industries submarine photometer equipped with selenium barrier-type photocells sensitive in the range 400-640 mm. Unfortunately, leakage at greater depths eventually ruined the photocells and cancelled further measurements. Simultaneous Secchi disc measurements allow extrapolation to other water masses.

The colour of the surface waters was measured by comparing the apparent colour of the Secchi disc as it disappeared to a series of coloured solutions prepared according to the Forel-Üle recipe provided by Hutchinson (1957). The series of ten colour standards ranged from blue to green. Screw cap test tubes containing the solutions were mounted over a white perspex sheet. When held in direct sunlight and viewed from above, the colour standards matched those of the sea very well.

2.2.2 Supplementary physical information

Meteorological data, including daily total irradiance, run of wind and maximum and minimum air temperature, were provided by Mr. P. Roachford, Chief Climatologist, Caribbean Meteorological Institute, Husbands, St. James. Irradiance measurements were in the 0.3-2.0 μm range using a Kipp and Zonen type pyranometer, mounted at C.M.I. approximately 7 km southeast of Bellairs Research Institute.

Hourly values for windspeed and daily totals for percent possible sunshine (as calculated using a Campbell-Stokes sunshine meter) were also obtained from Grantley Adams International Airport, courtesy of Mr. D.F. Best, Chief Meteorologist. These measurements are considered more representative of the conditions at sea, since the airport is near the weather coast of the island on a low plateau, and little effect of the island is felt.

Supplementary information on surface drift currents was obtained from National Oceanographic Data Service in Washington, D.C. These unpublished data are summaries of surface layer current velocity and direction as calculated from ships' drift observations. Also provided by NODC were data concerning physical conditions away from the island. These included a large number of bathythermograph transects

across the western tropical Atlantic conducted between 1957 and 1974, and complete hydrographic-station data for several cruises in the area along the Guiana coast.

2.2.3 Measurements of pigment concentrations

One liter volumes were measured out for chlorophyll analyses and filtered under low vacuum (not exceeding 350 mm Hg) through 47 mm Whatman GF/C glass fibre filters. During filtration of the last few hundred ml, 3 or 4 ml 3% $MgCO_3$ suspension was added and the sides of the funnel washed down with a few ml of filtered sea water. Filters were then removed from the funnel, folded in half face inwards, blotted dry between paper towels, and inserted into glassine envelopes. They were then stored at -10°C over desiccant until analysis.

Difficulties in obtaining acetone from suppliers forced long term storage of most of the chlorophyll samples obtained during 1974 and 1975. An experiment designed to study the possible decomposition of chlorophyll on filters during storage (see Appendix A.2) demonstrated no significant change of pigment concentration for at least six months and probably for periods up to a year. No corrections have been applied to any of the data discussed here, but the reader should be aware of the possibility that the 1974 chlorophyll values may be somewhat low.

When acetone became available, analyses were carried out after the methods of Holm Hansen, Lorenzen, Holmes and Strickland (1965) and Strickland and Parsons (1968). Filters were ground to a slurry in a few ml of 90% v/v acetone using a motor-driven Potter Elvehjem tissue grinder. After rinsing down the pestle and walls of the tube with a few more ml of 90% acetone, the volumes were made up to 12 ml, and the tubes were covered and set aside for 20-30 minutes in a cool dark location to permit full extraction of the pigments. Filters and

extracts were then separated by centrifuging for approximately 10 minutes on a swinging bucket centrifuge. After precipitation of the glass fibre, approximately 5 ml of each extract were removed by Pasteur pipette and transferred to cuvettes for fluorometric analysis of chlorophyll *a*. Measurements were made using a Turner model 110 filter fluorometer, fitted with a blue pass Corning 5-60 primary filter and a red pass Corning 2-64 secondary filter, in conjunction with a Turner 'blue' lamp (#110-853) and standard equipment photomultiplier. This combination allowed measurement of as little as 0.02 µgm chlorophyll *a*.

The fluorescence (F_b) of the extracts was measured on any of the three largest apertures such that F_b was as close to 90 as possible. The extract was then acidified with 2 drops 0.1N HCl and remeasured after 5 minutes (F_a). Acidification converts chlorophyll *a* to the breakdown product phaeophytin *a* which has a smaller emission fluorescence at the wavelengths used; F_a is therefore less than F_b. Chlorophyll *a* is determined by difference ($F_b - F_a$), since F_a is due solely to fluorescence by phaeophytin and a variable group of other breakdown products including chlorophyllide and phaeophorbide. (For a complete discussion, see Yentsch, 1965). The specific acid ratio F_b/F_a used in calculations will depend upon the configuration of the machine used and must be determined for each machine. The maximum acid ratio observed in the natural Barbados phytoplankton was 1.95. When chlorophyll *a* from a brackish water pond undergoing a bloom was chromatographed to separate it from other pigments, measurement by the above technique gave acid ratios between 2 and 2.1. A ratio of 2 has therefore been utilized in calculating pigment concentrations, according to the formula suggested by Schumann and Lorenzen (1975).

$$\text{Chlorophyll } a(\mu g/l) = \frac{\dfrac{F_b/F_a{}_{max}}{(F_b/F_a \text{ max})-1}\,(F_b - F_a)\cdot K_x \text{ Dil}}{\text{liters filtered}}$$

$$\text{Phaeopigment } (\mu g/l) = \frac{F_b/F_{a\max}}{(F_b/F_{a\max})-1} \left(F_b/F_{a\max}\,(F_a) - F_b\right) K_x \text{ Dil}$$

where:
F_b = fluorescence before acidification
F_a = fluorescence after acidification
F_b/F_a max = maximum acid factor found in nature, or in chromatographed chlorophyll a
K_x = calibration constant for each aperture of the fluorometer (μgChla/F units)
Dil = dilution factor.

The K factors were determined by cross calibration with a Gilford Model 240 spectrophotometer. Eighty 3 and 4 liter samples were extracted in the normal manner and, their chlorophyll contents measured spectrophotometrically according to Strickland and Parsons (1968). The same samples were then analyzed on the fluorometer, usually after dilution with more acetone.

All pigment data were card punched, verified and submitted to the McGill IBM 360 computer for calculation of the basic parameters. Acid ratio, chlorophyll a, phaeopigment and percent chlorophyll a were computed and listed by cruise, station and depth. It should be noted that the total chlorophyll calculated by methods not utilizing the acidification technique (and hence most historical data at Barbados) will not exactly equal chlorophyll a and phaeopigment as calculated here because of variable interference by natural phaeopigment in the former method. Further, the phycobilin pigments* of Trichodesmium are thought to interfere with the determination of chlorophyll, giving anomalously high values for chlorophyll a and total chlorophyll by both fluorometric and spectrophotometric methods (Strickland and Parsons, 1968; Saijo et al., 1969). There is no obvious solution to this possible interference.

* Repeated attempts to measure the accessory phycobilin pigment phycoerythrin by the fluorescence method of Moreth and Yentsch (1970) were unsuccessful.

and no corrective measures have been applied to insure fluorometric measurements were only of chlorophyll a.

2.2.4 Enumeration of Trichodesmium

Plankton from 1 liter subsamples from each depth were concentrated for examination by gentle filtration through a sintered glass extraction funnel to about 10-15 ml volume, then transferred to 25 ml Utermöhl counting chambers. The funnel was thoroughly washed and the rinse added to the chamber to bring the volume up to 25 ml. Lugol's iodine was added as a preservative. Counting usually was completed within a week of sampling.

This concentrating procedure was adopted after trials with the more familiar settling method revealed that most Trichodesmium colonies disintegrated during the three or four transfers that were necessary from one settling chamber to the next. Fewer colonies were disrupted when the filtration method was employed. Difficulties were also encountered with the tall settling chambers when 2% formalin was initially used as a preservative, since the gas vacuoles of Trichodesmium were not always collapsed. The algae therefore possessed residual buoyancy and could be found at the surface or only partially settled after long periods. This problem has also been noted by Sournia (1968). The filtration technique was much more rapid and insured collection of all the Trichodesmium in a water sample.

Filtrates were often collected and settled, siphoned down, and examined as a check on loss of material through the coarse sinter, since its effective mesh size was unknown. At no time did significant amounts of Trichodesmium pass through the funnel. Small, spherical cells, less than about 25μ diameter, and very short fragments of Trichodesmium (5-10 cells or less) were occasionally observed, but these never amounted to more than 1% of the total Trichodesmium for

those samples. There was probably rather consistent loss of small individual plankters, but in any case only Trichodesmium was enumerated. Qualitative notes were made regarding the most common, and unusually large or abundant other species. Trichodesmium was recognized as either T. thiebautii or T. hildenbrandtii on the basis of filament-diameter and differential staining with Lugol's iodine. Single filaments of T. erythraeum, relatively rare at Barbados and very similar to T. thiebautii at low magnification, were not counted separately except where occurring in intact colonies. The entire bottom of each counting chamber containing the filtered and settled concentrate from 1 liter of water was counted at low magnification (63x) using a Zeiss inverted microscope. All of the Trichodesmium in single filaments and in intact colonies was enumerated.

Filaments were counted in three size classes (less than 3/4 mm, 3/4 - 1-1/4 mm, and greater than 1-1/4 mm in length) chosen to grossly reflect the distribution of filament length observed. The totals in each size class were then multiplied by 3/4, 1 and 1-1/4 respectively to convert the frequencies to total filament length.

Where intact radial colonies were encountered, the number of filaments per colony was estimated by counting the filaments protruding around one half of the colony, while focusing up and down to cover as much of the sphere as possible. For parallel colonies, the filaments exposed at both ends were counted and the total divided by two. Filament length of the colonies was estimated to the nearest 1/4 mm by comparison with the visible field which was adjusted to 1 mm square.

This method may sound crude, but in practice it worked rather well since the microscope depth of field at that magnification was large in relation to the colonies. When colonies counted in this manner were flattened under a coverslip and the number of filaments

counted under higher magnification, it was evident that the technique underestimated by about 25% throughout the range of colonies encountered, with an error of ± 20-25%. Accordingly, total filament length in each colony has been calculated by number of filaments per colony x average filament length (diameter of radial colonies, length of parallel colonies) x 5/4. The mean difference between 10 duplicate 5 m samples gathered at different times during the study was 13%. Recounts of single samples agreed to within 10% (n = 8). The technique is therefore considered to be accurate to within about 15%. The more accepted technique of counting filaments encountered in 1 percent of the field is much faster and the obvious choice for studies where the other plankton are also enumerated, but it will not be accurate unless colonies are completely disrupted. Experience during this study indicated that intact colonies were usually present, and during blooms they contributed as much as half the biomass of the sample. No technique could be found which insured that all of the colonies would always break up without loss of some cells by lysis. Even long term storage in formalin would not release filaments bound in the polysaccharide which accumulates around the central portion of some radial colonies.

2.3 Observations

2.3.1 The physical environment

2.3.1.1 Sea temperature

The annual march of sea surface temperature off Barbados roughly followed that of the air. Waters were coldest (25.2°C) in March when the mixed layer was very deep, and warmest (28.4°C) in September and October when the pycnocline was shallow, wind velocity was less and air temperature was higher.

The temperature regime in the upper 150-m appears closely related to the presence or absence of the brackish surface layer. The shallow thermocline was nearly always situated in close proximity to the halocline, except where the latter was weak. Usually, however, density stratification was strongly developed and thermal mixing occurred only to the halocline, that is to between 15 and 35 m. On a few occasions (February 10 and March 12, 1976) temperature inversions were observed beneath the shallow low density layer - the result of colder but very low salinity (and therefore low density) water sliding over a more saline, heavier layer. Below the pycnocline, temperatures decreased more or less uniformly.

2.3.1.2 Salinity

The seasonal march of surface salinity during 1974-76 is illustrated in Figure 2.2, from data collected during this and three other simultaneous studies (Partlo, 1975; R. Kidd*, and C. Hawkins*, pers. comm.). Surface salinity at all stations was near 36°/oo at the beginning of each year and fluctuated about a decreasing mean to near 32°/oo in August. This irregularity is a common feature in the first half of the year as illustrated by the wide envelope enclosing the published surface data since 1962. The nearly synoptic data gathered on short cruises around the island (May 21, 1975; July 21, 22, 23, 1975; and January 19, 1976) and the nearly simultaneous data from other locations, further emphasize this horizontal heterogeneity of the surface layer during the first six months of the year.

After August in both years, the low salinity summer waters were slowly replaced by more homogeneously saline water masses, and

* Robert Kidd and Christopher Hawkins, Bellairs Research Institute, St. James, Barbados.

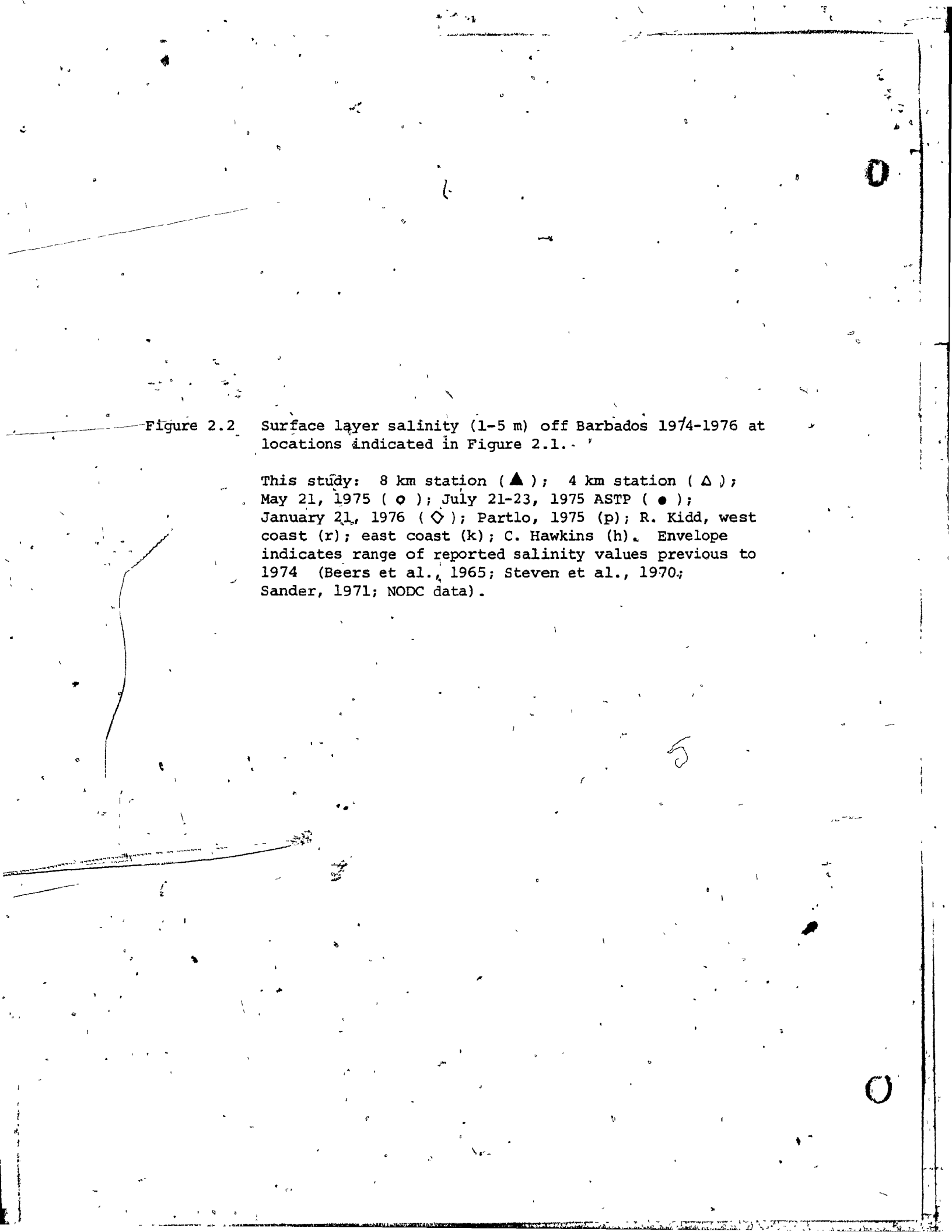
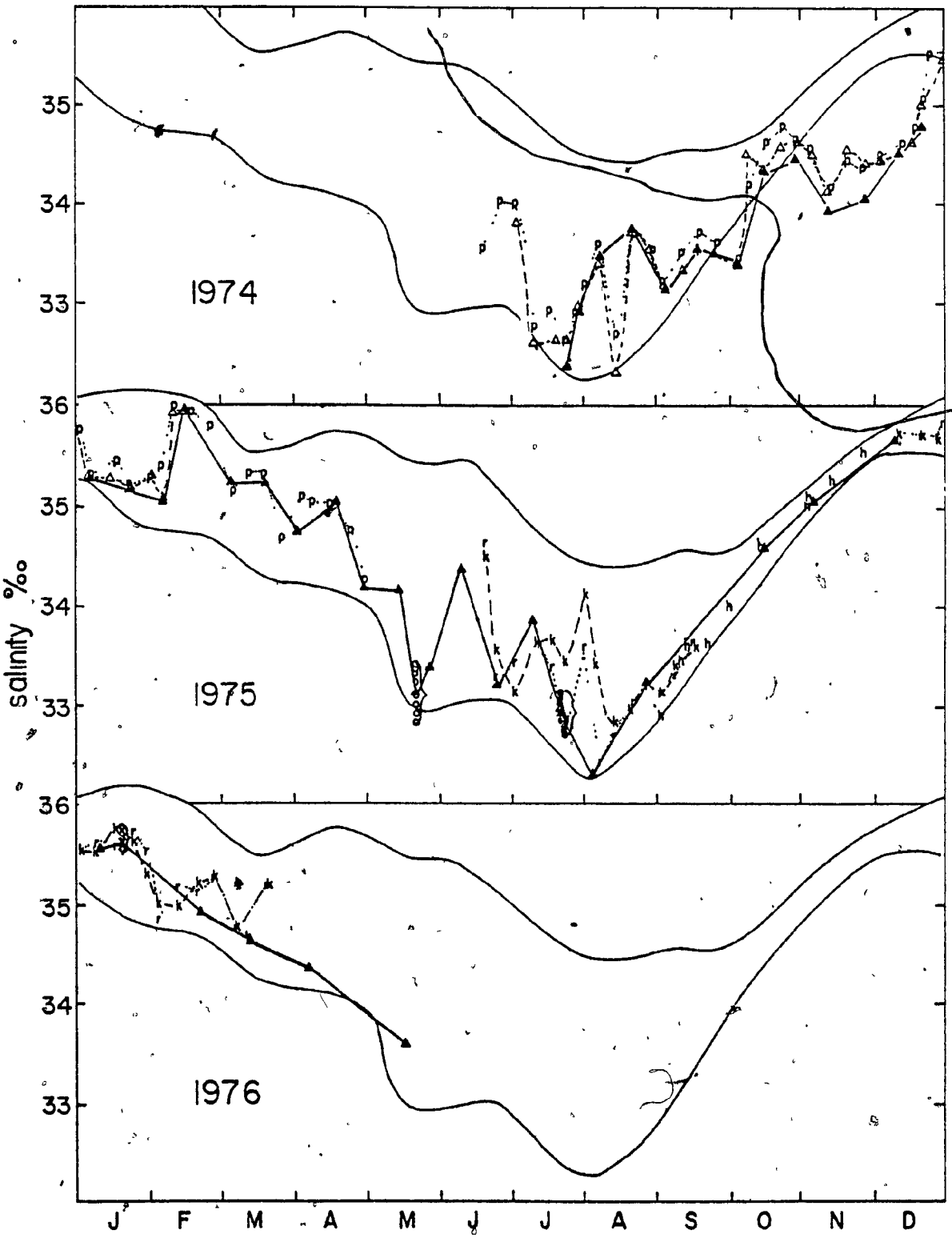


Figure 2.2 Surface layer salinity (1-5 m) off Barbados 1974-1976 at locations indicated in Figure 2.1.

This study: 8 km station (▲); 4 km station (Δ); May 21, 1975 (o); July 21-23, 1975 ASTP (●); January 21, 1976 (◇); Partlo, 1975 (p); R. Kidd, west coast (r); east coast (k); C. Hawkins (h). Envelope indicates range of reported salinity values previous to 1974 (Beers et al., 1965; Steven et al., 1970; Sander, 1971; NODC data).


1974
1975
1976
salinity ‰
35
34
33
36
J
F
M
A
M
J
J
A
S
O
N
D

maximum surface salinities were observed early in the new year (February of 1975, January and March of 1976). In 1974 this usually very constant increase was temporarily interrupted by passage of a large pool of brackish water with salinity near 34°/oo. Conditions in 1975, however, were more normal, and the changing salinities very closely approximated both the rate of increase and absolute values observed in several other years.

Regardless of the changes in salinity of the surface waters, the water between 50 and 75 m was always close to 36°/oo. In February 1975, when the brackish surface waters were absent, this 36°/oo water extended from below 100 m to the surface, and possessed characteristics very similar to water masses of the South Sargasso or North Equatorial areas. These waters were quickly replaced by more stratified waters however. Brackish low density waters driven off the South American coast by the Northeast Trade winds slide over the more saline, denser waters of the North Equatorial current (Ryther et al., 1967; Mazeika, 1973) and arrive at Barbados as 'bubbles' or 'pools' of low salinity water superimposed on a more expansive freshening. The major source of this fresh water is recognized as being the Amazon River (Steven and Brooks, 1972), but heavy seasonal rains over the oceanic region may contribute up to 35% (Froelich and Atwood, 1976).

The shallow brackish layer, and the pools themselves, were usually well mixed and homogeneous. Below this surface layer, salinities increased to a maximum in the 'subtropical underwater' at depths between 100-150 m. This layer varied somewhat in depth and in thickness, but the salinities observed at the standard depths bore no particular relation to events at shallower depths. There are noticeable increases in the salinity of this layer in data presented by Steven et al. (1970) (their Figure 3), and these seem to occur with a period similar to the plankton cycles described by them. It is probable that changes in the surface currents are associated with subsurface

phenomena (see 2.4.3.2), but a much more intensive sampling program would be necessary to adequately describe the features. Temporary increases in salinity of the subtropical underwater were observed during the present study, but these were not as regular as in the 1968-1970 data, probably partly due to differences in depths sampled.

2.3.1.3 Stratification and stability

Sigma-T and stability calculated for all of these data and those from the 1968-70 study (Steven et al., 1970) showed essentially the same picture as described by Beers et al. (1965). During the summer, when surface salinities are low, sigma-T at 5 m may be as low as 20.9. During the first eight months of the year, there were large changes in the density structure and stratification over short intervals, resulting from the advection of low salinity pools into the sampling area. The very large temporal variations of sigma-T at a given depth emphasize the sharp separation of the mixed layer into large cells or patches (changes of as much as 1 unit of sigma-T were observed at 5 m within 2 weeks). At 100 m there was generally less variation of sigma-T, but lower densities at this level were usually associated with pools of low salinity surface water.

The water column was always stratified and possessed positive stability, but there is a great deal of variation. No perceptible trends or patterns could be recognized in these data, except for a reduction of stability in January and February associated with vertically more homogeneous water masses at that time.

2.3.1.4 Solar irradiation

Barbados receives approximately 80% of the irradiation possible at that latitude, or about 450 ly/day. There are quite small day to day

variations (± 10%) but decreases to around 50 or 60% possible sunshine occur at 5 to 10 day intervals, apparently associated with features which tropical meteorologists refer to as 5 day waves (Mr. D.F. Best*, pers. comm. and meteorological data supplied by him, not presented here). Very large decreases (to 10 or 20% of possible sunshine) occurred with greatest frequency during the fall and winter of 1974-1975, when almost total overcast was experienced on four widely separated occasions.

Typical of the daily variations of irradiation are those for June 4, 1975, which are illustrated in Figure 3.8. Widely scattered cumulus cloud was responsible for the short duration decreases in irradiation.

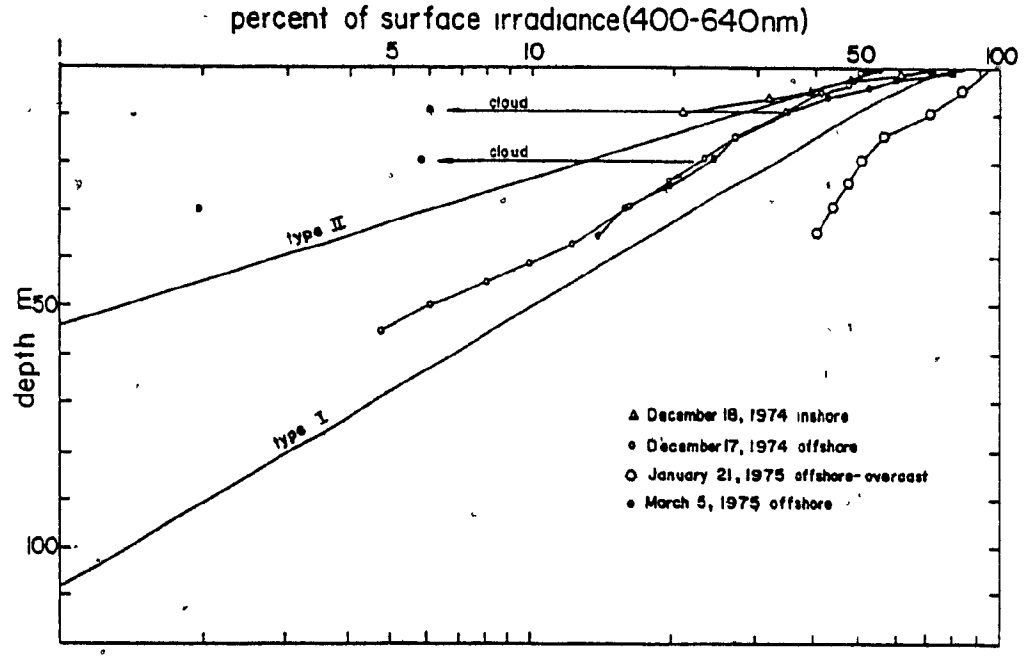
2.3.1.5 Light penetration into the sea

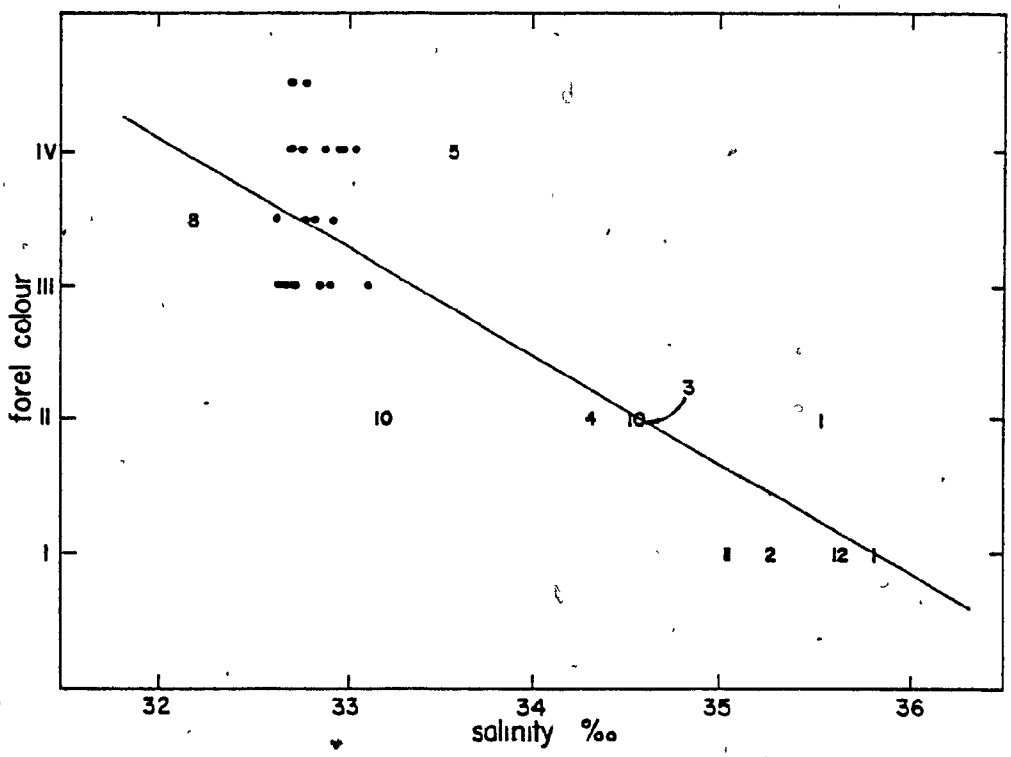
The irradiance climate for Trichodesmium and other phytoplankton near Barbados is summarized in Figure 2.3. The offshore waters were similar to Jerlov's (1968) class I water, that is, the clearest oceanic type with very low particle content. Chlorophyll measurements in the upper 30 m on these two days averaged 0.07 µg/l (December 17) and 0.15 µg/l (March 5). On December 18, 1974, percent transmittance in the inshore region (3/4 km offshore in 20 m of water) was considerably different than recorded at the 8 km station the previous day. The slope of the curve is closer to Jerlov's type II water - still very clear but with a greater extinction coefficient than that of the offshore waters. This decrease in transparency is a result of large increases in suspended particulate matter close to the island (cf. Sander, 1971) including phytoplankton and zooplankton. In absolute terms, the irradiance received during each of these three

* Mr. D.F. Best, Chief Meteorologist, Barbados Government.

Figure 2.3 Percent of surface irradiance in the 500-640 nm range received at various depths in the sea off Barbados. Surface conditions: calm sea and bright sun on December 17, 18 and March 5 (3500, 2600 and 4200 arbitrary units respectively); rough sea and heavy overcast on January 21 (600 units). Secchi depth on December 17 and March 5 was 27 m, that on January 21 was 23 m. Two measurements on March 5 made under passing cumulus cloud illustrate the large reduction of irradiance in upper euphotic zone caused by cloud.

Figure 2.4 Relationship between surface salinity and Forel colour off Barbados, July 1975-May 1976. Dots represent ASTP stations (July 1975) in water of more than 100 m depth; numbers represent months during which data were collected after July at the 8 km station (January indicated by 1, February by 2, etc. Regression equation $F = 30.03 - 0.81\ S$ ($r = 0.71$). Forel I is deep oceanic blue. Forel IV is an equal parts mixture of blue and green.


percent of surface irradiance(400-640nm)
1
5
10
50
100
cloud
cloud
type II
type I
depth m
50
100
▲ December 18, 1974 inshore
• December 17, 1974 offshore
○ January 21, 1975 offshore-overcast
• March 5, 1975 offshore


forel colour
IV
III
II
I
8
5
10
4
18
3
1
11
2
12
32
33
34
35
36
salinity ‰

measurements (December 17 and 18, 1974; March 5, 1975) was nearly the same. Two measurements made on March 5 illustrate the very large fluctuations in the irradiance climate of the upper euphotic zone caused by passing cumulus cloud. The % transmittance profile measured on January 21, 1975 under heavy overcast reflects the difference in spectral composition of the surface irradiance. Absolute irradiance at 10 and 20 m on January 21, 1975 was approximately the same as on March 5, 1975, when the sun was obscured.

Extrapolation of the offshore transmittance to 1% surface irradiance shows that the lower limit of the euphotic zone, when defined by this irradiance level, was between 80 and 90 m. The Secchi depth (SD) was 23 m on both days and thus 3 x SD, or even 4 x SD, would be the best measure of the depth of the euphotic zone in the offshore region.

During most of this study, the Secchi disc disappeared at depths between 20 and 30 m, except on two occasions when it was still visible at 35 m. No correlation with other parameters measured could be detected, except that on the two days on which SD was greater than 35 m, the surface salinity was near 35°/oo. While the depth of the euphotic zone was generally less, and varied more in the first half of the year than after August, there was no correlation between surface salinity, chlorophyll, or Trichodesmium with Secchi depth.

2.3.1.6 Apparent colour of the sea

Casual observation during 1974-1975 had suggested that the summer waters were a much different colour than those encountered during the winter months, and conversations with Barbadian fishermen and boatmen confirmed that variations were indeed observable and that they may have biological significance. Barbadian fishermen have long

sought out 'green water' in which to set their nets in the belief that these waters contain more fish (see also Parr, 1938).

The colour of the surface layers, as measured with the Forel scale did change appreciably, even over short distances. During the ASTP cruises (July 21-23, 1975) Forel colour measured at alternate stations varied from II to IV-V. After July, when higher salinity waters moved in, colour decreased from values around III to I in November and December, then increased to IV in May of 1976. Fifty-one percent of the variation of FOREL colour was associated with variations in surface salinity (Figure 2.4). A similar relationship between salinity and sea colour data was reported by Fukuoka (1965) for the north coast of Venezuela and off the Orinoco River.

Hutchinson (1957) considers the changes in colour as measured by the Forel scale to be primarily due to the presence of Gelbstoff, or fulvic and humic compounds of terrestrial origin. At Barbados, these low salinity waters which Forel measurements show to be greener, are regarded to be principally of Amazon River origin since their silicate concentrations are negatively correlated with salinity (Steven and Brooks, 1972). Ryther et al. (1967) mention that the fresh waters encountered off Cape Orange retained a characteristic deep brown colour even though suspended particulate matter was very low. The spreading of this discoloured surface water across the western tropical Atlantic to Barbados was observed directly from spacecraft altitudes by the ASTP astronauts, who marked the northern limit of the discolouration as near 13°N, about 500 km east of Barbados (Borstad, in press). It would be interesting to know if the known chelating properties of these materials are significant to the biology and chemistry of this large area.

2.3.1.7 Wind

Barbados is situated in the Trade Wind belt and experiences generally constant easterly winds around 5 m/sec. In 1974, daily mean velocities at Grantley Adams International Airport averaged 6-7 m/sec from June until August (D.F. Best, pers. comm.). Near the beginning of September winds slackened appreciably for a short time, then resumed velocities between 3 and 6 m/sec. This period of weaker and more variable winds continued until January when there was a slight increase in the monthly mean. The range of daily average velocities during the first half of 1975 was between about 4 and 6 m/sec.

Coincident data on wind direction are not available, but meteorological atlases (cf. Meteorological Office of the British Air Ministry, 1948; U.S. Chief of Naval Operations, 1955) show that the stronger winds during May through August are about 45% northeasterly and 50% easterly. The period of relative calm from September to December is a time of lower barometric pressure and more variable winds (10% southeasterly, 35-45% easterly, and 35-45% northeasterly) associated with the northward shift of the Intertropical Convergence Zone (ITCZ) (the zone of weak and variable winds known as the Doldrums, where the northeast and southeast Trade Winds meet). After the ITCZ retreats to the south in January, the Northeast Trades again strengthen and winds at Barbados increase (in 1975 to around 5-6 m/sec) and are more northerly (40-70% northeasterly, 30% easterly).

During the present study, casual observation indicated the presence of a substantial wind shadow close to the island's lee shore, and anemometer measurements made at various locations confirmed this. Wind velocity measured at the 8 km station on ten separate cruises was 9 ± 1 m/sec (average of five 1 min velocities measured 3 m above sea surface). By comparison, wind velocities at the Martlet mooring, only 3/4 km from shore, averaged 5 ± 1 m/sec on these days (means of two

measurements - one before leaving the mooring and another after return). The difference between the velocities was highly significant.

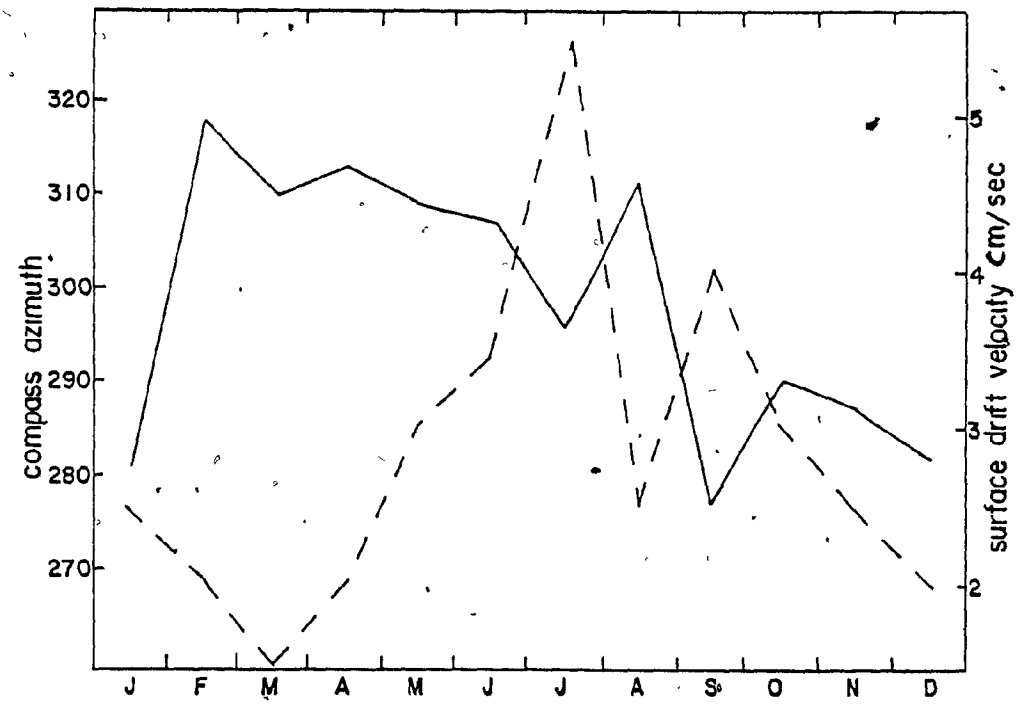
2.3.1.8 Water movements

Drift bottles released during July 1975 travelled northwest at a net velocity of 30 km/day, in agreement with similar measurements by Emery (1972). There was, however, no evidence of any large scale deformation of the water mass into which the bottles were released, as suggested by Emery. Bottles released over the northern parts of the cruise track were recovered from the northern coast of St. Lucia, while those released further to the south were found along the St. Lucia southwest coast. None of the bottles released in January were recovered.

Description of the average surface currents is possible using unpublished data made available by National Oceanographic Data Center (NODC) in Washington. The mean monthly surface drift velocity and direction for the Barbados area are summarized in Figure 2.5. During the period February to August, waters arrive at Barbados from the south-east with velocities slowly increasing until July. In September there is an abrupt change in direction and, until February, currents are more westerly.

It is immediately obvious that these changes in water movements are directly related to changes in the zonal wind field described earlier. Mazeika (1973) has shown that the surface layer travelled about 40° to the right of the mean wind during the period of his study. During the first half of the year therefore, the east-northeasterly winds should be expected to drive the surface layers to the northwest, and the fresh waters from the South American rivers will be carried offshore and hence to Barbados. After August, the decrease in wind speed and change in direction result in slower and more westerly drift. With the

Figure 2.5 Mean monthly sea surface drift velocity (--) and direction (—) near Barbados, for the area between 13° and 14°N, and 59° and 60°W (from data provided by National Oceanographic Data Center, Washington, U.S.A.).


compass azimuth
320
310
300
290
280
270
surface drift velocity cm/sec
5
4
3
2
J
F
M
A
M
J
J
A
S
O
N
D

departure of fewer pools of fresh water from the South American coast (the Amazon River discharge begins to decrease in May), the waters of the oceanic region become more homogeneous with respect to salinity. Beginning in August or September, the predominantly westerly currents bring progressively more saline North Equatorial Current waters to Barbados.

2.3.2 Chlorophyll in Barbados waters

Chlorophyll *a*, as one of the most important phytoplankton pigments, is a good index of phytoplankton standing stock and primary production (Lorenzen, 1970). The ratio of live chlorophyll *a* to total chlorophyll (chlorophyll *a* and its breakdown products)* can be used as an indication of the condition of the plankton, since very little, if any, phaeopigments are present in actively growing 'blooms' or lab cultures in logarithmic growth. Larger amounts of phaeopigments are present in senescing, remineralized or partially digested (as in herbivore guts or faeces) phytoplankton (cf. Spence and Steven, 1974; Schumann and Lorenzen, 1975).

At the 8 km station, chlorophyll *a* concentrations in the surface layer (Figure 2.6) were very low, between 0.05 and 0.1 µg/l during much of the year. These amounts of chlorophyll are similar to other stable systems of low fertility such as the Sargasso and the open Caribbean Seas (Margalef, 1971). Periodically, however (January-February, May and August), surface layer chlorophyll increased substantially to between 0.25 and 0.35 µg/l, levels more characteristic of fertile ascending systems (Margalef, 1971). These events were temporary, usually only encountered at one or two consecutive hydrographic stations which were two weeks apart. There may have also been a small and short duration increase in October 1974.

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* This definition of 'total chlorophyll' is used throughout this thesis.

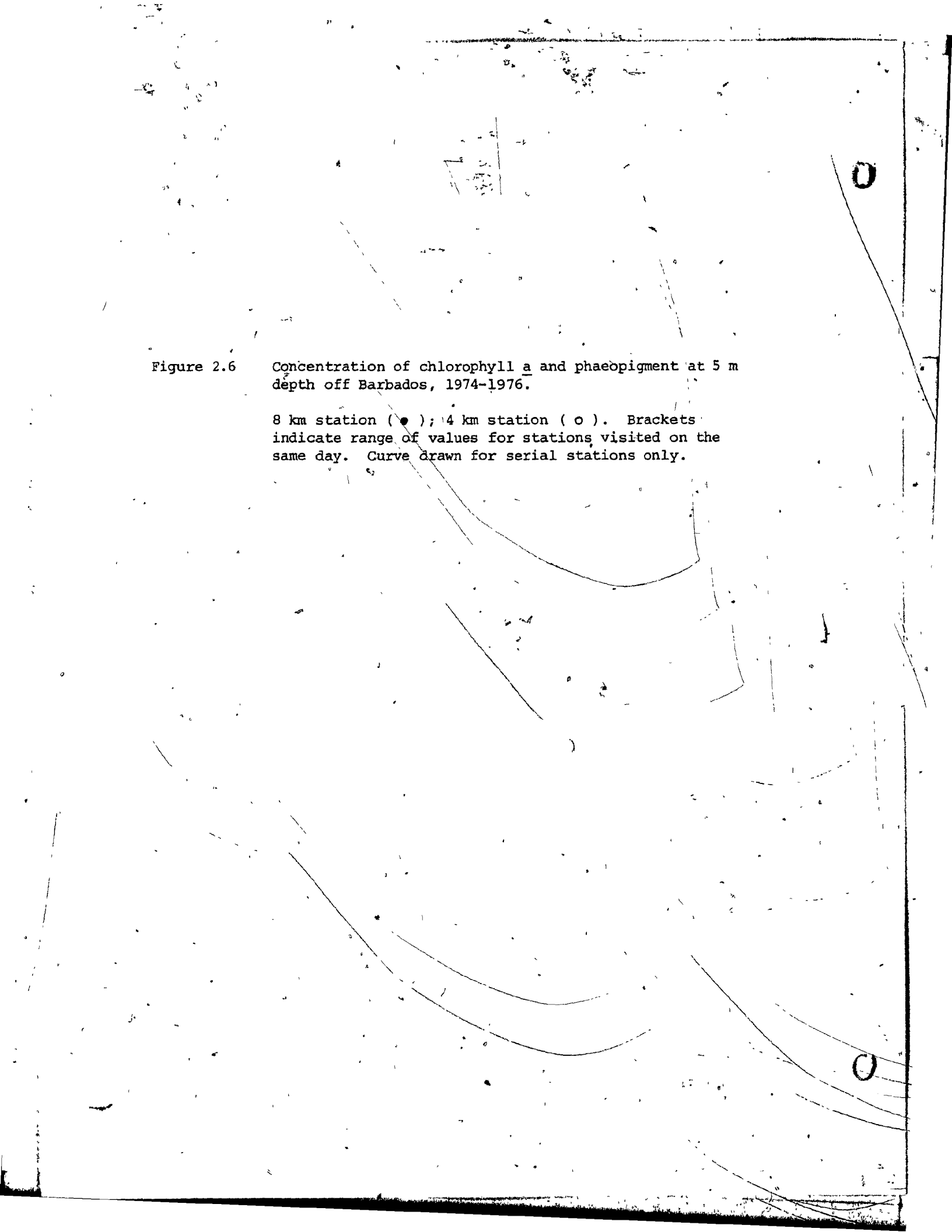
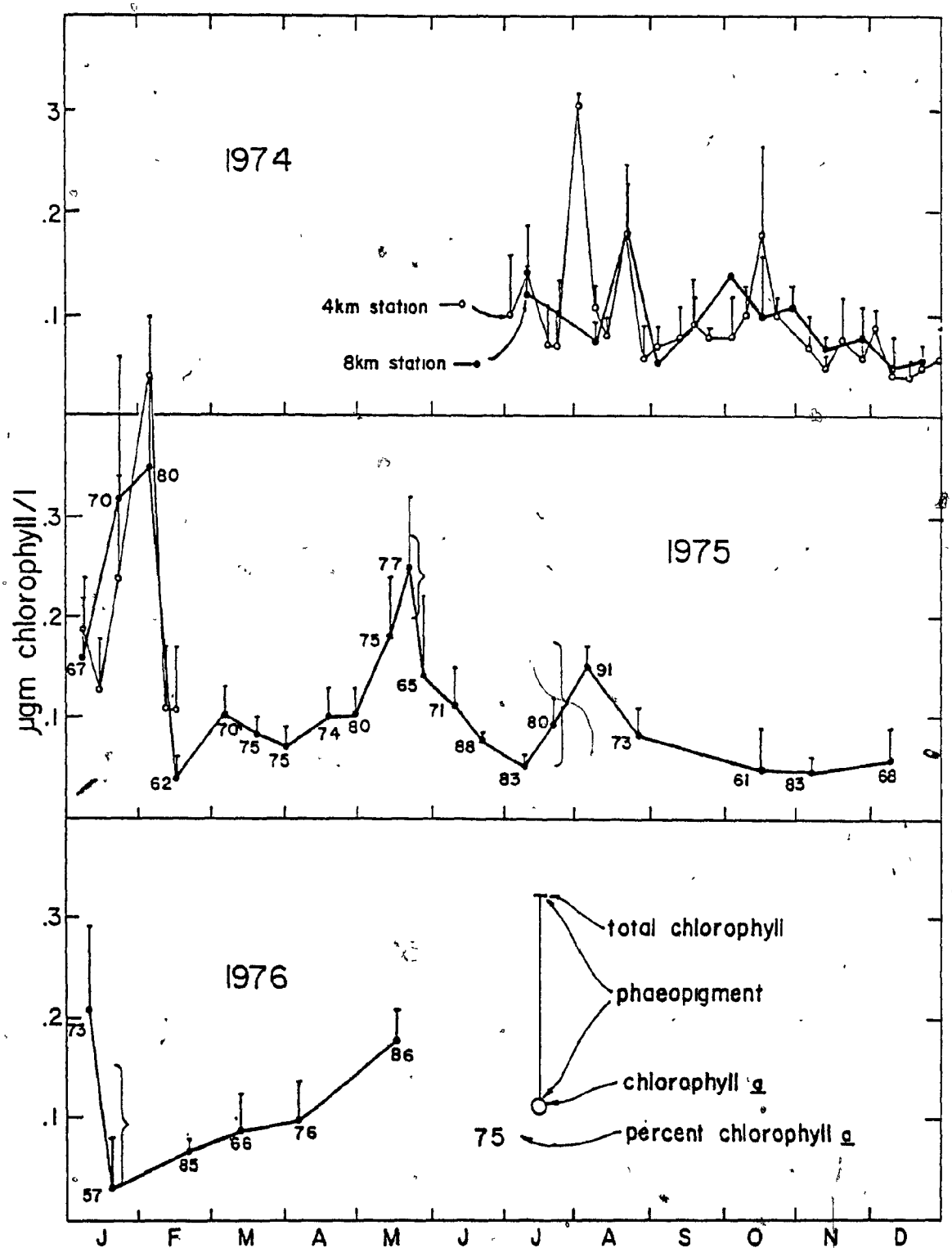


Figure 2.6 Concentration of chlorophyll a and phaeopigment at 5 m depth off Barbados, 1974-1976.

8 km station (●); 4 km station (o). Brackets indicate range of values for stations visited on the same day. Curve drawn for serial stations only.


1974
4km station
8km station
1975
1976
μgm chlorophyll/l
3
.2
.1
.3
67
70
80
62
70
75
75
74
80
75
77
65
71
88
83
80
91
73
61
83
68
73
57
85
66
76
86
total chlorophyll
phaeopigment
chlorophyll a
75
percent chlorophyll a
J
F
M
A
M
J
J
A
S
O
N
D

The phaeopigment concentrations in the surface layer are also shown in Figure 2.6 as vertical bars between the live chlorophyll a and total chlorophyll. The two digit number associated with each point is the percent chlorophyll a of the 5 m sample. Phaeopigment ranged from less than 0.01 to 0.1 µg/l during the study, and % chlorophyll a from 55 to 95% (mean 78%). Contrary to what might have been expected, the % chlorophyll a during the 'blooms' was not very high, indicating that the plankton were not in logarithmic growth when they reached Barbados.

The vertical distribution of chlorophyll a and phaeopigment at the 8 km serial station are illustrated in Figure 2.7 for comparison with hydrographic conditions and vertical distribution of Trichodesmium (to be discussed later). Pigment concentrations were generally low and homogeneous in the mixed layer and closely approximated the distribution of Trichodesmium. Near the bottom of the mixed layer there was generally a chlorophyll a maximum and large amounts of detrital chlorophyll associated with remineralization of sinking phytoplankton. Steven et al. (1970) have already demonstrated that the water at this depth usually contains dissolved nitrite in appreciable quantities, one of the initial products of remineralization. Below about 100-150 m there were never significant amounts of chlorophyll a, and phaeopigment also decreased.

The distribution of surface chlorophyll a during the ASTP cruises (July, 1975), as illustrated in Figure 2.8, shows the effect of the island on phytoplankton carried in the surface water masses. At this time, the general set of the offshore drift was to the northwest, and the movements of waters inshore were probably much like those described by Murray et al. (1977) who studied the movement of subsurface drogues in July 1973.

Away from the island and 'upstream', the surface chlorophyll concentrations were very low (less than 0.1 µg/l). In the region along

Figure 2.7 Vertical distribution of chlorophyll a and phaeopigment concentration, and of Trichodesmium numbers at the 8 km station during 1974-1976.

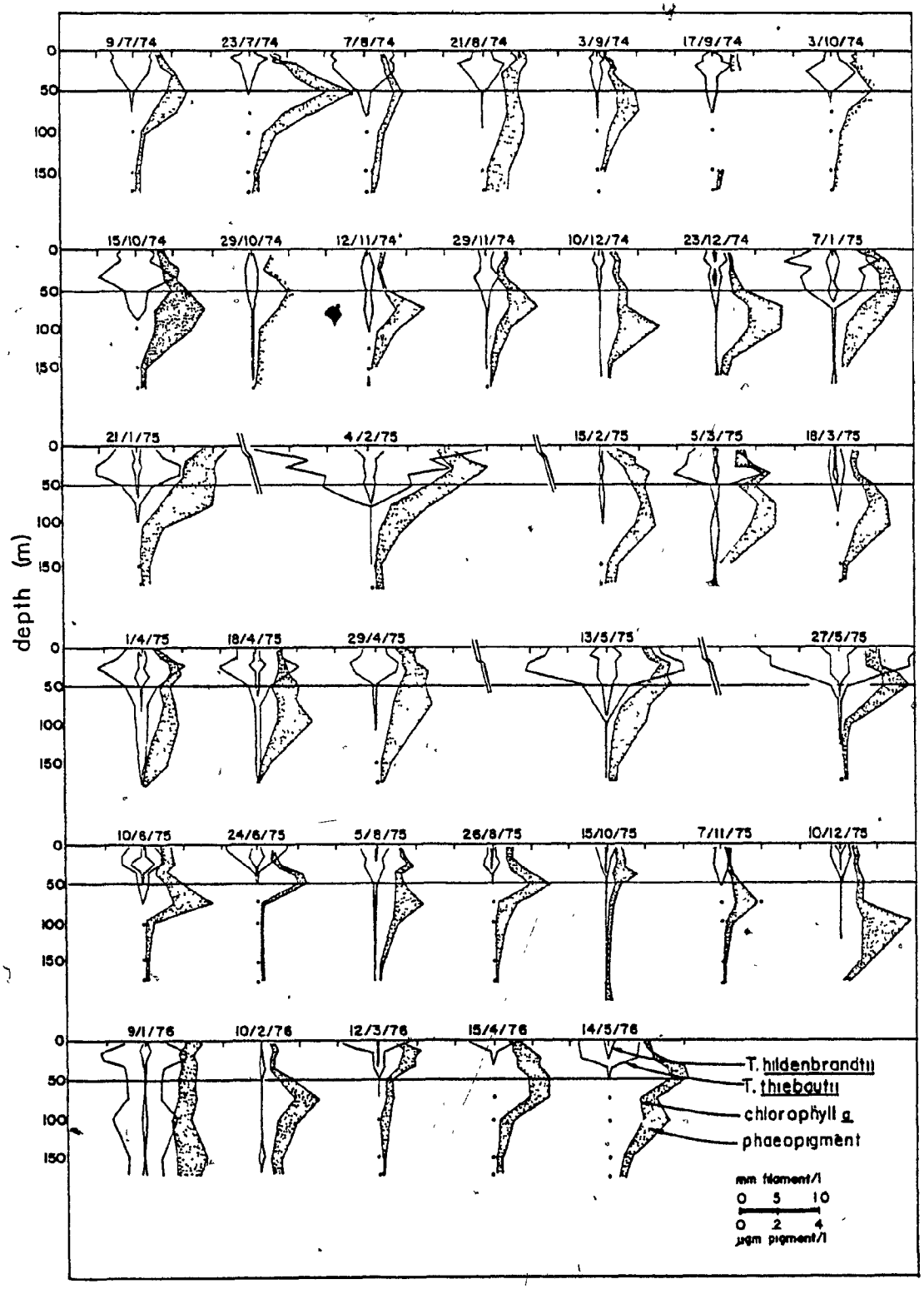
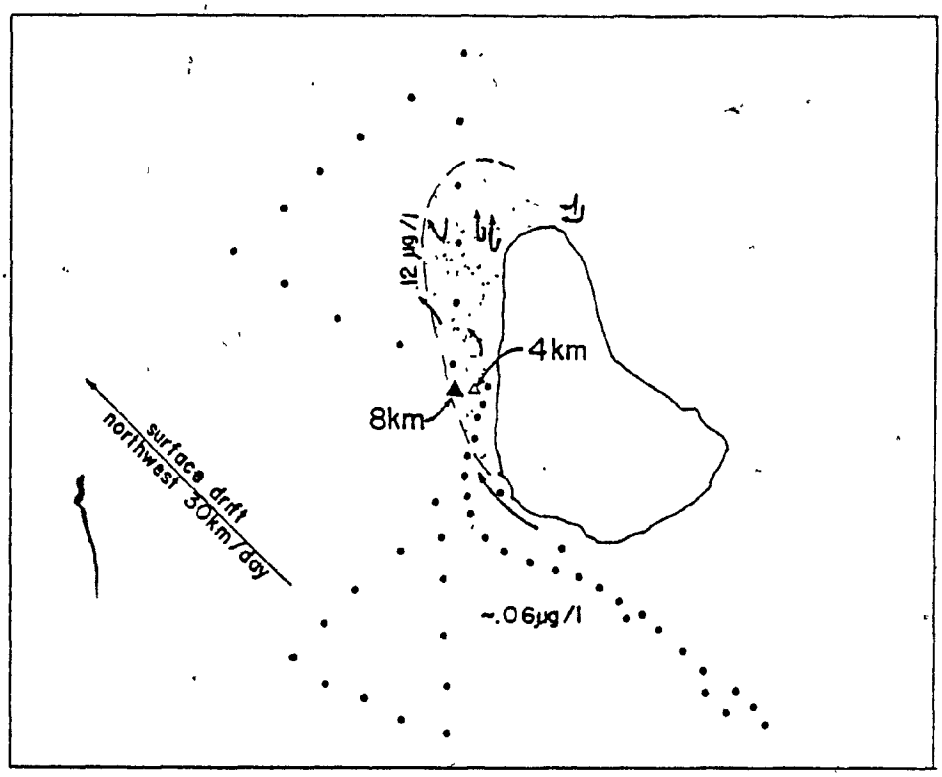

depth (m)
9/7/74
23/7/74
7/8/74
21/8/74
3/9/74
17/9/74
3/10/74
15/10/74
29/10/74
12/11/74
29/11/74
10/12/74
23/12/74
7/1/75
21/1/75
4/2/75
15/2/75
5/3/75
18/3/75
1/4/75
18/4/75
29/4/75
13/5/75
27/5/75
10/6/75
24/6/75
5/8/75
26/8/75
15/10/75
7/11/75
10/12/75
9/1/76
10/2/76
12/3/76
15/4/76
14/5/76
0
50
100
150
T. hildenbrandtii
T. thiebautii
chlorophyll a
phaeopigment
mm filament/l
0 5 10
0 2 4
µgm pigment/l

Figure 2.8 Horizontal variation of surface chlorophyll a concentration, July 21-23, 1975 (ASTP) illustrating augmentation in the island current lee. Small arrows indicate current patterns for July 1973 described by Murray et al. (1977). Large arrow indicates net surface drift calculated from drift bottle returns. 8 km station (8), 4 km station (4).


12 µg/l
4km
8km
surface drift
northwest 30km/day
~.06µg/l

the island's lee coast, which Murray et al. (1977) demonstrated is an area of significantly slower drift and confused circulation, pigment concentrations were elevated. This increase in chlorophyll concentrations close to Barbados' lee shore is now well known (cf. Sander and Steven, 1973) and has been considered a result of a retention of water masses and plankton close to the island (Sander, 1971, 1976; Emery, 1972; and others). While data collected during the present study cannot refute this possibility, it seems more likely that the slow passage of water along the lee coast and weak fertilization of the water masses due to the island (Sander, 1973) provide sufficient impetus to phytoplankton to produce the observed increases in pigment concentrations. Water masses pass quickly along the south and southwestern coasts, and the phytoplankton in these waters will not remain in these areas long enough to build up chlorophyll concentrations. In the region very close to the lee shore, water movements are much slower, and tidal movements should provide sufficient time for the phytoplankton to respond to fertilization. Correspondingly, pigment concentrations, phytoplankton cell counts and carbon fixation rates are elevated in these regions (Sander, 1971; Vezina, 1974; Partlo, 1975; and others). This effect extended downstream of the island during the ASTP, but did not persist more than about 10 km offshore, indicating that the fertilization was slight and cut off after the water mass passed the island.

The island appears to have little effect in elevating pigment concentrations at the 8 km station in July, when the latter was out of the island current lee. There was no significant difference between surface layer (0 and 5 m) chlorophyll concentrations at the two serial stations during the first seven months of the study (the coefficient of determination indicates that chlorophyll concentrations at the two stations are highly correlated - $r^2 = 0.94$). On only two occasions did the surface chlorophyll concentrations at the 4 km station differ significantly from those at the 8 km station; these were during the 'bloom' encountered during January and February 1975.

2.3.3 *Trichodesmium* in Barbados waters

2.3.3.1 Colony size

Whereas in the formalin preserved samples studied by Steven (1970) the average *Trichodesmium* filament was only about 12-25 cells long, *Trichodesmium* filaments in Lugol's preserved material observed during the current study were much longer. There was a very great range of filament length, from 4 or 5 cell fragments to very long filaments, sometimes greater than 4 mm (ca. 500 cells). Within this range, the filaments fell roughly into three groups with lengths around 0.5 mm, 1 mm and 2 mm, corresponding with the filament lengths in intact colonies.

Table 2.1 illustrates the range of filament length and number of filaments per colony observed in the 1 liter discrete samples from 5 m at the 4 km and 8 km stations. Consistent differences between radial and parallel *T. thiebautii* colonies and between *T. thiebautii* and *T. hildenbrandtii* colonies with respect to filament length are apparent.

The differences in number of filaments per colony may be related to colony architecture and to the structural strength of the two conformations. Manipulations in the laboratory showed that radial colonies, in which trichomes all cross through a central tangle of filaments, were quite resistant to mechanical disruption, and where a mucilaginous matrix was present the strength of the conformation was further improved. Filaments of both *T. thiebautii* and *T. hildenbrandtii* exhibit a tendency to coil and, in parallel colonies, this assists the trichomes in twisting around each other like fibres in a rope. This twisting proceeds to a variable extent and adds considerable strength. Parallel colonies are generally more fragile than radial colonies, even with this coiling, and the lower mean for filaments per colony and the greater number of colonies with few filaments is a reflection of this.

Table 2.1 Mean dimensions of *Trichodesmium* colonies observed in discrete samples from 5 m depth at the serial stations during 1974-1976.
Brackets indicate too few radial *T. hildenbrandtii* colonies were encountered to calculate meaningful standard errors.
T. hildenbrandtii colonies made up 10% of the total observed in these samples.

species	colony conformation	filaments/ colony ± SE	avg. length of filaments (mm) ± SE	n
T. thiebautii	radial	55 ± 3	0.5 ± 0.02	113
T. thiebautii	parallel	25 ± 2	1.2 ± 0.05	158
T. hildenbrandtii	parallel	21 ± 4	2.2 ± 0.04	22
T. hildenbrandtii	radial	44(± 9)	1.1(± 0.07)	8
				301

Many of these were obviously fragments of larger colonies which had broken apart either in the sea or during the sampling procedure.

Multiplication of the average filament length by the number of filaments per colony permits rough calculation of the total filament length. Further, a very approximate estimate of the number of cells per colony can be obtained by dividing by the average cell length (about 9μ for both species, although this varies through 100% due to longitudinal cell division). The mean number of cells for T. thiebautii colonies of both conformations is then around 3000, while T. hildenbrandtii colonies are larger with approximately 4500 cells/colony.

The size of Trichodesmium colonies observed at Barbados compared well with estimates for Trichodesmium from the Kuroshio by Marumo et al. (1975), from the Indian Ocean by Qasim (1970) and Ramamurthy et al. (1972), and from the Atlantic by Sieburth and Conover (1965), who variously report colonies with from 12 to 50 filaments with an extreme of 150. Carpenter and McCarthy (1975), however, have conducted experimental work on colonies with around 30,000 cells which were selected from plankton tows. While such large colonies were never observed in the discrete samples at Barbados, they were present in plankton tows in small numbers. The photosynthesis experiments reported in Section 3 were also conducted on larger than average colonies because these were much easier to work with and because a larger change in the experimental variable (particulate ^{14}C uptake) could be measured where more algal cells were present.

While there was a tendency towards larger colonies during the 'blooms', little can be said about the variation of lengths of single filaments with respect to the cyclical oscillations of the population. If any relationship between filament length and growth phase does exist in Trichodesmium populations, it was not obvious in

data from Barbados. The distribution of filaments within the three chosen size classes varied erratically from one station to another and within the samples from the mixed layer, from one depth to another. Shorter filaments were usually more abundant than longer ones at all depths, and below 50 m there was a consistent absence of filaments longer than about 1 mm in length. At 100, 150 and 175 m, where Trichodesmium was never abundant, only small numbers of short fragments were ever observed.

2.3.3.2 Vertical distribution

The vertical distribution of the Trichodesmium populations sampled during 1974-1976 is illustrated in Figure 2.7. More than 90% of the population was always located above about 50 m, and in nearly every case there was a subsurface maximum between 15 and 35 m. On a few occasions there were near surface (5 m) maxima in place of, or in addition to, the subsurface maxima, and these usually coincided with 'blooms'.

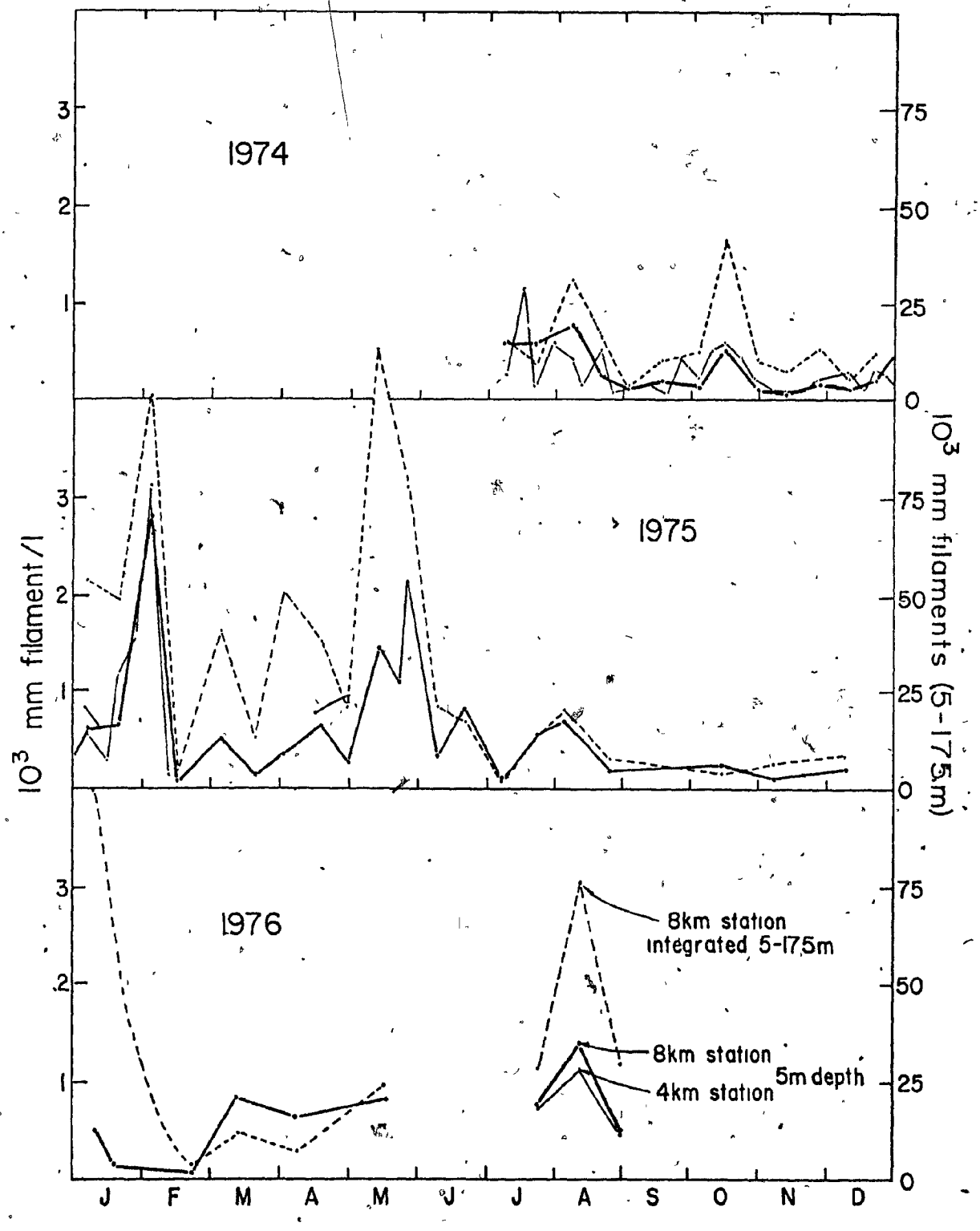
Although no data are presented here, field notes always noted a much greater number of parallel colonies in plankton tows closest to the surface. Radial colonies, by comparison, were more evenly distributed between the surface and 35 m, with a decline below that. In many instances, where colonies of both morphologies were required from 5, 25 and 50 m for comparison of morphology, pigment content, or other character, insufficient numbers of parallel colonies were collected from 50 m to make comparison. These trends, so obvious in the plankton tows, could unfortunately not be corroborated with data from the counts of the discrete samples. No matter how carefully the water samples were transported and transferred from one container to another, some colonies always fell apart. Parallel colonies were the most fragile.

Unlike the other phytoplankton, a larger part of which accumulates lower in the euphotic zone in or just below the pycnocline, Trichodesmium is definitely a mixed layer dweller. Like other cyanophytes, Trichodesmium possesses gas vacuoles which afford it considerable buoyancy. Some blue-greens have been shown to be capable of regulating their buoyancy through photosynthetic control of vacuolation (Walsby, 1972) and are thus able to stratify at depths optimal for growth. It is possible that this is also the case with Trichodesmium since the apparent differences in vertical distribution between the two colony types noted above correspond to differences in their photosynthetic response to the irradiance climate in the upper euphotic zone.

2.3.3.3 Temporal variations

The temporal variation of the Trichodesmium population can best be illustrated by Figure 2.9 in which total filament length at 5 m and throughout the layer sampled here are presented. It is evident that the oscillatory variations described by Steven and Glombitza (1972) were still operating during 1974-1976. There were regularly appearing increased standing stocks of Trichodesmium (predominantly T. thiebautii) in January-February, May, August and perhaps in October. While the timing of the increases coincided well in both years of this study with those observed by Steven and Glombitza, the amplitudes did not. In January 1976, the 5 m population was smaller than that observed a year earlier, and microscopic observations of colonies collected during January 1976 indicated that much of the population was lysing and deteriorating. A large number of partially disintegrated colonies with only a few intact filaments were observed in the discrete samples from 5 and 15 m on January 9, 1976. A series of nine surface bucket samples taken 10 days later, along a 20 km transect to the southwest of the 8 km station, revealed that this situation existed over a wide area. Chlorophyll a concentrations at 5 and 15 m on January 5, and in the surface samples on January 19,

Figure 2.9 Variations of Trichodesmium standing stock (mm of filament/liter) at two stations off Barbados during 1974-1976.


1974
1975
1976
10^3 mm filament/l
10^3 mm filaments (5-175m)
8km station
integrated 5-175m
8km station
5m depth
4km station
J F M A M J J A S O N D

were also low, with large proportions of detrital phaeopigment present indicating the poor state of health of the phytoplankton population generally. Instead of being distributed close to the surface, the population was more equally distributed throughout the upper 100-150 m.

On January 14, 1976, the Trichodesmium population below 15 m appeared in much better condition than that near the surface, and was similar to that present in January 1975, at those depths. In March and April 1976, the very small populations present were concentrated near the surface, and the 5 m populations therefore give a false impression of the alga's abundance. The 5 m Trichodesmium population is therefore not always a good indicator of the entire mixed layer population because of these variations in vertical distribution. Regression of the entire Trichodesmium population (integrated 0-175 m) on the 5 m population (T_5) gives the equation:

$$T \int_0^{175} \text{(mm)} = 8153 + 38.73\ T_5\ \text{(mm)}$$

The coefficient of determination indicates 55% of the variation of $T \int_0^{175}$ is associated with variation of T_5.

2.4 The cyclical phenomenon

2.4.1 Hypotheses concerning its cause

2.4.1.1 Biological control of growth

The hypotheses concerning the cause of the cyclical appearance of Trichodesmium off Barbados put forward by Steven and his coworkers (Steven et al., 1970; Steven and Glombitza, 1972) have already been outlined in Section 1. Their suggestion that the cycles were free-running

and the result of the growth of surface blooms from deep subsurface populations and their decay in the nutrient impoverished surface layer, was one of the working hypotheses in the first part of the current study. The finding that the timing of Trichodesmium 'blooms' observed during 1974-1976 was essentially the same as that during 1968-1970 casts doubt on the free-running hypothesis, especially since the length of time between 'blooms' does not appear to be constant. A free-running cycle would be expected to be fairly constant and exhibit a fourth peak annually in November. This increase was absent in both studies.

Carpenter and Price (1976) are the only other authors to have considered the cause of the cycles recorded by Steven et al. (1970). Their own findings that nitrogen fixation seems to supply nearly all of the alga's nitrogen and that the process was adversely affected by turbulence led them to suggest that Trichodesmium blooms, which usually occur in calm and sunny conditions (Brengersma-Sanders, 1957), do so because nitrogen fixation is allowed to proceed. Accordingly, they compared the Trichodesmium standing crops recorded by Steven et al. (1970) to coincident meteorological data from Grantley Adams International Airport and concluded that there was a significant correlation between the 'blooms' and calm, sunny weather. They interpreted this to indicate the cycles were not free-running but controlled by physical factors affecting nitrogen uptake and growth. Neither Steven et al. (1970), Steven and Glombitza (1972) nor Carpenter and Price (1976) have apparently considered lateral transport as a possibility in determining the timing of events.

2.4.1.2 Lateral transport of already large populations

The sudden appearance of very large populations, sometimes already in a state of decline, and their equally rapid disappearance, suggests that horizontal advection of discrete patches of Trichodesmium is important in regulating the populations encountered at Barbados. The general movements and heterogeneity of the surface water masses have already been discussed, and comment has been made on the intermittent appearance of 'pools' of slightly fresher water. A comparison of surface Trichodesmium and salinities is therefore interesting.

The algae could almost always be found in the surface waters, both inshore and offshore. The TSP plot (Temperature-Salinity-Plankton) in Figure 2.10 illustrates the euryhalinity of Trichodesmium within the range of conditions at Barbados and the lack of a relationship between absolute salinity and abundance of the algae. The salinity range for the genus seems to be about 32°/oo - 37°/oo (Wille, 1904; Sournia, 1968; and many others). The apparent differences in temperature optima evident between the 1968-70 study (Steven et al., 1970) and this one are probably related to the methodological differences mentioned in Section 2.2.4.*

There is no apparent relation between Trichodesmium standing stocks and absolute salinity, but a plot of surface salinity and Trichodesmium (Figure 2.11.1 and 2.11.2) shows that much more alga appears around Barbados in the first nine months of each year. Further,

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* Whereas Steven et al. (1970) recorded recurring maxima of nearly the same amplitude, this was not the case during the present study where all of the Trichodesmium in 1 liter samples was enumerated. The abundance of the alga at 28° indicated in the 1968-70 data is a reflection of the relatively large populations observed in the August 'blooms' of 1969 and 1970.

Figure 2.10 Temperature-salinity vs. Trichodesmium at 5 m depth off Barbados.

Solid circles: this study (1974-1976); open circles: Steven et al., 1970 (1968-1970).

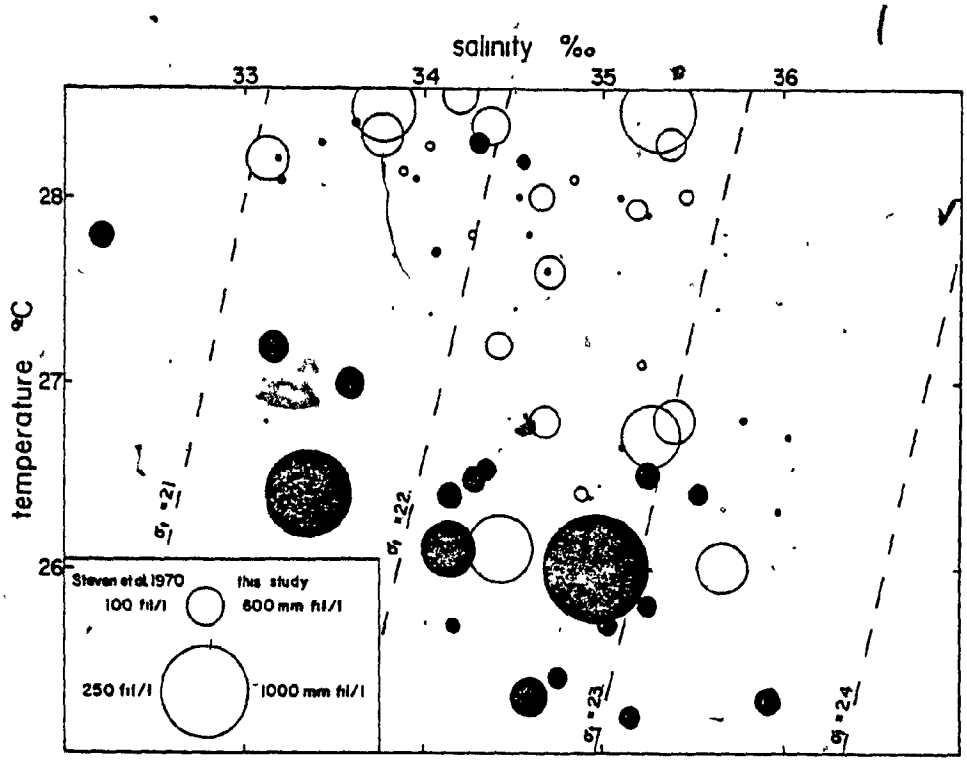
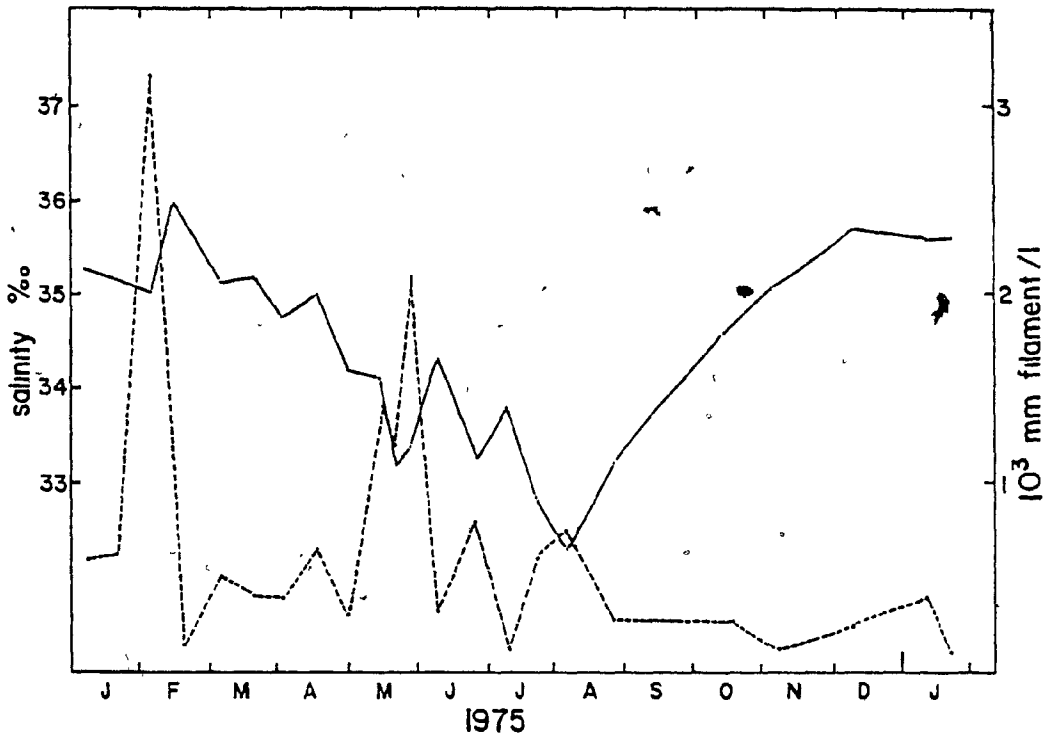
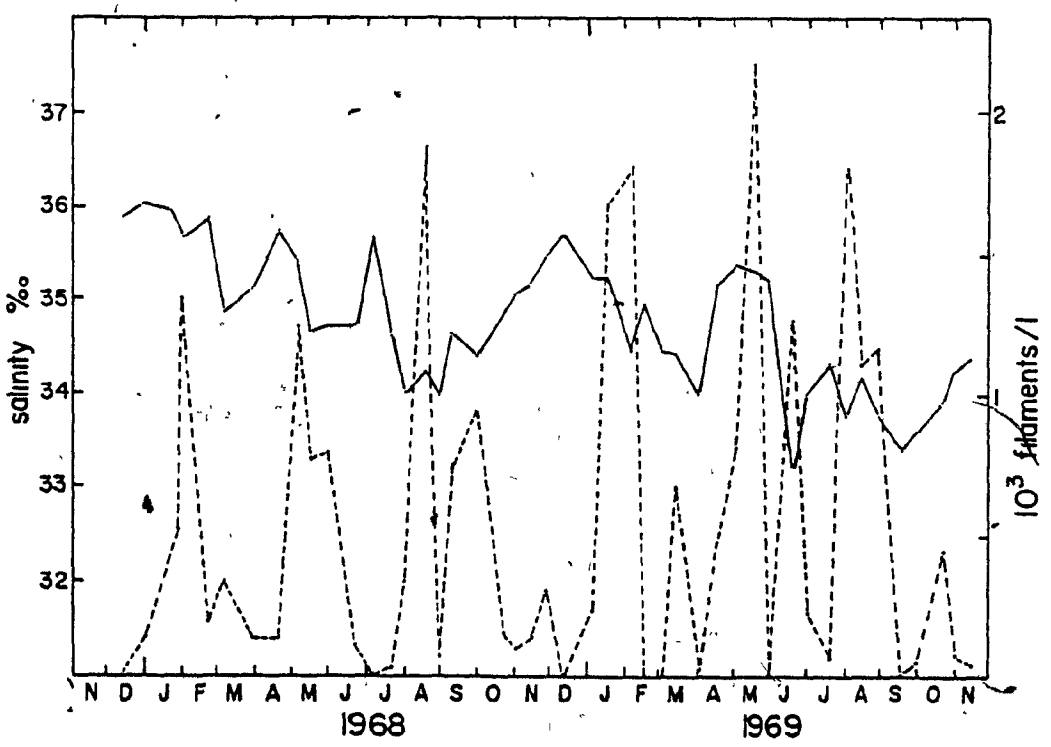

salinity ‰
33
34
35
36
temperature °C
28
27
26
σ_t = 21
σ_t = 22
σ_t = 23
σ_t = 24
Steven et al 1970
100 fil/l
250 fil/l
this study
600 mm fil/l
1000 mm fil/l

Figure 2.11.1 Relationship between Trichodesmium standing stocks (---) and salinity (——) at 5 m depth at the 8 km station during 1975 (this study).

Figure 2.11.2 Relationship between Trichodesmium standing stocks (---) and salinity (——) at 5 m depth at station 2B during 1968-1969 (Steven et al., 1970).


37
36
35
34
33
salinity ‰
3
2
1
10^3 mm filament/l
J F M A M J J A S O N D J
1975


37
36
35
34
33
32
salinity ‰
2
1
10^3 filaments/l
N D J F M A M J J A S O N D J F M A M J J A S O N
1968
1969

the rapid changes in Trichodesmium abundance from one station to another were associated with slight changes of surface salinity, indicative of changing water masses. Most large increases in algal numbers coincided with temporary declines in surface salinity, suggesting that Trichodesmium is carried to Barbados in 'pools' of Guiana Current water.

Steven et al. (1970) discussed the heterogeneity of the surface salinities at Barbados and observed that at least three large pools of low salinity water passed the island between February and August 1968. They did not relate this to the rhythmical appearance of Trichodesmium. The same inverse relationship exists between surface salinity and algal abundance in their data as in 1975 (see Figure 2.11.2). The negative relation between silicate concentration and salinity has been interpreted by them to indicate that these waters are largely of Amazon River origin.

In both data sets, Trichodesmium was most abundant between January and September. The 1974 data suggest that there may have been a fourth small increase in mid-October, and other data to be discussed later support this suggestion.

The fact that Trichodesmium was most abundant in waters with slightly lower salinities suggests that the temporal variations of the standing crop of this alga off Barbados are in some way controlled by hydrology. If this is so, and the water mass carrying the large Trichodesmium populations are quite separate from the masses surrounding them, as they appear to be, then it is logical to expect evidence of rhythmicity in data concerning other plankton.

As already mentioned, the variations of chlorophyll a concentrations in the top layers of the ocean closely approximated those of the Trichodesmium population in those layers. A regression of

chlorophyll a on Trichodesmium at 5 m for the 8 km station gives:

$$Chla_{5m}\ (\mu g/l) = 8.0 \times 10^{-5}\ T_{5m}\ (mm) + 0.062$$

The coefficient of variation indicates that 49% of the variation of the chlorophyll concentrations was associated with variations of the Trichodesmium population. This is almost exactly the fraction arrived at by calculating the µgm chlorophyll/mm filament (0.00012) from measurements of isolated colonies and multiplying this by the average standing crop (523 mm). By these calculations Trichodesmium contributes, on the average, 0.062 µg chlorophyll/l or 50% of the annual mean concentration. The fraction may be higher or lower on specific days, but it is in good agreement with the estimate of 60% made by Carpenter and Price (1977) for four stations in the Caribbean Sea.

Steven et al. (1970) did not calculate the contribution by Trichodesmium to total chlorophyll or cell numbers in this way, but observed that when their Trichodesmium counts fell to zero, the chlorophyll concentrations were about 0.12 µg/l. They assumed that this represented the phytoplankton other than Trichodesmium, and that since the numbers of other phytoplankton did not seem to vary significantly, oscillations in the numbers of the blue-greens were responsible for fluctuations of chlorophyll concentration.

During the current study, phytoplankton other than Trichodesmium were not enumerated because of the rather tedious method chosen to enumerate the blue-green. Qualitative notes made of the other plankton, however, showed clearly that while dinoflagellates and coccolithophorids were the most common other phytoplankton when Trichodesmium numbers were low, large mats of very small Chaetoceros spp., Rhizosolenia spp., and Navicula spp., were very abundant in samples containing large numbers of the cyanophyte. In the May 1975 'bloom' fish eggs and larvae were also abundant. The realization that the numbers of the 'other' phytoplankton

changed radically during the so-called Trichodesmium 'blooms', and that diatoms were much more abundant at such times, called for a re-examination of the historical data.

2.4.2 Re-examination of historical biological data

2.4.2.1 Phytoplankton

Steven et al. (1970) regarded the offshore phytoplankton excluding Trichodesmium as being rather stable numerically; however, they point out that the range of variation was from about 500-5,000 cells/liter*, and mention marked fluctuations of diatoms in particular. Two stations for which they refer to 'diatom mini-blooms' also happen to be occasions on which large Trichodesmium populations were encountered. While their published data include 'phytoplankton cell counts', they do not mention whether or not these include Trichodesmium cells or filaments, and it is not possible to examine the annual variations of the two groups separately.

The observation made during the course of the current study, that diatoms were very much more abundant when Trichodesmium appeared in greater numbers, led to a re-examination of the personal data of the late Dr. D.M. Steven. These unpublished data included cell counts for Trichodesmium, totals of phytoplankton 'excluding Trichodesmium', and in some cases notes on numbers of diatoms, dinoflagellates and coccolithophorids. These data are summarized in Figures 2.12 - 2.14.

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* Corrected value; the original cell counts were apparently 6x too high, and have been corrected by Sander (1971) and Sander and Steven (1973) (F. Sander, pers. comm., Bellairs Research Institute, St. James, Barbados).

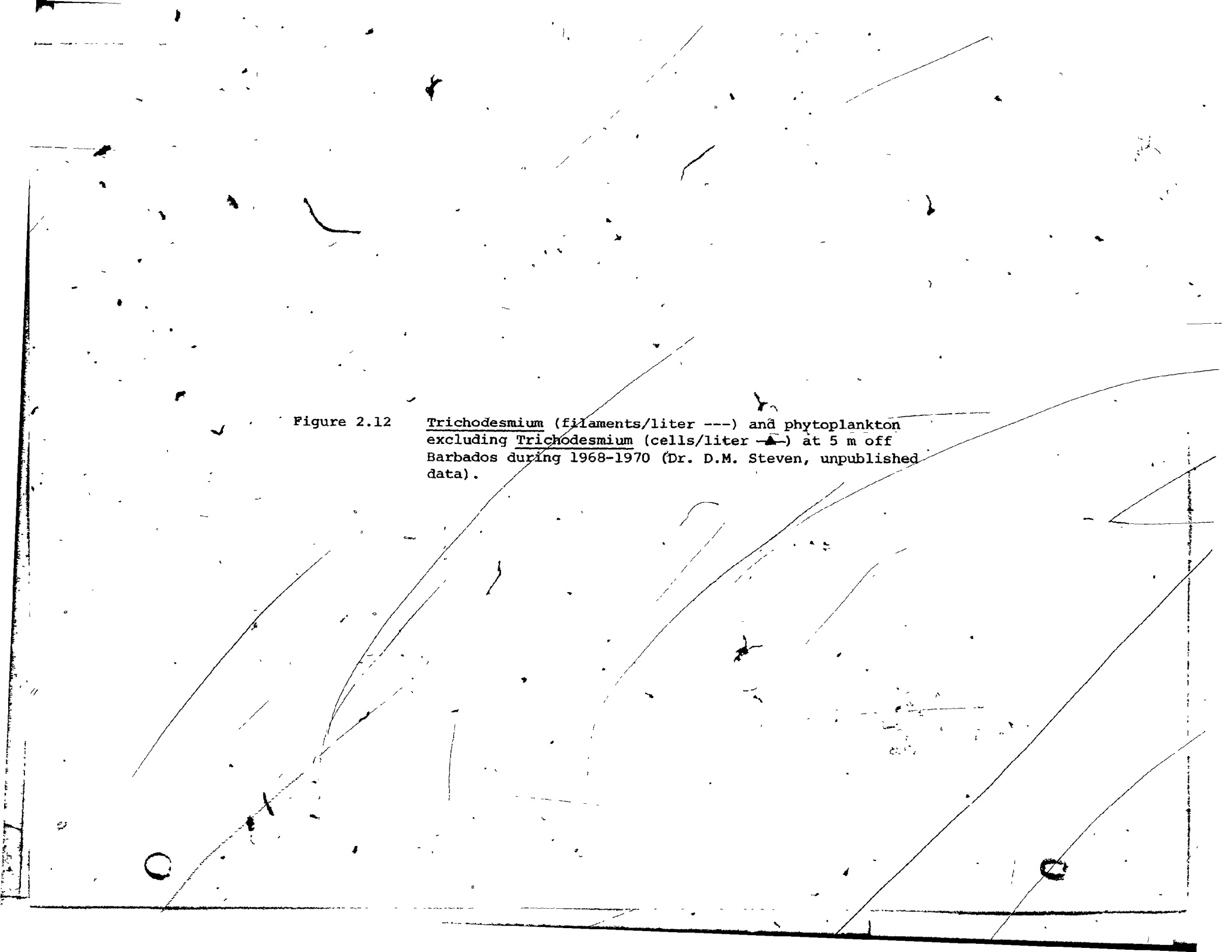


Figure 2.12 Trichodesmium (filaments/liter ---) and phytoplankton excluding Trichodesmium (cells/liter —▲—) at 5 m off Barbados during 1968-1970 (Dr. D.M. Steven, unpublished data).

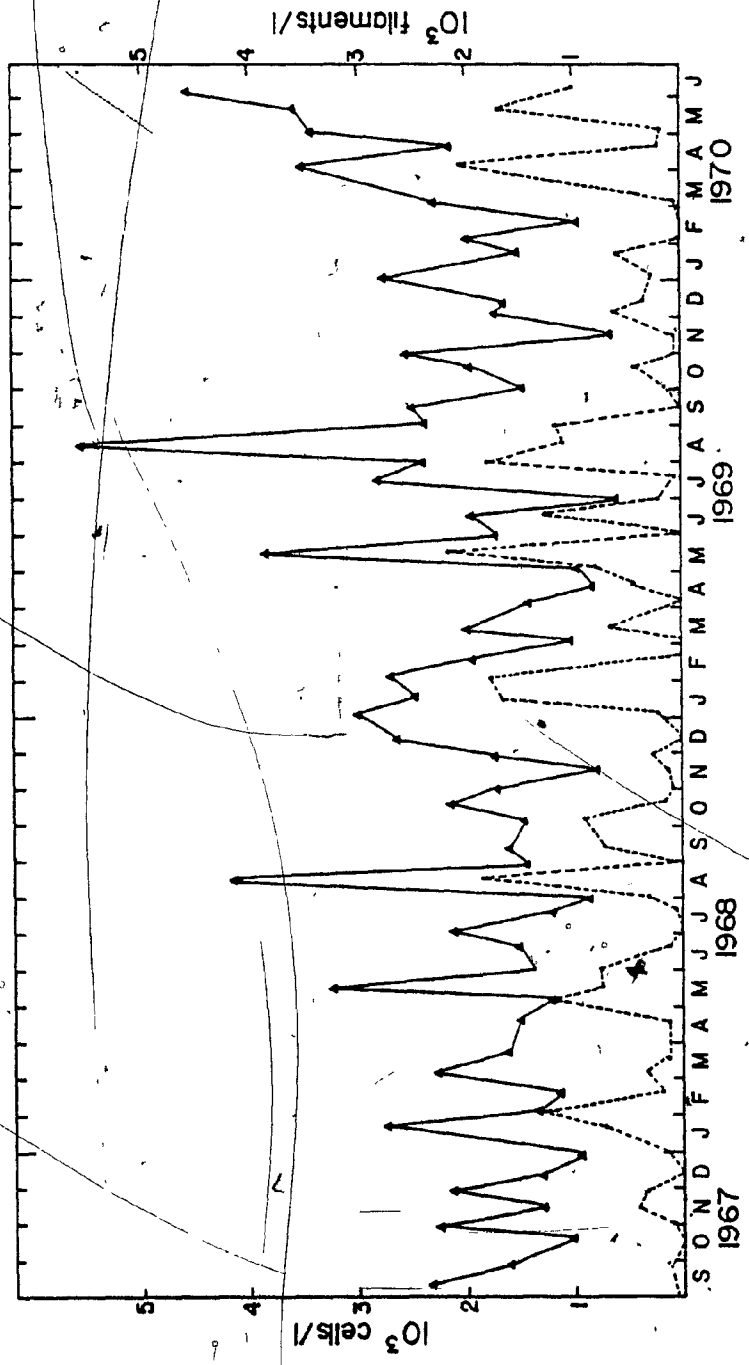
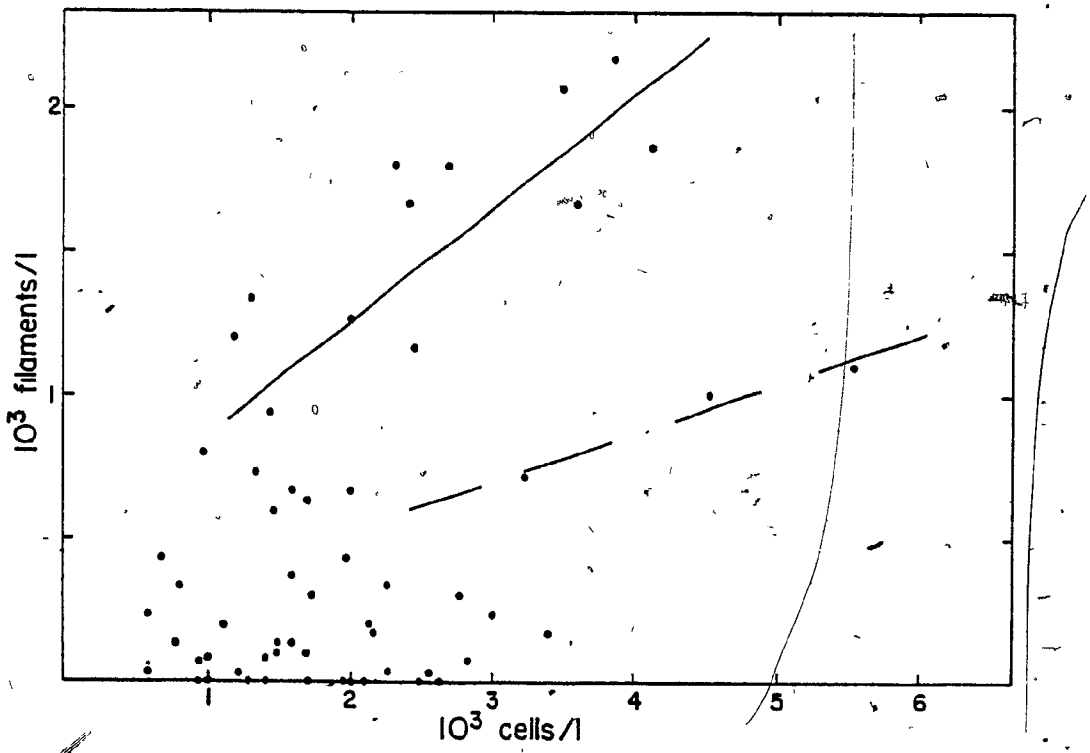
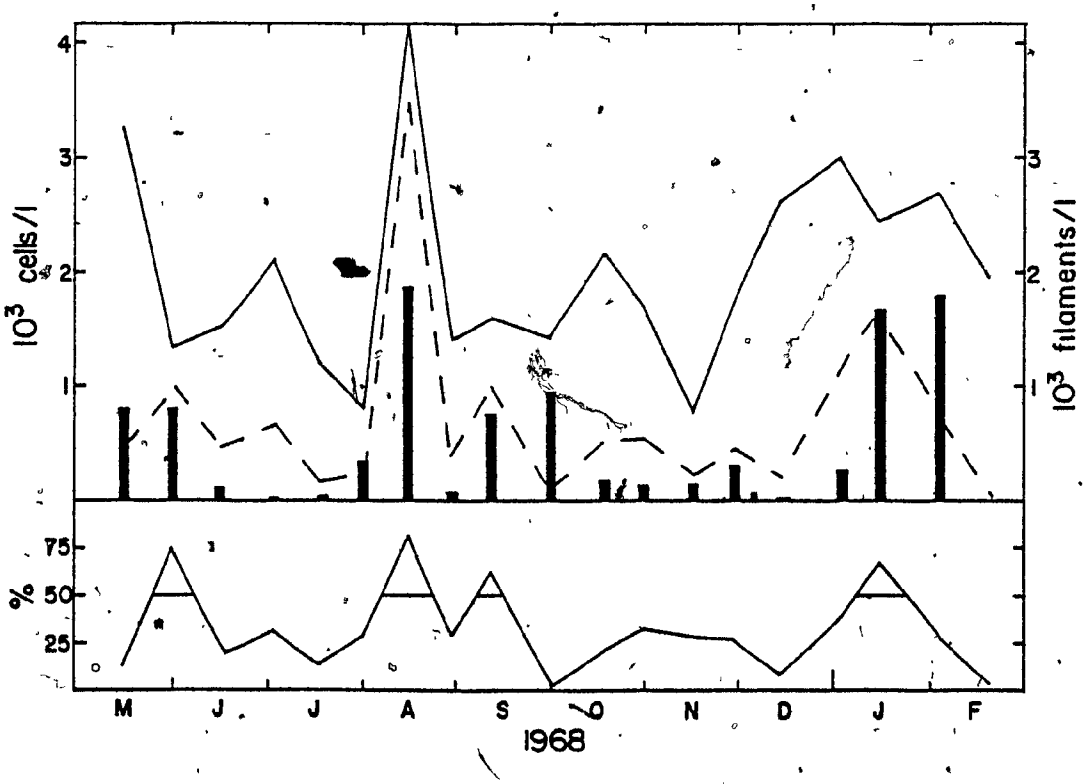

10^3 filaments/l
10^3 cells/l
1
2
3
4
5
S O N D J F M A M J J A S O N D J F M A M J J
1967
1968
1969
1970

Figure 2.13 Relation between Trichodesmium and phytoplankton excluding Trichodesmium at 5 m during 1968-1970.

The three points along the lower dashed line are all from stations where the increase in other phytoplankton followed that of Trichodesmium by two weeks (Dr. D.M. Steven, unpublished data).

Figure 2.14 Temporal variations of Trichodesmium (filaments/liter: bars), total other phytoplankton (cells/liter:——); diatoms (cells/liter:---), and of the percent contribution to total other phytoplankton by diatoms (below) (Dr. D.M. Steven, unpublished data).


10^3 filaments/l
10^3 cells/l
1
2
3
4
5
6


10^3 cells/l
10^3 filaments/l
%
75
50
25
M
J
J
A
S
O
N
D
J
F
1968

While the phytoplankton numbers are very low and the fluctuations miniscule compared to those at higher latitudes, the phytoplankton excluding Trichodesmium show marked oscillation in phase with the blue-green. There is a linear relation between the two groups at 5 and 50 m for most stations (Figure 2.13); and in every case the 'peaks' agree to within one interval on the sampling schedule (two weeks). Further, the increases in 'other phytoplankton' are apparently largely due to increases in numbers of diatoms which appear with the same periodicity as Trichodesmium (Figure 2.14).

Observations during the present study, and these previously unpublished data, show that in the region offshore, all of the surface phytoplankton (but mostly Trichodesmium and the diatoms) fluctuate numerically with a rhythm that is constant and fairly predictable from year to year.

All of the other phytoplankton studies at Barbados with sampling twice a month or more have been conducted close to the island. A study of the Bridgetown careenage area (Partlo, 1975), conducted simultaneously with the current work, permits comparison of the timing of events in the Bridgetown harbour area with that offshore. Figure 2.15 illustrates the close temporal agreement. Both major increases of chlorophyll a encountered offshore during this period were also observed at the Bridgetown station at the same time and surface salinities at Partlo's station number 4 and the 4km and 8 km stations agreed well (Figure 2.2), indicating that the same water mass was usually being sampled at the three locations. It is apparent that the largest variations observed in Partlo's chlorophyll data for this station are caused by invasion of new water masses carrying different sized phytoplankton populations. The fact that the increases and decreases coincide well both near Bridgetown and at offshore stations halfway up the west coast indicates that the water masses had discrete boundaries with abrupt changes in

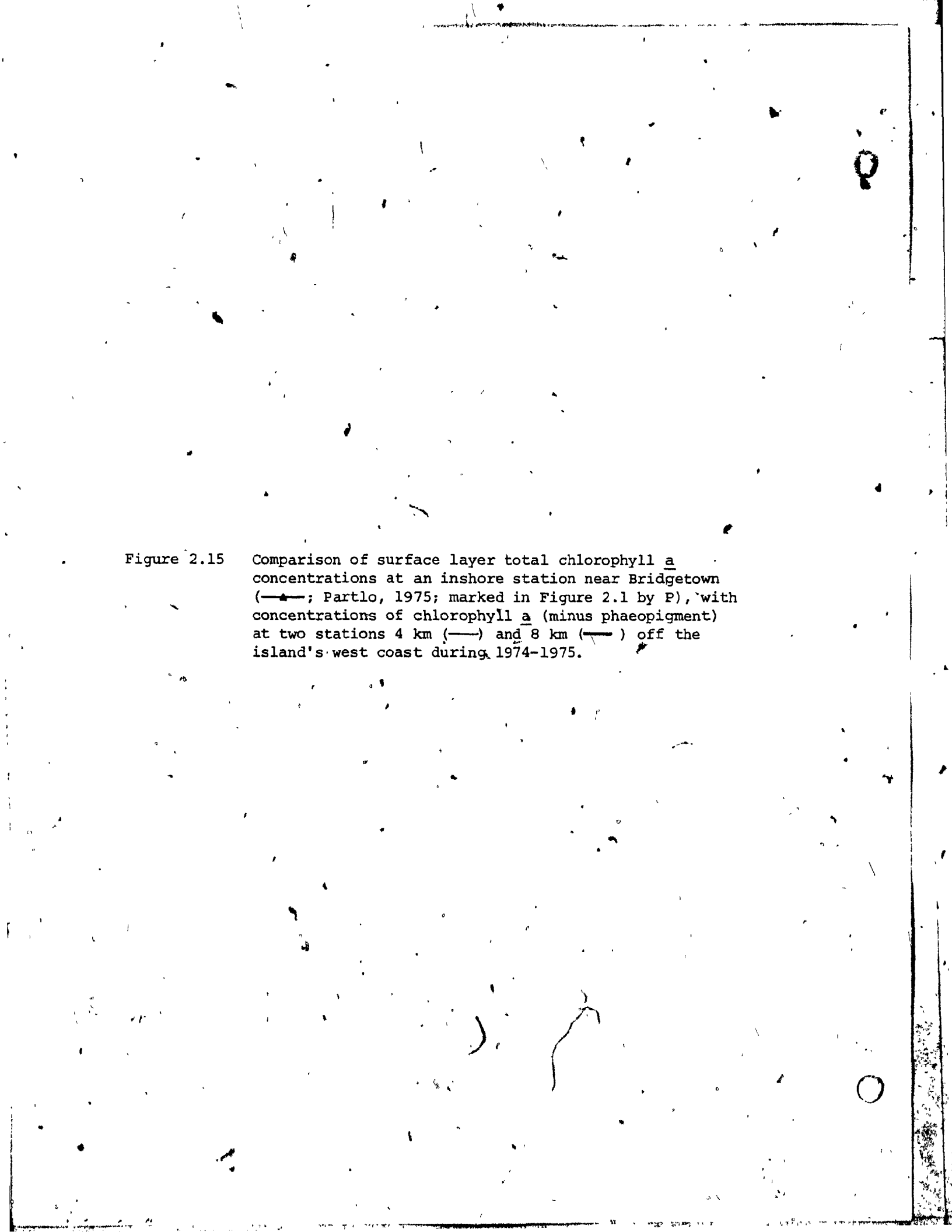
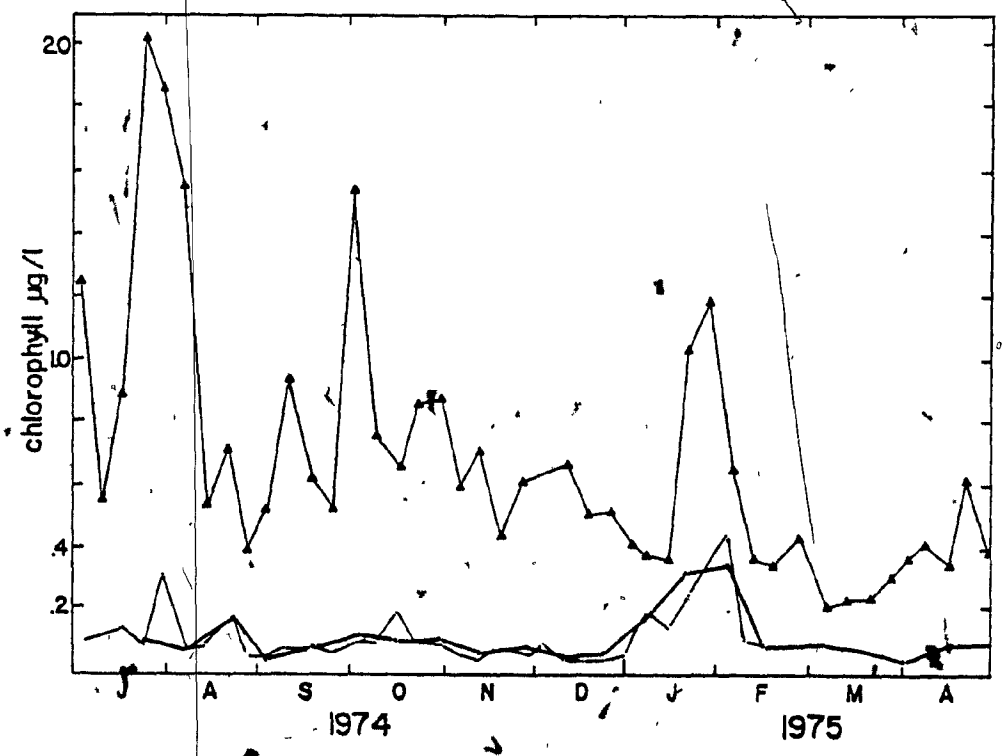


Figure 2.15 Comparison of surface layer total chlorophyll a concentrations at an inshore station near Bridgetown (—▲—; Partlo, 1975; marked in Figure 2.1 by P), with concentrations of chlorophyll a (minus phaeopigment) at two stations 4 km (——) and 8 km (——) off the island's west coast during 1974-1975.


20
10
.4
.2
chlorophyll µg/l
J
A
S
O
N
D
J
F
M
A
1974
1975

pigment concentrations and cell numbers. The combined data show that the July and January 'patches' of phytoplankton were large enough, and their passage by the island slow enough, that they were detectable at stations about 15 km apart for two or three weeks. The patch in which Partlo encountered high chlorophyll in October must have been rather small because it was only sampled once. The small increase at the 4 km station a few days later may represent the periphery of the same patch.

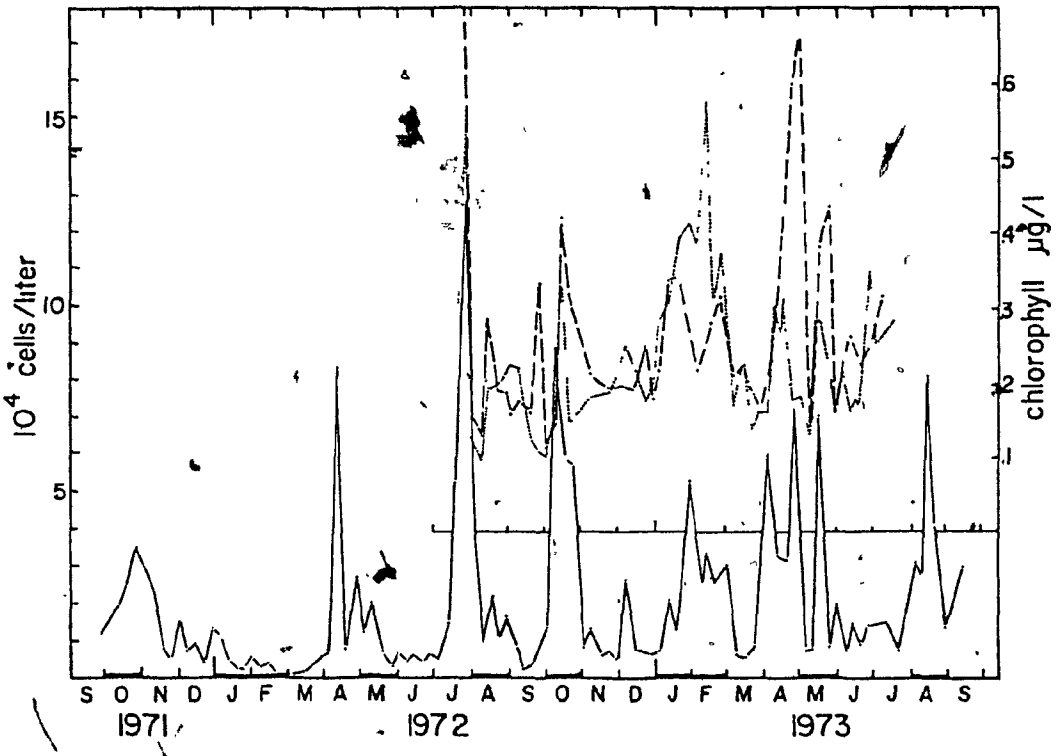
Two other studies conducted by Vezina (1974) and Sander (1976) present data allowing further examination of the fluctuations along the southern half of Barbados' west coast during 1971-1973. Vezina occupied eleven stations close to shore at weekly intervals, between Bellairs Research Institute and Bridgetown during 1972 and 1973, while Sander examined the numbers and species composition of surface phytoplankton at a 10 m station near Bellairs from 1971-1973. Figure 2.16 compares the temporal variations of chlorophyll concentration at two of Vezina's stations (V and P on Figure 2.1) with phytoplankton numbers recorded by Sander (1976) (H on Figure 2.1) and allows comparison with the timing of events offshore in 1968-1970 and 1974-1976.

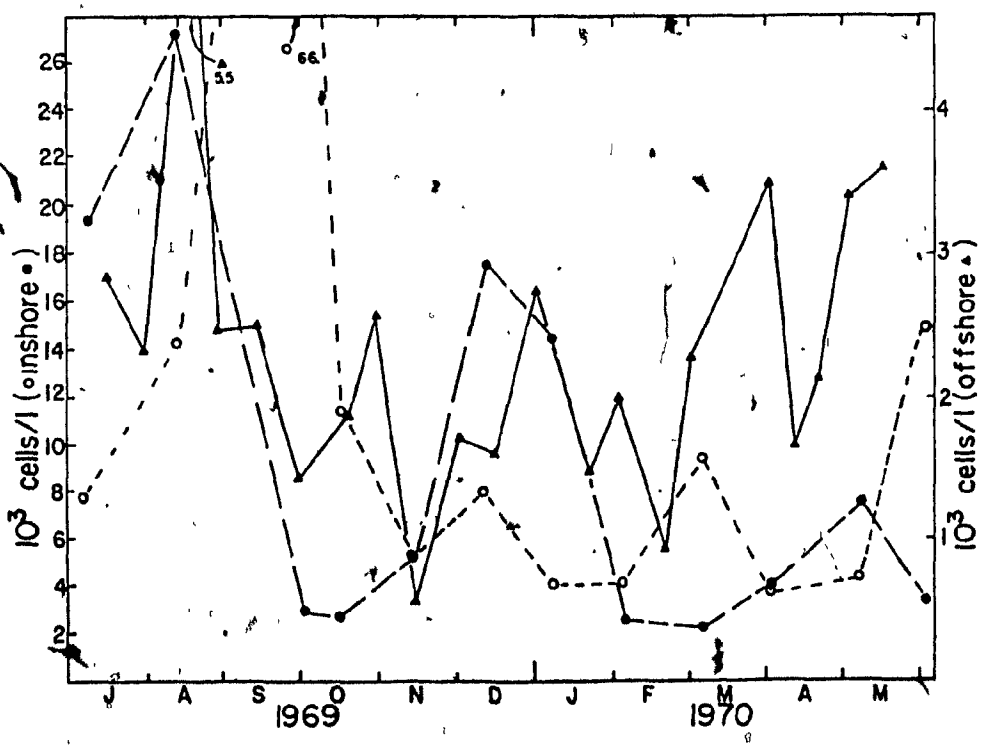
Vezina's study was not long enough in itself to allow detection of recurring maxima, but comparison with the studies by Sander (1971, 1976), Steven et al. (1970), Partlo (1975), and the current work, show that phytoplankton appears and disappears all along the southern west coast with much the same rhythmicity as offshore. Whether the differences in maximal total chlorophyll observed by Vezina at different stations along the coast are reflections of rapid growth as the water moved by, patchiness in the phytoplankton distribution within the larger 'patches', aliasing due to the sampling interval, or a combination of all three, is difficult to say.

Sander's (1976) data show that the increases in chlorophyll measured by Vezina were primarily due to increases in the numbers of

Figure 2.16 Temporal variations of surface layer (1 m) total chlorophyll a concentration (interrupted lines - Vezina, 1974) and phytoplankton cell numbers (continuous line - Sander, 1976) at three inshore stations along the southern half of Barbados' west coast. Vezina's stations are indicated in Figure 2.1 by V and P. Sander's data are from H. Bars along the abscissa indicate the timing of Trichodesmium and/or phytoplankton maxima observed in 1968-1970 (Steven et al., 1970) and 1974-1976 (this study).

Figure 2.17 Temporal variations of surface layer (1 m) phytoplankton (excluding Trichodesmium) offshore —▲— (D.M. Steven, unpublished data) and of total phytoplankton at two inshore stations along the northern half of Barbados' west coast (Sander, 1971 ●- indicated by S in Figure 2.1, o- indicated by R in Figure 2.1).


10^4 cells/liter
chlorophyll µg/l
S O N D J F M A M J J A S O N D J F M A M J J A S
1971
1972
1973


10^3 cells/l (o inshore •)
10^3 cells/l (offshore ▲)
J A S O N D J F M A M
1969
1970

diatoms. He also states that dinoflagellates and coccolithophorids were a larger proportion of the population during the periods of low numbers.

The phytoplankton data collated here indicate that the rhythmic passage of water masses containing larger phytoplankton populations with a more important diatom component is important along the southwestern coast where little distortion of the water masses is evident. The northern half of the west coast, however, is known to be an area of slower currents and eddying (Murray et al., 1977) and nearly synoptic chlorophyll data collected during July 1975, revealed an area of higher surface chlorophyll in this island 'wake'. Sander's earlier study (Sander, 1971) was concentrated in this area and was simultaneous with part of the offshore work of Steven et al. (1970). Sander has already described increases in average chlorophyll, cell numbers and photosynthesis in this inshore region, but the data can also be examined for synchrony with the offshore station. Figure 2.17 illustrates that while the agreement is not nearly so good as along the southern half of the west coast, major increases offshore were usually observed at at least one of the inshore stations at the same time. The slower passage of water through this area may be responsible for development of asynchrony with the offshore station.

Along all of the coast the arrival of water masses carrying larger diatomaceous populations capable of response to fertilization near the island seems responsible for the timing of increases in chlorophyll and cell numbers at inshore stations. Off the northwest coast, where water movements are more complex, the timing is somewhat modified.

Data from research by Steven et al. (1970), Vezina (1974), Partlo (1975), Sander (1976) and the current study all suggest the alternating appearance at Barbados of two groups of phytoplankton: one with low population densities, dominated by dinoflagellates and coccolithophorids; and a second group usually appearing in larger numbers, in which

Trichodesmium and diatoms were abundant. This division of the phytoplankton into diatomaceous and nondiatomaceous groups seems to be quite a natural one, since the diatoms are more common in neritic and coastal waters, while dinoflagellates and coccolithophorids dominate the blue oceanic regions (Hargraves et al., 1970; Sander, 1971; Steidinger, 1973). Hulbert (1962) has shown that standing crops of these latter groups were more or less equal along a transect between the southwest Sargasso Sea and Grenada in February, 1961. Diatoms and Trichodesmium, however, were both more abundant at the surface at the southern stations where slightly lower surface salinities were observed. In 1964 and 1965, Hulbert and Corwin (1969) observed large diatomaceous populations in isolated low salinity pools far off the South American coast north of Cape Orange. They considered these to be neritic populations which had been carried offshore in freshwater lenses produced near the Cape. Their experimental work with several different types of 'neritic' and 'oceanic' phytoplankton from the western tropical Atlantic revealed that diatoms responded well to fertilization in batch culture while coccolithophorids and dinoflagellates did not. Eppley et al. (1969) have since shown that the species usually regarded as 'neritic' have higher K_s for nutrient uptake than do 'oceanic' species; that is to say, 'neritic' species' uptake mechanisms saturate at much higher nutrient concentrations than do those of 'oceanic' species. Recent evidence suggests that Trichodesmium also requires considerably higher concentrations of ammonium and nitrate than do other 'oceanic' species (Carpenter et al., 1975; Wada et al., 1975). Its appearance off Barbados in concert with large numbers of supposedly neritic diatoms, therefore may be related to their nutrient kinetics, since the low salinity waters in which it arrives are derived from the Guiana Current. These waters contain a large riverine component and pass along the coastal areas of South America where nutrients are supplied by upwelling.

2.4.2.2 Zooplankton

The discussion of the temporal variations of the Trichodesmium and other surface phytoplankton populations suggests that alternation of Guiana Current water and North Equatorial Current water is responsible for the rhythmical fluctuations. There is now a great deal of information available regarding the temporal variations of zooplankton stocks near Barbados, and a short review of this literature, while not directly related to Trichodesmium, may be enlightening.

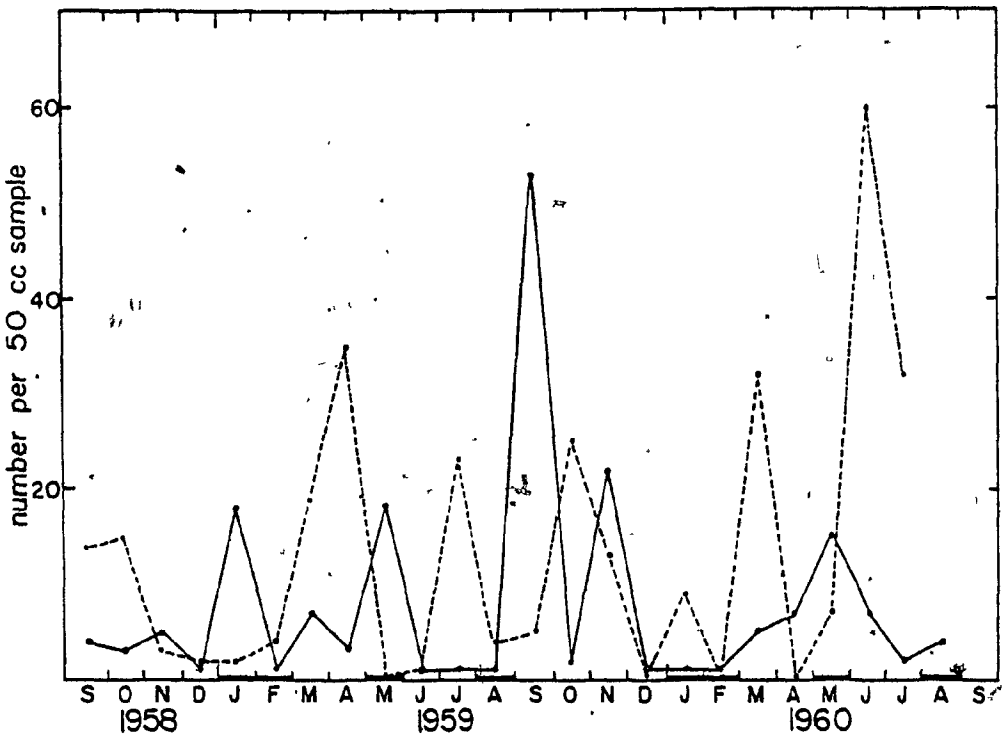
Many zooplankton migrate appreciable vertical distances and thus spend part of each day below the surface mixed layer, in water masses which move in different directions and at different velocities than the surface masses. There are, however, many mixed-layer dwellers with only feeble migrations and others which curtail migrations to remain in certain water masses, and these types can be used as water mass indicators (Bary, 1963; Michel and Foyo, 1976).

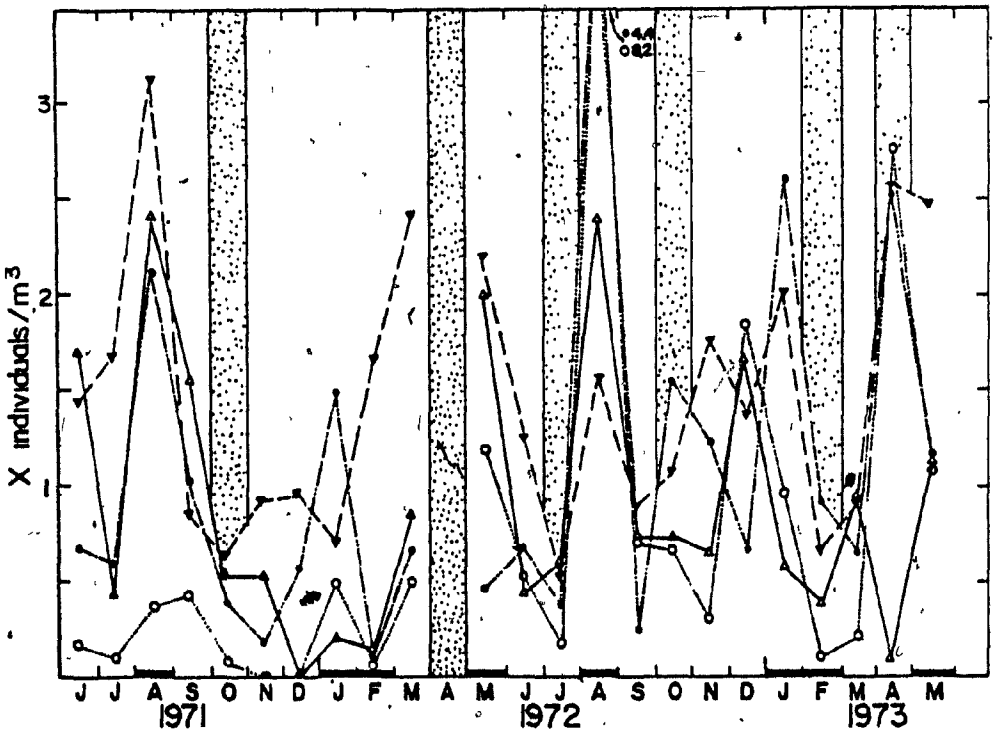
One of the first zooplankton studies near Barbados was conducted by Lewis and Fish (1969) between 1958 and 1960. They recorded great month to month fluctuations in surface zooplankton, with no apparent seasonality. Their data suggested to them an irregularity of distribution associated with variable hydrographic conditions rather than seasonal changes in production. In this connection, they specifically mentioned the surface dwelling forms such as the siphonophore Abylopsis eschscholtzii. Abylopsis appeared with a fairly regular 3 month variation (see Figure 2.18) which is out of phase with the phytoplankton 'cycle' described by Steven et al. (1970) and this study. Siphonophores and medusae are more abundant in oceanic, more saline North Equatorial waters than in the neritic freshened Guiana Current (Urosa and Rao, 1974), and thus the variations of Abylopsis standing stocks recorded by Lewis and Fish (1969) support the hypothesis proposed here regarding alternation of water masses. Their data also include information on fish larvae which

Figure 2.18 Temporal variations of Ablyopsis eschscoltzii (a surface dwelling siphophore ---) and fish larvae (——) abundance in night plankton tows taken off Barbados during 1958-1960 (from Lewis and Fish, 1969).

Figure 2.19 Temporal variations of the abundance (monthly means of weekly tows) of four species of euthecosomatous pteropods in 0-400 m oblique plankton tows off Barbados during 1971-1973 (Wells, 1974). Stippled bands indicate months of phytoplankton maxima recorded by Sander (1976) at a near shore station also sampled during this time. Black bars along the abscissa represent months of Trichodesmium and/or phytoplankton maxima during 1968-1970 (Steven et al., 1970) and 1974-1976 (this study).

- ▲ Spiratella inflata x 2 x 10^3 individuals/m^3
- △ S. lesueuri x 10 individuals /m^3
- ● Creseis virgula conica x 10^3 individuals/m^3
- o C. v. virgula x 10^2 individuals/m^3


number per 50 cc sample
60
40
20
S O N D J F M A M J J A S O N D J F M A M J J A S
1958
1959
1960


X individuals/m³
3
2
1
J J A S O N D J F M A M J J A S O N D J F M A M
1971
1972
1973

indicates that this group fluctuated more or less out of phase with Abylopsis (see Figure 2.18).

A more intensive study of a smaller group of zooplankton, the euthecosomatous pteropods, was carried out in 1971-73 by Wells (1974). These herbivorous holoplanktonic molluscs, while they constitute an insignificant fraction of the Barbados zooplankton (Sander, 1971) are often used as water mass indicators (Myers, 1969; Chen and Hillman, 1970), and Wells' data are therefore particularly interesting here. The temporal variations of four species recorded by Wells have been re-plotted in Figure 2.19 to illustrate the remarkable agreement between members of the group and their periodic nature.

There are unfortunately no coincident data for phytoplankton or salinity for this study, but Wells did subjectively note an inverse correlation between Trichodesmium and the pteropods. Closer examination of Sander's (1976) inshore phytoplankton data shows that the phytoplankton maxima were early during 1972. Pteropods represent oceanic offshore waters (Björnberg, 1971) and thus Wells' data provide a clear indication of alternations of two water masses with the same period as already established for the Trichodesmium and phytoplankton cycles.

In a recent publication considering the seasonality of the pteropods at Barbados, Wells (1976) mentions the two water types but, like most authors to date, only considers salinity in absolute terms; the low salinity surface waters of summer and the higher salinity waters in winter. The slight changes of surface salinity which signal the arrival of a new and different water mass can probably also be related to arrival of a new pteropod population in a fashion similar to that described earlier for Trichodesmium (apparently in the reverse sense).

Wells (1976) suggested that the reason pteropods were less abundant during Trichodesmium 'blooms' might be that the blue-green depleted

the nutrient levels in the euphotic zone, thereby excluding the other phytoplankton on which pteropods feed. In certain circumstances, such as in true Trichodesmium blooms or red tides observed elsewhere (Qasim, 1970), other phytoplankton may indeed be scarce. If this is indeed a result of exclusion by the blue-green, there is no evidence of such competition at Barbados. As has been shown here, diatoms and other phytoplankton are more abundant when Trichodesmium is present in greater numbers, not less so. The fact that Trichodesmium is unable to efficiently assimilate combined inorganic nitrogen also diminishes the possibility of it excluding other oceanic phytoplankton in this manner. A much more plausible explanation lies in the fact that two water masses with different histories are being sampled alternately - one with abundant Trichodesmium, the other with abundant pteropods.

Steven (1971) pointed out a very rough 'coupling' between fluctuations of total chlorophyll (integrated 0-100 m) and zooplankton from 0-400 m oblique tows in the first half of the 1968-1970 study, but this relation was less visible in later data (Steven et al., 1970). It seemed likely to Steven and Glombitza (1972) that the oscillations of the system were controlled biologically. They suggested the key factor might be the generation time of one or more important species of zooplankton, and therefore the grazing pressure on the phytoplankton, or the rate of regeneration of plant nutrients.

Moore and Sander (1976, 1977), and Sander and Moore (in press) have now studied the zooplankton gathered during the 1968-1970 study in greater detail and have examined the abundance and temporal variations of individual species. They found no consistent relation between the phytoplankton and the major groups of the zooplankton. Like most other authors, they conclude that "hydrographic factors are the most important factors controlling temporal variation", since very large zooplankton populations appeared and disappeared at short intervals. They detected no seasonal variation in abundance or breeding of the group, or of any

individual species of the copepods, and observed that "reproductive activities of various species lack synchronization and seasonal regularity. For most species, breeding appears to take place sporadically." Stated another way, this could be 'most species arrive only sporadically at Barbados in breeding condition', since it is fairly obvious that the same water mass is rarely, if ever, sampled twice at the offshore station. Presumably conditions at some time in the past history of the water mass, and factors such as vertical migrations, predation and food supply, determine the zooplankton population and breeding condition observed when the water mass is near Barbados. The observation by Calef and Grice (1967) of large actively growing populations of a neritic cladoceran and mysid far off the coast of South America north of Cape Orange is a case in point. Calef and Grice regarded these populations as residents of an originally neritic water mass which had been carried offshore.

2.4.2.3 Summary of biological evidence

It is quite apparent that the largest fluctuations of surface plankton, both phytoplankton and zooplankton, around Barbados are related to the continuously changing water masses. While there are admittedly other factors operating inshore, even in this region the rhythmical appearance of large populations of phytoplankton is almost certainly controlled by water movements.

It has been shown here that there is a loose inverse relationship between the salinity of the surface layer and phytoplankton abundance, not an absolute relation but one in which departures from the running mean signal more abundant phytoplankton. The 1968-1970 data (Steven et al., 1970) further indicated that this was water with high silicate concentration, therefore water diluted by South American rivers.

Semiquantitative observations of the Barbados plankton during 1974-76 revealed that Trichodesmium did not appear alone in the 'blooms', but in concert with large numbers of other phytoplankton, principally diatoms of the genera Chaetocerus, Nitzschia and Rhizosolenia. Examination of the late Dr. D.M. Steven's unpublished data for the 1968-1970 study confirmed this coincident oscillation of the other phytoplankton and showed that diatoms contributed between 50 and 75% of the 'other phytoplankton' numbers during 'blooms'. Dinoflagellates were the most common group during the periods between 'blooms'. In the inshore regions of the southwest coast, rhythmical increases in cell numbers and chlorophyll concentrations appear with the same periodicity as offshore, and all of the variations in surface plankton are closely related to passage of differing water masses, the best label of which seems to be salinity. Phytoplankton standing crops in the region of weak and stagnant currents off the northwest coast are more variable. Some of the zooplankton data gathered from serial stations by other workers also show rhythmical oscillations, but the vertical migrations of many zooplankton and the longer generation times will mean that most members of this group show apparently erratic fluctuations.

All of the biological evidence seems to point towards hydrological control of the Trichodesmium (and other plankton) temporal variations. The fact that large Trichodesmium standing crops arrive at Barbados in slightly fresher surface waters with higher silicate concentrations suggests that the water masses have been influenced by riverine discharge from South America. Any attempt to identify the factors determining the timing of events at Barbados must therefore begin with a thorough review of the oceanography of the area, particularly of the Guiana Current.

2.4.3. Regional oceanography

2.4.3.1 A review of the oceanography of the western tropical Atlantic to 1975

The picture of water movements in the western tropical Atlantic presented by most textbooks (Sverdrup et al., 1947; Neumann and Pierson, 1966) is a very simple one. Until very recently, little information was available other than for ship drift, drift bottle studies and distribution of physical properties such as temperature, salinity and oxygen.

The general set of surface ocean currents in the region is from east southeast to west northwest (see small arrows in Figures 2.22 and 2.24 for example), and these movements are driven largely by the zonal winds. The northeast trade-winds blow constantly from the northeast and east over most of the area at velocities of 5-10 m/sec during the first half of the year. During the period of strong winds the Guiana Current reaches velocities of up to 55 km/day (see Figure 2.28). As summer comes to the southern hemisphere and the large high pressure cell over the South Atlantic moves north, the Intertropical Convergence Zone (the zone of weak and variable winds known as the doldrums where the northeast and southeast trades meet) also moves north. The effect of this in the western tropical Atlantic is that the winds in the southeastern part of the region near Cape Orange and the Amazon estuary become weak and variable after June. As the southeast trades are felt north of the equator, the winds become southeasterly or southerly and the surface waters, which had been moving northwesterly in the first half of the year, are directed north and east. This recurving of the surface current is discussed later in Section 3.3.2.3 in relation to events at Barbados. In the western part of the region the southeast trades have little effect, but the general decrease in wind speed causes a decrease in surface ocean currents to around 25-35 km/day.

The rainy season over the oceanic tropical Atlantic and the vast inland regions of Amazonia occurs early in the year, and the ocean receives very large inputs of fresh water during the first half of the year. The surface waters of the region close to the South American coast receive fresh riverine discharge throughout the year, but the massive discharge of the Amazon, which reaches its maximum in May and June, completely overshadows contributions by other smaller rivers (J.G. de Amorim Coelho, pers. comm.*).

The low density, turbid water is directed northward along the Brazilian coast by the trade winds and becomes entrained in the fast flowing Guiana Current (Gibbs, 1970). Considerable mixing takes place as the water moves northwestward, but the mass maintains its low salinity signature as far as Puerto Rico and Jamaica (Froelich and Atwood, 1976).

Not all of this relatively fresher water is retained along the Guiana coast, however, since a very large region of the western tropical Atlantic experiences decreasing salinities during the summer. Several authors have studied 'pools' of fresher water north of Cape Orange which apparently have broken off the main Guiana Current and are surrounded by surface waters of greater salinity (Ryther et al., 1967; Metcalf, 1969; and others). These 'lenses' of brackish water have been shown to possess greater quantities of dissolved silicate than the surrounding ocean and have thus been considered to be of riverine origin. The inverse relationship between surface salinity and silicate which Steven and Brooks (1972) demonstrated for Barbados waters can be seen over very large regions of the western tropical Atlantic, and Froelich and Atwood (1976) have by this means calculated that the Amazon contributes more than 65% of the total freshwater input to the area.

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* J.G. de Amorim Coelho, DNAEE, Ministerio das Minas e Energia, Brazilia, Brazil.

Beers et al. (1965), Steven et al.(1970) and Steven and Brooks (1972) have all remarked on the complex nature of the fluctuations of sea surface salinity at Barbados, noting that more than one low salinity, high silicate water mass appears there each year. Indeed, the last two papers concluded that at least three reasonably distinct pools of riverine waters invaded the Barbados region during both 1968 and 1969.

The Caribbean Sea receives the majority of its water through the channels at the south end of the Antilles Arc , and since the area west of the island chain is ultimately the beginning of the Gulf Stream system there has been considerable interest in the currents of the region. It is, however, a massive area and synoptic data have been impossible to obtain until very recently. There have therefore been several attempts at calculating geostrophic currents from time-averaged historical data (Glombitza, 1971; Mazeika, 1973; Ortega et al., 1976). All of these studies have presented similar pictures showing a very complex situation of eddies and counter eddies, of flows as often easterly as westerly. Mazeika (1973) regarded this as evidence of water flowing from the east piling up against the Antilles and washing back to the east.

Brucks (1971) combined a study of thermocline topography and release of drift bottles to demonstrate a northerly flow along the Antilles during February and August 1970 which also was considerably different from the general conception of the flow at that time. The picture presented by Wüst (1964) and confirmed by direct current measurements by Johannessen (1968) near Barbados and Trinidad and by Stalcup and Metcalf (1972) in the Grenada Passage, showed that a major part of the surface water crossing the Caribbean enters from the Atlantic, flowing westerly through the southern passages.

A considerable amount of physical oceanographic work has been carried out by Venezuelan scientists in the past ten years; and Fukuoka (1971) has presented further evidence of the complexities of circulation in the area. His quasisynoptic temperature and oxygen data showed large cyclonic and anticyclonic gyres under the core of the Guiana Current during August 1968 and April 1970. He interpreted the data to show stationary meanders in the current caused largely by bottom topography.

Much of this recent evidence depicting complex circulation patterns is difficult to reconcile with the analyses by Wüst (1964) using the core method, drift bottle returns, and direct measurements (Michel and Foyo, 1976). Therefore, considerable effort has been directed here to resolve the inconsistencies apparent in the literature. The vertical and horizontal distribution of Trichodesmium (and a very large number of other plankton) at Barbados are greatly influenced by water movements.

2.4.3.2 Re-examination of historical hydrological data

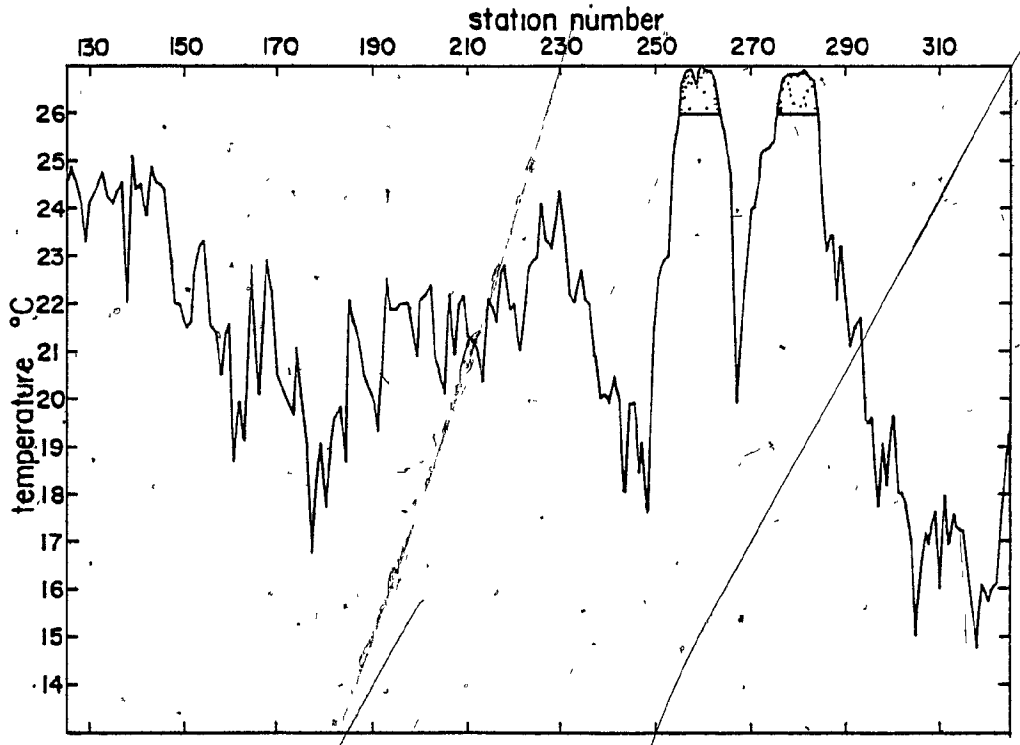
Examination of the archived bathythermograph data, provided by NODC for the area of the western tropical Atlantic to the east of Barbados, revealed little significant variation in thermocline topography north of 11°N. Strong convergence and divergence were not in evidence in this region in the cruise data surveyed* (see for example Figure 2.20.1) except within about 300-400 km of the South American coast in association with the Guiana Current, where large vertical

* NODC cruises 31-0433, 31-01277, 31-01604, 31-02508, 31-03462, 31-06113, 31-06121, 31-06124, 31-06125, 31-06127, 31-06130, 31-06132, 31-06186, 31-8070 and 31-21290.

Figure 2.20.1 Horizontal variation of temperature at 100 m in the western tropical Atlantic, January 25 to February 12, 1968 on a cruise by RV Crawford.

Figure 2.20.2 Variation of temperature at 100 m in the western tropical Atlantic, April 4 to April 7, 1968.

Station locations of RV Crawford cruise in Figures 2.20.1 and 2.20.2 are illustrated at right.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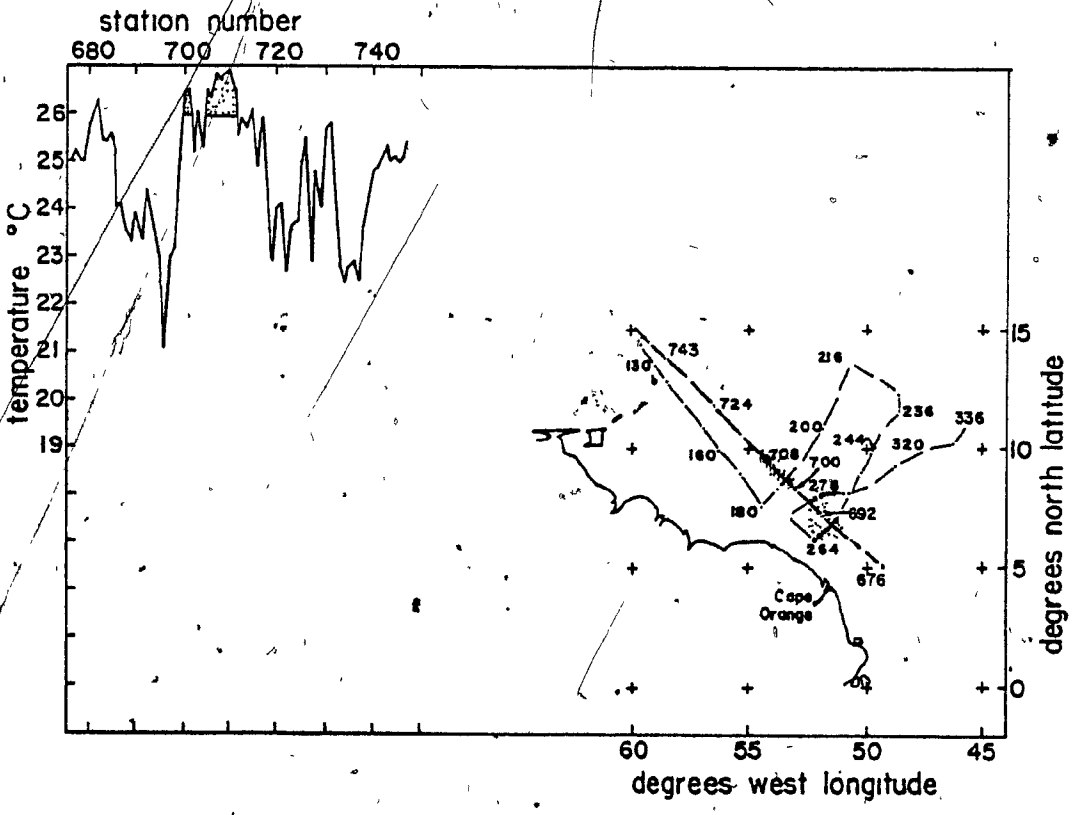
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200
244
320
160
708
700
273
180
692
264
676
Cape
Orange
15
10
5
0
degrees north latitude
60
55
50
45
degrees west longitude

fluctuations in the thermocline were observed over relatively short horizontal distances. Figure 2.20.1 (transects by R.V. Crawford in 1968) illustrates the presence of an anticyclonic eddy north of Cape Orange as indicated by the very rapid changes in temperature at 100 m. When the same area was crossed a second time two months later (Figure 2.20.2), the feature was displaced. A similar phenomenon has been recorded in this area by Calef and Grice (1967) and Metcalf (1968).

At about the same distance from the coast, but further west, complete hydrographic station data from several cruises were available (Figure 2.21-2.26). The temperatures at 150 m on two R.V. Lasalle cruises (July-August 1968 and April 1970) are plotted in Figures 2.21 and 2.23. In both figures the distribution of temperature suggests cyclonic circulation centered at about 56°W, 9°N and anticyclonic circulation to the east and west. The distribution of dissolved oxygen concentrations at the same depth (not shown) also corresponded, showing high values where cold oxygen-poor waters were upwelling (Fukuoka,1971). Figure 2.25 is a plot of NODC data for a third Lasalle cruise in the area in April 1972, which was not considered by Fukuoka. The pattern of convergence and divergence presented by these data is considerably different from those in Figures 2.21 and 2.23.

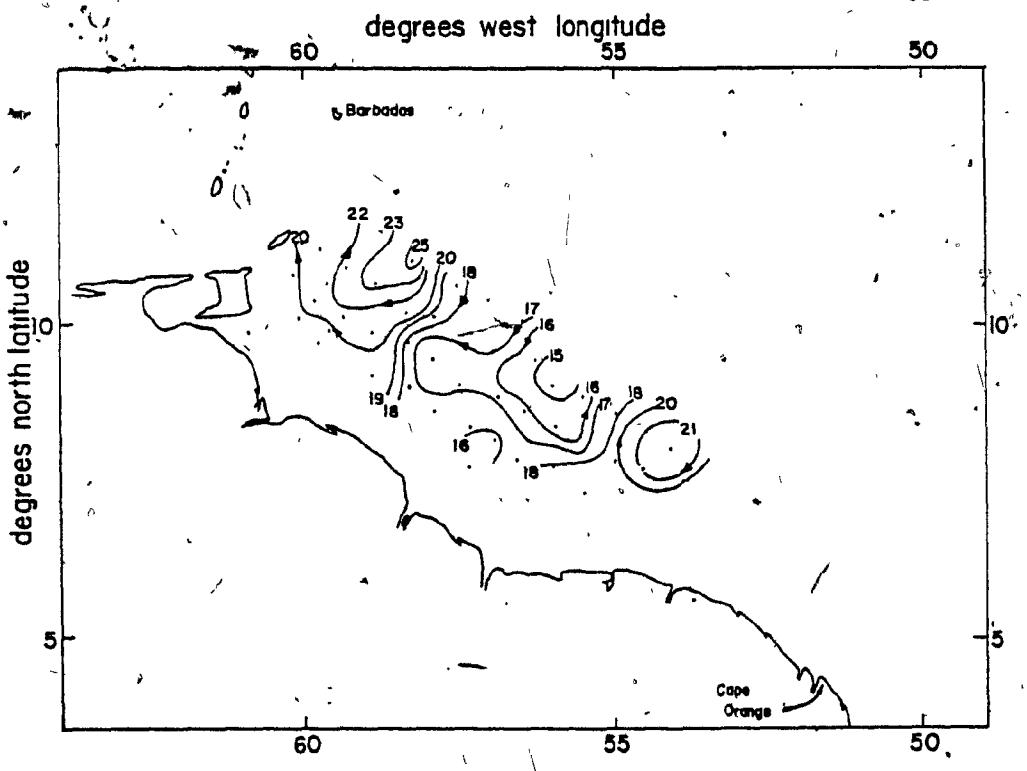
The only other available data concerning the distribution of temperature with depth in this area is a bathythermograph transect run more or less parallel to the coast in March 1958 by R.V. Westwind. Very large fluctuations of temperature, evident in Figure 2.27, are consistent with the presence of the meanders indicated above. The convergences and divergences are of approximately the same dimensions as those revealed in the Lasalle data, but they are in different locations. Note that the regular fluctuations continue into the Caribbean.

Figure 2.21 Temperature at 150 m off the Guiana coast, July 7 to August 17, 1968.

Arrows mark inferred circulation (after Fukuoka, 1971).

Figure 2.22 Surface salinity off the Guiana coast during July 7 to August 17, 1968 (from data presented by Urosa and Rao, 1974).

Arrows indicate mean August surface drift velocity and direction for 1° squares of latitude and longitude from NODC-SCUDS file.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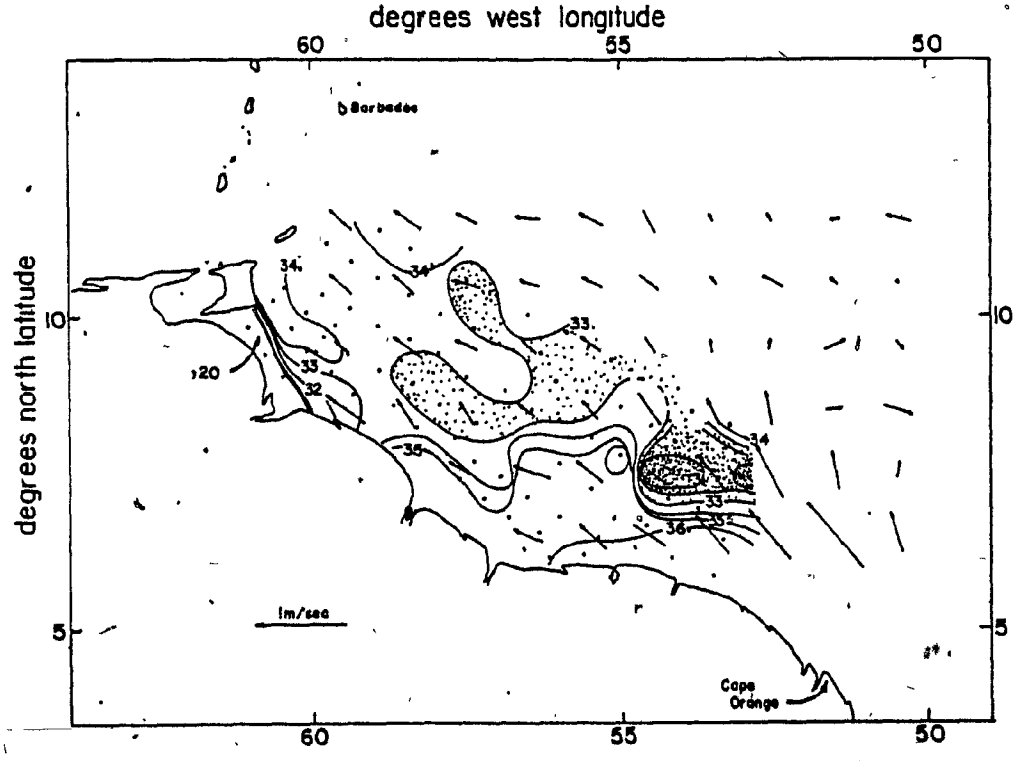
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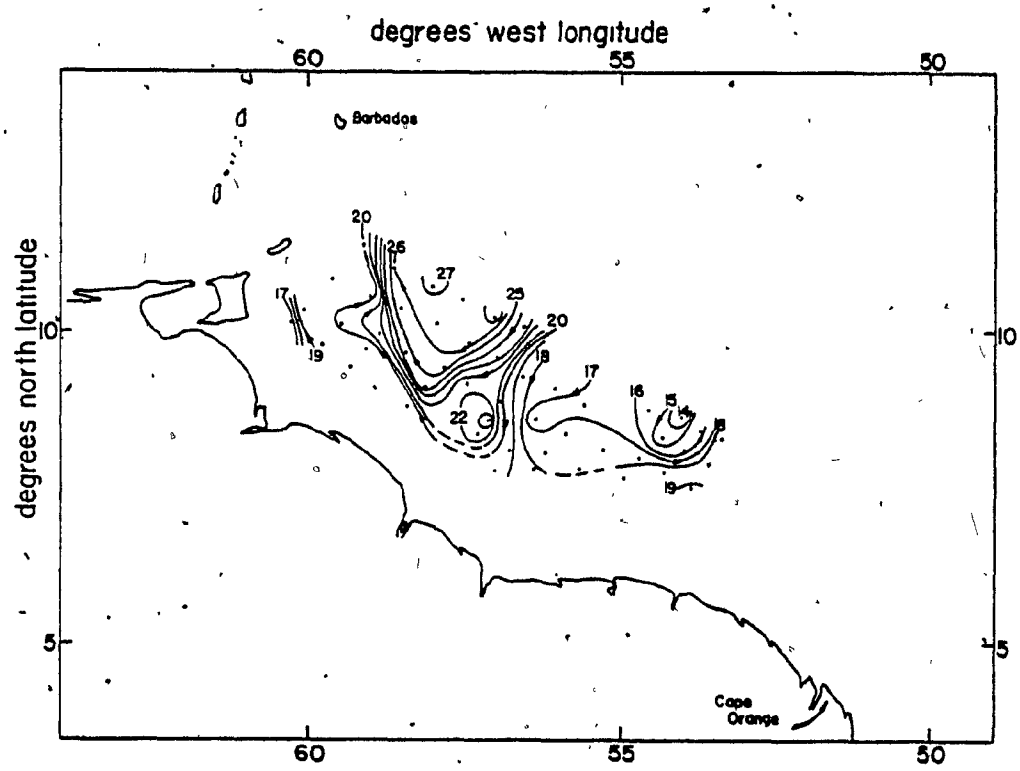
35
36
1m/sec
Cape
Orange

Figure 2.23 Temperature at 150 m off the Guiana coast, April 7-23, 1970.

Arrows mark inferred circulation (RV Lasalle cruise, NODC data).

Figure 2.24 Surface salinity off the Guiana coast during April 7-23, 1970 (from NODC data of a RV Lasalle cruise).

Large arrows indicate mean April surface drift velocity and direction for 1° squares of latitude and longitude from the NODC-SCUDS file. Small arrows join the noon positions of two parachute drogues tracked by RV Calamar, May 5-18, 1970 and May 21-30, 1971 (the more northerly of the two tracks) (Anon. 1971a, 1971b).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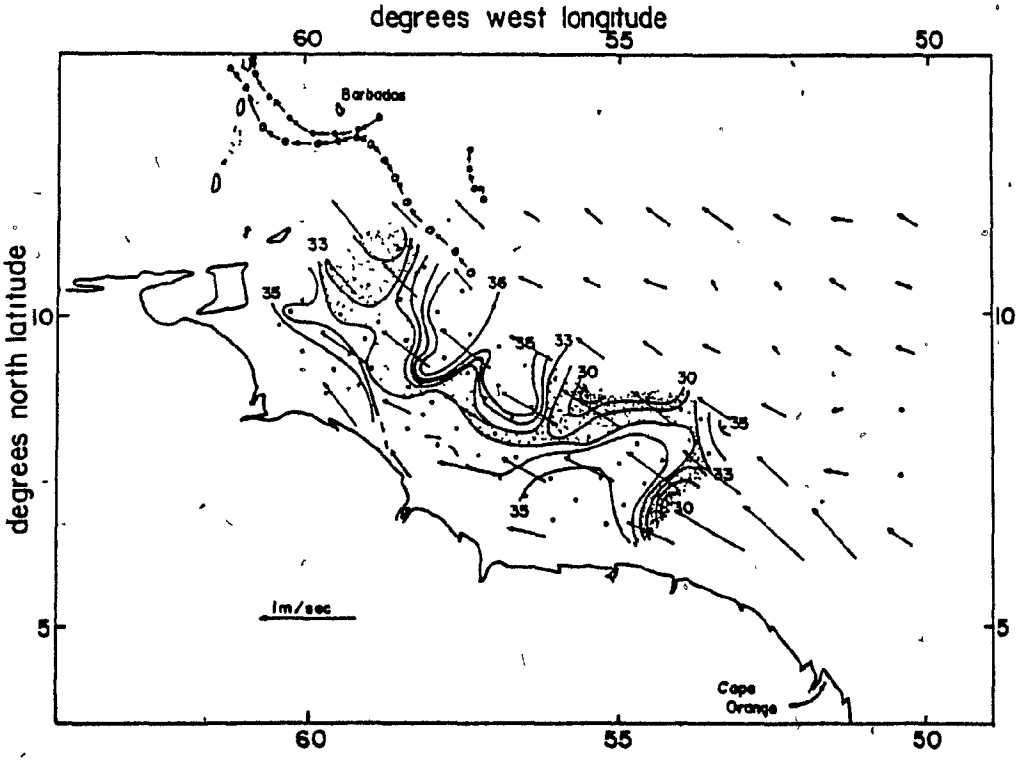
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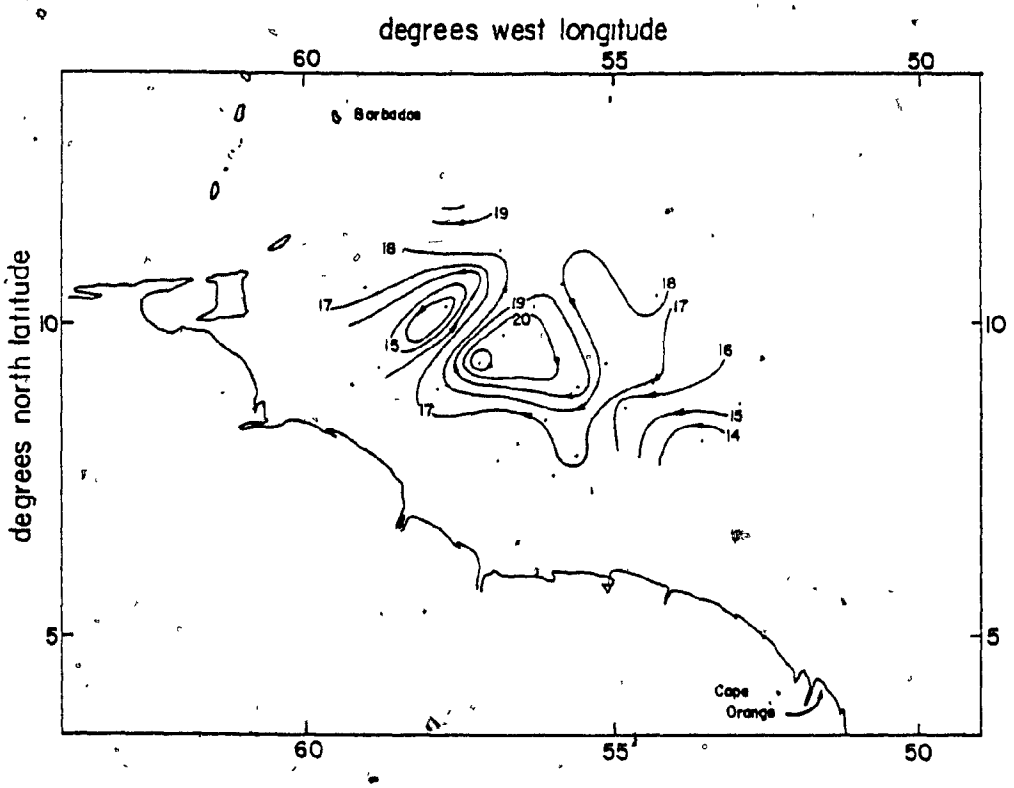
1m/sec
degrees north latitude
10
5
Cape
Orange

Figure 2.25 Temperature at 150 m off the Guiana coast, April 15-28, 1972.

Arrows mark inferred circulation (RV Lasalle cruise, NODC data).

Figure 2.26 Surface salinity off the Guiana coast during April 15-28, 1972 (from NODC data of a RV Lasalle cruise).

Large arrows indicate mean April surface drift velocity and direction for 1^{o} squares of latitude and longitude from the NODC-SCUDS file. Small arrows join the noon positions of two parachute drogues tracked by RV Calamar May 5-18, 1970 and May 21-30, 1971 (the more northerly of the two tracks (Anon. 1971a, 1971b).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Cape
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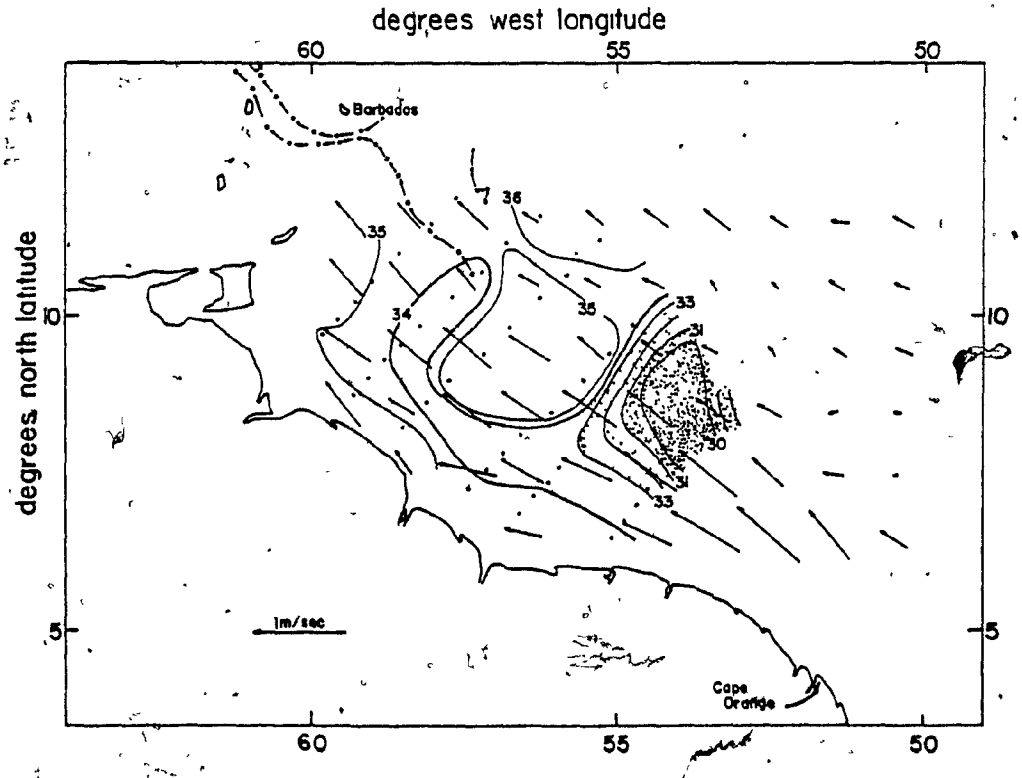
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degrees north latitude
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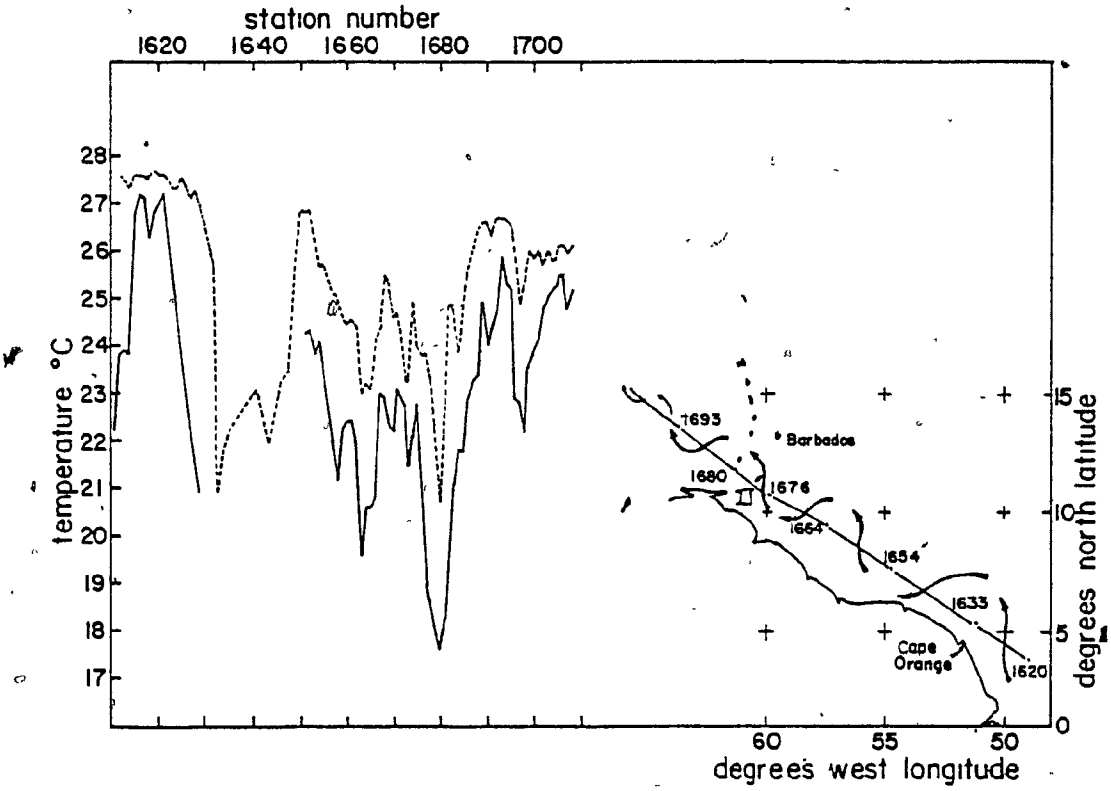
Cape
Orange

Figure 2.27 Horizontal variation of temperature at depths at 70 m (---) and 100 m (——) along the Guiana coast, in March 1958 (RV Westwind cruise, NODC data).

Arrows indicate inferred circulation.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1693
Barbados
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1676
1664
1654
1633
Cape Orange
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degrees north latitude
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50
degrees west longitude

Surface salinity data for the two April Lasalle cruises, and the mean monthly surface drift for this month as provided by the NODC-SCUDS file, are illustrated in Figures 2.24 and 2.26. While the mean monthly drift is towards the northwest, the quasisynoptic salinity data clearly show the low salinity tongue closely following the meanders in the subsurface current. Under the influence of westerly winds the surface layer, which is separated from the more dense water masses below it by a sharp discontinuity, can be expected to be driven offshore as the current turns at the north end of the meanders. The lobes thus formed are partly visible in both figures, and the apparently isolated pool at 56°W, 12°N has probably been driven off the lobe at 54°W.

Also plotted on Figures 2.24 and 2.26 are the tracks of two parachute drogues followed by the FAO-UNDP fisheries research vessel Calamar (Anon., 1971). Both drogues were released in May at locations very near the lobe at 58°W, and their paths indicate that water in the position of the lobe can and does travel to Barbados in a curving path consistent with the shape of the meandering current.

The surface salinity distribution over the area in August 1968 is shown in Figure 2.22, from data presented by Urosa and Rao (1974). Comparison with the pattern of temperature at 150 m (Fukuoka, 1971) shows that the low salinity waters follow the meandering subsurface current rather closely. While the absolute value of the salinities is about the same as in April, the broader plume and more homogeneous conditions are probably reflections of the slower surface currents and greater mixing at this time.

No-one has pointed out the control of surface salinity in this region by the subsurface meanders, but Metcalf (1968), considering the area near Cape Orange, stated that the Amazon outflow was probably "associated in its position and movements with the subsurface current

structure rather than the local wind pattern only". It is apparent that this is the case along the coast of the Guianas also. Most authors to date (Ryther et al., 1967; Steven and Brooks, 1972; Mazeika, 1973; and others) have considered that the fresh waters of Amazon origin leave the coast at Cape Orange and travel north and then west to Barbados. It is evident from these data that at least part of this low salinity surface water is carried back along the coast of the Guianas before it is brought to Barbados.

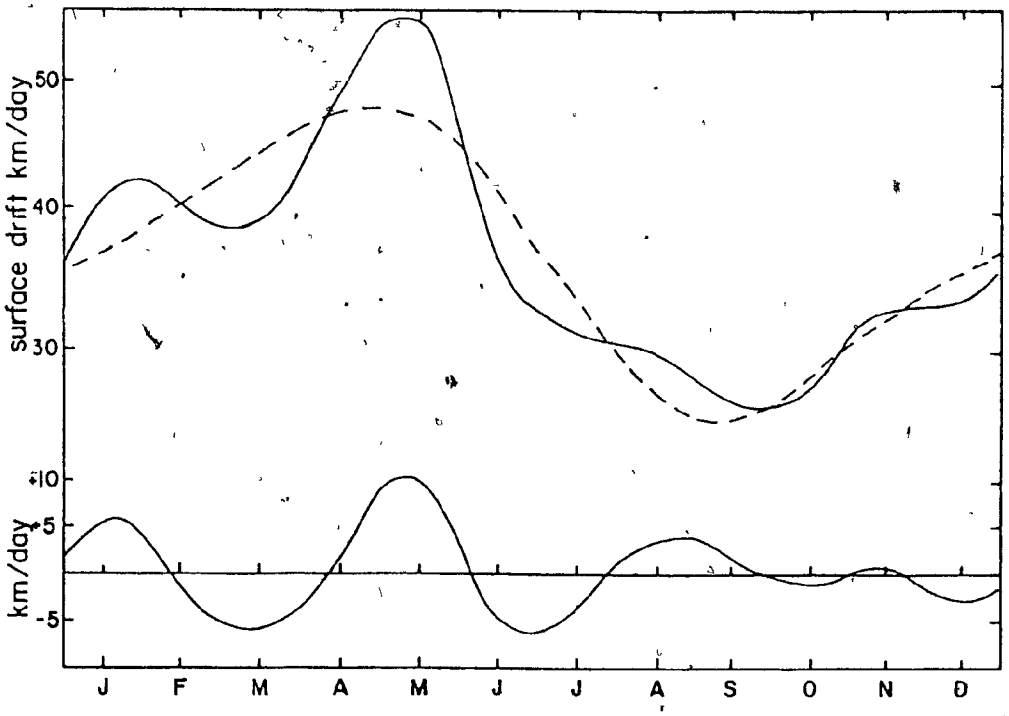
Fukuoka (1971) was the first to show that the Guiana Current meandered, but the data available to him at the time suggested the current pattern was stationary. Consequently, he considered the meanders were evidence of stationary Rossby waves, since the wavelength corresponded to that predicted by classical theory when constant current velocity was assumed. As pointed out above, however, other data not analyzed by Fukuoka suggest that the meanders must move, since the alternate convergences and divergences are in considerably different locations in different months. In recent years, reports of open ocean eddies have become increasingly common (cf. Phillips, 1966; Beckerle, 1972, 1976; Berstein and White, 1974; Gill, 1975; Swallow, 1976; Kerr, 1977; and others), and now they are sometimes likened to atmospheric weather systems, mesoscale systems which derive their energy from the larger mean flow (McWilliams, 1976). Theory predicts baroclinic-barotropic Rossby waves will have wavelengths of 500 to 600 km depending upon latitude and a mean lateral movement of around 4 cm/sec to the west (Longuet-Higgins, 1968; Rossby, 1937). The phenomenon most commonly reported - alternating convergence and divergence as indicated by thermocline topography and sound speed measurements - have now been observed in almost all parts of the world ocean. Most of the major ocean currents (the Gulf Stream, Kuroshio, Antarctic Circumpolar and West Australia Currents) have recently been shown to be complex systems of migrating meanders (Swallow, 1976; Kerr, 1977). Kerr concludes that meandering and ring formation are inevitable wherever narrow swift

currents exist. As these features usually have similar dimensions and movement to the planetary waves described by theory, they are most often regarded as evidence of Rossby waves.

Bernstein and White (1974) have shown that oceanic eddies near Hawaii are wavelike in nature and have a wavelength and phase velocity giving them a characteristic period of around 3 months. Beckerle (1972, 1975) has found features of comparable dimensions in the area north of the Bahamas, and it seems possible therefore that the Guiana Current meanders are also planetary waves. It is a simple matter to measure their wavelength (500 to 600 km), but the data available do not allow calculation of reliable phase velocity or period because of the relatively long time the grids of stations took to complete (2-3 weeks) and the fact that the data are from different years. If one can assume the meanders' positions are similar in the same month of every year, and the 2-3 week sampling time 'averaged' the position for the month, crude estimates may be possible. The difference between the March and April positions is about 1/3 to 1/2 the wavelength, making the period 2-3 months. The corresponding difference between April and August is about 1/2 (or 1-1/2) wavelengths, and the period in this case would be either 8 months or 2-2/3 months (more likely the latter since this agrees with the March-April calculations).

There is also a hint of a similar periodicity in the velocity of the Guiana Current as calculated by Fuglister (1951) from mean monthly surface current data in the U.S. Navy Hydrographic Office (1947) Atlas of surface currents, North Atlantic Ocean. These monthly means, which are plotted by 1° squares in the Atlas, were averaged for an area in the core of the current; a plot of Fuglister's curve is shown in Figure 2.28. When the annual and semi-annual components are removed, this current can be seen to fluctuate with a three month period, which is consistent with the hypothesis that current meanders move westward with a period of three months. When surface Ekman drift

Figure 2.28 Temporal variations of surface drift in the Guiana Current (——), the calculated annual and semi-annual components (---) and the residual calculated by difference (below) (after Fuglister, 1951).


surface drift km/day
50
40
30
+10
+5
km/day
-5
J
F
M
A
M
J
J
A
S
O
N
D

(directed northwest) and the subsurface meander are both directed offshore, the surface currents measured in that area should be greater than when the subsurface current is turned back towards the continent. For any one area then, one should expect positive and negative deviations from the mean current as meanders pass underneath.

Passage of meanders along the coast should also be expected to result in variation of the strength and position of coastal upwelling as divergences pass. The charts of oxygen anomalies for the Atlantic Ocean compiled by Mazeika (1968) do show considerable month to month fluctuations of the anomaly in the area to the west of Cape Orange. During much of the year the anomalies oscillate from positive (downwelling) to negative (upwelling).

Finally, there are other phenomena in the area with coincident periodicities. Fukuoka (1966) noted that the data for tidal height, water temperature, and air pressure along the north coast of Venezuela during 1961 to 1965 exhibited strong periodicities at 3, 4, 7 and 8 months and were significant at the one percent confidence level. Somewhat fewer data for water density and oxygen anomaly at one station suggested upwelling with about the same period. Fukuoka could offer no satisfactory explanation at the time, but it is possible in light of the evidence discussed above that, at least under certain circumstances (see Figure 2.27), the current may continue to meander after it has passed through the Antilles Arc . Such meandering can be expected to result in periodic upwelling similar to that in the region west of Cape Orange.

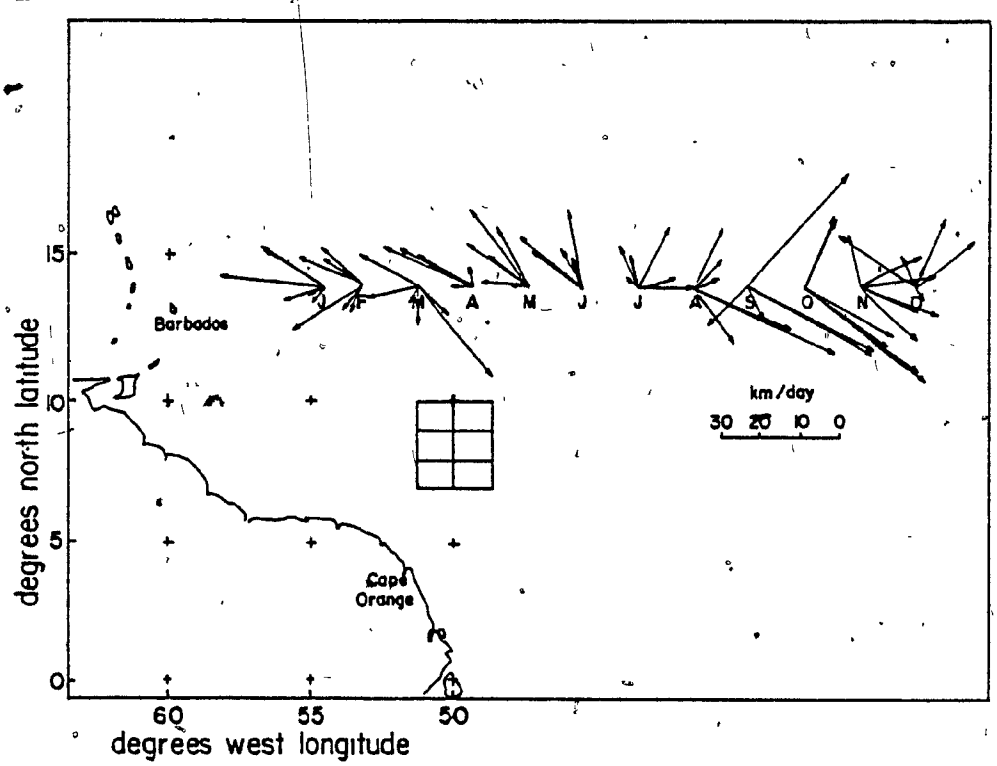
If these meanders do pass westward along the South American coast as is hypothesized here, Barbados will alternately receive more saline oceanic (North Equatorial) water and fresher, less dense Guiana Current water. As indicated in Figures 2.22 to 2.26, the Current possesses relatively sharp salinity boundaries. The very abrupt and

temporary changes in salinity and density visible during the first half of the year at serial stations off Barbados are consistent with the suggestion that the meanders move, and there is considerable biological evidence to confirm that distinctly different water masses pass Barbados at regular intervals during this time.

2.4.3.3 Annual seasonality

The question arises as to why this oscillating regime is not observed throughout the year. Most authors (Cochrane, 1965; Metcalf and Stalculp, 1967; Metcalf, 1968; Mazeika, 1973) have considered the recurving of the Guiana Current north of Cape Orange to be a more or less permanent feature, and have explained the production of lobes of low salinity surface waters in this region as the westward limb of a stationary eddy to the northeast of the Cape. The United States Navy Oceanographic Atlas (1947) and data from the NODC-SCUDS file show, however, that the Guiana Current does not recurve throughout the entire year with the same strength. The arrows in Figure 2.29 indicating the mean monthly direction and velocity in six 1^{o} squares north of Cape Orange clearly demonstrate that recurving only occurs between July and December. This change in current speed and direction can be directly related to changes in zonal winds mentioned earlier (Section 2.3.1.7). In the area north of Cape Orange the winds are generally northeasterly from January until July, when they weaken and gradually become easterly and southeasterly (Meteorological Office of the British Air Ministry, 1948). Under such changing winds the seasonal changes in current direction are to be expected. The low density surface waters are very responsive to wind stress (Herrara and Snooks, 1969; Mazeika, 1973), and Mazeika has shown that at least during the months of July and August these surface waters travel about 40^{o} to the right of the mean wind direction.

Figure 2.29 Temporal variations of mean monthly surface drift velocity and direction in six 1^{o} squares of latitude and longitude north of Cape Orange (data from U.S. Navy Hydrographic Office (1947) Atlas of surface currents).


15
10
5
0
degrees north latitude
Barbados
Cape Orange
J F M A M J J A S O N D
km/day
30 20 10 0
60
55
50
degrees west longitude

The seasonal recurving of the current in the late summer and fall, but not before, is consistent with the surface salinity data from Barbados. As already pointed out, the decline of salinity during the first half of the year is erratic and is associated with the arrival at Barbados of fresher waters of South American origin. The very steady increase in surface salinities beginning in August is directly related to a series of events, including reduction of the Amazon discharge and decrease in wind speeds everywhere over the western tropical Atlantic. Under the influence of more southerly winds, much of the low salinity waters are carried north and east off Cape Orange. In the west, the Guiana Current slows significantly (Figure 2.28). The consequent reduction of its influence and the movement of the more saline oceanic waters from the North Equatorial Current into the Barbados area are responsible for the changes of surface salinity observed during this time.

2.4.4. Conclusions regarding the cyclical phenomenon and the occurrence of Trichodesmium off Barbados.

Physical and hydrographic data from a variety of sources indicate that the wavelike nature of the Guiana Current and the alternate appearance of these waters with higher salinity North Equatorial waters are responsible for the observed cyclical fluctuations of Trichodesmium standing stock off Barbados. It has also been demonstrated here that this alternation of water types is related to marked in-phase variations of the stocks of other phytoplankton. Diatoms are much more abundant in the surface waters with slightly lower salinity and greater Trichodesmium numbers, while dinoflagellates and coccolithophorids are most common in the intervening periods. This oscillatory variation of the phytoplankton has been detected in five other separate studies at Barbados, and the phenomenon appears to be one of the most

important mechanisms determining the phytoplankton standing crop and species composition off Barbados, both in the oceanic waters offshore and in the region close to shore. There is also evidence that the seasonal distribution of some zooplankton is controlled in this manner.

By the reasoning presented here, the periodic phytoplankton 'blooms' off Barbados are pools of plankton-rich water carried north from the productive regions off the Guiana Shelf. This area benefits from fertilization through remineralization of terrestrial detritus and dissolved organic compounds brought down by the Amazon River and from local upwelling (Cadée, 1975) and supports prolific diatom growth. As waters of the Guiana Current move away from the shelf and these sources of nutrients, their large phytoplankton populations will rapidly strip the water of dissolved nutrients. Because the surface layers are essentially isolated from the deeper waters, little vertical exchange of nutrients can be expected, and by the time the pools reach Barbados (three to six weeks), compounds such as nitrate and orthophosphate will be nearly undetectable (cf. Steven et al., 1970). This explains why previous authors have found no relation between surface layer nutrient concentrations and phytoplankton standing crop off Barbados.

The onset of oligotrophy does not necessarily bring about an immediate decrease in phytoplankton numbers, however. Most phytoplankton are capable of storing carbon, nitrogen and phosphorus, and as Dodson and Thomas (1977) have demonstrated, Chaetoceros affinis and Gymnodinium splendens can survive more than 65 days of oligotrophy after simulated upwelling without significant decreases in population densities. The ability of Trichodesmium to survive oligotrophy will be even greater because of its ability to fix molecular nitrogen.

The seasonal distribution of Trichodesmium in the western tropical Atlantic and the peculiarities of its abundance at Barbados are also better understood in light of the hydrology of the region.

The alga is common over the tropical Atlantic extending north to about 40°N by late summer (Dugdale et al., 1961). Its population densities in the Sargasso Sea during August to October are about the same as in the Caribbean during February and March (Carpenter and Price, 1977), and at Barbados in the 'nonbloom' phase. During the first half of the year, drift across the western tropical Atlantic is generally northwestward. The Guiana and Caribbean Currents strengthen, and low salinity waters along the Guiana coast spread across the Caribbean during the summer (Wust, 1964) carrying plankton from the Atlantic into that sea.

At Barbados the large increases in phytoplankton standing crop appear closely related to fluctuations in the horizontal extent of the Guiana Current. It seems likely therefore that the large populations of Trichodesmium observed by Carpenter and Price (1977) in the eastern Caribbean in August 1974 are reflections of the transport from the Guiana shelf area. (The population densities observed by Carpenter and Price at 15 m were between 120 and 290 x 10^6 cells/m^3. This is very close to the densities of Trichodesmium blooms observed in Guiana water off Barbados - 1500 to 2800 mm fil/l or about 160 to 310 x 10^6 cells/m^3.). The observation by Goering et al. (1966) of a large Trichodesmium bloom in low salinity waters off Cape Orange in 1964, and small populations at nearby stations in high salinity water, lends further support to the hypothesis that the abundance of Trichodesmium in the western tropical Atlantic is related to the spread of low salinity surface waters across this region during the summer. What little quantitative information is available regarding the distribution of Trichodesmium in the Atlantic indicates that it is not found off the Amazon delta (Wood, 1966), nor in the area near Cape Orange (Dr. G.C. Cadée*, pers. comm.), but that it is found further offshore.

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* Dr. G.C. Cadée, Netherlands Institute for Sea Research, Texel, Netherlands.

Trichodesmium is known to exhibit very inefficient uptake of combined nitrogen for growth in oligotrophic regions (Wada et al., 1975; Carpenter et al., 1975) and therefore might be expected to thrive in nutrient rich waters. To a certain extent this is true, since it is very abundant all across the tropical Atlantic in the region of equatorial divergence (Lohmann, 1920; Hentschel, 1936; Zernova, 1975), around the periphery* of upwelling zones, such as off Isla Margarita (Margalef, 1971) and Columbia (Corredor, 1976) and in waters in the Caribbean and Gulf Stream rings with increased phosphate supply (Carpenter and Price, 1977). In the Indian Ocean, Jayraman (1970) has pointed out that Trichodesmium blooms occur near regions of upwelling; Sournia (1968) considers T. thiebautii a neritic species in this area. Like the situation at Barbados, the abundance of the alga off northern Madagascar is related to the appearance of low salinity surface waters. Whether this is due to the stability of such water masses or their original nutrient supply (the Guiana Current-Amazon River at Barbados) is difficult to judge from the data available. There was no consistent relationship between Trichodesmium standing stocks and stability during this study or from the 1968-70 data (Steven et al., 1970). In view of the fact that Trichodesmium is abundant in waters influenced by riverine waters, Fogg et al. (1973) consider it possible that nutrients required by the alga are derived from land runoff.

After August and the change of the wind and current regimes over the western tropical Atlantic, Trichodesmium and all of the diatomaceous phytoplankton is less abundant off Barbados. The re-curving of the currents off Cape Orange, the decrease in velocity of the Guiana Current, and the generally more westerly drift over the area, will mean that the water and phytoplankton arriving at Barbados are from the oceanic region east of the island. These waters have had

*It will be washed out of the upwelling areas because of its buoyancy.

no contact with coastal areas, upwelling or river runoff, and the phytoplankton standing crops are low - dominated by dinoflagellates and coccolithophorids. Trichodesmium is common but not abundant. In northern regions, the alga is rarely found after September or October (Cleve, 1960; Goering et al., 1966), coinciding with a sharp reduction in transport from further south and decreasing stratification of the water column in these regions at this time (Dugdale et al., 1961).

3 SOME CHARACTERISTICS OF PHOTOSYNTHESIS BY *TRICHODESMIUM*

3.1 Introduction

It very quickly becomes obvious when examining the phytoplankton collected off Barbados, and in many other parts of the tropical oceans, that *Trichodesmium* is important numerically. Calculations of the percent contribution to total cell numbers and chlorophyll *a* by *Trichodesmium* demonstrate that this alga is very often dominant.

When this study began in 1974, very little was known about the biology and physiology of the alga. Only one preliminary study of photosynthesis had been made (McLeod et al., 1962) and this was beset by problems of apparent extreme variation in the alga. The following is an account of a series of experiments conducted utilizing the ^{14}C technique to expand on this aspect of the alga's physiology.

3.2 Materials and methods

3.2.1 Experimental procedures

Measurements of *Trichodesmium* photosynthesis were made on isolated colonies essentially after the ^{14}C method of Steemann Nielsen (1952). Most plankton collections were made shortly after dawn from a small open boat approximately 3/4 km offshore, in water of 100 m depth. A few experiments were conducted on *Trichodesmium* collected further offshore.

All collections were made with a 1/2 meter diameter, No. 6 (0.24 mm mesh) plankton net, except those from below the surface. In these instances collections were with a Clarke-Bumpus opening and closing

net, or throttle nets lowered cod-end first. Immediately after completion of the tow, the plankton was transferred to a large container and diluted with surface sea water. Great care was taken to guard against light shock to the organisms. The covered container was immediately returned to the laboratory, where individual Trichodesmium colonies were removed with wide bore Pasteur pipettes. Isolated colonies were placed in freshly collected HA Millipore filtered seawater, and then transferred by pipette to a second container of filtered water to reduce possible transfer of zooplankton or other unassociated phytoplankton.

Washed colonies were placed in 125 ml pyrex bottles filled with HA Millipore filtered seawater from the corresponding depth, and 1.0 ml sterile solutions of $NaH^{14}CO_3$ in distilled water (New England Nuclear Corp.) buffered at pH 9 (activity 19.44 μcuries/ml) were then added by syringe to each bottle. Each empty ampoule was rinsed with water from the experimental bottle and the rinse added to the bottle to insure complete transfer of the label.

After inoculations, the bottles were stoppered, inverted gently two or three times to insure mixing of the label, and inserted into black nylon mesh bags (GM Manufacturing Co. Ltd.) which transmitted 1.8 ± 0.8%, 5.6 ± 0.4%, 17 ± 4%, and 56 ± 4% of the incident irradiation (I)*. Trichodesmium was also incubated in bottles without cover (100% I), and with a heavy black plastic wrapping (0% I). Bottles containing Millipore filtered seawater but no Trichodesmium were similarly incubated in most experiments as checks on adsorption and washing errors and any other form of contamination.

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* Transmittances were considerably different than those claimed by the manufacturer for new bags.

Except where noted otherwise, incubations were conducted under natural illumination, in a temperature controlled (27° ± 2°C) water bath on the roof of the laboratory. The bottles were laid on their sides, in a clear plastic tray under about 5-10 cm water and were thus protected from infrared irradiation. The bottles themselves absorbed strongly in the ultraviolet (96% absorbance at 360 nm). Most incubations began around 0800 hrs local time and continued for four hours. Immediately after incubation the bottles were covered and taken to the laboratory where photosynthesis was terminated by filtration of the bottle contents.

The in situ experiments were conducted offshore near the 8 km station utilizing filtered water and Trichodesmium collected from just below the surface, 25 and 50 m. Except for the fact that incubations were in situ, manipulations were similar to the other inshore experiments. Incubations were for 3-1/2 hrs, beginning at 1230 hrs. In these two experiments, photosynthesis was terminated by addition of formalin, and filtrations were made after return to shore.

In all cases, the whole contents of each bottle were filtered at negative pressures of less than 250 mm mercury, and rinsed with two 10 ml aliquots of filtered, unlabelled seawater. These rinses were then also filtered, serving to rinse inorganic dissolved label from the filter. After filtration, the filters were dried, examined, and rough notes made on the appearance of the colonies. The dried filters were then labelled, glued to aluminum planchettes with rubber cement and sent to Dr. J. Kalff, Biology Department, McGill University, for counting, using a thin window gas flow Nuclear-Chicago Geiger-Müller counter. All filters were counted for 5 minutes, or 10,000 counts.

Radioactivity on the filters not associated with Trichodesmium colonies was between 30 and 300 cpm, and this was always less than apparent dark uptake of label by Trichodesmium colonies. When this background activity was subtracted, dark fixation by Trichodesmium was

less than 5% of the corresponding Pmax in every experiment except two.

Where photosynthesis is presented in terms of µgm C/colony·hr production has been calculated in the following manner:

$$\mu gmC/colony \cdot hr = \frac{(L - D)\ W}{A \times H \times N}$$

where

L = counting rate (cpm) of light bottle containing Trichodesmium

D = counting rate (cpm) of dark bottle containing Trichodesmium

W = weight of available carbonate carbon in the bottle, assumed to be 25,000 µgm/l in seawater

A = ^{14}C (cpm) added to each bottle

(1 ml x 19.33 µcurie/ml x 2.22 x 10^6 $\frac{dpm}{\mu ci}$ x E = 15 x 10^6 cpm)

H = length of incubation, in hours (usually 4)

N = number of colonies per bottle (usually 3)

The factor accounting for differential uptake of ^{14}C and ^{12}C has not been applied since the assumption of constant carbonate alkalinity reduces the accuracy of the calculation by about 5% in these waters.

Apparent counter efficiency, represented in A above by E, was between 28 and 34% as calculated from dry standards of known activity. The accuracy of these calculations was checked by combusting precounted Trichodesmium and counting the liberated $^{14}CO_2$ by liquid scintillation. Scintillation counting agreed to within 2% of that calculated from the G.M. counter measurements.

Release of newly fixed carbon was measured according to the method of Watt (1966). The filtrate from each incubation bottle was acidified with concentrated HCl to below pH 2 and bubbled vigorously with air for 45 minutes to remove inorganic ^{14}C as carbon dioxide. One

half ml aliquots of the bubbled filtrate were then dried onto aluminum planchettes and sent to McGill University for counting. Release of dissolved material was also examined fluorometrically using a Turner model 110 fluorometer equipped with a 'blue' light source (Turner #110-853) high sensitivity door, primary filter Corning No. 7-60 and secondary filter Wratten No. 48. These filters were chosen according to excitation and emission fluorescence spectra given by Traganza (1969) for water from a Trichodesmium bloom. As the fluorophor was not identified the machine could not be calibrated in absolute terms. The machine was blanked against a black dummy cuvette and all data expressed in terms of arbitrary fluorescence units for 5 ml filtered aliquots of seawater. Deionized distilled water consistently gave low fluorescence throughout the period of this study.

Routine photosynthesis experiments were also conducted on colonies in which the gas vacuoles had been completely collapsed, in order to investigate the possibility that the vacuoles were providing protection for the photosynthetic apparatus. To collapse the gas vacuoles, colonies were subjected to increasing pressures of oxygen, using a Parr bomb calorimeter as a pressure chamber. Their complete collapse was verified microscopically.

3.2.2 Treatment of data

Studies of homogeneous cultures of organisms are relatively easy, but, as has been pointed out by Steemann Nielsen (1975), difficulties arise when one wishes to compare photosynthesis of natural phytoplankton populations, because of differences in biomass, cell number and chemical content (chlorophyll, for example) among populations. In colonial organisms such as Trichodesmium, each colony contains a variable number of dead and dying cells, and cells in a wide variety of

physiological states. Each colony can therefore be legitimately regarded as a separate population, and experimental variance can be expected to be higher than in studies involving homogeneous cultures in log-phase growth.

Photosynthetic rates are often normalized to carbon or chlorophyll content of the samples, and thus successful comparisons can usually be made between different populations or species. In this work there were, however, several difficulties with this means of normalizing the data: a) Trichodesmium colonies may often be 'contaminated' by large numbers of chlorophyll and carbon-containing organisms (see Section 5) which would bias estimates of Trichodesmium biomass; b) Trichodesmium possesses the phycobilin pigment phycoerythrin, which is thought to interfere with spectrophotometric and fluorometric measurement of chlorophyll (Saijo et al., 1969), and c) phycoerythrin, not chlorophyll, is considered by Shimura and Fujita (1975) to be the main photosynthetic pigment in Trichodesmium. If this is so, normalizing photosynthesis on a chlorophyll basis may be misleading.

In view of this very large variation in biomass and chemical content from colony to colony, the best normalization procedure would have been one which measured the actual Trichodesmium colonies tested, either on the filters, or before incubations began. The fragility of the colonies, however, dictated that incubations begin as soon as possible after their removal from the sea, with very little handling. Weighing the filters and colonies after the experiment was not possible because of the very low weight of the algae and the retention of salt by the filters. The carbon content of three colonies was also below the limits of detection by techniques available, and chlorophyll analyses were impossible because the filters had to be sent to Montreal to be counted. Where chlorophyll values are reported here, they are for colonies of size similar to those used in the experiments, and selected at the same time.

Incubations of larger number of Trichodesmium would have allowed normalization by one of these means, but trials indicated considerable autoinhibition when more than three colonies were incubated in one bottle (see Section 3.3.2). Three colonies per bottle was chosen as an experimental condition which allowed sufficient counts at lower irradiances and averaged out some variations due to colony size, or the presence of contaminants.

Experiments involving Trichodesmium must begin as soon as possible after their removal from the sea, as decline and death of the alga begins within a few hours. A crude division of the genus on the basis of colony morphology (radial or parallel colonies) allowed experiments to begin within an hour of collection where surface collections close to shore were made., Where studies were made of offshore populations (in situ experiments) or of the deeper-living 'shade' population, logistical difficulties were greater and the delay between collection and incubation was longer. For this reason, the study concentrated on the near-surface inshore populations (0-5 m). The variations of colony morphology and the relation of this to the taxonomy of the alga are discussed in Appendix A.1. While radial colonies were mostly T. thiebautii, and parallel colonies mostly T. hildenbrandtii, there was some overlap as illustrated in Figures A.1 and A. 2. The systematics of the genus is controversial but experience has suggested that colony morphology, while not a good taxonomic character, certainly had ecological significance (see Section 5). T. erythraeum was seldom present in large numbers at Barbados (Section 2.3.3.) and when it was, colonies adhered to the walls of any vessel containing them, thus making them difficult to manipulate. No data are presented here for this species.

As a result of the difficulties in normalization mentioned above, the data are presented here on a 'per colony' basis. At the beginning of the study, a subjective choice of a 'standard size colony' was made. In all succeeding experiments, considerable effort was made to select colonies of approximately equal size and gross appearance. Within each experiment the biomass in each bottle could be equalized fairly well, and the variability of C uptake rates from replicates were usually within about 20% (see Figure 3.2). Larger variations probably occurred between experiments because of changes in the physiological condition and nutrient status of the population in the sea between experiments.

Biomass determinations of 'standard' size colonies drawn from the same samples as experimental colonies, and performed according to the methods outlined in Section 2.2.4 are presented in Table 3.1 and allow rough calculation of assimilation number and comparison of these rates with other data.

Table 3.1. Size range and chlorophyll content of Trichodesmium colonies utilized in the photosynthesis experiments.

Colony form*	Total filament length mm ± SE (n)	chlorophyll a µgm ± SE (n)
'Standard' radial colonies	108 ± 11 (21)	0.013 ± .001 (24)
'Standard' parallel colonies	165 ± 15 (19)	0.018 ± .002 (23)

* Colony morphologies illustrated in Figure A.1.

There were also a number of possible sources of experimental error other than variations of biomass. These included loss of Trichodesmium during incubations through fragmentation, cell lysis or adsorption to walls of the bottle, uptake of radiocarbon by contaminating organisms, adsorption of the label by the polysaccharide mucilage present in some colonies, and loss of labelled ^{14}C during desiccation of the filters. In forty-eight of sixty-two measurements, however, replicates of particulate carbon uptake agreed to within ± 30%. Microscopic examination of the divergent pairs revealed considerable particulate material other than Trichodesmium on six of the filters having high activity. In one case this could have been contamination from the bottles, but in the others, particulate contamination of the ^{14}C ampoules themselves is suspected. (Fee (1975) and Platt and Irwin (1968) have also reported particulate contamination of ampoules from New England Nuclear Corporation.) The filters were not routinely fumed over concentrated HCl, but when filters with very high counting rates were, their activity dropped markedly indicating adsorption of inorganic ^{14}C had been a problem. The counting rates did not decrease to 'normal', however, and it is assumed that the particles on the filter had also absorbed the label internally. Fuming of filters containing Trichodesmium with normal counting rates did not show a decrease in activity, thus indicating that adsorption to the colony mucilage was not a serious problem.

3.2.3 Irradiance measurements

Meteorological data, including irradiance measurements for the days on which photosynthesis experiments were made, were provided by Mr. P. Roachford, Caribbean Meteorological Institute, Husbands, St. James, Barbados. Total irradiance in the 300-2000 μm range was measured by a Kipp and Zonen type pyranometer located at the Meteorological

Institute approximately 7 km from Bellairs Research Institute.

Irradiance in the Photosynthetically Active Range (PAR), that is, in the 400-700 μm range, is almost independent of atmospheric conditions and nearly constant at 0.50 ± 0.03 of the total irradiance (Monteith, 1972; Szeicz, 1974; Suckling, 1975). In this study, the pyranometer total irradiation measurements have been divided by two to convert them to PAR. All irradiance values discussed here are PAR unless noted otherwise.

A note is in order here concerning the multiplicity of units in the literature by which irradiance is measured. This confusion has resulted in errors in the literature, and has made comparison of the present data with those of other studies tedious. Published data have been recalculated using the rough conversion factors in Table 3.2. As these factors are approximate only, the comparisons are also.

Table 3.2. Conversion factors between photometric units (lux)† and radiometric units of light energy (ly/min)*.

Light source (1 lux)	ly/min (PAR)	Reference
Natural sunlight	6×10^{-6}	Strickland, 1958
Tungsten lights	8×10^{-6}	Vollenweider, 1969
Fluorescent lights	4×10^{-6}	Westlake, 1965

* 1 gm cal/cm^2 = 1 langley/min (ly/min)

† 1 lux = 0.0929 ft c

3.3 Results and discussion

3.3.1 Photosynthesis vs Irradiance

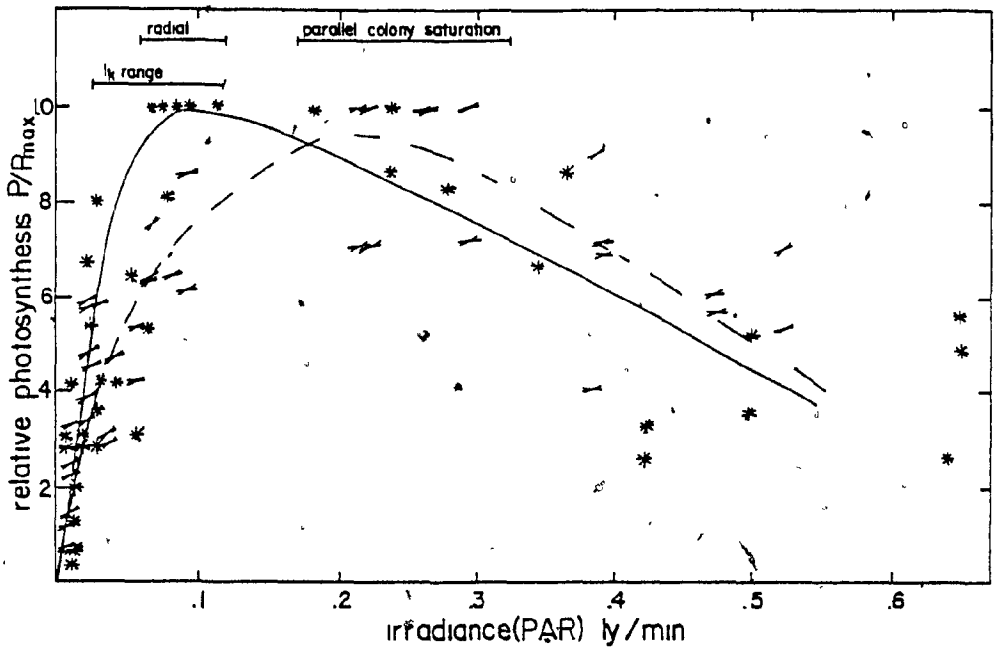
The photosynthetic response to irradiance occurs in two semi-independent stages. Water is split and the reductive high energy compounds ATP and NADPH are supplied by the photochemical processes which utilize light between about 350 and 700 nm wavelength. Chlorophyll and the accessory pigments are responsible for collecting the light energy and hence the first linear part of the photosynthesis vs irradiance (P vs I) curve (see Figures 3.1 and 3.2) is a function of the pigment content per cell and the rates of the light reactions.

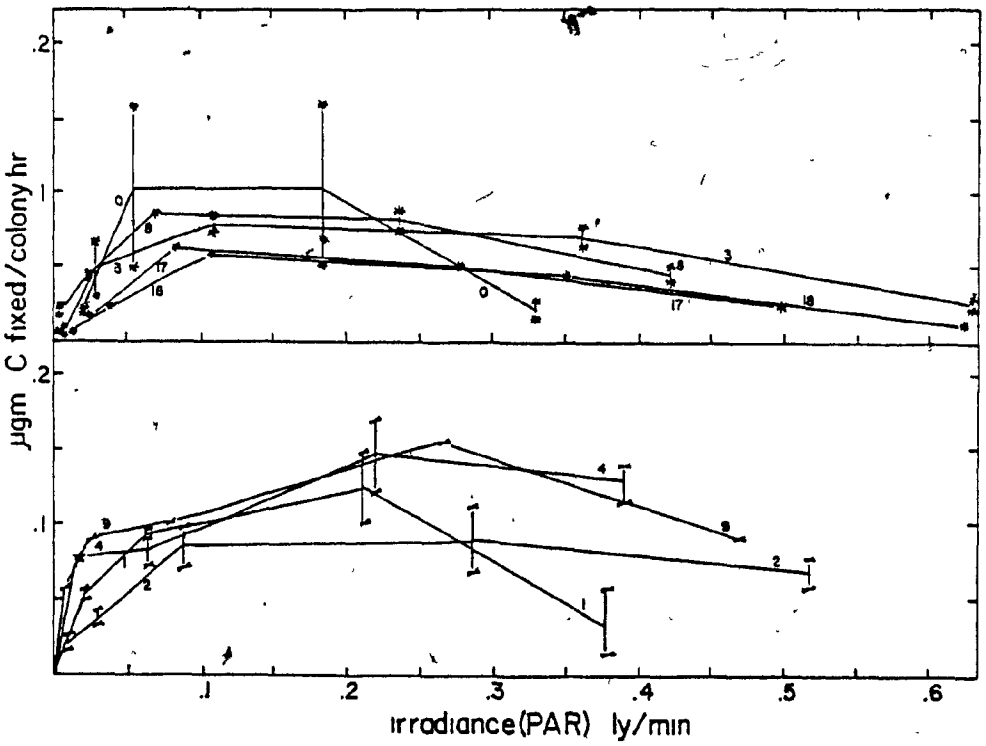
The processes which utilize the energy collected by the photochemical reactions are collectively referred to as the dark reactions. This collection of reactions involving enzymatic synthesis and utilization of the newly fixed CO_2 determines the maximum rate of photosynthesis (Pmax) (Steemann Nielsen, 1975). Photosynthesis as a whole is a balance between the light and dark reactions, and can usefully be described by the term I_K which was introduced by Talling (1957), as a ratio between the two processes. The extrapolation of the light limited portion of the P vs I curve to intersect Pmax yields I_K - the saturation intensity. Both I_K and Pmax are useful in describing the physiological state of an alga, and can be used to compare populations or species.

Changes in the environment, such as temperature or nutrient availability, can drastically affect the magnitude of photosynthesis (Yentsch and Lee, 1966), and thus Pmax/Chla (Pmax normalized to chlorophyll a content of cells). This 'assimilation number' is often used to roughly compare photosynthesis between species or geographical areas, or as an indication of nutrient status. Thomas (1970) has demonstrated that for a tropical Pacific diatom, Chaetoceros gracilis,

Figure 3.1 Relative photosynthesis by Trichodesmium vs. irradiance in the photosynthetically active range (PAR). Each datum is plotted as a fraction of the maximum carbon uptake in the respective experiment; radial colonies (*), parallel colonies (⁀).

Figure 3.2 Absolute photosynthetic carbon fixation (µgm C/colony.hr) vs. irradiance in the photosynthetically active range (PAR) for Trichodesmium gathered from the near surface layer at various times of the year. (0 - Jan. 21, 1975;1 - Mar. 12, 1975; 2 - Mar. 18, 1975; 3 - Mar. 22, 1975; 4 - Apr. 11, 1975; 8 - May 11, 1975; 9 - June 14, 1975; 17 - Jan. 28, 1976; 18 - Mar. 3, 1976). Radial colonies (*), parallel colonies (⁀).


radial
parallel colony saturation
I_k range
relative photosynthesis P/P_{max}
irradiance(PAR) ly/min


µgm C fixed/colony hr
irradiance(PAR) ly/min

the assimilation numbers are less than 1 during extreme nutrient deficiency, but rise to 6 or more when nutrients are readily available. Data may also be normalized with respect to maximum photosynthesis in each experiment (Pmax) and be presented as relative photosynthesis (Steemann Nielsen, 1975). The resulting P/Pmax vs I. curves can then be compared without distortion resulting from variations of the magnitude of photosynthesis.

Data from ten experiments conducted at various times during 1975 and 1976 have been normalized to Pmax and presented in relative units in Figure 3.1. The response of Trichodesmium of both colony types was variable at very low irradiances and I_K's for both types fall in a wide envelope between about 0.02 and 0.11 ly/min. Uptake rates by radial colonies increased in a nearly linear fashion, and saturation occurred around 0.1 ly/min. The rate of carbon uptake by parallel colonies, however, decreased around 0.03 ly/min and Pmax was reached around 0.2 ly/min at which irradiance inhibition began for radial colonies. Parallel colonies were not inhibited until above 0.3 ly/min. The shapes of the curves for the two colony types (species) are rather different, suggesting adaptation to different irradiance climates (see later - Section 3.3.6). The very great reduction of photosynthesis in a few instances at higher irradiances may be evidence of nutrient limitation, which is known to amplify photorespiration at high irradiance (Whittle, 1977).

In absolute terms, the P vs I curves for the near surface population (Figure 3.2) show essentially the same features as the relative photosynthesis plot, but with variations of Pmax due to biomass differences between experiments and/or nutrient status. Four of the five curves for radial colonies reach a Pmax between 0.05 and 0.08 µgm C/colony·hr. These experiments were conducted on colonies taken from 'nonbloom' populations, on the dates indicated. In January 1975,

colonies from a 'bloom' (curve 0) were tested which were photosynthesizing considerably more at irradiances between 0.05 and 0.2 ly/min. These very high counts were verified by recounting and did not decrease after fuming with concentrated HCl, as did most other abnormally high counts. Microscopic examination of the filters did not reveal excessive particulate contamination or large differences in the amount of Trichodesmium on the filters, and thus the high counting rates have been accepted as correct. As well as demonstrating much higher absolute uptake, these colonies also possessed a very low I_K, characteristics which are consistent with the deduction that 'bloom' colonies at Barbados are recent arrivals from nutrient-rich waters along the South American coast (see Section 2.4.4) and therefore have greater internal nutrient stores than 'nonbloom' colonies (the effect of nutrient status on I_K will be discussed later in this section). In January 1976, when colonies from another large 'bloom' population were tested, the alga showed a very low absolute rate of carbon fixation and considerably higher I_K (curve 17). As has already been discussed in Section 2.3.3, the water mass present around Barbados at that time did contain a large phytoplankton population, but it was declining and senescent. Cell counts, percent chlorophyll a and microscopic observations confirmed that this was so for the Trichodesmium and much of the other phytoplankton as well.

In these experiments, parallel colonies demonstrated a higher Pmax than did the radial colonies. This is considered to be primarily due to the fact that the 'standard' parallel colonies contained more cells than the 'standard' radial colonies. The choice of standard colonies was based on gross size, and since parallel colonies have a more compact arrangement of filaments than standard radial colonies, they contained considerably more biomass (see Table 3.1). The fixation rates expressed as a function of a mm of filament length are approximately equal (1.2×10^{-3} µgm C/mm fil·hr for radial colonies; 0.9×10^{-3} µgm C/mm fil·hr for parallel colonies), and so are assimilation

numbers (6.2 µg C/µg Chla·hr for radial colonies; 8.3 µg C/µgmChla·hr for parallel colonies). It is possible that there are differences between the colonies (species?) because of morphology or pigment composition, but these data are too few and variable to confidently make such a statement.

The assimilation numbers for Trichodesmium collected near shore indicate that the alga must have benefited from the well known 'island-mass effect' (Sander, 1971, 1977, and others), since these values are considerably higher than those for Trichodesmium offshore during this study (1.5-5.5). In Table 3.3, assimilation numbers calculated from these data are compared to those reported by others. Phytoplankton from oligotrophic waters generally have values between 1 and 3, while inshore or nutrient rich areas have values above 5.

Assimilation numbers for Barbados Trichodesmium are in good agreement with these general values, as well as with those reported by Moreth (1970) for Trichodesmium from the Florida Current, and that of Aruga and Ichimura (1968) for a Trichodesmium bloom in the Kuroshio. They do not, however, agree with values given by, or calculated from the data of Aruga et al. (1975), Mague et al. (1977) or Carpenter and Price (1977), all of whom report assimilation numbers less than 1. It is not clear why this is so, but it is likely that the low incubation temperatures (20-23°C) used by Aruga et al. (1975) limited photosynthesis. The same authors showed a sharp decrease in carbon fixation by Trichodesmium below 25°C and above 30°C. Mague et al. (1977) did not report their incubation conditions, but it appears that they used very small vials, as did Carpenter and Price (1977). In view of the fact that Trichodesmium colonies isolated from the sea do poorly in small containers (McLeod et al. 1962; B. Taylor, pers. comm.*; this study, Section 5.2),

* Dr. B. Taylor, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, U.S.A.

Table 3.3 Assimilation numbers of near-surface natural phytoplankton

situation	assimilation number µgC/µg Chl*a*·hr. min.	max.	avg.	reference
MIXED PHYTOPLANKTON				
S. W. Caribbean - off Venezuela			2*	Margalef,1971
W. Atlantic - off Barbados	0.5*	3.2*	1.4*	Steven et al.,1970
Tropical Pacific	1.3*	3.5*		Saijo & Ichimura,1962
Tropical Pacific			2.1	Eppley et al.,1973
Tropical Pacific (nitrogen deficient)			3.1	Thomas,1970
Tropical Pacific	1.1	5.2		Takahashi et al.,1972
Tropical Pacific (nitrogen rich)			4.95	Thomas,1970
Near Barbados - neritic	0.2*	22*	4.7*	Sander,1971
ISOLATED TRICHODESMIUM				
Sub-tropical Pacific			.38	Mague et al.,1977
Oceanic Kuroshio	.11	.16		Aruga et al.,1975
Sargasso & Caribbean	.13	.28		Carpenter & Price,1977
Kuroshio - red tide			7	Aruga & Ichimura,1968
Florida Current	3	5		Moreth,1970
Radial colonies - offshore	1.5	2.9	2	This study
Parallel colonies - offshore	3.8	5.5	4.5	This study
Radial colonies - inshore	3.8	6.1 (bloom 12.3)	4.1	This study
Parallel colonies - inshore	3.8	8.3	6.1	This study

* Assimilation numbers based on total chlorophyll will be somewhat low compared to those based on 'live' chlorophyll *a*, depending upon the recent live chlorophyll. In surface layers near Barbados chlorophyll *a* represented 78% of total; in the Kuroshio, it was 60-80% (Saijo et al., 1969). These assimilation numbers should be increased by about 30% to make them comparable with others on this table.

and of the fact that Carpenter and Price utilized very high algal densities (1 colony/ml), the carbon fixation rates on which these assimilation numbers are calculated may be low (see Section 3.3.2, in which autoinhibition is discussed).

Both types of colonies exhibited considerable variability in the slope of the initial, light limited portion of the curve, and in I_K. On some days colonies were present which possessed an I_K of 0.02 ly/min, while at other times I_K's as great as 0.1 ly/min were recorded.

Two other studies of photosynthesis by Trichodesmium surface populations can be found in the literature. McLeod et al. (1961) in experiments with Trichodesmium from near Bermuda, measured photosynthesis with an oxygen probe under tungsten lights. Extrapolation of oxygen production rates from very low irradiance led them to believe that Trichodesmium would saturate at 500-700 ft-candle/cm^2 (0.05-0.06 ly/min), values similar to lower values reported here. They also reported very great variations in photosynthesis among colonies taken from the same tow. Compensation as measured with the oxygen probe was around 20 ft-candle/cm^2 (0.001 ly/min) equal to about 0.2% of noon surface irradiance at Barbados.

Aruga et al. (1975) have studied photosynthesis by Trichodesmium from the Kuroshio, the East China Sea and Japanese coastal waters. Their data also show a great variability in saturation irradiances (5-20 Klux or 0.03-0.12 ly/min) in good agreement with the Barbados data (see Table 3.4 for comparison). Neither McLeod nor Aruga discuss their data, or provide possible explanations for this variability.

The light limited portion of the P vs I curve is a direct function of the pigment concentration of the alga and this is perhaps

Table 3.4 Photosynthetic parameters of *Trichodesmium* and other phytoplankton.

	irradiance (ly/min PAR) I_K	Pmax*	Reference
BLUE-GREENS			
Oscillatoria agardhii (temperate lake)	.035-.045		Baker et al., 1969
O. agardhii var. *isothrix* (temperate lake)	.045-.055		Wohler and Hartmann, 1973
Oscillatoria and *Anabaena* (temperate lake)		.078-	Takahashi et al., 1970
Trichodesmium (Kuroshio, E. China Sea)	.03-.12		Aruga et al., 1975
Trichodesmium (off Bermuda)		.05-.06	McLeod et al., 1962
Trichodesmium (near Barbados)			
mostly *T. thiebautii* (radial colonies)	.02-.11	.06-.26	This study
mostly *T. hildenbrandtii* (parallel colonies)	.02-.09	.18-.31	This study
OTHER PHYTOPLANKTON			
dinoflagellates			
Goniodoma (Puerto Rico *in situ*)	.18	.18-	Burkholder et al., 1967
Peridinium (Puerto Rico *in situ*)	.24	.24-	Burkholder et al., 1967
Dinophysis (India - cultures)	.21	.21-	Qasim et al., 1972
diatoms			
Rhizosolenia (India - cultures)	.13	.14-.22	Qasim et al., 1972
several species (India - cultures)	.07-.13	.13-.20	Qasim et al., 1972

* range of irradiance within which maximum photosynthesis is maintained. Upper value of each range represents the irradiance at which photoinhibition begins. Where no upper value appears above, no data are available.

the most likely explanation for the variability of the I_K recorded in all three studies. While Aruga et al. normalized their data to chlorophyll, the data in the current study and those of McLeod et al. were normalized to biomass. Certainly, if the chlorophyll concentration varies, most algal photosynthesis rates expressed on biomass will vary, but this does not explain the variation of I_K noted by Aruga. The explanation may depend upon the importance of phycoerythrin in Trichodesmium photosynthesis. Shimura and Fujita (1975) have concluded that phycoerythrin is the main photosynthetic pigment in Trichodesmium after observing that wavelengths exciting phycoerythrin stimulated photosynthesis as much as irradiation exciting only chlorophyll a. This in itself is not strange. The phycobilins of other blue-greens are also very important in photosynthesis (Wolk, 1973), but Trichodesmium apparently possesses phycoerythrin which absorbs strongly at three separate wavelengths - quite unlike other known phycobilin pigments. Most other blue-greens possess much larger amounts of phycoerythrin relative to chlorophyll a than that measured by Shimura and Fujita (1975). They ascribed the low phycoerythrin content of the Trichodesmium they collected to nitrogen deficiency.

Nutrient limitation is known to have important effects on photosynthesis by phytoplankton, but in most cases the dark reactions seem to be more affected than the light reactions. The photosynthetic efficiency at low irradiances is usually not greatly affected, but Pmax is decreased and as a result I_K is also lowered (Yentsch and Lee, 1966). Such a decrease of Pmax also evidently occurs with Trichodesmium, but in blue-greens in general and Trichodesmium in particular, there is reason to believe the effect of nutrient deficiency on I_K might be somewhat different. The phycobilin pigments (phycoerythrin in Trichodesmium) are nitrogen containing proteins and are known to be important as internal nitrogen reserves during times of nitrogen starvation. Allen and Smith (1969) have demonstrated rapid decreases in cell phycobilin concentrations in Anabaena with the onset of N starvation.

and a subsequent resynthesis of the pigment when nitrogen is again available. It is hypothesized here that this reduction in the phycobilin pigments will decrease the photosynthetic efficiency at low irradiance, and result in an increase in I_K. A test of this hypothesis requires sensitive C/H/N analyses of colonies whose carbon uptake rates have been measured (suitable instrumentation was not available during this study).

The waters in which Trichodesmium is found commonly contain very low concentrations of all plant nutrients, and phytoplankton growth is generally considered to be controlled by nutrient limitation (cf. Sverdrup et al., 1942; Parsons and Takahashi, 1975). The nitrogen uptake capabilities of Trichodesmium have been the subject of considerable research by several authors (Goering et al. 1966; Wada et al., 1975; Carpenter and McCarthy, 1975). Wada et al. and Carpenter and McCarthy have demonstrated the apparent inability of the alga to take up sufficient combined nitrogen for growth at ambient oceanic concentrations, and consider that nitrogen fixation must supply nitrogen for growth of the alga. The extreme variability of this activity by Trichodesmium is well documented, but no suitable explanation has yet been presented. It may relate to a rather precarious morphological protection of the nitrogenase enzyme from oxygen deactivation (cf. Carpenter and Price, 1976).

The 'neritic' nature of Trichodesmium's nitrogen uptake kinetics and the fact that the specimens tested in these experiments were taken at different times of the year from a very complex and patchy series of water masses with different origins and past nutrient conditions (see Section 2.4.3), undoubtedly means that the colonies tested were in various stages of nitrogen starvation. It seems very likely that the variability of the photosynthetic response of Trichodesmium at low irradiances was closely determined by the

nitrogen-status of the cells and therefore by their past history and any number of other factors limiting nitrogen uptake.

Literature concerning the I_K and saturation irradiances for various phytoplankton have been collated, converted to units of Langleys per minute (PAR) using the conversion factors listed in Table 3.2, and compared in Table 3.4. It is immediately obvious that Trichodesmium and other blue-greens exhibit much greater rates of photosynthesis at low irradiances than do diatoms or dinoflagellates. The range of I_K values for Trichodesmium is 0.02-0.1 ly/min, whereas diatom I_K's are above 0.01 ly/min and those of dinoflagellates above 0.15 ly/min. The photosynthetic characteristics of all algae are changeable and a function of their history, age and environment, but it is apparent from Table 3.4 that there are fundamental differences between the various taxonomic groups (Ryther, 1956), especially at lower irradiances.

Most surface phytoplankton appear to saturate in the range of 30-50% of the surface irradiation (Steemann Nielsen, 1975; Strickland, 1958) which, for tropical species, will be at higher irradiances than for temperate species. By contrast, Trichodesmium is, at least on occasion (periods of nutrient sufficiency?), able to saturate at lower irradiances because of the increased photoreceptor capacity provided by phycoerythrin. Radial colonies perform more like diatoms, whereas the parallel colonies saturate at higher irradiances, more like dinoflagellates.

3.3.2 Autoinhibition

In two experiments conducted under tungsten and fluorescent light (I = 0.07 ly/min) in a temperature controlled incubator, the

number of colonies per bottle was varied as indicated in Table 3.5.

At concentrations of 3 colonies per bottle (24/liter) uptake per colony was greatest in both cases, and declined significantly (25-35%) at concentrations of 10 and 30 colonies per bottle (80 and 240/liter). In the second experiment fixation was generally lower and the decline in photosynthesis per colony at great concentrations was only about 10% at 9 and 18 colonies per bottle. The decrease in carbon fixation rate at higher algal density is not considered to be due to self shading since the colonies were small relative to the size of the bottle. Nutrient limitation within the bottles during the 4 hr incubations can also be ruled out if the colonies were taking up combined nitrogen at rates comparable to those observed by Carpenter and McCarthy (1975) and Wada et al. (1975).

Trichodesmium was not present during this study in numbers greater than about 40 colonies per liter and population densities were usually much less. Autoinhibition in the sea at Barbados is therefore not likely to occur except where the algae are concentrated by convergences or similar phenomena. The data in Table 3.5 are few and the agreement between the two experiments is not perfect; however, experimental work with Trichodesmium should be conducted using low numbers of colonies wherever possible until such time as autoinhibition is more fully investigated.

3.3.3 Release of dissolved materials

Exudation, or release of dissolved organic material by phytoplankton, is now considered to be an integral part of photosynthesis in all waters (Fogg et al. 1965) and has been considered to be a large

Table 3.5 Effect of Trichodesmium population density on photosynthetic rate and percent extracellular release on two occasions.

colonies/liter	carbon fixed µgm/colony/hour (± SD)*	percent extracellular release (99% confidence limits)†
24	0.13 ± .016	4 ± 1
80	0.08 ± .031	18 ± 3
240	0.11 ± .003	18 ± 1
24	0.07 ± .004	ND (<4)
72	0.06 ± .008	ND (<4)
144	0.06 ± .011	ND (<4)

* Standard deviations calculated for duplicates.

† PER ranges represent 99% confidence limits for the counting procedure itself, since counts were low. Duplicate filters gave identical counting rates in each case.

fraction of the particulate carbon fixation in oligotrophic waters (cf. Parsons and Takahashi, 1975). Trichodesmium has been implicated as the source of either inhibitory substances (Ramamurthy, 1970; Menzel, 1962) or surfactants (Sieburth and Conover, 1965). At Barbados, Trichodesmium was often the apparent source of a refractive oil which could be observed trailing behind colonies on the sea surface film, or in containers which had held Trichodesmium for some time.

Several attempts were made to measure release of recently fixed organic carbon during routine photosynthesis experiments following the technique of Watt (1966); however, the carbon uptake in absolute terms was always low and the labelled organic compounds released to the medium were at the limits of detection by this method. Loss was less than 4% of the particulate fixation at low population densities (3 colonies/125 ml = 25 colonies/liter), but where many more Trichodesmium colonies were present in each bottle, the particulate fixation in each bottle was much greater and the organically bound label was present in sufficient concentrations to allow satisfactory estimation. At population densities of 80 colonies/liter the greater release of organic ^{14}C amounted to about 18% of the particulate fixation. This was under conditions of about 30% autoinhibition (see Table 3.5). Even though the absolute amount of activity observed in the water was small, the agreement of duplicates and the 99% confidence intervals of the counting rate itself indicate that there was a significantly different excretion at the greater Trichodesmium densities. If nutrient deficiencies do develop in the incubation flasks at high algal densities, either because of increased uptake of combined nitrogen over that reported by Carpenter and McCarthy (1975) and Wada et al. (1975), or by restrictions on nitrogen fixation, then carbon fixed during photosynthesis may be in excess of requirements. In many species of phytoplankton this leads to excretion of glycolate, which is a major intermediate in photorespiration (Whittle, 1977).

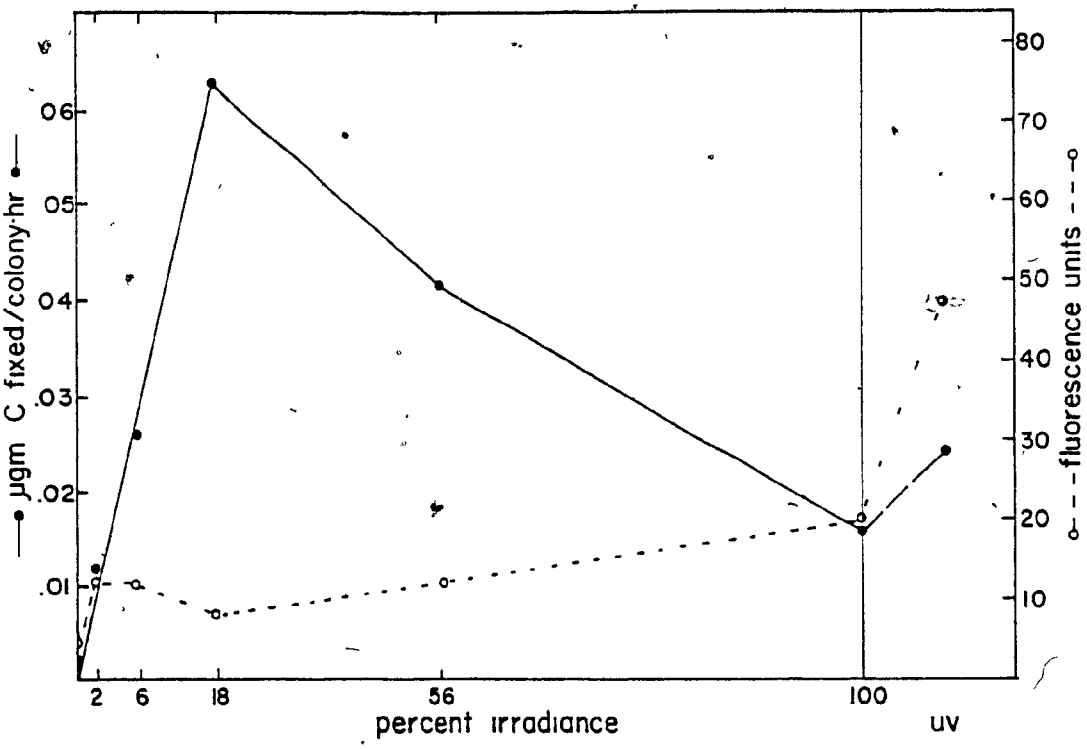
The low percentage release at low Trichodesmium densities made the Watt technique impractical, and difficulties encountered with attempts at sending liquid samples to Canada for scintillation counting eventually forced abandonment of this technique. McLeod et al. (1962) had, however, noted a red fluorescence of Trichodesmium colonies when they were excited by light of 360 nm, and Traganza (1969) observed similar fluorescence in seawater from a Trichodesmium bloom. The excitation and emission spectra for this bloom 'fluorophor' presented by Traganza allowed selection of interference filters to selectively measure for this (these) compound(s) at Barbados. Traganza did not identify the(se) compound(s) but recorded similar fluorescence from cultures of twelve species of other phytoplankton, and suggested the fluorophor might be one of several fluorescent biochemicals (many phenols, aromatic amines, hetercyclic and polycyclic compounds are fluorescent).

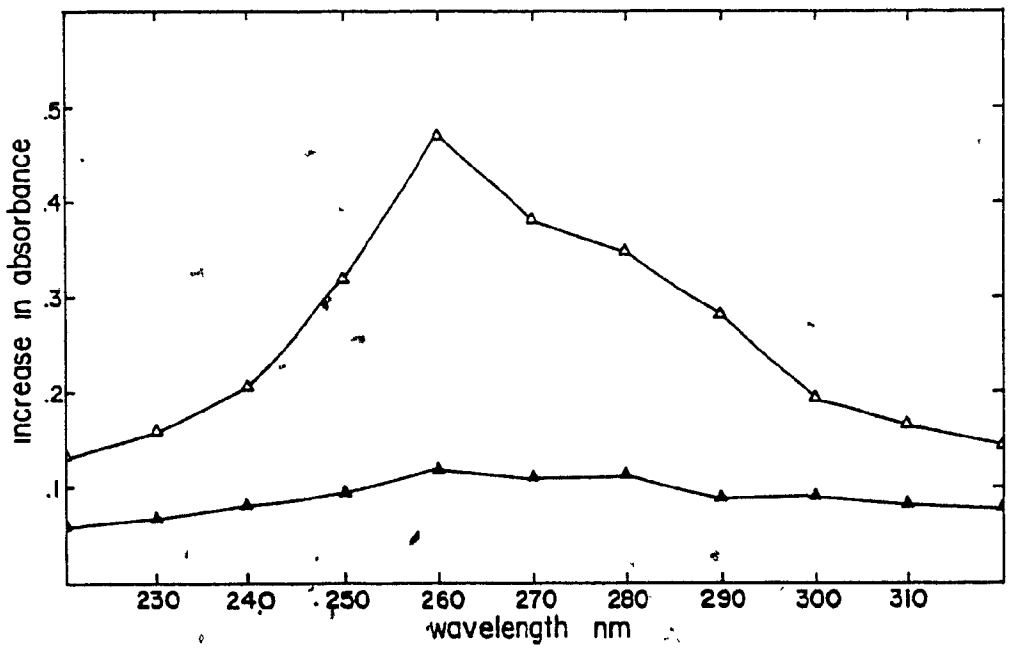
The fluorometric assay was used to investigate the effect of irradiance on release of organic material, since it was sensitive enough to record changes even at low Trichodesmium population densities. Figure 3.3 illustrates that, in the dark, the fluorescence of the Trichodesmium filtrate was low (the same as that of deionized distilled water). At low and moderate irradiance the dissolved fluorescence was somewhat greater, but increased substantially at 100% PAR. Where Trichodesmium colonies were incubated in open finger bowls, thereby exposing them to ultraviolet wavelengths which are normally blocked by the pyrex bottles and the water bath, the fluorescence increased sharply. Such increases in excretion or release of organic compounds at high irradiance are often observed in studies of other algae, and are thought to be a result of increased photorespiration at high irradiance (Whittle, 1977).

As has already been mentioned, Trichodesmium colonies on the sea surface were often observed to be the apparent source of a refractive

Figure 3.3 Effect of increasing irradiance on exudation of a dissolved fluorescent material by Trichodesmium (radial colonies). Carbon taken up by the alga (—●—); fluorescent material released (--o--). UV indicates incubation in open bowl, alga exposed to ultraviolet radiation from the sun.

Figure 3.4 Increase in absorbance of filtered seawater after four hour photosynthesis experiment illustrated in Figure 3.3. Colonies exposed to ultraviolet radiation (▵), colonies in dark bottle (▲).


µgm C fixed/colony·hr
fluorescence units
.01
.02
.03
.04
.05
.06
10
20
30
40
50
60
70
80
2
6
18
56
100
percent irradiance
uv


increase in absorbance
.1
.2
.3
.4
.5
230
240
250
260
270
280
290
300
310
wavelength nm

oil. In the laboratory, Alcian blue stain for polysaccharide indicated release of an otherwise invisible exudate near the terminal ends of many filaments in colonies drawn from the surface population. Trichodesmium does not secrete a thick mucilaginous sheath as do many other blue-greens, but the older, often plasmolyzed and bleached cells near the ends of some filaments, seem to leak considerable quantities of a carboxylated polysaccharide material, primarily through their intercellular junctions. Further reference to these observations will be made in Section 5.3.2.

Sieburth and Conover (1965) observed T. erythraeum in a natural surface slick in the Sargasso Sea, and suggested that secreted carbohydrates from this alga were responsible for the surface effect. During several routine experiments in the current study, where the acidification and bubbling technique of Watt (1965) was in use for estimation of released organics, differences in the amount of foam and the size of bubbles produced in some bottles were noted, suggesting the presence of a surface active compound. Some Trichodesmium filtrates definitely produced less foam than others, but no consistent relationship could be established between the amount of foam produced and any other experimental variable.

In the 4 hr experiments cell lysis may have been occurring to an extent sufficient to cause appearance of freshly labelled organic ^{14}C in the water. However, trials with Trichodesmium freshly collected proved that an increase in fluorescence could be detected in the water after as short a time as 15 minutes, coinciding with an increase in the optical density at 260 nm (see Figure 3.4). This was long before lysing and general morphological deterioration was microscopically visible. An increase in absorbance around 260-270 nm is commonly observed in filtrates of algal cultures and in the sea, and has been suggested to be due to excreted organic material (Fogg and Boalch, 1958;

Sournia, 1965; Brown, 1977). Butler and Ladd (1969) have studied the spectrum of humus, which is often suggested to be responsible for the 'Gelbstoff' in the sea, and have found a close correlation between carboxyl groups and absorption at 260-280 nm.

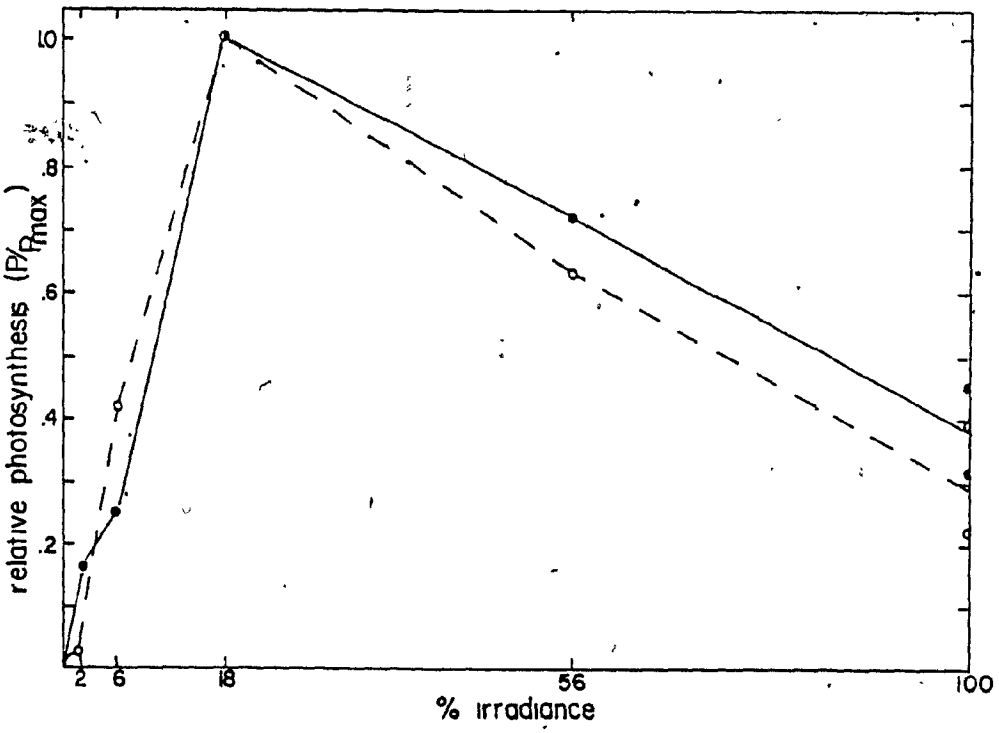
Taken together, all of the observations discussed above suggest that Trichodesmium may be the source of considerable dissolved organic material in the sea, but primarily at the surface. At low irradiance and low population densities, exudation was not great. At high irradiance and in crowded conditions, however, release of a fluorescent and newly synthesized compound increased markedly. Such conditions as would obtain in the microconvergences found in Langmuir vortices, that is, crowding, high irradiance and ultraviolet wavelengths, can be expected to cause a reduction in photosynthesis and excretion of large amounts of a dissolved compound, possibly a carbohydrate.

3.3.4 Light shielding by gas vacuoles

Since Trichodesmium is often encountered in the harsh, high-irradiance surface layer and because of the peripheral location of its gas vacuoles, Van Baalen and Brown (1969) have postulated that the vacuoles serve as a light shield protecting the photosynthetic apparatus which is located just inside.

When radial colonies from the near surface population were exposed to twenty atmospheres' pressure, their vacuoles collapsed. Compared with normally vacuolated colonies of similar size collected at the same time, these 'pressure treated' Trichodesmium colonies showed essentially the same P/P max vs I curves (see Figure 3.5). It

Figure 3.5 Photosynthesis vs. irradiance by normally vacuolated *Trichodesmium* (●) (radial colonies) and colonies in which vacuoles have been artifically collapsed (o).


relative photosynthesis (P/P_{max})
1.0
.8
.6
.4
.2
2
6
18
56
100
% irradiance

is apparent that, on this occasion at least, the gas vacuoles were not providing significant protection from high irradiance since the photosynthetic response of the alga was not seriously affected by their collapse (in absolute terms, the pressurized colonies C uptake was 20-25% higher at medium irradiances (5.6, 18 and 56% I) than that of normal colonies).

The suggestion that gas vacuoles act as light shields in blue-green algae has often been made, but as Walsby (1972) has also noted, Anabaena flos-aquae shows no difference in photosynthesis at high irradiance with or without their gas vacuoles. This appears to be the case for Trichodesmium also and it seems likely, therefore, that their primary function is not related to light shielding but to that of providing buoyancy and mobility to the alga (Walsby, 1972).

3.3.5 Diurnal changes in photosynthesis

Two experiments were conducted to describe the diurnal changes of photosynthesis by the near surface Trichodesmium population, and to provide data allowing extrapolation from forenoon incubations to daily production.

On June 4, 1975, parallel Trichodesmium colonies were collected at 0700, 0900, 1100 and 1300 hrs and otherwise routine 4 hr experiments begun at 0800, 1000, 1200 and 1400 hrs respectively. If the colonies collected at different times of the day can be regarded as representative of the population at large, then the data summarized in Figures 3.6 and 3.7 demonstrate the diurnal changes in photosynthesis of the near surface Trichodesmium population.

Figure 3.6 Photosynthesis vs. irradiance response for Trichodesmium (parallel colonies) incubated at different times of the day. Four hour incubations beginning at 0800, 1000, 1200 and 1400 hrs. Stippled area represents range of forenoon incubations illustrated in Figure 3.2.

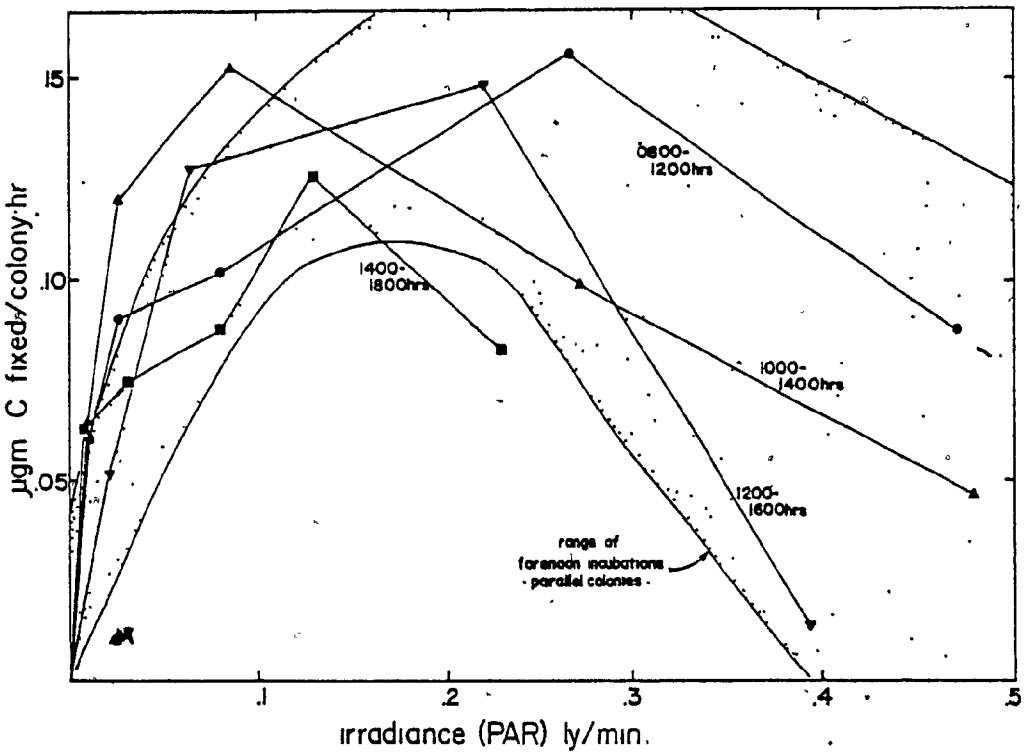
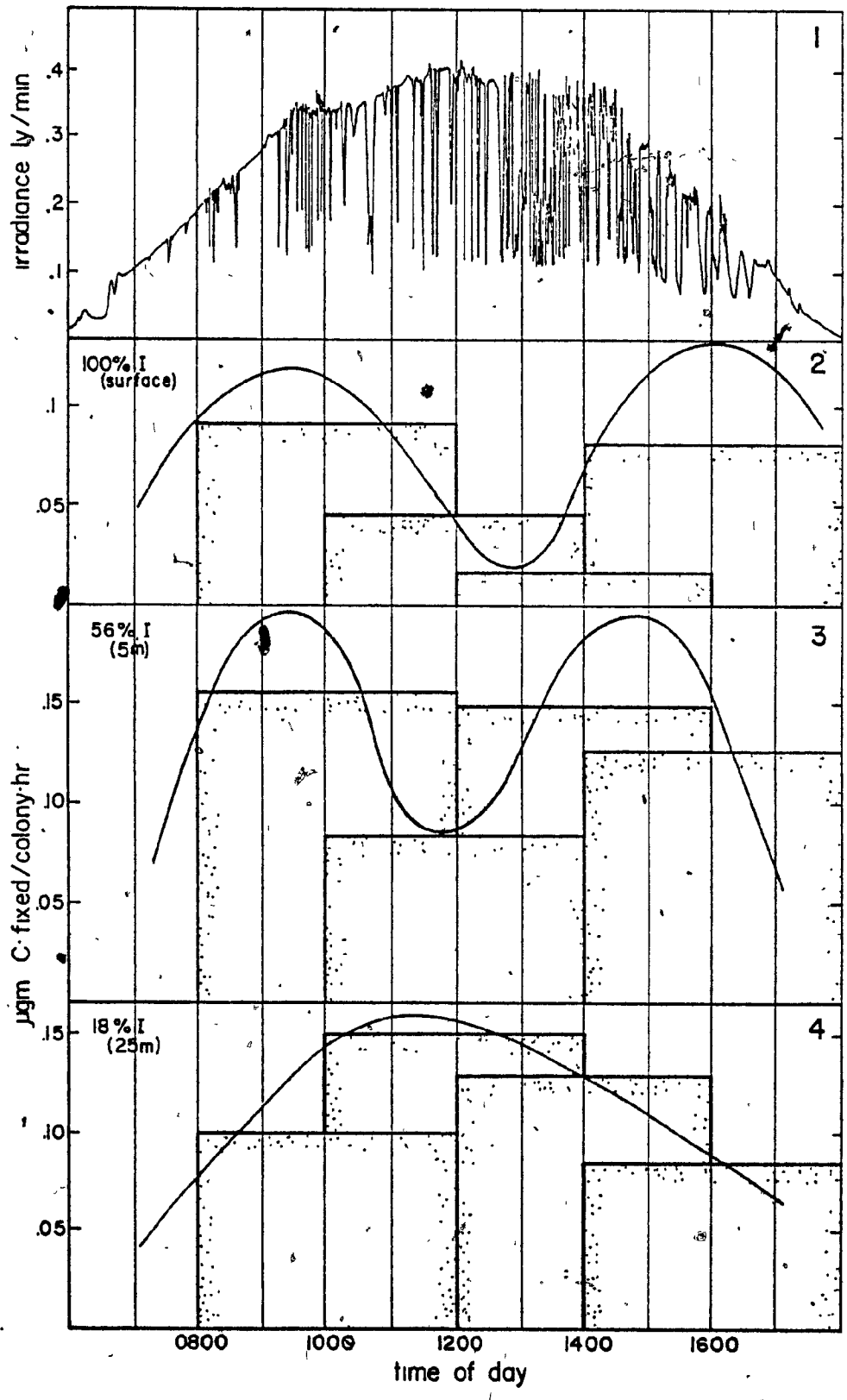

.15
.10
.05
µgm C fixed/colony·hr
0800-
1200hrs
1400-
1800hrs
1000-
1400hrs
1200-
1600hrs
range of
forenoon incubations
- parallel colonies -
.1
.2
.3
.4
.5
irradiance (PAR) ly/min.

Figure 3.7 Diurnal variations of surface irradiance and of photosynthesis at three simulated depths by Trichodesmium (parallel colonies) from the near surface population.

Bars represent average carbon fixation rate in each four hour incubation. Curves represent possible instantaneous rates based on P vs I curves in Figures 3.6 and variations of irradiance indicated here.


irradiance ly/min
.4
.3
.2
.1
1
100% I
(surface)
2
.1
.05
56% I
(5m)
3
.15
.10
.05
µgm C·fixed/colony·hr
18% I
(25m)
4
.15
.10
.05
0800
1000
1200
1400
1600
time of day

The absolute level of Pmax remained constant during the first three periods, but dropped in the late afternoon. The irradiance at which Pmax was attained changed also. In the first forenoon incubation (0800-1200 hrs), the alga performed in a manner similar to other forenoon experiments, attaining Pmax near 0.25 ly/min. In the noon incubations period (1000-1400 hrs), however, the shape of the P vs I curve changed drastically. Photosynthesis was considerably depressed at high irradiances, and Pmax had shifted to less than 0.1 ly/min. In the afternoon periods (1200-1600 hrs and 1400-1800 hrs) Pmax returned to higher irradiances and the shape of the P vs I curves was more like those of forenoon incubations.

In Figure 3.7 the data are presented as a function of the percent irradiation the alga received, and therefore can be regarded as representing the daily changes of photosynthesis in colonies situated at constant depths. Figure 3.7.1 shows the changing irradiation as measured by the pyranometer, and the spacing of the four incubations. The two hour overlap permits interpolation for shorter periods. Figure 3.7.2-4 shows the fixation during each 4 hr experiment, and the estimations for each 2 hr period throughout the day.

In the forenoon incubations, the P vs I curve in Figure 3.6 demonstrates that the total fixation in the uncovered bottles simulating 100% irradiance near the sea surface was depressed. According to this curve, Trichodesmium should have been inhibited during the latter part of that incubation period, when irradiance passed 0.3 ly/min (at around 0900 hrs). This inhibition increased over noon, and reached a maximum in the early afternoon (1200-1600 hrs) when irradiance was greatest and C uptake in the 100% bottles was only about 0.2 Pmax. During this period, the alga was evidently respiring the largest part of the carbon being fixed. With a decrease in irradiation in the late

afternoon, the irradiance in the uncovered bottles was low enough that photoinhibition was reduced and a sort of afternoon recovery was possible.

At the 56% irradiance level (simulating about 5 m depth) photosynthesis was high during the forenoon, but dropped in the noon period. The P vs I curves and interpolations from the 4 hr incubations suggest that the fixation rate during the first half of the forenoon (0800-1000 hrs) must have been much higher. The photoinhibition which was evident in the 100% I bottles beginning at about 1000 hrs also occurred in the 56% I bottles, but was not as severe and did not last as long. With decreasing irradiation in the afternoon the alga recovered more quickly and was fixing rapidly for a short period in the afternoon before light limitation began.

At the 18% irradiance level (simulating about 25 m depth) energy appears to have been limiting for Trichodesmium from the surface layer at least, for most of the day. Pmax was attained during the noon incubation when maximum irradiance was received.

Fixation in dark bottles containing Trichodesmium colonies was, on this occasion, less than 0.05 Pmax in all periods. On April 23, 1976, when the experiment was repeated with radial colonies, dark fixation increased linearly from 0.15 Pmax in the forenoon to 0.44 Pmax in the late afternoon. While the June experiment had utilized parallel colonies which have significantly lower bacterial populations (L. Borstad, in prep.), the April experiment was conducted on radial colonies, and it is assumed that a growing bacterial population in situ was responsible for the increase in dark counts later in the day. Fixation in light bottles containing Trichodesmium was low during all incubation periods, with little change from one period to another. The combination of low photosynthesis and high bacterial contamination suggests the Trichodesmium

population off Barbados on this day was waning. These data have therefore not been used in the extrapolations to daily rates.

Based on the interpretation of the data in Figures 3.6 and 3.7, carbon fixation during the forenoon (0800-1200 hrs) represented about 0.4 of the daily carbon uptake both at 56% and 100% of the surface irradiance and around 0.35 of the daily fixation at 18% I. Extrapolation of daily production from forenoon incubations will be approximately correct therefore, if the forenoon hourly production rates are multiplied by 10. This should hold for the Trichodesmium population in the top 10 to 20 m of the water column.

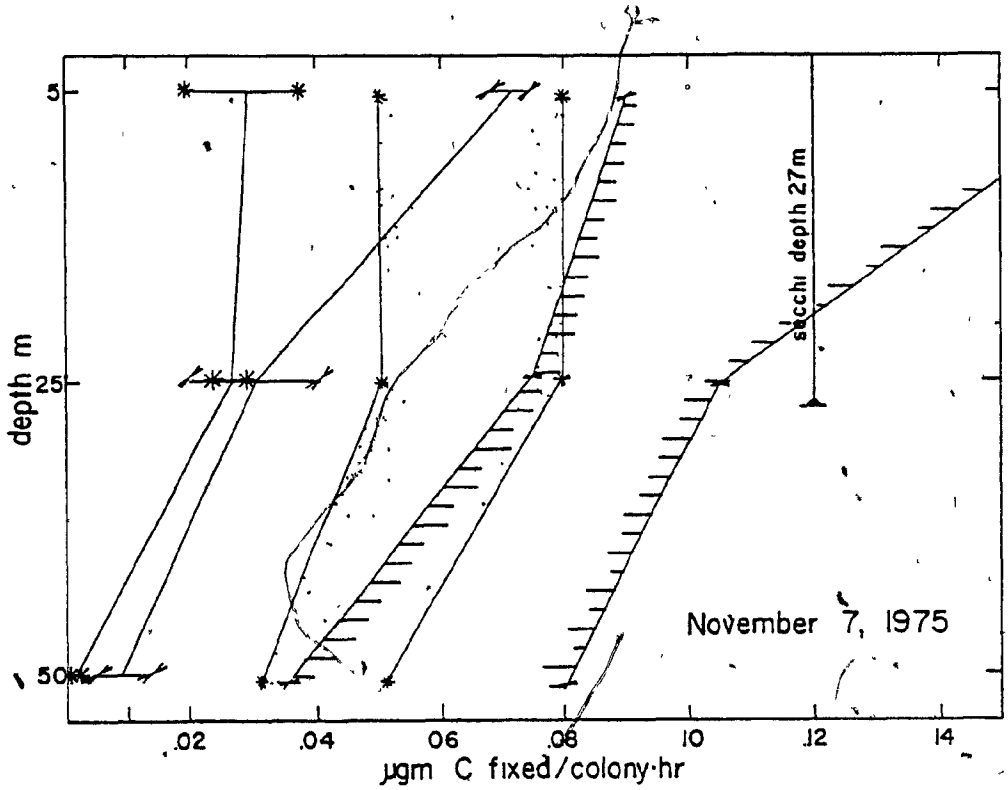
3.3.6 Photosynthesis in situ

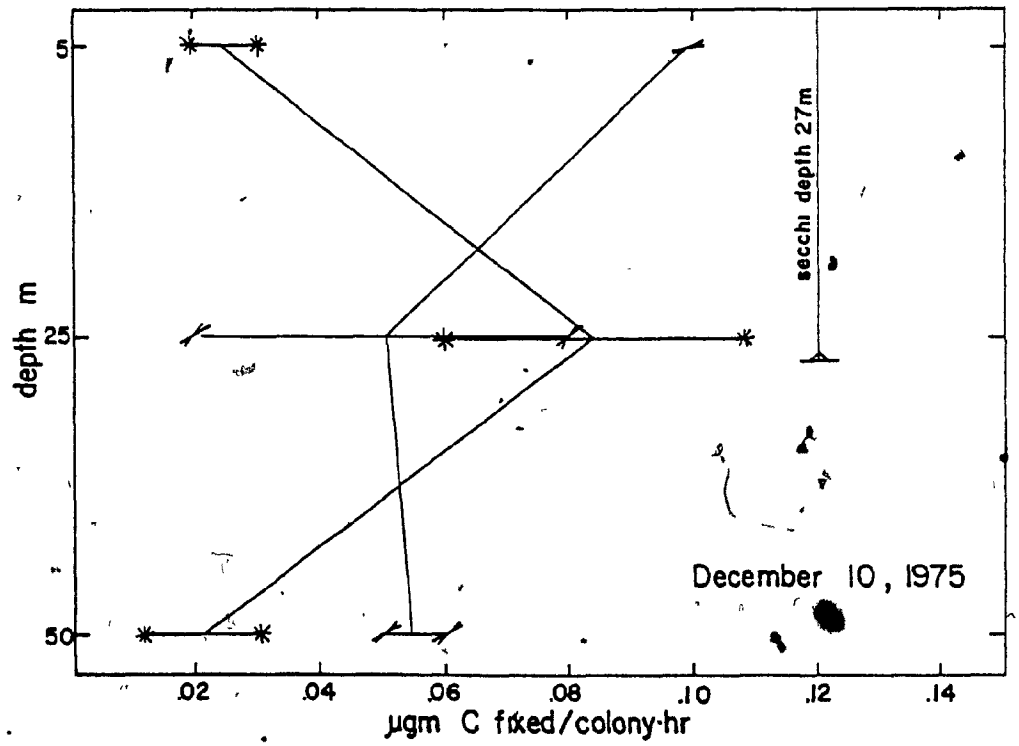
Carbon fixation by Trichodesmium measured in situ near the 8 km station on November 7 and December 10, 1975, is illustrated in Figures 3.8 and 3.9. Surface irradiance averaged 0.46 ly/min during the November experiment and 0.40 ly/min during the December incubation.

In November, fixation by radial colonies was approximately equal at 5 and 25 m (approximately 0.2 µg C/colony·hr) but decreased to near zero in the 50 m bottles. Parallel colonies, by contrast, were fixing more than twice as much as the radials at 5 m and this rate decreased more or less linearly to around 0.01 µgC/colony·hr at 50 m. The change of rates of both colony types with depth was similar to what might have been predicted from the P vs I curves (Figure 3.2 and light penetration data (Section 3.3.1), but the absolute magnitude of photosynthesis at all depths was about 50% of that measured for inshore Trichodesmium at comparable irradiances.

Figure 3.8 *Trichodesmium* photosynthesis *in situ*, November 7, 1975, near the 8 km station. Stippled envelope indicates response of radial colonies from the near surface population to irradiance regime similar to that received at 5 m (50% I_S), 25 m (18% I_S) and 50 m (3% I_S). Dashed envelope illustrates range for parallel colonies.

Figure 3.9 *Trichodesmium* photosynthesis *in situ*, December 10, 1975, near the 8 km station.


5
25
50
depth m
secchi depth 27m
November 7, 1975
.02
.04
.06
.08
.10
.12
.14
µgm C fixed/colony·hr


5
25
50
depth m
secchi depth 27m
December 10, 1975
.02
.04
.06
.08
.10
.12
.14
µgm C fixed/colony·hr

In December, fixation rates were higher than in November (except for the 5 m radial colonies) and more variable. Photosynthesis by parallel colonies again decreased from 5 m to 50 m, but the radial colonies demonstrated greatly accelerated rates at 25 m. This is in the irradiance range in which the 'bloom' radial colonies tested in January 1975 inshore (Figure 3.1, curve 0) also exhibited a much higher Pmax, and corresponds to the depth of the population maximum noted in Section 2.3.3.2. The differences in vertical distribution between the two colony types (radial colonies found more or less evenly throughout the upper 35 m or concentrated at 15-25 m; parallel colonies more common near the surface) are partly explained by their photosynthetic responses to the irradiance climate.

3.3.7 Potential photosynthesis by Trichodesmium from 5, 25 and 50 m.

'Shade adapted' phytoplankton growing at lower irradiances generally exhibit either increased chlorophyll content (thereby increasing their photosynthetic efficiency at low irradiances and decreasing their I_K), or decreased Pmax (thereby decreasing their I_K, but also decreasing their growth rate) (Steemann Nielsen, 1975). In order to investigate possible differences in photosynthesis by Trichodesmium found at different levels of the water column, radial colonies were collected at 5, 25 and 50 m depth and exposed to the full range of irradiance in the mesh bags as described earlier.

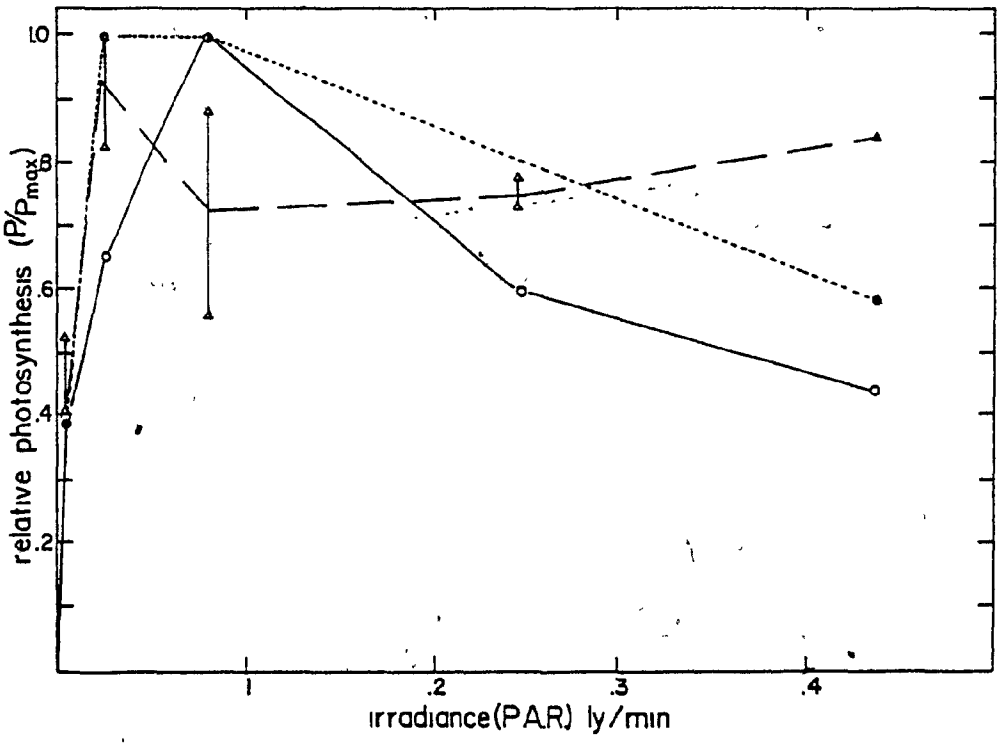
Carbon uptake in absolute terms was approximately equal in colonies from each depth when dark counts were subtracted. As is often the case when photosynthesis measurements are conducted near the base of the euphotic zone at low latitudes (Steven et al., 1970; Steemann Nielsen, 1975), very high dark fixation was recorded by Trichodesmium colonies at 50 m. High dark fixation at the bottom of the mixed layer

is usually assumed to be due to bacterial contamination (Steemann Nielsen, 1975) and since L. Borstad (in prep.) found increased numbers of bacteria in Trichodesmium colonies at 50 m, this is also assumed to be the case here. The darkened Trichodesmium from 25 m also gave high counts, but the filter (which gave an equivalent of 2 µg C/colony.hr) was found to be seriously contaminated by particulate material, as was the filter for the 50 m Trichodesmium at 0.2 ly/min. When recounted, these two filters exhibited substantially less radioactivity. They have therefore been considered spurious.

Figure 3.10 illustrates the P/Pmax vs I response of colonies from 5, 25 and 50 m, and the decrease in I_K by the algae at 25 and 50 m. This was not due to an increase in chlorophyll content; measurements indicated that colonies from all three depths contained similar amounts of this pigment. The obvious suggestion, that phycoerythrin was more abundant in the alga from deeper depths, could not be investigated because this pigment was not measured (see p. 14).

On the basis of these few data, one might expect photosynthesis in situ (during the early afternoon at least - the period during which this experiment was conducted) to be approximately equal at all depths, or perhaps slightly higher at deeper depths. The consistently low fixation at 50 m in the in situ experiments in November and December 1975 is difficult to explain unless it is related to differences in the quality of available irradiance. At 50 m in situ only wavelengths around 500 nm are available, whereas the spectral distribution of energy available in the bags was fairly uniform across the photosynthetically active range. Trichodesmium possesses phycoerythrin which absorbs efficiently at 495 nm and could be expected to be capable of considerable photosynthesis in these wavelengths, but as noted already, phycoerythrin's role as an internal nitrogen supply may lower the concentration of pigment in the cells. Under conditions of nitrogen starvation Trichodesmium might then lose the ability to utilize the blue wavelengths available in the lower euphotic zone.

Figure 3.10 Potential relative photosynthesis vs. irradiance response of radial Trichodesmium colonies from 5 (o), 25 (Δ) and 50 m (●).


1.0
.8
.6
.4
.2
relative photosynthesis (P/P max)
1
.2
.3
.4
irradiance(PAR) ly/min

3.3.8 Calculation of the contribution by *Trichodesmium* to total production

The contribution made by *Trichodesmium* to total primary production can be calculated from these photosynthesis data and the standing crop measurements reported earlier in Section 2.3.3. Conversion of the hourly carbon fixation rates from a per colony basis to values expressed as a function of total filament length (mm), and multiplication by the *Trichodesmium* standing crop (total filament length (mm) per liter), will give µgm carbon fixed by *Trichodesmium* in one liter per hour.

In Table 3.6 hourly per colony fixation rates from the *in situ* experiments at 5 m have been grouped and a mean production rate by *Trichodesmium* standing stocks on those two days calculated. The large standard errors and lack of coincident data for total production data make the estimate crude, but it is evident that on these two occasions production by the *Trichodesmium* population at 5 m was a very considerable fraction of the mean rate for the entire phytoplankton reported by Steven et al. (1970)*.

Somewhat more data are available for the inshore region,

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* A mathematical error in calculations performed by Dr. D.M. Steven was discovered during the course of the present study, which requires a revision of all the production estimates arising out of the 1968-1970 study (Steven et al., 1970; Steven, 1971; Sander and Steven, 1973) and Sander's 1969-1970 study (Sander, 1971). Their values should all be divided by two. Note, however, that production estimates based on GM counting of dried filters may be low due to loss of activity during drying (Steemann Nielsen, 1975).

Table 3.6 Comparison of estimated Trichodesmium production rate with those of the entire phytoplankton population near the surface.

	Trichodesmium carbon uptake rates pgmC/mm fil·hr ± SE	Trichodesmium standing stock mm fil/l ± SE	Estimated Trichodesmium production rates µgmC/l·hr ± SE	Mean total production rates µgmC/l·hr. ± SE	Trichodesmium production percent of total
Offshore	0.5 ± 0.04 (7)	180 ± 60 (2)	0.09 ± 0.04	0.22 ± 0.05*† (43)	41
Inshore	0.7 ± 0.1 (12)	535 ± 116 (8)	0.37 ± 0.13	1.05 ± 0.07* (92)	35
Inshore (coincident data) August 13, 1975	1.0 ± 0.07 (8)	450	0.45 ± 0.03	0.92 ± 0.05 (6)	49

* indicates the corrected production figures of Steven et al. (1970) and Sander (1971).

Figures in brackets refer to the number of data for which standard errors are calculated.

† corrected values agree well with those given by Margalef (1965) and Cadée (1975) for offshore regions.

where Trichodesmium fixation rates at 80% I (irradiance received at 1 m) on the P vs I curves are compared to the mean rate for the entire phytoplankton at 1 m depth reported by Sander (1971)*. If the diurnal variations of photosynthesis by the entire phytoplankton are similar to those reported here for Trichodesmium, then production by the blue-green amounted to about a third of the mean total production near the surface. Coincident measurements of carbon uptake by Trichodesmium and the entire phytoplankton collected from just below the surface in this region are available for August 13, 1975. The calculated production rate by the Trichodesmium standing stock on that day was 0.4 µgC/l·hr (eight replicates), about half of the total production (0.92 µgC/l·hr - six replicates).

Other estimates of production by Trichodesmium in the Atlantic area have been made by Goering et al. (1966), Moreth (1970) and Carpenter and Price (1977). Moreth incubated Trichodesmium colonies in bottles of unfiltered sea water and removed the colonies after one hour. On the average ($\bar{n}$ = 100) Trichodesmium fixed about 46% of the total carbon taken up. This estimate may be slightly low if the recovery of Trichodesmium was incomplete. At Barbados, colonies often fragmented in the bottles during incubations, and experiments showed that individual filaments photosynthesized at the same rates as those in intact colonies (colonies completely disrupted by shaking gave the same counting rate as similar size intact colonies).

Carpenter and Price measured carbon fixation at four stations in the Caribbean and compared these rates with total production reported by Beers et al. (1970) from Jamaican waters. Their estimate of Trichodesmium's contribution to the total production - 20% - may be low however, because of the problems of autoinhibition mentioned

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* See footnote, previous page.

earlier (Sections 3.3.1 and 3.3.2).

Goering et al. (1966) conducted simultaneous experiments with isolated Trichodesmium and the entire phytoplankton in larger bottles, but only four measurements are available for near-surface plankton. Their data indicate that Trichodesmium contributed up to 35% of the total production.

The data discussed above indicate that Trichodesmium plays an important role in the euphotic zone, both offshore in oligotrophic waters and close to shore. Previous calculations (Section 2.3.3) indicating that the alga contributes up to half of the chlorophyll a in the upper layers of the sea make this to be expected. More data are required to make a more precise estimate of the percent contribution in specific areas.

Note here that the presence of Trichodesmium colonies may lead to large increases in the variability of routine ^{14}C measurements in tropical oceans, since one medium size colony is capable of fixing between 0.10 and 0.15 µgC/hr. In oceanic areas where the average carbon fixation is only 0.22 µgC/liter.hr or 0.028 µgC/hr in the 125 ml bottles in which experiments are usually conducted, the fortuitous presence of one colony will significantly affect the results. Even in the near-shore environment where fixation rates are high, the presence of one colony could double the amount of carbon uptake measured.

4 DECOMPOSITION AND DETRITUS FORMATION BY TRICHODESMIUM

4.1 Experimental decomposition of Trichodesmium

4.1.1 Introduction

Much has been written about decomposition and remineralization of detrital material in the sea, particularly in stratified tropical oceans where nutrient limitation is severe. In these environments where remineralization is thought to be of overriding importance in supplying nutrients for phytoplankton growth (Wangersky, in press), the implications of the death and decomposition of large Trichodesmium populations demand attention. Several authors have referred to this supply, mentioning the alga's ability to fix atmospheric nitrogen and store it in nitrogenous iron-containing pigments (Wood, 1965; Steidinger, 1973; Wolk, 1973). The only data available are a few presented by Moreth (1970), showing that considerable quantities of phosphate were released from Trichodesmium even in the presence of formalin. In order to further investigate the active remineralization of Trichodesmium by active bacteria, fungal and protozoan populations, experiments were conducted in which the changes in dissolved plant nutrients and bacteria were monitored.

4.1.2 Materials and methods

Surface plankton was collected as described in Section 3.2.1. Small volumes of the bucket plankton were removed and diluted with larger volumes of surface seawater. Two thousand radial colonies were then isolated using Pasteur pipettes and deposited in 2 l millipore filtered, autoclaved seawater. Two flasks, one containing streptomycin and sulphadiazine to inhibit bacterial growth*, were inoculated.

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* The antibiotics may also have affected the Trichodesmium, but this is not considered important in this context since the alga always died within a short time.

placed in indirect sunlight in an airconditioned room (T^{o} 25 ± 2^{o}C) and stirred continuously with glass paddles. Each was initially covered with sterile cotton plugs, but these fouled the stirring rods and were replaced with tin foil dust covers after five days.

The resultant lack of sterility may represent a possible source of error however, it is assumed that the autotchonous bacterial and fungal populations of the Trichodesmium colonies provided a very large inoculum, and these organisms were responsible for at least the initial degradation of the algal material.

Bacterial growth in both flasks was monitored by L. Borstad, by plating homogenized aliquots of water samples onto Zobell's 2216E medium. Details will be discussed in a thesis by L. Borstad (in prep.) as will be the results of a third, smaller experiment similar to these in which external contamination was more limited. Bacterial numbers and gross colony morphology in the latter experiment closely followed those observed in flask 1 (no antibiotics). Bacterial numbers in the second flask (flask 2) were inhibited by periodic addition of antibiotics.

At intervals of several days, aliquots were taken from each flask, filtered through Whatman GF/C filters and frozen for later analysis of dissolved ammonium, nitrite-nitrate and orthophosphate concentrations, according to Strickland and Parsons (1968). The small number of samples taken from each flask was determined by the volumes required for the analyses and the desire to decrease the total volume of the flask by no more than 40%. The pH of the unfiltered water was measured each day a sample was taken.

4.1.3 Results

The changes recorded in the two flasks are summarized in Figures 4.1 and 4.2. In both cases the Trichodesmium colonies became lighter coloured, lysed and fragmented by day 2 or 3, and clumping of the detrital material occurred. Bacterial growth in the water made flask 1 turbid by day 3. Neither of the flasks contained intact Trichodesmium colonies by day 7 and by day 14 or 15 a white flake-like detritus had appeared in both. In flask 1 these particles were amorphous flocs laden with bacteria, while in flask 2 they were entirely bound by fungal mycelia. Both types of particles carried abundant microphagous and carnivorous protozoa by day 28.

Growth of diatoms on the walls and bottom of the flasks was noted on day 28, and increased until, at termination of the experiments on day 54, large sheets of the pennate diatom Navicula sp. 1 (see Section 5.3.3.4) were present on the glass in flask 1.

In flask 1, bacteria viable on 2216E increased to more than 10^6/ml within 30 hours of inoculation. Numbers of this rapidly growing form began to decline around day 6. Total numbers increased again after day 10 due to the appearance of a slower growing type forming smaller colonies. By about day 26 the differences between the two types became less obvious, and the total numbers, which had been declining between days 20 and 28, increased temporarily. Bacteria viable on 2216E from flask 2 were always less than 100/ml.

In flask 1, ammonium appeared in large amounts by day 14, following the initial burst of bacterial activity, then quickly disappeared. By day 21 concentrations were similar to that measured on day 1. Nitrite-nitrate concentrations began to increase after day 6, reached a maximum around day 28, and declined thereafter. Phosphate concentration increased sharply after day 6 and attained a maximum

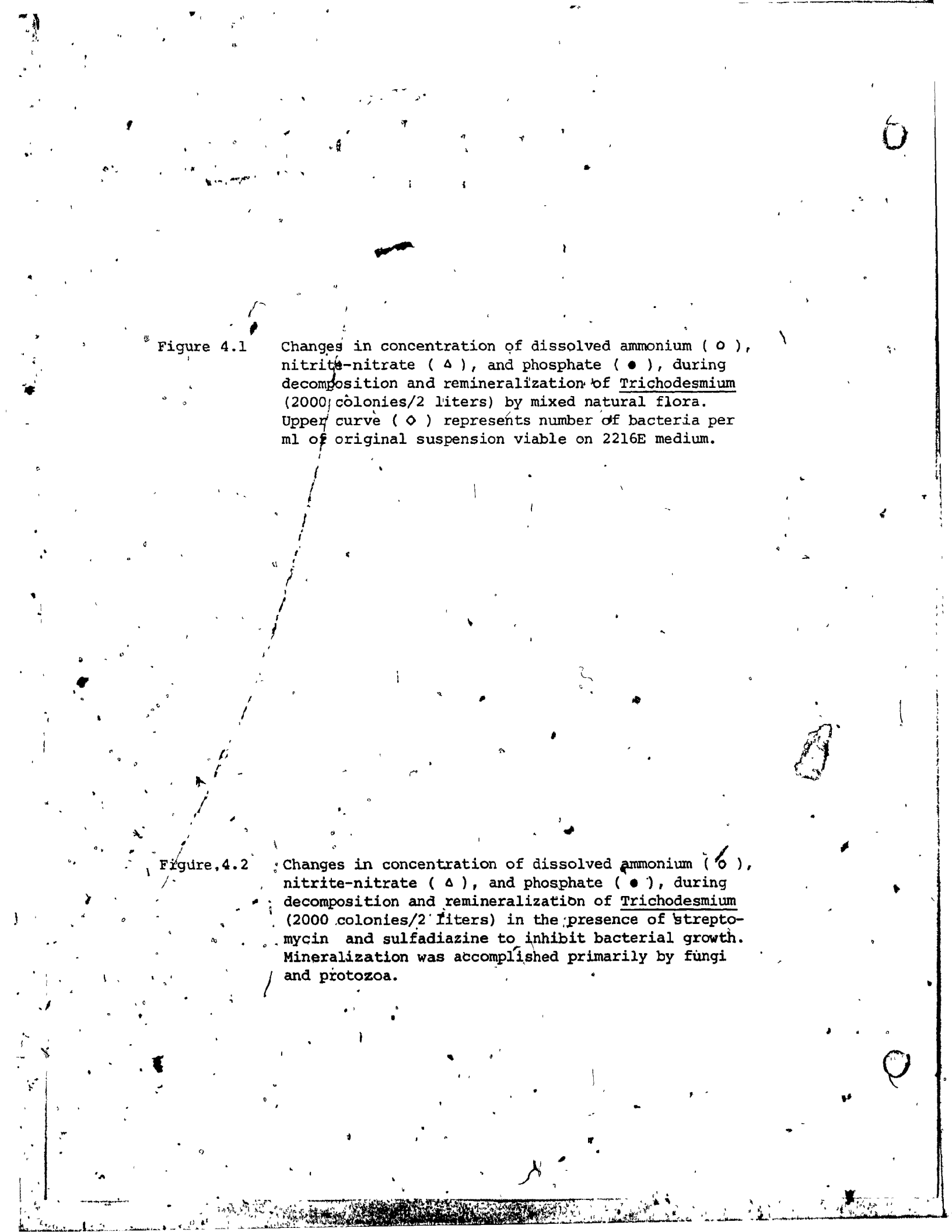
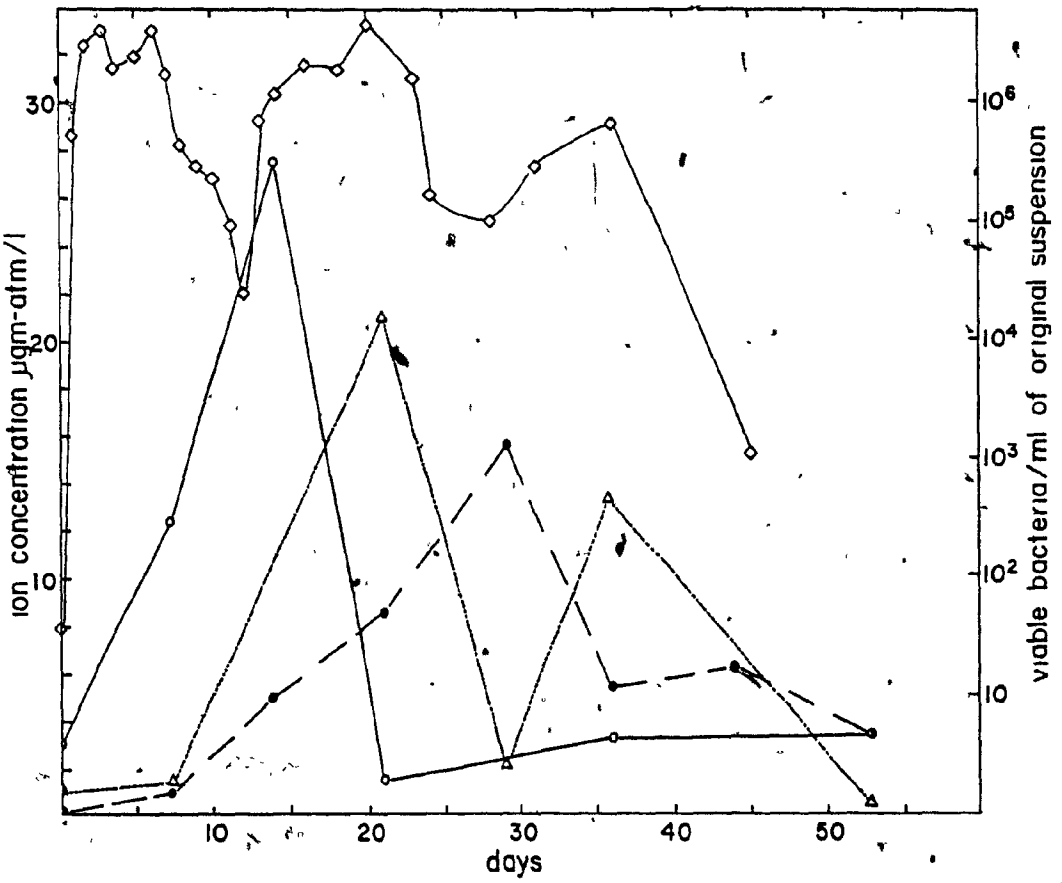
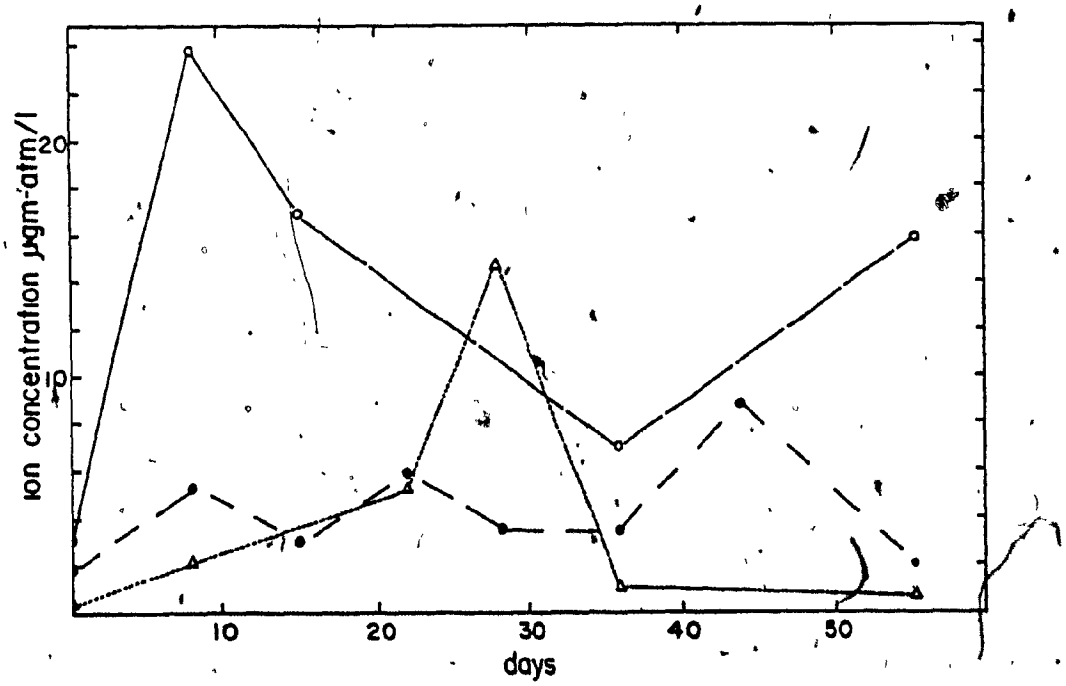


Figure 4.1 Changes in concentration of dissolved ammonium (o), nitrite-nitrate (Δ), and phosphate (●), during decomposition and remineralization of Trichodesmium (2000 colonies/2 liters) by mixed natural flora. Upper curve (◇) represents number of bacteria per ml of original suspension viable on 2216E medium.

Figure 4.2 Changes in concentration of dissolved ammonium (o), nitrite-nitrate (Δ), and phosphate (●), during decomposition and remineralization of Trichodesmium (2000 colonies/2 liters) in the presence of streptomycin and sulfadiazine to inhibit bacterial growth. Mineralization was accomplished primarily by fungi and protozoa.


ion concentration µgm-atm/l
viable bacteria/ml of original suspension
days
10
20
30
40
50
10⁶
10⁵
10⁴
10³
10²
10


ion concentration µgm-atm/l
days
10
20
30
40
50

around day 21.

In flask 2, where antibiotics did not permit growth of bacteria, remineralization was accomplished by fungi and protozoa which were not enumerated. The changes in dissolved chemical species were somewhat different than in flask 1. Ammonium appeared in large amounts within 8 days, and declined thereafter, but nitrite-nitrate did not show appreciable increase until around day 44. Phosphate levels also remained low, increasing only temporarily around day 28.

The pH in both flasks did not change throughout the experiment (8.15 ± .05).

4.1.4 Discussion

The rates of appearance and amounts of ammonium released in each flask during the first two weeks were similar, but in flask 1 where a large and varied bacterial population was present (introduced as inhabitants of the original Trichodesmium inoculum) this dissolved ammonium was subsequently converted to nitrite and/or nitrate. In flask 2, where bacterial growth was restricted by antibiotics, nitrite and nitrate did not accumulate to any great extent. Phosphate liberation in flask 2 was also less, and occurred more slowly than where a complete mixed flora was active.

If the amounts of ammonium and orthophosphate released in flask 1 are any indication of the quantities of nitrogen and phosphorus which may be mobilized from decaying Trichodesmium in situ, then it should be possible to crudely estimate the 'fertilization potential' of the Trichodesmium 'blooms' observed off Barbados.

About 0.025 µgm-atms ammonium were released from each colony in the experimental situation. At such quantities, 'blooms' like those of January and May 1975, where the Trichodesmium population above 35 m was around 40 colonies per liter, presumably represented the potential addition of approximately 1 µgm atm-ammonium per liter to the water (40 colonies/liter x 0.025 µgm-atms ammonium/colony). In the upper mixed layer, this addition would temporarily double the average ammonium concentration if added all at once.

The release of orthophosphate may be more significant, however, since about 0.02 µgm-atm phosphate was released per colony. Forty colonies, therefore, represent the potential addition of 0.8 µgm-atms phosphate per liter, or thirteen times the average concentration in the mixed layer (Steven et al., 1970).

In both flasks, the large increase in dissolved ammonium and nitrite-nitrate concentration encountered during the second week represents the release of about 0.35 µgm nitrogen from each colony. This was for colonies of about 10,000 cells (see Table 3.1 'standard' radial colonies) and 1.5 µgm carbon*. Using C/N ratios and cell nitrogen content data from the literature (5.6 - Marumo, 1975; 4.1 - Mague et al., 1977; 5 pgm nitrogen/cell - Carpenter and McCarthy, 1975) to estimate the nitrogen content of these colonies, one arrives at values between 0.3 and 0.5 µgm nitrogen/colony. If these values are correct they indicate a very large fraction of the Trichodesmium cell nitrogen was remineralized early in the experiment.

While the total amount of the various chemical species released in the experimental flasks may be relevant to the situation

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* Analysis provided by H. Reiswig using the wet oxidation technique outlined in Strickland and Parsons (1968).

in situ, their rates of appearance cannot be extrapolated. The experimental Trichodesmium biomass was unnaturally high compared to that in the western tropical Atlantic, and the near simultaneous lysis of the colonies in the enclosed volumes must have led to extremely high concentrations of dissolved organic material. The explosive growth of bacteria which this permitted made the water in flask 1 turbid between days 3 and 6, a phenomenon which does not occur in solution in situ because of rapid dispersion of localized concentrations of dissolved nutrients around the particles by turbulence. The in situ rates of remineralization are probably somewhat different than in these experiments, since in the sea the largest part of the processes must take place on the Trichodesmium particles themselves.

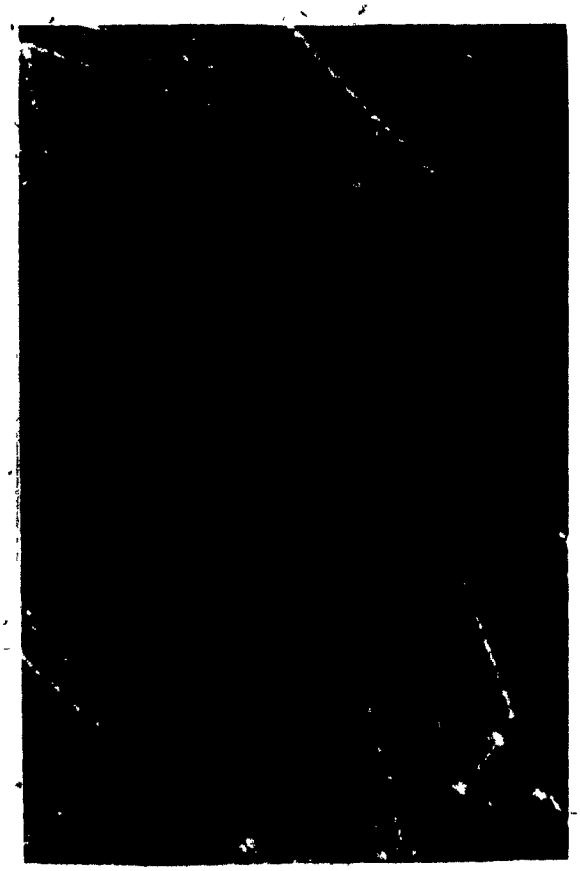
4.2 Trichodesmium detritus and decomposition in situ

The fate of the Trichodesmium biomass in the sea is of considerable interest. In the laboratory, Trichodesmium colonies inevitably died and lysed leaving an amorphous aggregate in which bits of Trichodesmium cellular debris, diatoms, dinoflagellate thecae and other matter could be recognized. Particles such as illustrated in Plate 4.1 were also commonly encountered in the counting chambers during the enumeration phase of the field work, and it became evident that a large part of the degradation and mineralization of Trichodesmium biomass must occur in the mixed layer. In the sea, the Trichodesmium filaments do not all lyse, as is usually the case in the laboratory. One or two well vacuolated filaments appear capable of providing buoyancy sufficient to retain the whole particle (often with one or two large hydrozoans) in the mixed layer, since the particles were often observed in discrete samples from 5, 15 and 25 meters.

Plate 4.1 *Trichodesmium* detrital particle; short fragments bound in an extensive mucilage. Scale bar at lower left indicates 50μ.

Plate 4.2 Close-up of detrital particle in Plate 4.1. *Trichodesmium* fragments, numerous diatoms (*Nitzschia* sp. 1 and *Mastogloia capitata* ? - see later Section 5.3.3.4) and extensive organic debris bound together by mucilage. Scale bar indicates 10μ.

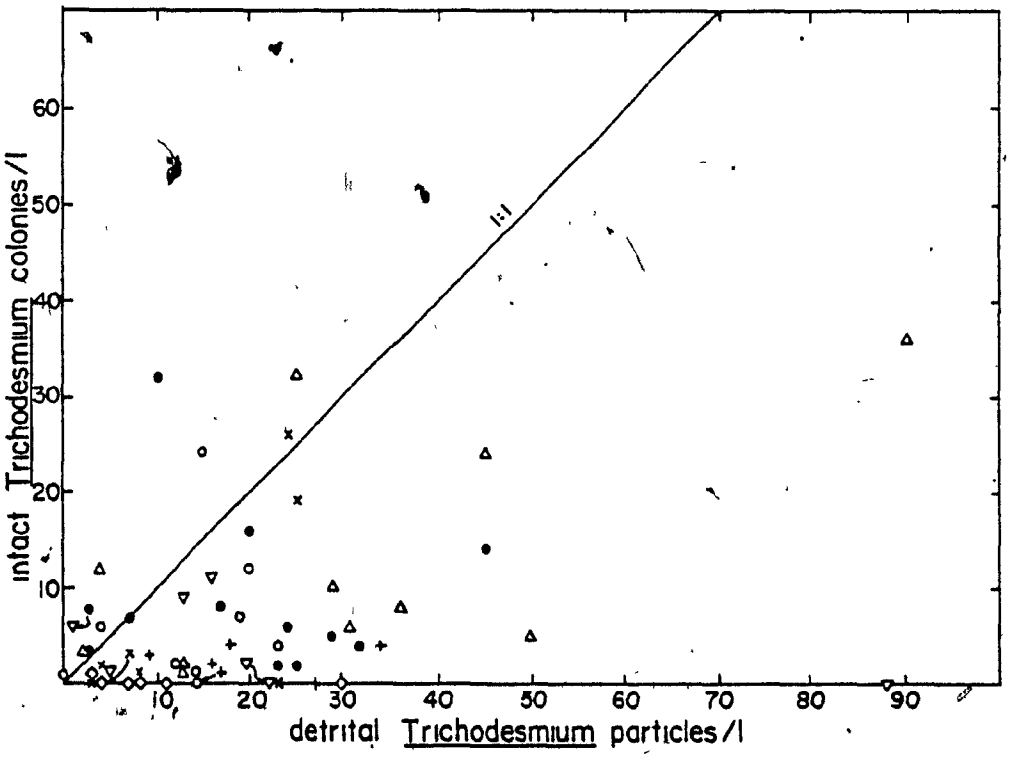
4.1



4.2

In sixty-two 1 liter, discrete samples from 5 to 100 m depth, collected between April and July 1975, these detrital aggregates containing a few recognizable Trichodesmium cells and/or filaments were counted. Figure 4.3 illustrates that, in most of these samples, the detrital Trichodesmium was more abundant than the intact healthy colonies. Unlike dead or dying diatoms or dinoflagellates, a large proportion of dying Trichodesmium cells benefits from the buoyancy of the other cells in the colony and does not sink immediately. In fact, completely lysed Trichodesmium debris formed in decaying plankton in the laboratory was on several occasions kept for as long as two weeks in the refrigerator. At the end of this time the masses were still floating, evidence that the gas vacuoles had not all collapsed when the cells lysed. The fact that the large ammonium and phosphate release observed during the decomposition experiment occurred before the complete disintegration of the detrital particles suggests that similar release might occur in situ in the mixed layer.

Figure 4.3 Comparison of the number of intact Trichodesmium colonies and detrital particles of Trichodesmium origin in one liter samples from various depths taken at the 8 km station between April and July, 1975. 5 m (●); 15 m (o); 25 m (▲); 35 m (▽); 50 m (+); 75 m (×); 100 m (◇).


intact Trichodesmium colonies/l
detrital Trichodesmium particles/l
1:1
10
20
30
40
50
60
70
80
90

5 THE TRICHODESMIUM PERIPHYTON

5.1 Introduction

Early in the field work, high power microscopic observations of Trichodesmium demonstrated that large numbers of other microorganisms could frequently be found associated with the algal colonies, either loosely lodged among the filaments at the edges or ends of the colonies or deeply embedded within the central tangle of filaments. Further extensive examination of Trichodesmium collected at various depths, distances from the island and times of the year, established that the phenomenon was common in colonies taken from the North Equatorial Current waters, but less so in younger Trichodesmium populations which arrived at Barbados in fresher water masses of Guiana Current origin (see Sections 2.4.3 and 2.4.4).

A search of the literature revealed only a comment by Wood (1965) that Trichodesmium sometimes accumulated a pseudoperiphyton, and mention by Margalef (1968) that "epiphytic bacteria often occurred in (sic) the pseudovacuoles of the algal cells". The same author noted attached bacteria and fungal sporangia in some colonies. Bjornberg (1965), Calef and Grice (1966) and Tokioka and Bieri (1966) had described the association between the larval stages of the harpacticoid copepod Macrosetella gracilis and Trichodesmium colonies in the western tropical Atlantic and in the Kuroshio. There was no mention of the presence of other autotrophs or of the hydrozoan which may be observed in colonies collected near Barbados, and no indication as to the extent of the phenomenon.

What follows is a general description of the community of microorganisms commonly associated with Trichodesmium colonies collected from 'nonbloom' populations. The relationships between the alga and other members of the community are also considered, and the importance of the Trichodesmium colonies as pelagic substrates discussed.

5.2 Materials and methods

As has been described earlier, Trichodesmium was regularly collected at two serial stations located 4 km and 8 km off the west coast of Barbados, and irregularly at various other locations further offshore. Much more frequent collections were made from small open boats operated close to shore. Plankton was collected at the surface and at various depths using 0.24 mm mesh (no. 6) plankton nets of 1/2 m diameter. Collections below the surface were made with either Clarke Bumpus opening and closing nets, or throttle nets lowered cod-end first.

Plankton collected from offshore locations was usually preserved with formalin or Lugol's iodine immediately; however, on occasion Trichodesmium colonies were isolated from the bulk of the plankton using Pasteur pipettes into cool filtered seawater and brought ashore live. Every effort was made to guard against exposure to the bright tropical sun, and live plankton was accordingly kept in the dark in ice coolers. Most observations of live material were from collections made within 2 km of the coast, since on these occasions observations could begin within 10 or 15 minutes of the collection.

In the laboratory, a portion of the plankton was immediately transferred to a larger volume of seawater. Individual Trichodesmium colonies were picked out using large bore Pasteur pipettes and carefully transferred to large volumes of cool filtered seawater where they were held until required (only one or two colonies per 100 ml*). Single colonies were transferred to glass slides in a large drop of water and a coverglass laid on. Microscopic examinations using a Leitz Ortholux microscope equipped with phase optics began with general observations on the colony morphology and size, and of any macro-symbionts such as copepod nauplii or hydroid polyps. Water was then slowly removed from under the coverglass with a scrap of paper towel, thereby flattening

* where colonies were kept in very small containers they lysed sooner.

the colony and allowing observations at higher magnification. Very few symbionts could ever be detected during low magnification observations of intact 'unsquashed' colonies. Trichodesmium colonies collected and handled in the manner described above remained at least morphologically intact for up to 24 hours. Under even low natural sunlight (15% I), however, photosynthesis and nitrogen fixation declined after three or four hours. At higher irradiance this decline occurred earlier and under the very intense irradiance necessary for high power microscopy some colonies bleached and lysed almost immediately.

During 1974 and 1975 microscopic observations were primarily concerned with identification and recognition of the various community members. Beginning in November 1975 and continuing until May 1976, collections were made at about weekly intervals at the surface approximately 1 km offshore. Five or six colonies of each conformation were examined from each tow and the presence or absence of each group noted.

Several attempts were made at prolonging the life of the Trichodesmium colonies in the laboratory, so that growth and development of the community could be followed. These were unsuccessful, but test tubes mounted on a vertically revolving wheel proved useful in maintaining polyps of the hydrozoan described in Section 5.3.3.6. The Trichodesmium colonies always lysed within a few days, but occasionally the detrital particles, held together by mucilage, adhered to the walls of the test tubes. Polyps of the hydrozoan embedded in three such particles were maintained for nine weeks in this apparatus with frequent changes of water and introduction of small copepod nauplii, newly hatched brine shrimp or very finely ground fish meal.

Diatoms could easily be observed in live, water mounts, but for identification they were cleaned of organic material leaving only their siliceous frustules. Unpreserved individual Trichodesmium colonies were

dried onto microscopic slides, and concentrated 30% v/v hydrogen peroxide was then applied directly to the alga. Gentle warming hastened the oxidation and evaporated the peroxide. After several re-applications to insure complete clearing the peroxide residue was washed off with distilled water.

This procedure worked reasonably well for unpreserved material, but formalin or alcohol preserved material had to be incinerated for five to ten minutes at 500°C to remove all of the organic matter. Both techniques cleared the opaque organic material and did not severely damage the diatoms. The Trichodesmium filaments themselves conveniently produced a thin clear residue which allowed delineation of the trichomes and location of the diatoms within the colony.

Cleaned colonies were mounted in Hyrax (a medium of very high refractive index) which sufficiently accentuated the striations of the larger and heavier species so that they could be identified by light microscopy using a Leitz Ortholux research microscope or a Zeiss Ultraphot photomicroscope. Smaller, highly silicified species were examined in colonies which were dried directly onto aluminum mounting stubs, combusted and prepared for electron microscopy by coating with atomized carbon. Examination and photography was done using a Cambridge Stereosan Scanning Electron Microscope.

5.3 Observations and discussion

5.3.1 Description of the Trichodesmium colony as a substrate

The filamentous and colonial habit of the two Trichodesmium species most common in Barbados waters will be discussed in Appendix A.1, and the differences in colonial morphology illustrated in Figure A.1. The parallel colonies of both T. thiebautii and T. hildenbrandtii, where filaments are aligned in parallel like the bristles in a broom, present

a similar physical aspect - long relatively smooth particles having frayed ends and long narrow interfilamental spaces at the center of the colony. In contrast, the radial colonies of both species possess a more complex construction. In apparently younger, more rapidly growing radial colonies of T. thiebautii collected from 'blooms', the filaments were very tightly arranged in a concise symmetrical fashion, providing a very complex outer surface and network of peripheral interfilamental spaces but very little space at the center of the colony. Colonies of this species drawn from the water masses of the North Equatorial Current generally contained fewer filaments which were arranged in a less compact manner. These colonies and the very loose asymmetrical radial colonies resulting from the disruption of parallel colonies of either species present vastly increased networks of small enclosed irregular spaces within their actual framework. In purely physical and morphological terms, the differences between the species are not as great as the differences between the two colony types.

5.3.2 The Matrix

Related to the physical architectural differences between the colony types and apparently more important than species differences, is the much greater accumulation in loose radial colonies than in parallel colonies of a mucilaginous material forming a 'matrix' at the center of the colony. This material is not present in the majority of symmetrical, concisely arranged T. thiebautii colonies from 'blooms' but accumulates in considerable quantity in loosely arranged colonies.

Staining with alcian blue at pH 0.5 and 2.5 essentially after the method of Parker and Diboll (1966) shows that the mucilage is a carboxylated polysaccharide material, and the uneven nature of the uptake of the stain suggests variability in its consistency. Handa

(1975) has found the hotwater slime fraction of Trichodesmium collected from the Kuroshio contains principally glucose and mannose. It seems likely that these two components were derived from the matrix since observations at Barbados indicated that there is very little other external mucilage in Trichodesmium colonies. Trichodesmium does not produce thick extracellular investments like some other blue-greens (Fritsch, 1965), but only a very thin sheath which apparently may be absent in some cases (Van Baalen and Brown, 1969). Examination of Trichodesmium collected at Barbados reveals a very thin, sometimes discontinuous layer of polysaccharide material along most of the length of the filaments. This material is clear and invisible except when stained, and appears in greater amounts along the unhealthy cells often encountered at the periphery of the colony (these cells, usually the last ten or fifteen at the end of some but not all trichomes, are often unpigmented, partially plasmolysed or even completely empty). Quite large sheets of this polysaccharide can occasionally be seen sloughing off the ends of these trichomes, and it is possible that the matrix represents an accumulation of material produced in this manner by the alga itself. Another possibility is that the alga is stimulated to produce large amounts of gelatinous material by a fungal infection, as has been noted by Jagg and Nipkow (1961) when Oscillatoria rubescens is infected by certain chytridaceous fungi. At least one chytrid is regularly found in the Trichodesmium matrix.

The origin of the matrix is unclear, however. L. Borstad (in prep.) has isolated bacteria from Trichodesmium colonies which produce copious polysaccharide on solid media and in liquid culture, and it therefore seems likely that the matrix is at least partially of bacterial origin. As well as the bacteria, there are frequently other organisms present which produce their own mucilage. At least one unidentified organism which appears to be a unicellular cyanophyte can be observed encapsulated in its own mucilage, and several species of benthic diatoms known to be capable of secreting sediment binding slime are also commonly

embedded deep within the colonies. The matrix therefore seems to be quite heterogeneous depending upon the organisms present.

The multicellular nature of the Trichodesmium colonies is also important. Freshly collected colonies reveal a great deal of variability with respect to pigmentation, vacuolation and cell size. Some trichomes contain groups of short, weakly pigmented nonvacuolated cells with only partially completed crosswalls. These young dividing cells alternate with darker (especially when stained with Lugol's iodine), well vacuolated cells, giving the trichome a banded appearance. Some trichomes may be completely comprised of younger cells while other trichomes in the same colony are older, with many completely empty and plasmolyzed cells. Like any population, Trichodesmium colonies contain cells in all phases of growth. As individual cells, especially those near the center of the colony, die and lyse, their protoplasm will further enrich the matrix and increase its heterogeneity. Just as populations age, so too do Trichodesmium colonies. More debris accumulating from a larger number of dead and dying cells will be present. The retention of Trichodesmium protoplasm, pigment and debris can be directly observed.

5.3.3 The community members

5.3.3.1 Bacteria

Bacteria were the most commonly observed microorganisms found in association with Trichodesmium colonies (Plates 5.1 and 5.2; all plates collected at end of this section). While nearly every colony examined during the course of this two-year study contained small numbers of bacteria, they were much more abundant in the apparently older colonies drawn from 'non-bloom' populations. Such Trichodesmium colonies

contained fewer filaments and cells, larger numbers of dead and dying cells than colonies from 'blooms' and usually had accumulated a significant amount of mucilage.

By far the largest number of bacteria associated with Trichodesmium colonies were intimately associated with the mucilage of radial colonies and detrital material contained in it, but small rod and corniform types could occasionally be observed directly attached to the Trichodesmium cells themselves. These were usually located around the intercellular junctions, a portion of the cell wall which Van Baalen and Brown (1969) have shown is considerably thinner than other parts. Walsby (1968) has observed secretion of mucilage at these locations in freshwater Oscillatoria, and similar production of polysaccharide was observed along Trichodesmium filaments during this study, making it likely that these bacteria are attracted to the localized source of nutrients. Whether they lead to breakdown of the blooms, as suggested by Carpenter and McCarthy (1975) is questionable. Observations at Barbados of intact colonies have shown that such attached bacteria only constitute a very small proportion of the total bacterial population. They could also be occasionally observed attached to diatoms, or the empty 'escape tubules' of fungal sporangia (Plate 5.2) found in some colonies. Bacteria were never recognized inside Trichodesmium cells.

Planktonic algae often have bacteria attached to or occurring within their slime sheaths, in fact a large part of the bacterioplankton may be epiphytic rather than truly planktonic except in very eutrophic waters (Wood, 1965). The role of these bacteria is uncertain. Campbell (1977) indicates that they are probably often saprophytic causing no harm. Intuitively, the location, abundance and physical relationship of the bacteria to the Trichodesmium colonies suggest their primary role on these particles is one of remineralization. This suggestion is supported by work of L. Borstad (in prep.) who reports that essentially

all bacteria isolated from Trichodesmium colonies are aerobic heterotrophs and many produce ammonium by breaking down more complex nitrogenous compounds. In this sense they may form the basis of the community of organisms found in the colonies, since their presence presumably leads to a local supply of inorganic nitrogen and other nutrients as Trichodesmium cells die. In the oligotrophic regions in which Trichodesmium can be found, this association may in fact be important in the alga's nutrition. Death of a few algal cells will ultimately lead to local production of compounds such as ammonium which may be scavenged by Trichodesmium cells or other autotrophs within the colony. Much of organic material accumulated in the Trichodesmium colonies as bacterial biomass appears to become food for protozoans (Section 5.3.3.3).

The bacteria observed in Trichodesmium colonies exhibited a very great diversity of morphologies and motilities, perhaps a reflection of the pleomorphic character of most marine bacteria. There were some data suggesting that the two different Trichodesmium colony types exhibited different types of bacteria (filamentous bacteria were much more common in parallel colonies than in radial colonies) and it is therefore perhaps possible that bacteria influence algal colony morphology as has been reported with other cyanophytes (cf. Wyatt and Henderson, 1971). This and other aspects of the occurrence and physiological characteristics of the bacteria associated with Trichodesmium colonies are the subject of a thesis by L. Borstad (in prep.), and will not be discussed further here.

5.3.3.2 The Fungi

One of the potentially most important groups of microorganisms in the Trichodesmium matrix community is the fungi. Fungi are extremely common in the sea, principally acting as decomposers (Lyles, 1969), and

it is therefore not surprising to find them in the Trichodesmium mucilage which is a readily available carbon source.

The fungi observed in Trichodesmium colonies are members of the primitive class Phycomycetes, possibly of the Thraustochytriaceae (Dr. E.B.G. Jones*, pers. comm.). There are very likely more than one species present, but it is difficult to be certain without culturing them and following their life cycle in detail. The flask-shaped cells in Plate 5.2, more often observed without the open tubes, were very common (those illustrated here are heavily infested by bacteria). Other stages often observed were the small, highly motile, biflagellate zoospores, the amycelial sporangia and small objects resembling fungal resting cells.

The aquatic phycomycetes commonly parasitize other micro-organisms, including the blue-greens (Canter, 1972) and are known to produce epidemics in which large populations of Anabaena flos-aquae are destroyed (Canter and Willoughby, 1964). In no case, however, was any of the forms recognized as fungi ever detected parasitizing living Trichodesmium cells or any of the other community members during this study. All were embedded in the mucilaginous matrix of the radial colonies, and while one or two cyst-like and sporangium-like cells could sometimes be observed adhered to the outside of parallel colonies or lodged within the filaments of radial colonies with no mucilage, it was in the matrix that large numbers occurred, and the rhizoid systems developed. In the Trichodesmium biocoenosis, the fungi appear to be primarily saprophytic, living in and absorbing nutrients from the matrix.

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* Dr. E.B.G. Jones, Department of Biological Sciences, Portsmouth Polytechnic, Portsmouth, England.

Fungi are important ecologically in many ecosystems as saprophytes and decomposers (Lyle 1969). They obtain all of their nutrient requirements through absorption of dissolved material from their surroundings and produce enzymes which act externally and over which they have no control. As a result they may be important factors influencing their own environment and that of other cohabiting organisms (Harley, 1972). In living Trichodesmium colonies the fungi apparently act principally on the matrix and on the mixture of waste products it contains, but after death of the alga they will compete with the bacteria in remineralizing the debris. In the decomposition experiments described in Section 4, fungi accomplished remineralization in the absence of bacteria.

5.3.3.3 The Protozoa

Trichodesmium colonies of both conformations harboured a small assortment of protozoa compared to that observed in filamentous algae attached to boats or moorings around Barbados. Unlike benthic substrates Trichodesmium never supported attached or sessile forms of the Suctoria or Sessilia. All of the protozoa observed in the algal colonies were small (less than 40μ long) freeliving and microphagous or saprophytic. There were no carnivores and none which attacked the diatoms or Trichodesmium itself.

Of 405 colonies of both conformations systematically observed during 1976, 24% of the radial colonies (56 of 236) and 14% of the parallel colonies (23 of 169) carried protozoa. The larger percentage of radial colonies infested (X^2 indicates significant difference at 1%) is probably related to the greater conformational complexity and larger bacterial populations of radial colonies. While the numbers of individual protozoans per Trichodesmium colony were not routinely

counted, the notes made of the observations often described them as 'abundant' or 'teeming'. One such colony in which a count was attempted contained more than 150 individuals, all of the same type. These nearly monospecific populations and their clear association with colonies containing abundant bacteria, suggest that they arise through rapid multiplication of one or two individuals in response to the plentiful and concentrated food supply (bacteria) in the Trichodesmium colonies. The variability in the type of protozoans present in colonies of the same size and conformation collected at the same time indicates the initial encounter is probably accidental.

Observations at Barbados indicate that the protozoans only inhabit the surface of the colonies, mostly the interfilamental spaces at the periphery of radial colonies and the frayed ends of parallel colonies. None were observed moving through the viscous mucilage, although they did graze its surface and the surface of the filaments where colonies were not squashed. In very loose disintegrating colonies and in decaying 'clumps' of Trichodesmium where greater access to the interior of the colony was afforded protozoans were abundant and no doubt very important in increasing the rate of remineralization of the particle. They could easily be observed ingesting bacteria and other small particles in the mucilage. Anderson (1977) has recently reported a bacteriophagous amoeba from Trichodesmium taken off Bermuda.

None of the protozoans exhibited obvious behavioural modifications restricting them to the colonies, and they seemed quite free to leave the filaments. Protozoa do, however, commonly exhibit positive chemotaxis and thigmotaxis (Hymann, 1940) and these reactions could serve to retain individuals where turbulence is not great or other surfaces are not encountered. Organisms not lost in these manners may encyst in the mucilage of the colonies. Fragmentation of decaying detrital particles will liberate other individuals.

No concerted efforts were made to identify the organisms observed. Rhizopods of the order Amoebida were seen on a few widely separated occasions. Most of the ciliates were recognizable at the family level and within the Hymenostomatida, one Tetrahymenid and three Cohnilemibid forms were recorded commonly. The Hypotrichida were represented by at least one species of Euplotidae and perhaps one of the Aspidiscidae.

Flagellates were as important as the ciliates numerically, but less diverse. There were two or three biflagellates, about 5-15μ long possibly of the Bodonidae, and one or two other unidentified forms.

5.3.3.4 Diatoms

Seventeen species of diatoms representing eleven genera were recorded as members of the Trichodesmium periphyton examined here (Figure 5.1, Table 5.1 and Plates 4.2, 5.3-5.7). Only nine species were common (i.e. present in more than 20% of those colonies with diatoms); the other eight species occurred in less than 5% of the colonies with diatoms. All were pennate species and many were types commonly regarded as benthic or epontic. While diatoms were recorded as present in 39% (n = 217) of the radial colonies and 32% (n = 168) of the parallel colonies examined systematically, the number of both individuals and species in any one Trichodesmium colony was highly variable.

Unlike diatom communities epiphytic on inshore benthic plants (cf. Lee et al., 1975), the diatom assemblages in Trichodesmium colonies were of low diversity, consisting of only two or three species (at most five) per colony. The species composition and the number of

Figure 5.1 Some of the diatoms commonly found in Trichodesmium colonies. All species to same scale (bar equals 10μ).

1. Nitzschia longissima
2. N. longissima var. reversa
3. N. closterium
4. N. sp. 1
5. Mastogloia (capitata ?)
6. Caloneis sp.
7. Amphiprora (paludosa ?)
8. Achnanthes sp.
9. Navicula sp. 2
10. Cocconeis scutellum var. ?
11. Epithemia sp.
12. part of a Trichodesmium thiebautii filament for comparison of size.

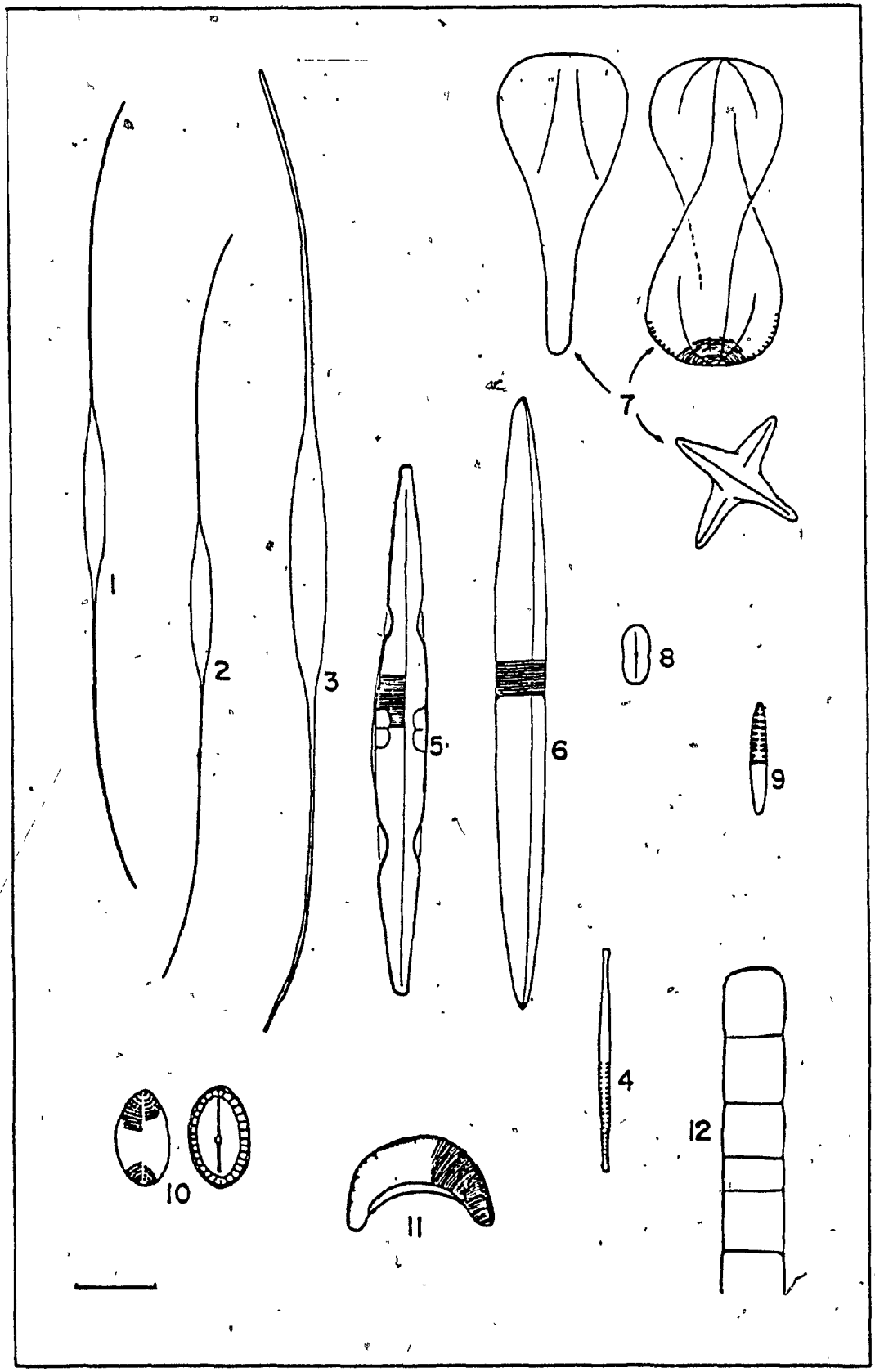
1
2
3
4
5
6
7
8
9
10
11
12

Table 5.1 Diatoms observed in Trichodesmium colonies.

	frequency of occurrence*	location in colony†
Achnanthes Bory		
A. sp. 1	C	M
Amphiprora Ehrenberg		
A. paludosa Wm. Smith ?	C	M
A. sp. 1	O	M
Caloneis Cleve		
C. sp. 1	C	P
Cocconeis Ehrenberg		
C. scutellum var. ?	O	M
Epithemia de Brebisson		
E. sp. 1	O	M
Grammatophora Ehrenberg		
G. angulosa	O	M
Hantzschia Grunow ?		
H. sp. 1	O	M
Mastogloia Thwaites ex Wm. Smith		
M. capitata (Brun) Cleve ?	C	P
Navicula Bory		
N. sp. 1	C	P
N. sp. 2	O	M
Nitzschia Hassall		
N. closterium (Ehr.) Wm. Smith	C	P
N. longissima (Breb.) Ralfs.	C	P
N. longissima var. reversa (Grun.)	C	P
N. sp. 1	C	P, M
N. sp. 2	O	M
N. sp. 3	O	M
Striatella Agardh		
S. sp. 1	O	M

* C - common; found in more than 20% of those colonies with diatoms.

O - occasional; found in less than 20% of those colonies with diatoms.

† P - found in parallel colonies and around the periphery of radial colonies.

M - found embedded in the matrix of radial colonies.

individuals per colony was highly variable, however, even between colonies of the same size and morphology collected at the same time. While it might be expected that particles as small as Trichodesmium colonies could not support many diatoms, it was common to observe between 5 and 50 in a colony. On occasion much larger populations were present; Plates 5.4 and 5.5 show an extremely large mixed population of Cocconeis scutellum and Nitzschia sp. 1. Plate 5.6 is a scanning electron micrograph of a single radial colony which has been incinerated to partially clear organic material and reveal embedded Nitzschia sp. 1.

As already mentioned in Section 5.2, few periphytic organisms of any kind could be observed associated with Trichodesmium colonies which had not been at least partially flattened under a coverglass. When this was done, the motile Nitzschia sp. 1, N. longissima and N. closterium could easily be observed moving among the filaments at the periphery of the colonies, and even deep within the parallel colonies in the interfilamental spaces. The larger Mastogloia capitata, Navicula sp. 1 and Caloneis sp. were also to be found, lodged in the outer edge of the radial colony matrix and between the filaments of parallel colonies. The awkwardly shaped Amphiprora paludosa was only observed associated with radial colonies.

Some of the smaller species such as Cocconeis scutellum, Achnanthes sp. and Epithemia sp. were difficult to detect as they were always deeply embedded within the matrix of radial colonies, in the jumble of Trichodesmium filaments. Several of these species, particularly Achnanthes, were difficult to recognize as diatoms until the colony was cleared and mounted in Hyrax. In live mounts these species were enveloped in an opaque mucilage of their own and were only discernible as oblate featureless cells. In this respect these species may be important contributors to the mucilage and to the strength of the matrix. Several species of benthic diatoms are recognized as important in binding loose sandy sediment by their mucilage (Round, 1971).

Like the diatoms belonging to the periphyton of floating Sargassum (Carpenter, 1970), the species found in Trichodesmium colonies are very lightly silicified and finely ornamented. This is rather unlike the heavier structure found in forms in the sediment or attached to benthic plants (see Lee et al., 1975) and may be a reflection of the pelagic existence of these forms. Wood (1966, 1971) has found a large number of benthic and epontic species in the oceanic regions of the western tropical Atlantic and eastern Caribbean, especially where water masses are passing over shallow shelves or banks. He assumes these banks and the pelagic Sargassum are the source of the benthic diatoms in the water column. The Trichodesmium diatoms may also be derived from the same sources.

The variability of the diatom assemblages observed in colonies of the same population indicates that several factors probably operate independently to determine the species composition and population size of any one Trichodesmium colony. After the initial accidental encounter in the sea, the success of the diatom in or on the colony can be expected to be affected by the community already established and hence the physical and chemical nature of the substrate.

As well as providing a substrate for primarily benthic species in the oceanic euphotic zone, it seems likely that the Trichodesmium colony also supplies nutrients or some other essential elements for diatom growth. There is evidence of widespread heterotrophy among marine diatoms (Lewin and Lewin, 1960; Lee et al., 1975; and references cited therein), and of excretion by many plants (cf. Fogg, 1966) including blue-greens. Some of the species recorded here are known to be capable of heterotrophic growth (Nitzschia closterium, Lewin and Lewin, 1960; Cocconeis scutellum, Lee et al., 1975). During the current study Nitzschia sp. 1 could be observed to demonstrate a strong chemotaxis to lysing Trichodesmium (see Plate 5.7).

Excreted organic compounds are not the only compounds expected in the matrix. The fact that many of the bacteria isolated from Trichodesmium by L. Borstad (in prep.) produce ammonium from complex compounds indicates that inorganic compounds may also be available locally.

5.3.3.5 The Dinoflagellates

In almost every radial Trichodesmium colony examined which possessed a matrix, some evidence was found of the presence of the non-motile stages of several individual dinoflagellates. The most common species represented was tentatively identified as Peridinium trochoideum (Stein) Lemmermann*. A second Peridinium, apparently P. avellana (Meunier) Lebour and a larger unidentified Gymnodinium-like species were also recorded.

The life cycles of many dinoflagellate species include one or more non-motile phases and in Peridinium, cell division occurs during one of these. There is cessation of movement, contraction of the protoplast and formation of a new thin membrane before the cell is released from the old theca (Plate 5.8). The thin-walled spherical cells thus formed may rest for a period (spherical cysts) or may soon divide (Fritsch, 1965) to form new thick-walled non-motile daughter cells which are also spherical and undifferentiated. The non-motile

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* P. trochoideum belongs to a group of species with very similar morphology which are difficult to identify with certainty (D. Wall, pers. comm., Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, U.S.A.).

stage terminates with the production of motile gymnodinoid, athecate individuals which eventually develop thecae as they mature. The adult, thecate Peridinium can undergo cell division again or produce hystrichospheres (resting cysts). In this case release of the protoplast from the theca results in production of a naked spherical cell which eventually acquires a thick wall and short calcitic spines. These cysts are resistant to conditions adverse to the motile stages and can remain viable for long periods of time (Wall et al., 1970). There is also evidence that they may serve a sexual function in at least some species (Fritsch, 1965; Von Stosch, 1974). Wall et al. (1970) consider them a naturally occurring stage in the flagellate's life cycle.

In Trichodesmium radial colony matrices, two or three orange, spherical, naked P. trochoideum protoplasts were nearly always present, very often in the process of ecdysis (release of the protoplast from the theca), or in close proximity to their thecae. The consistency of the mucilage appears to impede the loss of the jettisoned shells and they can often be found in the matrix where no protoplasts remain. P. avellana has been tentatively recorded in the Trichodesmium colonies in this manner, but other stages of its life cycle have not been recognized.

The early pear-shaped divisional stages of P. trochoideum were commonly recorded and so were the smaller paired daughter cells which immediately follow division. Division itself was only observed twice. Thick-walled daughter cells were common, and on four occasions the escape of small gymnodinioid swarmers from these cells were observed. The newly released gymnodinioids did not show any particular affinity to the Trichodesmium colonies and eventually swam away. These liberated naked individuals apparently secrete a new theca after some time (Fritsch, 1965). There is considerable variability in

the life cycles of different dinoflagellate species, however (Fritsch, 1965), and naked gymnodinioids were not always the product of the vegetative cells. The Gymnodinium-like cells recorded from the matrix were first observed as large nonmotile grey coloured cells, which then contracted within a very thin envelope, allowing the motile cells to work themselves free. The newly released individuals were thecate biflagellates and swam strongly.

As well as the various stages of the vegetative divisional phases of P. trochoideum described above, what may have been maturing spinous cysts of this species were observed on two separate occasions at Barbados. The idea that Trichodesmium could harbour resting cysts is attractive, but there is no evidence to suggest that this occurs to any significant extent at Barbados. While it is difficult to assess the quantitative importance of this association between dinoflagellates and the blue-green, it appears to be restricted (at Barbados) to a few species and then with the temporary non-motile phase accompanying cell division of the dinoflagellate.

Dinoflagellates as a group are exceedingly common in tropical oceans and P. trochoideum is one of the most widely distributed dinoflagellate species at low latitudes. It is, however, regarded as a neritic form, and is assumed to be meroplanktonic (Wall et al., 1970). The importance of its relationship with Trichodesmium may lie in the possibility that at least a portion of the P. trochoideum population is holoplanktonic. If the nonmotile stage can be prolonged, cells carried in Trichodesmium colonies may seed new growth in areas considerably removed from the location of the parent population.

This association has not been reported previously. If it occurs between Trichodesmium and other dinoflagellate species it could be important in red tide research.

5.3.3.6 Hydrozoa

The largest of the symbionts closely associated with Trichodesmium colonies for extended periods are the athecate hydranths of a previously undescribed hydrozoan which Borstad and Voss (in prep.) have named "Pelagiana trichodesmiae". The systematics of this cnidarian are not of direct concern here, and since they are largely the work of Dr. A. Voss*, of the University of Toronto, they will not be discussed in detail, except to mention that a new genus Pelagiana within the Pandeidae will be established within the order Anthomedusae. The new genus name will be used here for convenience only, but the reader should note that it is unpublished at the time of deposition of this thesis and is therefore not established.

The complete life cycle of this cnidarian is unknown at present, but Figure 5.2 represents a partial reconstruction of events, from microscopic observations of a large amount of freshly collected material taken during 1974-1976. Attempts at maintaining the hydrozoans in the laboratory were only partially successful. At Barbados, they lived for nine weeks but did not feed well, and succumbed before producing gonophores. Specimens shipped to Toronto also died, and this description of the organism and its life cycle is therefore complete only in so far as it is closely associated with Trichodesmium. The hydranths have only been observed in radial colonies with abundant mucilage. It is likely that their complete absence from parallel colonies is related to the weaker colonial structure and lack of a matrix in these colonies.

The earliest stage associated with Trichodesmium colonies which has been recognized is the planula (two slipper-shaped planulae,

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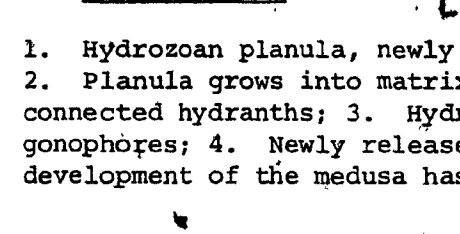
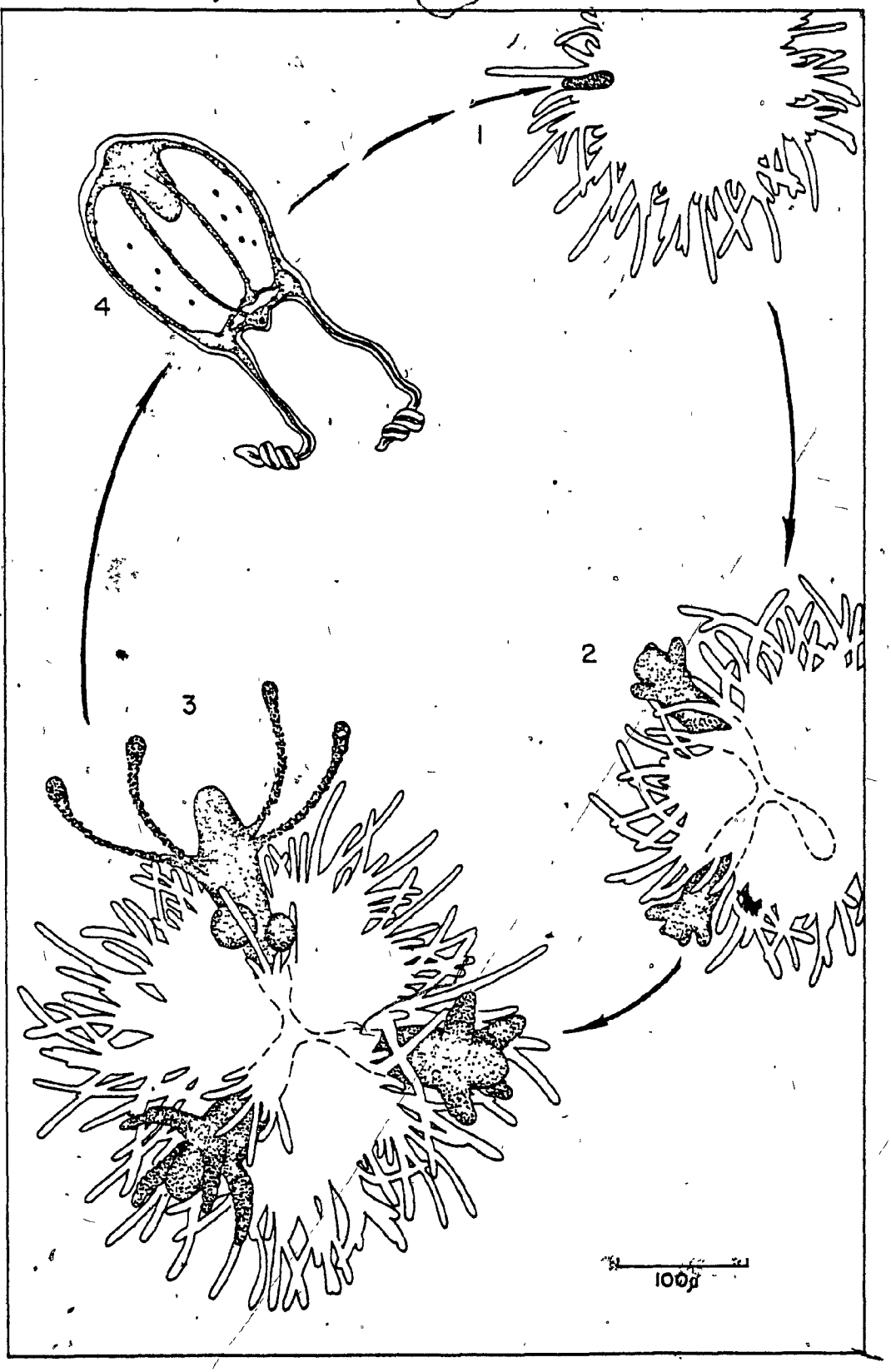
* Department of Zoology, University of Toronto, Toronto, Ontario, Canada

Figure 5.2 Relationship between the hydrozoan *Pelagiana trichodesmiae* and *Trichodesmium* colonies.



1. Hydrozoan planula, newly embedded in colony; 2. Planula grows into matrix, giving rise to interconnected hydranths; 3. Hydranths mature and produce gonophores; 4. Newly released medusa. Growth and development of the medusa has not been observed.


1
2
3
4
100µ

both approximately 30 x 40μ have been recorded lodged in the periphery of radial colonies, one in January and the other in May 1975). The planula grows into the matrix at the center of the colony and gives rise to as many as six identical hydranths which are connected by an irregularly branching stolon. The large maturing hydranth is the most frequently observed stage in the Trichodesmium collected near Barbados.

Mature polyps with medusa buds or gonophores (Plate 5.9) were seen less frequently - in May and October 1975, and June 1976. As many as four may grow on each hydranth. In June 1976, a "Pelagiana" polyp with a large apparently ripe gonophore was isolated from the plankton, and produced a minute two-tentacled medusa in the laboratory. The medusa, depicted in Figure 5.2 and in Plate 5.10, has not been recognized in the plankton, and nothing is known of its development, growth or reproduction.

The stage of "Pelagiana" life cycle most important to the Trichodesmium community is undoubtedly the sessile hydranth. These usually occur in groups of three or four but often as many as six may be present. The "Pelagiana" colony may have the ability to produce more individuals, but the polyps are relatively large compared to the Trichodesmium colonies. The hydranths are always spaced equidistantly around the surface of the Trichodesmium colony. Six polyps per colony appears to be the number above which interference between individuals becomes severe. The weight of each hydranth may also be important, since too much additional mass will cause the whole assemblage to sink.

Like most hydroids, "Pelagiana" hydranths are voracious feeders, and they can often be observed engorged on large copepods (Macrosetella gracilis adults) and even chaetognaths. Some of the most common prey for "Pelagiana" hydranths, however, seem to be the naupliar stages of M. gracilis. Trichodesmium colonies are known to attract the juvenile stages of this copepod, and are thought to be essential for the success of this species in oceanic regions (Björnberg, 1965; Calef

and Grice, 1966; Tokioka and Bieri, 1966). During the present study, the nauplii and early copepodites of M. gracilis were often observed clinging to Trichodesmium colonies where "Pelagiana" were not present, and were also noted as prey for the polyps on numerous occasions. The attraction which Trichodesmium seems to have for the copepod affords a great advantage to the hydrozoan, increasing the number of potential prey they would otherwise encounter only by chance. Conversely, the presence of the hydranths should very effectively reduce any predation on Trichodesmium and the enclosed microorganisms by all but very large zooplankton and fish.

An extensive search for "Pelagiana" hydranths on benthic algae, in the 'aufwuchs' of floating debris of all sorts, and on moorings at Barbados, failed to locate them. The search did not locate another substrate comparable to Trichodesmium, and it may be that "Pelagiana" is restricted to this alga. At Barbados, colonies bearing the hydrozoan polyps can usually be found throughout the year in the mixed layer. There is no apparent seasonality involved in the appearance of the hydranths or of their reproduction. As already mentioned, they occur only in radial colonies with abundant mucilage, and may occupy as much as 40% of such a population. Therefore, at Trichodesmium densities (radial colonies) of 700 per m^3 in the mixed layer of 'older' North Equatorial Current water masses, approximately 300 colonies per m^3 would possess "Pelagiana" polyps. The average Trichodesmium colony usually carried four polyps - amounting to about 1200 "Pelagiana" polyps per m^3. Such densities must be significant in the ecology of the euphotic zone.

While Trichodesmium colonies bearing "Pelagiana" polyps may be collected at any time of the year at Barbados, their abundance seems related to the condition of the Trichodesmium population. Further, it seems that the broadcast of eggs or planulae from the medusae must be a relatively sporadic or isolated event, since polyps may be abundant in

colonies collected one day and completely absent the next day in water of apparently the same origin.

However, sporadic or patchy the distribution of the hydrozoan is on the small scale, "Pelagiana" appears to be widely distributed throughout the North Atlantic, since Dr. E. Carpenter* (pers. comm.) found it to be very common in Trichodesmium colonies collected from the '18° Sargasso water' between Spain and Bermuda during June 1975, after being alerted to its presence at Barbados.

5.3.3.7 Copepod nauplii

As already mentioned, the association between the copepod Macrosetella gracilis and Trichodesmium has been previously recorded in the western tropical Atlantic. At Barbados, the naupliar stages of this copepod were also observed clinging to colonies. During systematic observations of 373 colonies of both conformations, 16 colonies (4%) were encountered which carried nauplii. Casual observations during 1974-1975 suggested that M. gracilis was more commonly found in parallel colonies than on radial colonies, and this was also noted during the systematic observations. (12 of 168 parallel colonies, 4 of 205 radial colonies carried nauplii.) A X^2 test indicated that the difference was significant at the 95% level.

This difference may be related to the greater ease of movement for the nauplii on the parallel colonies, upon which they can move about freely. On radial colonies their movement is severely restricted, and such colonies also harbour "Pelagiana" polyps for which M. gracilis is a potential prey.

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* Dr. E. Carpenter, Marine Science Center, State University of New York, Stony Brook, New York, U.S.A.

Björnberg (1965) found that M. gracilis nauplii could be reared more successfully if Trichodesmium colonies were added to the rearing vessel, and suggested that the alga provided a substrate and perhaps also a food source for the copepod. In the experience of the author, Trichodesmium always died and lysed within a few hours of its removal from the sea. The very large bacterial populations which resulted (see Figure 4.1) may in fact have provided the food for the nauplii in Björnberg's experiments. During observations of live material at Barbados, it was not possible to confirm that the nauplii were actually ingesting Trichodesmium cells. The copepods did move about actively on the colonies, often agitating the trichomes violently, but disappearance or lysis of Trichodesmium cells was never detected. The mouth parts of M. gracilis are quite small, and it seems more likely that the animal feeds on mucilage, bacteria, fungi or protozoans in the colonies.

5.3.4 Discussion

The open oceans in tropical and subtropical regions are generally extremely barren, and contain little particulate matter (Riley, 1963). For many meroplanktonic and benthic organisms this is an impossible environment because it is essentially bottomless. A few shallow water benthic organisms can traverse the areas by extending the length of their planktonic phase, or by attaching to other swimming organisms (Scheltema, 1971), and a few meroplanktonic microorganisms have been able to colonize particles such as organic aggregates (Riley, 1963), mucus structures (Aldredge, 1972) or foraminifera (Aldredge and Jones, 1973). It is evident that Trichodesmium colonies present similar colonizable particles. There are several advantages to be gained by the organisms grouped in the Trichodesmium community described here.

Trichodesmium colonies are abundant and widespread throughout the tropical and subtropical oceans, and are concentrated in the upper euphotic zone by virtue of the buoyancy provided by their gas vacuoles. Since many other cyanophyceae are capable of altering their position in the water column through photosynthetic control of their turgor pressure and inflation/deflation of their gas vacuoles (Walsby, 1972) it is possible that Trichodesmium may be able to do so also. The fact that a single colony can maintain itself in the near-surface zone while supporting several hydrozoans weighing many times its own weight, suggests that the alga can alter its buoyancy. The ability to even partially compensate for the added weight of other organisms will be greatly beneficial to all organisms associated with living Trichodesmium colonies, particularly the meroplanktonic dinoflagellate and hydrozoan which must return to the plankton, and the photosynthetic diatoms which must remain in the euphotic zone. Even after death and lysis of most of the algal cells, Trichodesmium detritus 'clumps' and floats because some gas vacuoles do not collapse*.

The aggregation of many individual filaments into colonies greatly increases the surface area and complexity of the Trichodesmium particle, and creates a complicated network of small 'internal' interfilamental spaces in which dissolved organic material from the water and from the alga itself may accumulate. In both radial and parallel conformations, a polysaccharide material accumulates in these spaces, but in radial colonies much greater amounts of the mucilage can be observed than in parallel colonies.

Accumulation of organic material in the small interfilamental spaces at the center of the colony will further reduce the already slow

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* Under polarized light, gas vacuoles are refractile, and can be observed in Trichodesmium debris after the cells have lysed.

diffusive loss of dissolved material from cells in this region. Where microorganisms are in close contact with each other and embedded in such material, it is logical to expect some exchange of dissolved metabolites.

Some cyanophytes release large amounts of nitrogenous material, chiefly peptides and amino acids (Jones and Stewart, 1969a) which are assimilable by various marine algae, fungi and bacteria (Jones and Stewart, 1969b). Others are known to produce vitamins or chelating compounds as by-products of their metabolism (Steidinger, 1973), and all blue-greens contain trace elements such as iron, molybdenum and cobalt which will be released after death and lysis of the cells. In Trichodesmium colonies, much of these materials may be retained in the mucilage.

The waters in which Trichodesmium is found are often extremely dilute nutritionally (cf. Steven et al., 1970) and the reduction of diffusive losses, or 'internal recycling' of nutrients within the colony community will be advantageous. The bacteria, fungi and protozoans in and on the Trichodesmium colonies appear primarily involved in remineralizing the mucilage, the complex organic molecules exuded into it by embedded autotrophs, and detrital material. Some of the products of this remineralization may be lost to the community through diffusion and emigration, but the nature of the matrix and the conformation of the Trichodesmium colonies leads to the accumulation and utilization of 'recycled' nutrients. The presence of large populations of actively dividing benthic diatoms embedded in the radial colony matrices supports this assumption.

The semisolid nature of the material forming the matrix at the center of some colonies may also restrict movement of dissolved gases. Postgate (1974) has pointed out that some bacteria rely on

layers of slime which retard oxygen diffusion and lead to the development of the microanaerobism necessary for nitrogen-fixation. The finding by L. Borstad (in prep.) that many of the bacteria isolated from Trichodesmium are microaerophilic and produce copious mucilage, suggests that microanaerobism may develop in Trichodesmium colonies in situ, at least in parts of the matrix. Jorgensen (1977) has shown that sulfate reduction (which requires anaerobic conditions) can proceed in detrital particles only 100μ in diameter, even when they are suspended in oxygen saturated seawater. In view of the fact that nitrogen fixation by Trichodesmium colonies is adversely affected by turbulence (Carpenter and Price, 1976), the barrier to diffusion provided by the mucilage may be significant, especially where respiration by embedded microorganisms creates an oxygen demand. Any mechanism which increases the activity of the nitrogenase enzyme, and the import of nitrogen to the particle, will benefit the whole community.

As well as nitrogenase and the extracellular enzymes of the fungii, alkaline phosphatase is also produced by Trichodesmium colonies (Yentsch et al., 1972). Whether this is produced by the blue-green or by one or more of its associates (many of the bacteria isolated from the colonies by L. Borstad produced it) is unimportant ecologically. The organic phosphates liberated will at least partially be available to all of the community members.

In addition to its role in retention of dissolved compounds, the mucilage accumulating in some colonies significantly increases their structural strength. This viscous and elastic material, when surrounding the tangle of filaments at the center of radial colonies, greatly improves the colony's suitability as a substrate for the larger symbionts, and prolongs the life of the particle. Even after death of most of the Trichodesmium cells in the colony, the matrix holds the particle together. The remains of colonies are regularly observed in

the mixed layer (see Section 4.2), recognizable as large mucilaginous flakes or particles with a few well vacuolated Trichodesmium filaments embedded in them.

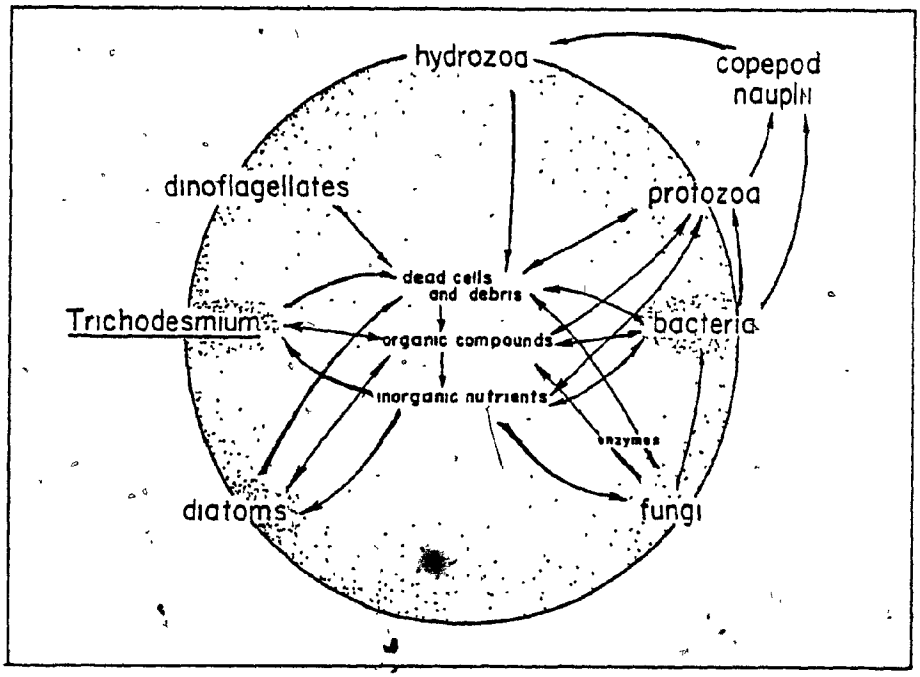
Figure 5.4 represents a simplified outline of some of the possible interactions within the community. The very small physical size of the colonies themselves and the variability among individual colonies will make any quantitative analysis of the interactions difficult. Studying the capabilities and requirements of each group in culture would contribute to an understanding of the system, but unfortunately the main organism - Trichodesmium - cannot yet be cultured.

Until the contributions of each group of organisms within the colonies can be separated, or Trichodesmium cultured axenically, field studies of the apparent physiology of the alga must take into account the potentially very diverse nature of the colonies. In most cases, Trichodesmium may dominate the flux of energy and compounds within the particle, but where other organisms are large or numerous this may not be the case. The variability from one colony to another will also be difficult to deal with.

The quantitative importance of the association described here is difficult to assess without considerable work on the physiologies of all of the organisms concerned. It can be said, however, that the numerically small and slowly growing Trichodesmium populations in the North Equatorial Current water masses contained much larger proportions of infested or 'colonized' colonies than the younger 'bloom' Trichodesmium populations swept to Barbados in Guiana Current waters. This is probably related to the finding by Meffert (1971) and others that in cultures of blue-greens such as Oscillatoria redeki, bacteria present in the media do not become abundant until the alga reaches the stationary or death phase of its growth.

Figure 5.3 Summary of possible interactions between organisms within the *Trichodesmium* community.

Shaded area represents physical confines of the matrix in which organisms are embedded.


hydrozoa
copepod
naupli
dinoflagellates
protozoa
dead cells
and debris
Trichodesmium
bacteria
organic compounds
inorganic nutrients
enzymes
diatoms
fungi

The invasion of Trichodesmium colonies by other microorganisms will therefore likely be most important in the older more stable water masses of the truly oceanic regions, such as the Sargasso Sea and the North Equatorial Current where Trichodesmium is growing slowly (Carpenter et al., 1975). The communication from Dr. E. Carpenter indicating "Pelagiana" was common in Trichodesmium colonies all across the North Atlantic Gyre confirms this supposition. The recent observation by Marumo et al. (1975) of other microorganisms in clumps of 20 to 30 Trichodesmium colonies gathered from the Pacific Ocean, suggests that phenomena similar to that reported here may also be found in that ocean. Such clumps were not observed in fresh material taken at Barbados, but could be generated by allowing the plankton to stand undisturbed in the bucket for an hour or two.

Trichodesmium presents the researcher with many problems, not the least of which will be the difficulties involved in culturing it or even maintaining it for short experiments. Workers conducting research on the physiology of the alga collected from the sea should be aware of the possible existence of other organisms which may significantly bias the results of biomass determinations or short-term uptake kinetics, by virtue of their size, numbers or level of activity.

Plate 5.1 Abundant bacteria in the organic debris near the periphery of a radial T. thiebautii colony.
Scale bar equals 10µ.

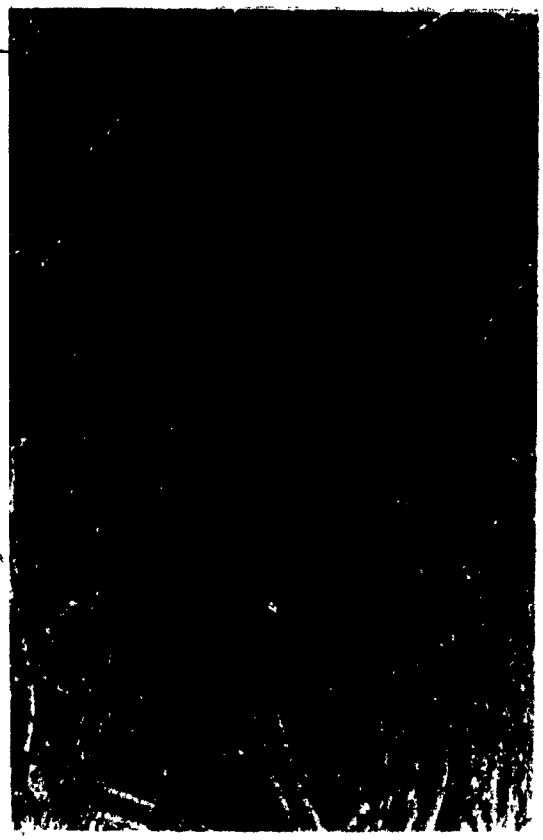
Plate 5.2 Filamentous phycomycete fungi embedded in the matrix of a radial T. thiebautii colony. Note heavy secondary bacterial infection of fungal escape tubules.
Scale bar equals 10µ.

Plate 5.3 Bacteria and diatoms (Nitzschia sp. 1) near the periphery of a radial T. thiebautii colony.
Scale bar equals 10µ.

Plate 5.4 Close-up of the very large population of Cocconeis scutellum and Nitzschia sp. 1 illustrated in Plate 5.5.
Scale bar equals 10µ.

5.1

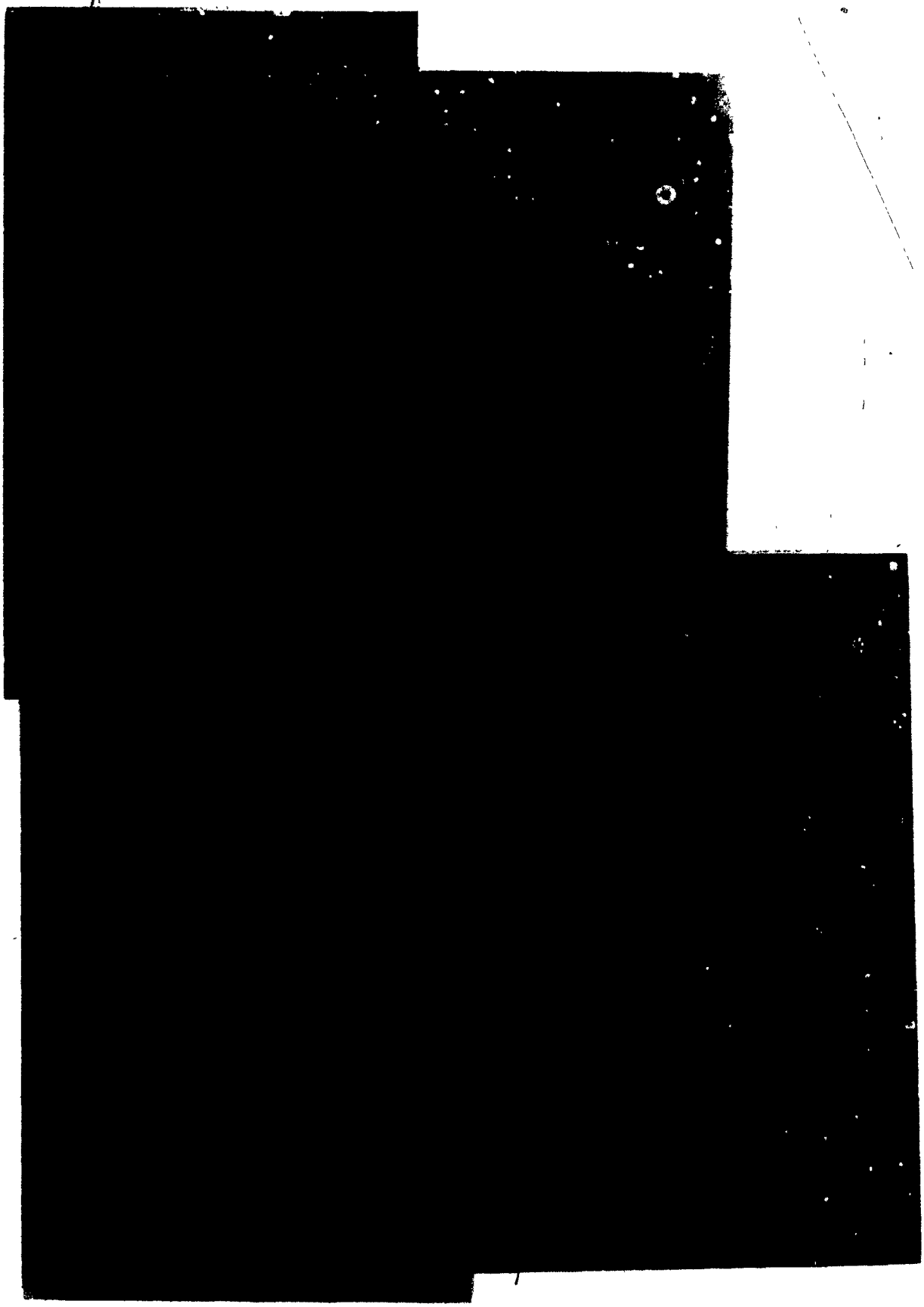
5.2



5.3

5.4

Plate 5.5 A single radial T. thiebautii colony of 5-10,000 cells, which has been incinerated and mounted in Hyrax to reveal a very extensive mixed population of Cocconeis scutellum and Nitzschia sp.-1. Trichodesmium filaments are partially visible around the periphery of the mount. Scale bar indicates 50μ.



5.5

Plate 5.6 Scanning electron micrograph of part of an incinerated T. thiebautii radial colony to show large population of Nitzschia sp. 1. Black scale bar at lower left indicates 50µ.

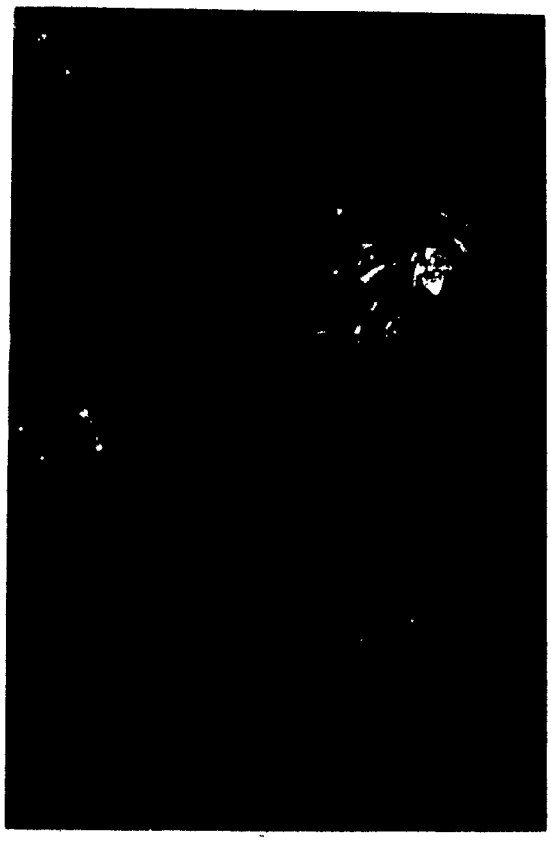
5.6

Plate 5.7 Diatom chematoxis to lysing Trichodesmium. Approximately five minutes before this photograph was taken, this field contained an intact Trichodesmium filament and no diatoms. After lysis Nitzschia sp. 1, N. closterium and N. longissima had congregated around the debris. The very fine needle-like projections protruding from the debris are very characteristic products of Trichodesmium lysis.
Scale bar indicates 10µ.

Plate 5.8 The dinoflagellate Peridinium trochoideum with partially released theca.
Scale Bar at lower left indicates 10µ.

Plate 5.9 A partially contracted 'Pelagiana trichodesmiae' hydranth with two unripe gonophores.
Scale bar equals 50µ.

Plate 5.10 A young 'Pelagiana trichodesmiae' medusa, released in the laboratory - less than six hours old.
Scale bar equals 100µ.



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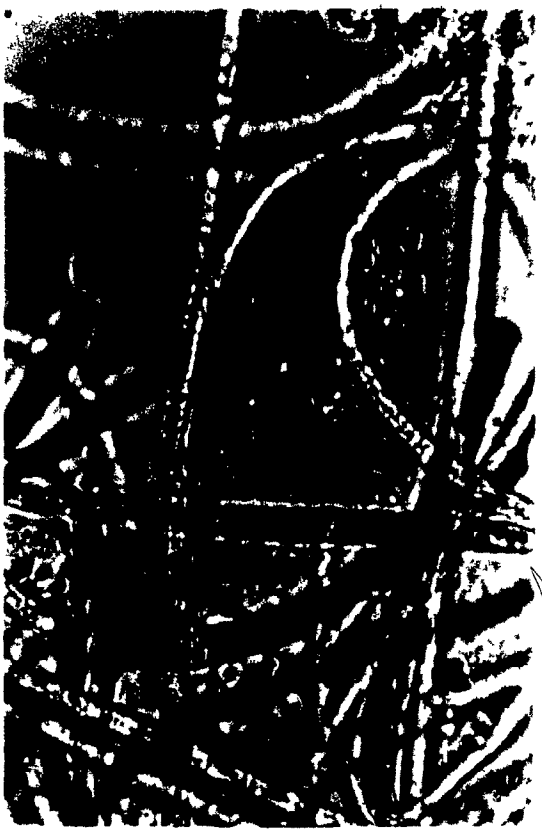

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6 SYNTHESIS

From the data discussed in Section 2 it has been shown that the appearance at Barbados of different water masses, and therefore of the temporal variation of phytoplankton species composition and abundance, is largely controlled by the timing and magnitude of several meteorological and hydrological phenomena occurring at a considerable distance from the island. Meandering of the Guiana Current seems largely responsible for the arrival of low salinity, neritic surface waters carrying large populations of diatoms and Trichodesmium, and the periodicity of the Barbados plankton appears related to the westward movement of the Guiana Current meanders as planetary waves. The resulting production of large lobes of freshened surface waters in the region north of Guiana at approximately 3 month intervals may explain the timing of many biological events at Barbados. The variations of many elements of the plankton community both offshore and close to the island have been shown to be related, and it now seems likely that this alternating appearance of two distinctly different surface water masses will have considerable importance in all aspects of marine productivity at Barbados.

Trichodesmium dominates the phytoplankton of the upper mixed layer off Barbados throughout the year, contributing on the average approximately 50% of the chlorophyll a and nearly the same fraction of the mean annual primary production at 5 m. The alga is always concentrated in the mixed layer, and rarely occurs below 75 m in significant numbers. The average standing crop in the upper 60 m during what has been referred to here as the 'nonbloom' periods is 200 mm³/l, but at three regularly occurring times of the year, populations up to twelve times larger can be observed. These periods are generally January and February, May and August. The length of time during which the high standing crops are present is variable and is related to current

velocity and direction. The large Trichodesmium populations arrive at Barbados in pools of low salinity surface water advected from the Guiana Current.

Photosynthesis experiments demonstrated that colonies from the 'bloom' which appeared off Barbados in January 1975 were fixing carbon very actively. Trichodesmium colonies collected from this and other 'blooms' usually gave the impression of being relatively younger than colonies collected from 'nonbloom' populations. The former were usually larger, generally lightly vacuolated, contained fewer plasmolyzed and empty cells, and were significantly less infested by other microorganisms.

It is hypothesized here that active growth of Trichodesmium in the divergence zones across the equatorial Atlantic, and off the northern continental shelf of South America (where essential elements in its nutrition may be provided by river runoff and/or upwelling) leads to the production of large standing stocks which are then transported to Barbados and into the Caribbean. As the populations are carried out of these zones, and the colonies' nitrogen, phosphorus and other cellular reserves are depleted, the alga will undergo a number of physiological changes. One possible result of nitrogen depletion is the alteration of the photosynthetic response as hypothesized in Section 3.

As individual cells in the colonies age and die, the leakage from and lysis of these cells contributes to a buildup of organic material in the interfilamental spaces of the colony. In apparently older, less robust radial colonies, which are more loosely bound together, a polysaccharide material accumulates to form a matrix around the filaments at the center of the colony. This 'matrix' forms the basic structural component of an identifiable microcommunity

including bacteria, fungi, protozoa, diatoms, dinoflagellates, a hydrozoan and copepod nauplii as well as Trichodesmium. The bacteria and fungi are primarily saprophytic, remineralizing the matrix and the metabolites and detrital material it contains. In vitro, where Trichodesmium colonies died more or less simultaneously, this autochthonous microbial population was capable of converting the algal material to ammonium and orthophosphate within about 10 days. In situ, however, it seems that most Trichodesmium colonies possess actively growing cells as well as dying ones, and some of the products of remineralization are therefore available to living Trichodesmium cells and to other organisms which find themselves in close contact with the algal colonies.

Some of the community members, particularly the diatoms and dinoflagellates, may benefit from the local concentration of nutritive elements, but the most important aspect of their association with Trichodesmium must be related to the buoyancy of the alga and its position high in the water column. Most of the diatoms are ordinarily benthic forms, the dinoflagellates are present in their nonmotile stage, the hydroids are meroplanktonic and the copepod is at least partly sessile. All apparently require a floating substrate in order to exist in the oceanic region. Like Sargassum, aging Trichodesmium colonies provide such a substrate, although on a smaller scale. The suitability of the alga as a substrate is greatly improved by its colonial nature and by the fact that even particles with only a few living Trichodesmium filaments are quite buoyant. Much of the algal detritus appears to remain in the mixed layer for a considerable time instead of sinking as is the case with non vacuolated phytoplankton. This may be important in recycling of elements such as nitrogen and phosphorus in the mixed layer.

7 SUMMARY

7.1 A two-year study was conducted off the west coast of Barbados, West Indies beginning in June 1974, with the purpose of investigating the spatial and temporal distribution of the planktonic cyanophyte Trichodesmium and elucidating the apparent regular blooming of this alga in these waters.

7.2 The oscillatory variations of Trichodesmium standing stock off Barbados (Steven and Glombitza, 1972) were confirmed. The period and synchrony of the fluctuations were identical to that observed in 1968-1970.

7.3 Diatoms were observed to be more abundant during Trichodesmium 'blooms', and re-examination of unpublished data belonging to the late Dr. D.M. Steven revealed close agreement between 'total other phytoplankton' and Trichodesmium at 5 m (and to a lesser extent at 50 m). Diatoms were responsible for the largest fraction of the 'other' phytoplankton during 'blooms'.

7.4 This regular periodicity can also be observed in serial data from five other phytoplankton studies and two other studies of zooplankton conducted at Barbados independent of this work.

7.5 In both periods, 1968-1970 and 1975-1976, there was a loose inverse relationship at 5 m between Trichodesmium standing stock and departures of salinity from the running mean.

7.6 A review of historical data and literature revealed the existence of large wave-like meanders in the Guiana Current off South America similar to planetary Rossby waves. These meanders do not appear to be stationary, and indirect evidence indicates that they move westward with a 3 to 4 month period.

7.7 The rhythmical appearance of low salinity, high silicate surface waters with high phytoplankton standing crops appears closely related to passage of northward lobes of these Guiana Current meanders by Barbados.

7.8 Recurving of the surface current north of Cape Orange has been demonstrated to occur only in the second half of the year, not year round as was previously supposed. This reversal of surface drift beginning in July appears to be responsible for the remarkably constant increase in sea surface salinity during the fall and winter at Barbados, and also for the reduction in standing stock of Trichodesmium as compared with the first half of the year.

7.9 In a series of ^{14}C photosynthesis experiments conducted on isolated Trichodesmium colonies, the photosynthesis vs irradiance response of the surface population has been demonstrated. The two colony morphologies tested showed rather distinct differences in this response, and this was similar to the variation of carbon fixation with depth in situ.

7.10 Trichodesmium was able to attain near maximal photosynthesis at low irradiance, and maintain those rates over a broad range of irradiance. It is hypothesized that the variability of photosynthesis at low irradiance demonstrated by the alga at Barbados is a reflection of varying degrees of nitrogen starvation and phycobilin depletion.

7.11 Release of recently fixed organic carbon compounds which were fluorescent and absorbed at 260 nm was recorded. This release was greatest in crowded conditions and high irradiance.

7.12 Gas vacuoles do not appear to offer significant protection to the alga's photosynthetic apparatus, since there was no change in the photosynthesis vs irradiance response where they were collapsed.

7.13 Most carbon fixation by Trichodesmium in the surface layer took place in the morning and afternoon, with intense photoinhibition occurring between about 1000 and 1400 hrs.

7.14 The near surface Trichodesmium population fixed carbon at between 40 and 50% of the mean rate for the whole phytoplankton population in these waters.

7.15 A large amount of Trichodesmium detrital material was present in the mixed layer, and at any one time may exceed the living fraction. Single well vacuolated trichomes and intact extracellular gas vacuoles embedded in the mucilage provide buoyancy to such particles.

7.16 These particles were usually infested with bacteria, fungi and protozoa whose primary purpose seems to be remineralization. In vitro decomposition and remineralization of Trichodesmium by these organisms was accomplished in about 10 to 14 days. The medium containing Trichodesmium lysate was an excellent medium for the growth of an unidentified species of Navicula (diatom).

7.17 Living Trichodesmium colonies of both conformations collected from both nearshore and far away from the island were found to harbour other microorganisms in the spaces between their filaments. In radial colonies a mucilaginous matrix accumulates which forms the structural (and nutritional) basis for a much more complex community of organisms including bacteria, fungi,

protozoa, diatoms, dinoflagellates, a hydrozoan and copepod nauplii. Parallel colonies demonstrated smaller, less complex associations.

7.18 Seventeen species of diatoms were commonly found embedded in Trichodesmium colonies. Some were common benthic species, but most were weakly silicified. Up to 1500 or more actively dividing individuals have been observed in a single Trichodesmium colony. Positive chemotaxis to Trichodesmium lysate has been observed.

7.19 The non-motile vegetative stages of the dinoflagellate Peridinium trochoideum and two other species of dinoflagellates were commonly found embedded in the mucilage of radial colonies.

7.20 A previously undescribed minute hydrozoan of the order Anthomedusa is commonly found anchored in radial colonies. Information regarding part of the life cycle and development of the hydranths has been presented here, including liberation of the medusa. The family, genus and species will be described elsewhere (Borstad and Voss, in prep.).

7.21 An experiment to monitor the possible degradation of chlorophyll a during long term storage on filters showed no significant changes up to 157 days, and only a 10% decrease after one year.

8 SUGGESTIONS FOR FURTHER INVESTIGATIONS

8.1 More information is desperately needed concerning the physical oceanography of the western tropical Atlantic, and the areas around the islands in particular. The water movements around Barbados should be studied in detail to provide support for biological and geological investigations there.

8.2 Some very interesting work could be done in the Guiana Current to monitor the meandering and the productivity of these waters. Synoptic studies using remote sensing could provide the large areal coverage necessary to examine the geography of the current, but many quasisynoptic cruises are also necessary to gather data concerning the plankton species composition and abundance throughout the area.

8.3 An interesting study of the temporal variations of surface salinity, chlorophyll and phytoplankton species composition could be mounted off the east end of Tobago, the south coast of Barbados and on one or more islands of the Antilles. Physical measurements would probably show fluctuations of the direction and velocity of the flow entering the Caribbean corresponding with the biological and chemical signatures of the surface water masses.

8.4 Since the Amazon River is known to introduce considerable iron to the ocean, and this element has been shown to limit phytoplankton growth, it would be worthwile to mount a study of the availability of iron off Barbados and in the Guiana Current. The availability of this element or chelating compounds present in the riverine water but not in the oceanic North Equatorial water, may ultimately be the factor determining the size of the phytoplankton standing stock observed at Barbados.

8.5 Future studies of planktonic organisms at Barbados would profit by use of TSP diagrams and continuous monitoring of salinity as an indication of the water mass sampled.

8.6 Recurrent group analysis of both phytoplankton and zooplankton data might prove valuable in studies of these organisms and relating the presence of individual species at Barbados to the past history of the water mass.

8.7 Interesting laboratory studies could be done to investigate the response of various individual species (both phytoplankton and zooplankton) to the environmental conditions operating close to the island.

8.8 Much more experimental data are required to completely describe the photosynthesis by Trichodesmium. P vs I data are needed for algae from 25 and 50 m, and during blooms. More in situ experiments both offshore and inshore should be conducted, and simultaneous measurements of the production rates of other plankton should also be made. Information on the action spectrum of algae from different depths and times of the cycle are also required, and C/H/N data are required for all experiments to prove or disprove the nitrogen starvation hypothesis. The diurnal variations of photosynthesis reported here require further study. If they reflect the activity of the alga in the top 25 m, then estimates of nitrogen uptake by the alga may have to be revised. (Any such study of photosynthesis by Trichodesmium or any other alga should wait until facilities are available in Barbados, if not at Bellairs Research Institute, for measuring radioactivity. Alternatively, this kind of study could be conducted by someone commuting between Barbados and a well equipped laboratory elsewhere.)

8.9 Barbados should be an interesting base from which to study nitrogen fixation by Trichodesmium, especially in relation to the periodic and predictable 'blooms'. Considerable time and effort were spent during the present study in this pursuit, but logistical difficulties ultimately caused the abandonment of this research. As with the photosynthesis study, this type of work could be done by someone commuting to and from a laboratory elsewhere.

8.10 More detailed studies of the decomposition of Trichodesmium and all of the other phytoplankton are required. The role of detritus of all types in tropical seas should be investigated further.

8.11 The possibility exists for some very interesting work on the internal recycling of nutrients within the Trichodesmium community itself. More information is required regarding the interactions of the various microorganisms found in the colonies, and their relative importance in experimental measurements of physiological activity by the entire colony.

8.12 More effort should be expended to try to get Trichodesmium into culture. Even a nonaxenic unialgal culture would greatly facilitate studies on this organism.

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APPENDICES

A.1 Taxonomy of the genus Trichodesmium

The taxonomy of Trichodesmium and the Oscillatoriaceae is problematical and unsatisfactory. Many synonyms appear in the literature, and the genus has been reorganized several times. The following is a short summary of the historical developments of the taxonomy as outlined by Sournia (1968) and Umezaki (1973), with comments in the light of experience with the alga at Barbados.

The genus Trichodesmium was established in 1830 by Ehrenberg with one species T. erythraeum. In 1892 Gomont divided T. erythraeum into three species, based on differences in trichome diameter, cell and colony morphology: T. erythraeum (Ehr.), T. hildenbrandtii (Gom.) and T. thiebautii (Gom.). In the same year Wille (in Schutt, 1892) ascribed the synonyms Xanthotrichum and Heliotrichum.

In 1932, Geitler united the marine Trichodesmium with the freshwater genus Oscillatoria based on the similarities of the algae. A few years later Detoni (1938) established a new genus - Skujaella - for the marine Oscillatoriaceae, and Fremy (1941) proposed lumping all of the marine species into one, also in the genus Skujaella. After the appearance of the name Skujaella, Geitler (1942) reconsidered his earlier work, and re-established the genus Trichodesmium in accordance with Gomont, thus redividing the marine and freshwater Oscillatoriaceae.

Trichodesmium, as described by Gomont in 1892, then stood for 26 years until 1968, when both Sournia and Drouet independently and simultaneously recommended reuniting the genus with Oscillatoria.

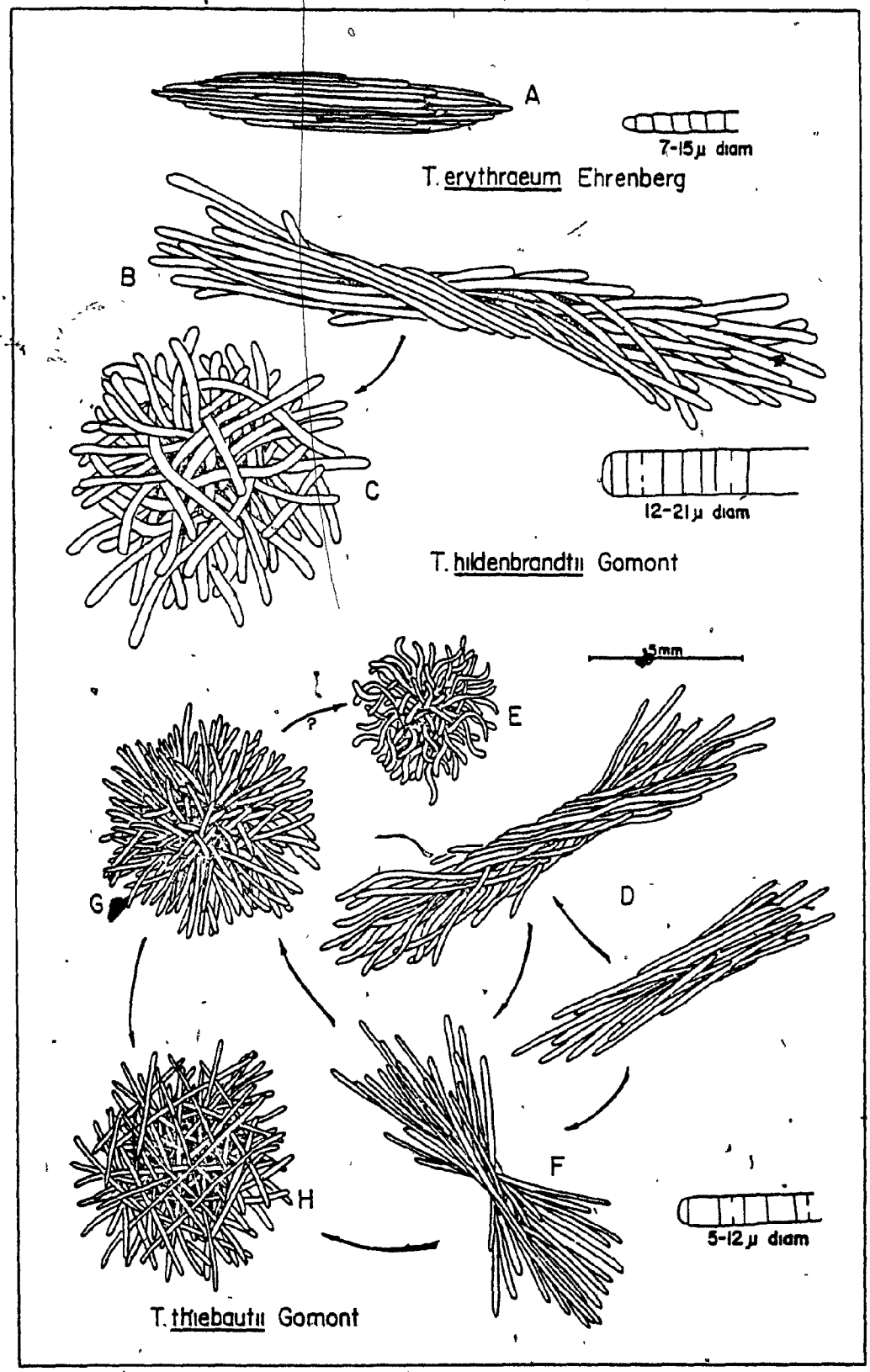
Sournia adopted Geitler's 1932 classification, with four species, but Drouet, in a major review of the whole family, lumped all three into O. erythraea (Ehr.) Kützing.

In the 1970's, the name Oscillatoria is gaining acceptance among some workers, especially Drouet's O. erythraea. The controversy is not over yet, however, since all of the Japanese and Indian workers still recognize the genus Trichodesmium. Several recent important publications concerning the blue-green algae (Fogg et al., 1973; Carr and Whitton, 1973) and nitrogen fixation (Mague et al., 1976, 1977; Hardy and Crisp, 1977) state that while the two genera are very similar, and Trichodesmium may indeed belong to Oscillatoria, the former name is preferable. Barker et al. (1967) have reported a significantly different fatty acid composition for Trichodesmium than for Oscillatoria, and several authors (Holton et al., 1968; Kenyon and Stanier, 1970) have discussed the phylogenetic and evolutionary significance of this. Umezaki (1974) concludes the differences in chemical composition between the two genera as further evidence for division of the family. (See, however, Olson and Ingram (1975) who report effects of environmental conditions on fatty acid composition.)

Taxonomy of the genus Trichodesmium is based primarily on trichome diameter and cell and colony morphology. Most authors agree that trichome diameter is the most important character, and that there are two broad groups within the genus: one with thin diameter trichomes (5-12μ) and another with wider filaments (12-25μ or more). The thin trichomes are commonly ascribed to the genera T. thiebautii and T. erythraeum, while filaments greater than about 12-13μ are referred to as T. hildenbrandtii (see Figure A.1). T. erythraeum is differentiated from both of the other species by constrictions at its intercellular junctions and fusiform colony morphology. It should be stressed here that observation of freshly collected Trichodesmium from Barbados waters

Figure A.1 The three species of Trichodesmium observed in Barbados waters and transformations of colonial morphology deduced from observations of live material.

See text for explanation of letters.


A
7-15μ diam
T. erythraeum Ehrenberg
B
C
12-21μ diam
T. hildenbrandtii Gomont
5mm
E
G
D
F
H
5-12μ diam
T. thiebautii Gomont

indicated that there was extreme variation in the degree of constriction at the extracellular junctions, within colonies and even within filaments. Meffert (1971) has also indicated such constrictions may be a result of nutritional variations in culture. This does not appear to be a reliable taxonomic character, and neither does the morphology of the terminal cells, for similar reasons.

At Barbados, both T. thiebautii and T. hildenbrandtii show the same range of cell length (7-16μ) but there are considerable differences in cell shape. T. thiebautii cells are relatively narrower (7 to 9μ in diameter) and are about 500μ^3 in volume. T. hildenbrandtii cells are between 12 and 15μ in diameter and approximately 1000μ^3 in volume. The thicker diameter T. hildenbrandtii cells are much more darkly pigmented than those of T. thiebautii, and they also stain much more heavily with Lugol's iodine. This deep brown colour, which disappears reversibly on warming, is indicative of a carbohydrate storage material commonly found in blue-greens, which is a polymer of glucose resembling glycogen (Fuhs, 1973). This consistent darker staining in the presence of Lugol's iodine greatly assists in species determination at low magnification.

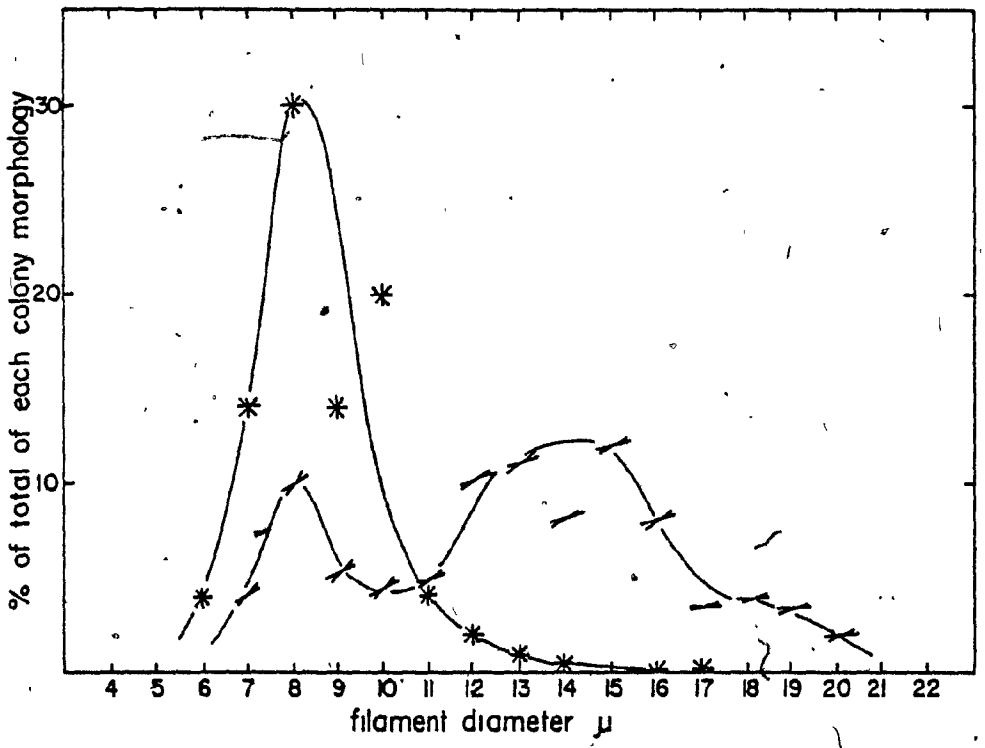
Most authors have divided the genus primarily on the basis of trichome diameter, but Marumo and Asaoka (1974) maintain that trichome diameter varies with depth as a function of vacuolation changes and consequently separate T. thiebautii and T. erythraeum on the basis of their colony morphology. For these two species this is probably the best means since their diameters are similar. Separation of T. thiebautii and T. hildenbrandtii can be grossly accomplished using colony morphology also, and in many cases this may be the most practical (see Section 3.2.2). As illustrated in Figure A.1 there are two fairly distinct colonial arrangements which have, in this thesis, been referred to as 'radial' colonies (c,e,g) in which trichomes all cross near their center, forming radially symmetrical colonies; and 'parallel' colonies

(A.1a, b, d) in which the trichomes are juxtaposed along most of their length either straight, or twisted about each other to varying degrees. This twisting of filaments in some parallel colonies led Sournia (1968) to establish O. contorta for colonies where the filaments were "twisted about each other like strands in a cable" (my translation). One often sees twisting to various degrees in colonies of T. hildenbrandtii and T. thiebautii and this character is not therefore considered by this author to be sufficient justification for establishment of a separate genus. Parallel colonies of both species gain considerable structural strength from this twisting, and the advantage is particularly noticeable in colonies with very long trichomes. In colonies with short trichomes, however, the tendency is a weakening influence, and mechanical disturbance can cause colonies (especially T. thiebautii) to break up completely or partially to form loose jumbled radial colonies (Fig. A.1c, f, h).

These possible transformations from one morphology to another mean that differences in trichome diameter and colony morphology are not mutually exclusive. Figure A.2 illustrates the overlap between the two characters in algae collected at the surface near Barbados at various times throughout 1974, 1975 and 1976. The curves represent the measurements (means of at least 3 filaments per colony) of 233 radial colonies and 145 parallel colonies, normalized to n = 100. While the preponderance of radial colonies examined had trichomes of diameters between 7-10μ, 7% of those examined had diameters greater than 12μ. These colonies were less symmetrical, loose jumbles of darkly pigmented trichomes which have been interpreted in this study as partially disrupted T. hildenbrandtii.

The 145 parallel colonies examined demonstrated a bi-modal distribution in accordance with the covariation of colony morphology and trichome diameter illustrated in Figure A.1. Parallel colonies formed by T. thiebautii (i.e. filaments less than 12μ diameter) constituted 34% of all parallel colonies examined, while 66% of all parallel colonies were T. hildenbrandtii.

Figure A.2 Relationship between colony morphology and filament diameter (normalized to % because of unequal n) of the near surface Trichodesmium population off Barbados (233 radial colonies, 145 parallel colonies).


% of total of each colony morphology
30
20
10
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
filament diameter μ

In the discrete samples, T. thiebautii was always the most abundant species of the three at Barbados, contributing approximately 80-90% of the total filament length at most times and depths. The larger percentage of T. hildenbrandtii in the parallel colonies observed microscopically, is probably a result of observer bias in selecting the colonies from the net plankton, since these colonies are larger than those of T. thiebautii.

All of the preceeding illustrates the difficulties involved in the taxonomy of the genus and why many authors prefer to lump all of these groups into one species. Evidence from unialgal cultures of freshwater Oscillatoriaceae has put much of the taxonomy based on morphology in question, since considerable variation in trichome diameter, pigmentation and cell morphology can result from changes in the algae's physiology (cf. Meffert, 1973). Similarly, the factors determining colony morphology are not well understood. Colony morphology in some cyanophytes appears to be influenced by environmental conditions or by symbiotic organisms (Wyatt and Henderson, 1971). Many authors (Drouet, 1968; Sournia, 1968; Moreth, 1970; J. Sharp, pers. comm.) consequently regard all of the marine forms as physiological variants of one species and use the species name O. erythraea. Until the alga can be cultured axenically, which so far has proven impossible, division of the genus into more than one species may seem to some to be a bit artificial. The species names as assigned by Gomont (1892) do remain useful, however, in describing the morphs and they have been used here when referring to differences in trichome diameter. The author prefers to use the generic name Trichodesmium in place of Oscillatoria in order to distinguish the marine forms from the freshwater forms, and also because of the unresolved significance of differences in fatty acid composition between the two forms.

A.2 Chlorophyll decomposition during storage of filters

At present there is no published experimental evidence regarding the possible decomposition of chlorophyll contained on filters during storage. Authors of most methods manuals recommend that analysis be done as soon as possible after collection of the sample, preferably within six weeks. (Strickland and Parsons, 1972). During the current study, this was not possible and many of the filters had to be stored for very long periods. The experiment described here was conducted to investigate the changes in chlorophyll a and phaeopigment content on filters stored for long periods.

A.2.1 Methods

Water was collected in opaque PVC Van Dorn bottles from a depth of 5 m approximately 4 km off the west coast of Barbados in 200 m water. Collections were made in the early morning before the sun became too intense, and strenuous efforts were made to protect the collected water and phytoplankton from direct sunlight. The water was stored for transit to the shore-based laboratory in a large opaque plastic container which had been thoroughly washed with fresh water prior to use.

In the laboratory, vigorous mixing was initiated immediately by bubbling air into the bottom of the container. One liter portions were filtered onto 47 mm Whatman GF/C filters, with a few ml $MgCO_3$ suspension to the last few hundred ml. After filtration the filters were laid out on paper towels to dry further, then folded in half and blotted to remove any excess moisture. Five filters, chosen at random, were analysed immediately. The remainder were inserted into glassine envelopes, and stored in air-tight containers over desiccant at

approximately -10°C. At intervals, five envelopes were chosen at random and the filters analysed for the contained chlorophyll *a* and phaeopigment as described in Section 2.2.3.

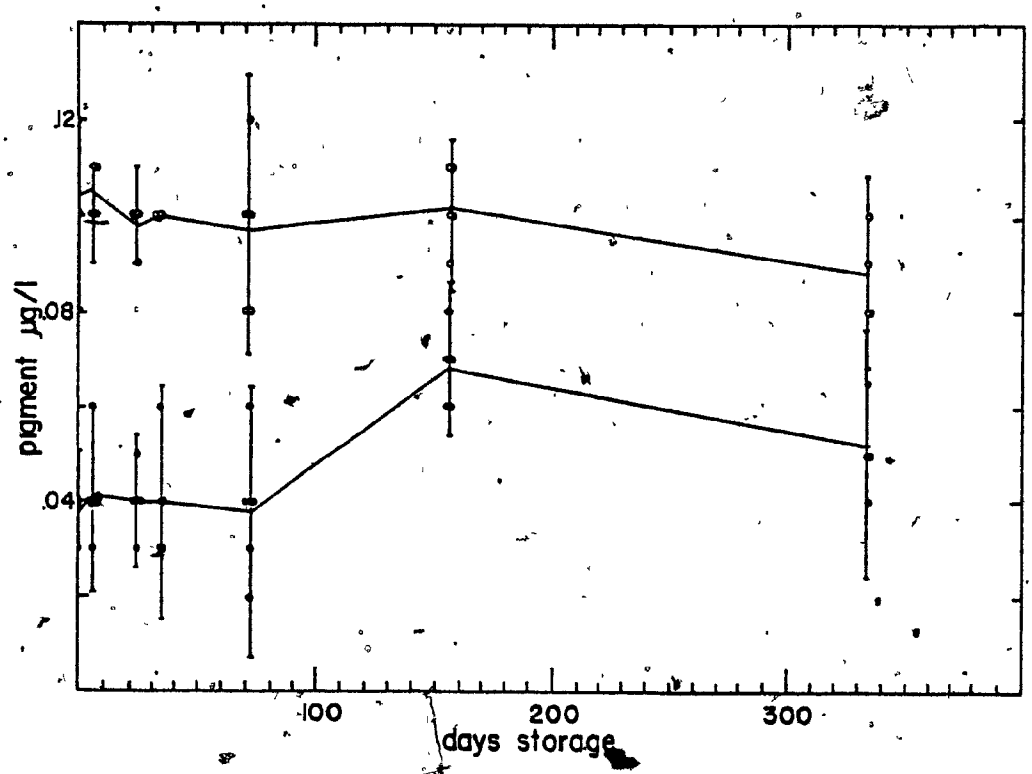
A.2.2 Results and discussion

The fate of the chlorophyll *a* and phaeopigment on filters as described above is summarized in Figure A.3. The large points represent the mean of five replicates. The vertical bars represent 95% confidence limits of the mean. Individual values are indicated by the smaller points. The high degree of variability is in part due to the presence of *Trichodesmium* colonies which may contain from 0.01 to 0.03µg chlorophyll *a* per colony, and also to less efficient mixing as the water level in the container dropped.

No significant changes ($p = 99\%$) in chlorophyll or phaeopigment content of the filters were evident within the limits of the sample variance until after 160 days. The changes apparent during the last period amount to about 10% of the day 0 mean (the 334 day mean is not significantly different from the others at $p = 95\%$), and are considered to be due to an unknown length of storage at higher temperatures. Sometime during the last period, the container with the filters was removed from the freezer compartment to the warmer refrigerator compartment. The increase of phaeopigment, but not of chlorophyll *a*, at day 157 may not be real, since notes made at the time of analysis indicate that the fluorometer was unusually unstable on that day. Re-centrifuging the extracts did not solve the problem and it was not encountered on other days. Line voltage fluctuations may have been the cause.

Figure A.3 Changes in chlorophyll a and phaeopigment content on replicate filters during long term storage in the dark and at -10°C.

Chlorophyll a (o); phaeopigment (●). Vertical bars indicate ± 2 standard deviations. Lines connect means.


.12
.08
.04
pigment µg/l
100
200
300
days storage

It is evident from these data that chlorophyll filters may be stored for periods of at least 5 months, and probably up to a year or more if they are kept reasonably dry, in the dark, and frozen to at least -10°C. Owen (1974) has recorded a decrease of 10% or more in chlorophyll concentrations if filters are stored (frozen) for more than a day. Such a decrease is not evident in the data presented in Figure A.3. There are no significant differences between filters analyzed on day 0 (unfrozen) and subsequent days, and therefore no corrections have been made to the data discussed here or in Section 2.3.2.

A.3 DATA LISTING

DAY -CONSECUTIVE DAY, NUMBERED FROM BEGINNING OF STUDY.

STATION -STATION NUMBER, BY NUMBER OF CONSECUTIVE WEEKS FROM BEGINNING OF STUDY.

FOREL -CCLOUR OF SECCHI AS IT DISAPPEARS. I=BLUE, V=BLUE-GREEN.

DEPTH -DEPTH OF SAMPLE, IN METERS. WHERE DEPTHS LISTED ARE NOT STANDARD, THEY HAVE BEEN CALCULATED FORM THE COSINE OF THE WIRE ANGLE AND THE NOMINAL DEPTH.

TEMP -TEMPERATURE IN DEGREES CENTIGRADE. BT WAS NOT OPERATIONAL FOR A PERIOD IN 1975.

SALINITY -SALINITY IN PARTS PER THOUSAND.

PHAEO-PIG -CONCENTRATION OF PHAEOPIGMENT IN MICROGRAMS PER LITER.

CHL-A -CONCENTRATION OF CHLOROPHYLL-A IN MICROGRAMS PER LITER.

TRICHO -TOTAL *TRICHODESMIUM* IN MM FILAMENT PER LITER.

ND -NO DATA

OFFSHORE STATIONS (8KM AND OTHERS)

DAY 15 STATION 3 9 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
0	27.5	32.669	20.83	.03	.12	668
5	27.5	32.787	20.92	ND	ND	580
10	27.5	32.544	20.73	.03	.20	685
15	27.5	32.795	20.92	.04	.14	511
25	27.0	33.438	21.56	.02	.19	432
50	26.1	35.876	23.68	.10	.17	43
75	25.2	36.461	24.42	.11	.11	5
100	24.9	36.774	24.73	.02	.04	3
150	23.3	37.044	25.41	.02	.01	ND
175	20.2	36.879	26.16	.02	.01	1

DAY 29 STATION 5 23 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
0	28.4	32.280	20.24	.03	.10	157
5	28.4	32.377	20.32	.04	.12	592
10	28.2	32.576	20.53	.04	.11	348
15	28.2	32.941	20.81	.05	.19	257
25	27.9	33.630	21.42	.09	.21	155
50	27.2	35.271	22.88	.14	.40	3
75	25.7	36.510	24.29	.17	.17	0
100	25.5	36.783	24.55	.07	.07	0
150	24.3	37.072	25.14	.02	.02	0
175	22.4	36.940	25.60	.03	.01	0

DAY 44 STATION 7 7 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
0	27.9	33.451	21.29	.02	.07	668
5	27.9	33.511	21.33	.03	.07	799
10	27.9	33.545	21.36	.05	.08	668
15	27.9	33.578	21.38	.03	.08	745
25	27.9	34.015	21.71	.04	.09	760
50	26.0	35.949	23.77	.04	.14	135
75	25.2	36.755	24.63	.04	.10	13
100	24.4	36.871	24.96	.04	.05	0
150	21.3	36.868	25.85	.04	.02	1
175	19.2	36.501	26.13	.01	.02	0

DAY 58 STATION 9 21 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
0	27.8	33.664	21.48	.07	.15	285
5	27.8	33.691	21.50	ND	.18	271
10	27.8	33.745	21.54	.06	.18	297
15	27.9	33.836	21.57	.07	.15	633
25	27.9	34.015	21.71	.09	.10	473
50	27.2	35.949	23.39	.07	.11	30
75	25.8	36.366	24.15	.09	.13	4
100	25.0	36.735	24.67	.11	.08	9
150	21.5	36.839	25.77	.11	.02	0
175	20.3	36.728	26.02	.12	.01	11

DAY 71 STATION 11 3 SEP. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.3	33.113	20.90	.01	.04	82
5	28.2	33.195	21.00	.01	.04	120
10	28.3	33.333	21.07	.02	.06	207
15	28.3	33.337	21.07	.02	.08	97
25	28.3	33.395	21.11	.02	.06	137
50	25.2	35.440	23.63	.10	.10	59
75	26.1	36.160	23.90	.10	.10	3
100	24.8	36.587	24.62	.07	.05	0
150	22.6	36.526	25.22	.01	.03	0
175	19.7	36.536	26.03	ND	ND	0

DAY 85 STATION 13 17 SEP. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.4	33.553	21.20	.02	.08	75
5	28.4	33.554	21.20	.03	.09	216
10	28.4	33.569	21.21	.03	.09	206
15	28.4	33.605	21.24	.04	.09	495
25	28.4	33.643	21.27	.05	.09	152
50	27.5	35.705	23.11	ND	ND	159
75	25.4	36.348	24.26	ND	ND	6
100	24.3	36.727	24.88	ND	ND	0
150	21.9	36.731	25.58	.03	.02	0
175	19.9	36.647	26.06	.02	.01	0

DAY 101 STATION 15 3 OCT. 1974 SECCHI: 28M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.3	33.146	20.93	ND	.14	122
5	28.3	33.420	21.13	ND	.14	ND
10	28.3	33.580	21.25	ND	.14	148
15	28.5	33.643	21.23	ND	.10	ND
25	28.3	33.647	21.30	ND	.14	759
50	26.4	36.931	24.38	ND	.22	51
75	25.3	36.622	24.49	ND	.08	0
100	24.2	36.825	24.98	ND	.05	0
150	21.9	36.718	25.57	ND	.02	0
175	19.7	36.351	25.89	ND	.00	0

DAY 113 STATION 17 15 OCT. 1974 SECCHI: 24M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.3	34.247	21.75	.05	.10	417
5	28.3	34.272	21.77	.07	.10	502
10	28.3	34.272	21.77	.05	.11	484
15	28.3	34.344	21.82	.06	.11	345
25	28.4	34.597	21.98	.08	.15	ND
34	28.0	34.436	21.99	.05	.15	1049
49	27.1	35.426	23.03	.08	.19	321
73	26.2	36.314	23.98	.25	.10	224
97	25.2	36.421	24.37	.18	.10	0
146	22.8	36.874	25.43	.02	.02	0
170	20.3	36.686	25.98	.04	.02	0

DAY 127 STATION 19 29 OCT. 1974 SECCHI: 28M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.0	34.540	22.07	ND	.11	77
15	28.0	34.539	22.07	ND	.07	ND
25	28.0	34.540	22.07	ND	.14	162
50	27.5	35.822	23.20	ND	.20	126
75	26.3	36.259	23.91	ND	.14	33
100	25.0	36.628	24.59	ND	.05	27
150	22.0	36.766	25.58	ND	.04	23
175	19.5	36.678	26.19	ND	.02	0

DAY 141 STATION 21 12 NOV. 1974 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.1	33.962	21.60	.01	.07	76
24	28.1	34.013	21.64	.02	.05	100
33	28.1	34.186	21.77	.02	.08	173
46	26.0	36.230	23.98	ND	ND	72
68	25.7	36.681	24.42	.15	.15	18
91	24.5	37.086	25.09	.10	.06	0
137	23.9	36.972	25.18	.02	.01	2
160	22.0	36.437	25.33	.09	.13	42

DAY 158 STATION 23 29 NOV. 1974 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.7	34.507	22.14	.03	.08	194
15	27.7	34.512	22.15	.04	.08	120
25	27.7	34.517	22.15	.03	.06	188
35	27.7	34.515	22.15	.03	.08	318
50	27.8	34.693	22.25	.06	.11	169
74	25.3	36.551	24.44	.16	.11	31
98	25.0	36.914	24.81	.07	.06	41
147	23.0	36.844	25.35	.02	.02	7
172	20.2	36.643	25.98	.02	.01	3

DAY 169 STATION 25 10 DEC. 1974 SECCHI: 36M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.4	34.518	22.25	.03	.05	105
15	27.4	34.513	22.24	.02	.08	179
25	27.4	34.513	22.24	.02	.06	55
34	27.4	34.516	22.25	.02	.07	44
49	27.5	34.812	22.44	.04	.09	33
73	26.4	36.475	24.04	.05	.08	9
97	25.2	36.777	24.64	.20	.10	4
146	23.5	36.957	25.29	.03	.01	2
170	21.4	36.804	25.77	.02	.02	10

DAY 182 STATION 27 23 DEC. 1974 SECCHI: 31M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.0	34.785	22.58	.00	.06	214
15	26.9	34.806	22.63	.02	.06	239
25	26.9	34.824	22.64	.03	.04	92
35	27.0	35.192	22.88	.03	.07	106
50	27.1	35.678	23.22	.04	.07	100
75	25.7	36.658	24.40	.19	.16	26
100	25.0	36.832	24.75	.19	.15	14
150	22.8	36.931	25.47	.05	.02	2
175	20.9	36.846	25.94	.02	.02	57

DAY 197 STATION 29 7 JAN. 1975 SECCHI: 24M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.6	35.268	23.07	.08	.16	642
15	26.7	35.354	23.10	.04	.17	1355
25	26.8	35.355	23.07	.09	.21	658
35	26.9	35.590	23.21	.06	.25	869
49	27.0	35.698	23.26	.10	.25	753
73	26.8	36.387	23.85	.17	.14	42
97	25.5	36.893	24.64	.16	.08	20
146	23.4	37.039	25.38	.04	.02	3
170	21.6	36.910	25.80	ND	ND	92

DAY 211 STATION 31 21 JAN. 1975 SECCHI: 23M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.4	35.162	23.05	.14	.32	637
15	26.4	35.165	23.05	.13	.26	854
25	26.4	35.168	23.06	.19	.22	1118
34	26.4	35.183	23.07	.11	.28	1157
47	26.6	35.450	23.20	.22	.18	396
71	26.4	36.310	23.92	.26	.11	16
94	25.5	36.950	24.68	.11	.02	2
141	24.3	36.962	25.06	.06	.02	0
165	23.0	36.911	25.40	.04	.01	0

DAY 225 STATION 33 4 FEB. 1975 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.0	34.997	23.05	.09	.35	2802
15	26.0	34.995	23.05	.13	.38	1525
25	26.1	34.992	23.02	.19	.44	2219
34	26.2	35.226	23.16	ND	ND	1070
47	26.2	35.238	23.17	.15	.29	1143
71	26.6	36.203	23.77	.20	.10	5
94	26.1	36.567	24.20	.11	.05	2
141	24.5	36.795	24.87	.04	.02	1
165	23.3	36.867	25.28	.05	.01	0

DAY 236 STATION 35 15 FEB. 1975 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.3	35.972	24.00	.02	.04	27
15	25.3	35.986	24.01	.09	.10	68
25	25.3	36.003	24.03	.08	.11	42
35	25.3	36.043	24.06	.12	.13	23
49	25.3	36.015	24.04	.06	.16	57
73	25.3	36.088	24.09	.05	.20	37
97	25.2	36.087	24.12	.04	.02	7
146	25.8	36.547	24.28	.11	.17	3
170	23.4	36.565	25.02	.06	.03	0

DAY 254 STATION 37 5 MAR. 1975 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.2	35.156	23.42	.04	.10	522
15	25.2	35.210	23.46	.03	.10	795
25	25.2	35.280	23.51	.09	.08	786
35	25.1	35.331	23.58	.01	.28	1196
50	25.1	35.626	23.80	.09	.11	84
75	25.1	35.881	24.00	.10	.21	13
100	25.3	36.525	24.42	.15	.16	86
150	23.2	37.042	25.44	.03	.01	7
175	22.8	36.913	25.46	ND	ND	14

DAY 267 STATION 39 18 MAR. 1975 SECCHI: 39M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.2	35.215	23.46	.03	.08	174
15	25.2	35.236	23.48	.02	.08	224
25	25.2	35.232	23.48	.03	.09	335
35	25.2	35.267	23.50	.03	.09	334
50	25.2	35.441	23.63	.07	.14	101
74	25.2	36.292	24.28	.09	.18	6
98	24.9	36.738	24.71	.17	.11	0
147	22.6	36.957	25.55	.04	.02	0
172	21.2	36.874	25.88	.02	.01	1

DAY 281 STATION 41 1 APR. 1975 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.4	34.747	23.05	.02	.07	369
15	25.4	34.945	23.20	.05	.11	656
25	25.3	35.308	23.50	.03	.16	1178
35	25.2	35.675	23.81	.04	.16	913
50	25.1	35.748	23.90	.05	.10	424
75	25.0	35.866	24.03	.05	.12	147
100	24.8	36.012	24.19	.10	.09	111
150	23.6	37.215	25.46	.10	.03	7
175	22.3	36.867	25.57	.02	.01	0

DAY 298 STATION 43 18 APR. 1975 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.7	35.040	23.18	.03	.10	663
15	ND	35.027	ND	.04	.12	642
25	ND	35.061	ND	.05	.11	1093
34	ND	35.058	ND	.06	.12	690
47	ND	35.577	ND	.15	.08	247
71	ND	36.252	ND	.10	.11	52
94	ND	36.995	ND	.20	.10	73
141	ND	37.041	ND	.06	.02	0
166	ND	36.874	ND	.02	.01	3

DAY 309 STATION 45 29 APR. 1975 SECCHI: 18M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.7	34.180	22.53	.03	.10	286
15	25.7	34.300	22.62	.05	.14	342
25	25.7	34.487	22.76	.08	.14	655
35	25.7	34.843	23.03	.10	.16	518
50	25.5	36.428	24.29	.12	.13	34
75	25.4	36.976	24.73	.20	.08	35
100	25.4	37.026	24.77	.16	.07	3
150	23.3	36.628	25.10	.06	.02	0
175	22.0	ND	ND	.02	.01	1

DAY 323 STATION 47 13 MAY 1975 SECCHI: 22M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.1	34.147	22.38	.06	.18	1462
15	ND	34.240	ND	.04	.25	1650
24	ND	34.471	ND	.04	.32	2212
32	ND	34.758	ND	.07	.28	2304
43	ND	35.543	ND	.12	.24	724
66	ND	35.970	ND	.13	.10	36
86	ND	36.513	ND	.15	.06	51
129	ND	37.116	ND	.05	.02	1
151	ND	37.159	ND	.03	.01	9

DAY 331 STATION 48-1 21 MAY 1975 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.3	33.080	21.52	.07	.25	1174
25	ND	33.270	ND	.15	.27	1285
50	ND	35.710	ND	.18	.23	43

DAY 331 SURFACE STATIONS 21 MAY 0075

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
48-2	26.3	33.068	21.50	.07	.24	ND	ND	ND
48-3	26.3	33.096	21.53	.04	.22	ND	ND	ND
48-4	26.3	33.075	21.52	.07	.24	ND	ND	ND
48-5	26.1	33.163	21.65	.04	.24	ND	ND	ND
48-6	26.1	33.273	21.70	.08	.28	ND	ND	ND
48-7	26.2	33.967	22.22	.09	.25	ND	ND	ND
48-8	26.3	33.631	21.86	.06	.18	ND	ND	ND

DAY 331 STATION 48-9 21 MAY 1975 SECCHI: 16M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
4	26.3	33.670	21.96	.05	.19	901
22	ND	33.670	ND	.11	.32	1598
44	ND	35.400	ND	.15	.27	388

DAY 337 STATION 49 27 MAY 1975 SECCHI: 28M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	ND	33.352	ND	.08	.14	2172
15	ND	33.348	ND	.14	.08	1774
25	ND	33.344	ND	.08	.14	1813
34	ND	33.416	ND	.06	.25	1211
47	ND	34.912	ND	.12	.23	221
71	ND	35.956	ND	.10	.13	19
94	ND	36.883	ND	.03	.02	2
141	ND	36.935	ND	.02	.02	7
165	ND	36.868	ND	.02	.02	0

DAY 351 STATION 51 10 JUNE 1975 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	ND	34.363	ND	.04	.11	381
15	ND	34.481	ND	.04	.11	535
24	ND	34.583	ND	.07	.10	560
34	ND	34.690	ND	.05	.07	182
45	ND	34.721	ND	.06	.12	165
67	ND	36.041	ND	.22	.17	10
90	ND	36.822	ND	.04	.02	0
135	ND	37.055	ND	.03	.01	0
157	ND	36.735	ND	.02	.01	4

DAY 366 STATION 53 24 JUNE 1975 SECCHI: 21M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	ND	33.185	ND	.01	.08	819
15	ND	33.225	ND	.05	.07	617
25	ND	33.655	ND	.01	.10	331
34	ND	34.613	ND	.04	.17	26
49	ND	35.829	ND	.05	.19	1
73	ND	36.070	ND	.01	.01	11
97	ND	36.966	ND	.02	.02	0
146	ND	36.914	ND	.01	.01	0
170	ND	36.435	ND	.01	.07	0

DAY 379 STATION 55 8 JULY 1975 SECCHI: 21M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	ND	33.835	ND	.01	.05	ND
14	ND	33.844	ND	.01	.07	76
24	ND	34.137	ND	.01	.07	9
33	ND	34.677	ND	.03	.10	2
48	ND	34.849	ND	.04	.09	0
71	ND	35.826	ND	.13	.23	3
95	ND	36.321	ND	.02	.02	0
143	ND	36.897	ND	.02	.05	2
166	ND	36.714	ND	.01	.01	0

DAY 332 ASTP STATIONS 21 JULY 1975 SURFACE SAMPLES

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
1	27.1	33.390	21.51	.02	.09	355	ND	III
2	27.1	33.320	21.46	ND	ND	ND	ND	II
3	27.3	33.320	21.49	.03	.08	ND	ND	II
4	27.2	33.260	21.39	.04	.12	ND	ND	II
5	27.2	33.250	21.36	.05	.13	ND	ND	II
6	27.2	33.220	21.34	.09	.17	ND	ND	III
7	27.1	33.220	21.34	.04	.08	ND	ND	II
8	27.1	33.080	21.28	.02	.06	ND	ND	III
9	27.2	33.140	21.28	.03	.09	ND	ND	III-IV
10	27.2	33.120	21.27	.04	.07	600	ND	III
11	27.2	33.090	21.24	.02	.05	ND	ND	ND
12	27.2	33.050	21.21	.02	.06	ND	ND	IV
13	27.2	33.020	21.19	.03	.05	ND	ND	ND
14	27.1	32.980	21.20	.02	.05	ND	ND	IV
15	27.1	32.930	21.16	.02	.05	166	ND	IV
16	27.2	32.970	21.15	.02	.06	ND	ND	ND
17	27.2	32.910	21.11	.03	.05	ND	ND	ND
18	27.2	32.880	21.09	.02	.05	ND	ND	IV
19	27.2	32.910	21.11	.02	.07	ND	ND	ND
20	27.4	32.790	20.96	.03	.04	337	ND	IV
21	27.4	32.780	20.95	.02	.04	ND	ND	ND
22	27.3	32.730	20.94	.04	.12	ND	ND	IV-V
23	27.3	32.690	20.91	.02	.04	ND	ND	ND
24	27.3	32.690	20.91	.02	.02	102	ND	III
25	27.3	32.720	20.94	.02	.06	ND	ND	ND
26	27.2	32.750	20.99	.01	.05	ND	ND	III-IV
27	27.2	32.830	21.05	.02	.04	ND	ND	ND
28	27.5	32.910	21.02	.02	.05	ND	ND	II
29	27.5	33.030	21.11	.02	.06	ND	ND	ND
30	27.5	33.140	21.1	.02	.13	600	ND	ND

DAY 393 ASTP STATIONS, 22 JULY 1975 SURFACE SAMPLES

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
31	27.3	32.880	21.06	.04	.14	490	14	II
32	27.3	32.950	21.11	.03	.05	ND	ND	ND
33	27.2	32.750	20.99	.02	.08	ND	14	II
34	27.2	32.740	20.99	.02	.10	ND	ND	ND
35	27.2	32.720	20.97	.02	.08	114	20	IV
36	27.2	32.800	21.02	.02	.07	ND	ND	ND
37	27.3	32.800	21.00	.02	.10	ND	19	III-IV
38	27.3	33.000	21.15	.01	.02	ND	ND	ND
39	27.3	32.820	21.01	.02	.07	ND	15	V
40	27.3	32.740	20.95	.03	.06	427	15	IV-V
41	27.3	32.720	20.94	.02	.07	ND	15	IV-V
42	27.3	32.630	20.87	.01	.06	ND	ND	ND
43	27.5	32.650	20.82	.02	.09	272	15	III
44	27.5	32.630	20.81	.01	.08	ND	ND	ND
45	27.3	32.660	20.91	.02	.08	ND	18	III-IV
46	27.3	32.720	20.94	.04	.14	ND	ND	ND

DAY 394 ASTP STATIONS 23 JULY 1975 SURFACE SAMPLES

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
50	27.1	32.680	20.88	.02	.14	441	15	III
51	27.1	32.770	20.94	.05	.15	ND	ND	ND
52	27.1	32.640	21.00	.02	.12	ND	20	III-IV
53	27.2	32.830	21.05	.04	.18	ND	ND	ND
54	27.2	32.930	21.12	.02	.11	ND	16	III-IV
55	27.3	33.110	21.23	.02	.08	464	ND	ND
56	27.3	32.910	21.08	.01	.11	ND	19	III
57	27.8	32.850	20.90	.01	.09	ND	ND	ND
58	27.5	32.860	20.98	.04	.10	ND	19	III
59	27.5	32.830	20.96	.03	.05	ND	ND	ND
60	27.5	32.740	20.89	.03	.05	449	18	III
61	27.5	32.710	20.87	.03	.08	ND	ND	ND
62	27.8	32.720	20.78	.02	.07	ND	15	III
63	27.8	32.770	20.81	.05	.11	ND	ND	ND
64	27.6	32.780	20.89	.06	.13	ND	16	IV

DAY 407 STATION 59 5 AUG. 1975 SECCHI: 20M FOREL: III-IV

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.8	32.247	20.41	.01	.13	704
15	ND	32.201	ND	.02	.15	487
25	ND	33.437	ND	.03	.17	510
34	ND	34.407	ND	.03	.11	330
48	ND	35.231	ND	.04	.11	60
72	ND	ND	ND	.14	.11	43
96	ND	36.775	ND	.05	.03	15
144	ND	36.773	ND	.02	.01	1
168	ND	36.469	ND	.01	.01	6

DAY 427 STATION 62 25 AUG. 1975 SECCHI: 25M FOREL: II

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.1	33.219	21.05	.03	.08	205
15	28.2	33.393	21.14	.03	.07	283
25	28.3	34.042	21.60	.05	.09	434
35	27.9	35.282	22.66	.09	.10	3
49	27.0	35.856	23.38	.10	.20	3
74	25.3	36.834	24.65	.08	.06	0
98	23.8	36.730	25.03	.04	.04	0
148	19.2	36.366	26.03	.02	.01	0
172	17.1	36.980	27.03	.03	.01	0

DAY 478 STATION 69 15 OCT. 1975 SECCHI: 30M FOREL: II

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.2	34.573	22.03	.03	.05	286
15	28.2	34.629	22.07	.03	.06	181
25	28.2	34.629	22.07	.04	.06	136
35	28.2	34.630	22.07	.14	.04	3
50	28.1	36.950	23.85	.05	.01	1
75	26.5	36.372	23.93	.03	.01	0
100	24.7	35.657	23.95	.02	.01	0
150	21.4	36.152	25.28	.02	.00	0
175	19.2	35.571	25.42	.02	.01	0

DAY 501 STATION 72 7 NOV. 1975 SECCHI: 28M FOREL: I

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.6	35.062	22.69	.01	.04	125
15	27.6	35.070	22.60	ND	ND	ND
25	27.6	35.158	22.66	.01	.03	191
35	27.1	35.110	22.79	.01	.04	170
50	26.3	36.264	23.91	.03	.06	22
75	25.3	37.082	24.84	.12	.06	0
100	24.5	37.162	25.15	.03	.03	0
150	22.2	36.884	25.61	.01	.01	0
175	19.4	36.276	25.91	.01	.01	0

DAY 534 STATION 77 10 DEC. 1975 SECCHI: 25M FOREL: I

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.4	35.649	23.10	.03	.06	239
15	27.4	35.655	23.10	.02	.07	231
25	27.4	35.664	23.11	.02	.07	ND
35	27.4	35.664	23.11	.08	.02	ND
50	27.4	35.705	23.14	.03	.09	46
75	27.4	35.734	23.16	.03	.08	22
100	27.2	36.377	23.71	.25	.12	6
150	25.3	36.807	24.63	.12	.07	6
175	22.0	37.097	25.83	.02	.02	0

DAY 564 STATION 82 9 JAN. 1976 SECCHI: 19M FOREL: II

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.4	35.540	23.34	.08	.21	553
13	26.4	35.544	23.34	.07	.18	1330
22	26.4	35.547	23.34	.07	.20	1131
31	26.4	35.547	23.34	.07	.18	742
45	26.4	35.549	23.34	.09	.17	402
67	26.4	35.651	23.42	.10	.17	318
89	26.8	36.397	23.85	.16	.16	438
134	24.0	35.579	24.10	.09	.15	422
156	22.7	35.652	24.53	.09	.18	485

DAY 574 STATION 83-1 19 JAN. 1976 SECCHI: 20M FOREL: I

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	26.1	35.579	23.46	.03	.05	123
5	26.1	35.582	23.46	.03	.03	164
23	26.1	35.583	23.46	.04	.05	213
45	26.1	35.582	23.46	.04	.04	160

DAY 574 SURFACE STATIONS 19 JAN. 0076

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
83-2	26.1	35.604	23.46	.05	.08	125	ND	ND
83-3	26.1	35.615	23.49	.05	.08	275	ND	ND
83-4	26.1	35.625	23.51	.04	.14	139	ND	ND

DAY 574 STATION 83-5 19 JAN. 1976 SECCHI: 18M FOREL: I

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	26.1	35.638	23.50	.04	.12	75
5	26.1	35.704	23.55	.03	.22	154
25	26.1	35.642	23.51	.03	.20	383
50	26.1	35.632	23.50	.04	.14	98

DAY 574 SURFACE STATIONS 19 JAN. 0076

STA.#	TEMP	SAL.	SIGMA-T	PHAEO	CHL-A	TRICHO	SECCHI	FOREL
83-6	26.1	35.705	23.57	.06	.16	212	ND	ND
83-7	26.1	35.618	23.50	.06	.13	281	ND	ND
83-8	26.1	35.656	23.53	.04	.06	121	ND	ND

DAY 596 STATION 87 10 FEB. 1976 SECCHI: 25M FOREL: I

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.8	34.885	23.03	.02	.05	31
15	26.0	35.108	23.14	.02	.09	ND
24	25.8	35.257	23.31	.01	.07	43
34	25.8	35.274	23.32	.02	.07	63
49	26.1	35.999	23.78	.05	.11	3
73	25.5	36.770	24.54	.12	.18	1
97	23.4	37.053	25.39	.13	.08	3
146	21.7	37.350	26.11	.05	.05	71
170	21.7	37.368	26.12	.03	.06	0

DAY 627 STATION 90 12 MAR. 1976 SECCHI: 27M FOREL: II

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	25.3	34.607	22.97	.04	.09	861
14	25.4	34.670	22.99	.09	.14	169
23	25.4	34.987	23.23	.07	.12	ND
33	25.7	35.058	23.19	.09	.11	106
42	25.5	36.919	24.66	.04	.04	1
63	26.2	37.072	24.55	.06	.02	4
84	24.1	36.887	25.06	.05	.01	0
125	20.8	36.112	25.41	.02	.01	0
146	22.3	36.043	24.94	.01	.01	0

DAY 661 STATION 96 15 APR. 1976 SECCHI: 24M FOREL: II

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.5	34.331	22.39	.03	.10	643
14	26.5	35.810	23.51	.09	.10	70
23	26.5	35.811	23.51	.11	.12	24
33	26.5	35.836	23.53	.08	.14	10
42	26.5	35.899	23.57	.09	.19	0
63	26.4	36.010	23.69	.10	.18	0
84	26.3	36.386	24.01	.09	.03	0
125	22.0	36.563	25.42	.02	.01	0
146	20.9	36.525	25.70	.03	.01	0

DAY 690 STATION 100 14 MAY 1976 SECCHI: 14M FOREL: V

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.1	33.590	21.65	.03	.18	802
15	27.1	33.594	21.65	.00	.22	ND
25	27.0	34.081	22.05	.03	.23	746
33	27.0	35.741	23.30	.09	.31	47
48	27.0	35.872	23.40	.10	.33	2
71	27.0	36.011	23.50	.08	.16	0
95	26.4	36.014	23.69	.13	.18	0
143	23.2	36.621	25.12	ND	ND	0
166	22.3	36.943	25.63	ND	ND	ND

4KM STATIONS

DAY 9 STATION 2 3 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	27.3	33.815	21.75	.07	.07	ND
5	ND	33.937	ND	.06	.10	ND
10	ND	33.983	ND	.06	.09	ND

DAY 15 STATION 3 9 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	27.5	32.613	20.79	.03	.07	361
5	27.5	32.626	20.80	.14	.05	374
10	27.5	32.678	20.83	.11	.04	882
15	27.4	32.688	20.87	.13	.10	ND
25	27.1	33.748	21.77	.15	.16	938

DAY 22 STATION 4 16 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	27.7	32.664	20.76	.09	.06	628
5	ND	32.764	ND	.13	.07	1444
10	ND	32.802	ND	.03	.15	1334
15	ND	33.010	ND	.05	.15	678
25	ND	34.244	ND	ND	ND	19

DAY 29 STATION 5 23 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	32.565	20.59	.03	.08	78
5	27.9	32.587	20.64	.04	.07	64
10	27.7	32.667	20.76	.04	.12	325
15	27.6	33.164	21.17	.07	.11	225
25	27.3	33.572	21.57	.12	.15	51

DAY 34 STATION 6 28 JULY 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	32.921	20.86	.03	.11	1174
5	ND	32.947	ND	.01	.14	781
10	ND	33.005	ND	.00	.18	711
15	ND	33.250	ND	.02	.17	429
25	ND	34.140	ND	.05	.14	7

DAY 44 STATION 7 7 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	27.9	33.243	21.13	.04	.08	312
5	27.9	33.398	21.25	.03	.11	406
10	27.8	33.517	21.37	ND	ND	685
15	27.7	33.585	21.45	.03	.10	440
25	27.6	33.590	21.49	.09	.40	411

DAY 48 STATION 8 11 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	32.265	20.36	.02	.08	65
5	ND	32.275	ND	.02	.08	144
10	ND	32.214	ND	.02	.09	212
15	ND	32.370	ND	.05	.14	168
25	ND	34.613	ND	.07	.19	196
50	ND	0.0	ND	.02	.10	73

DAY 58 STATION 9 21 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	27.6	33.716	21.58	.05	.18	386
5	27.6	33.716	21.58	.04	.19	478
10	27.7	33.747	21.57	.07	.16	356
15	27.8	33.791	21.57	.09	.14	438
25	27.3	34.190	22.03	.09	.21	238
50	26.2	36.063	23.79	.10	.14	36

DAY 64 STATION 10 27 AUG. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	33.770	21.49	.03	.08	129
5	ND	33.777	ND	.04	.07	24
10	ND	34.000	ND	.03	.06	90
15	ND	34.230	ND	.04	.08	120
25	ND	34.342	ND	.05	.09	544
50	ND	0.0	ND	.03	.18	3

DAY 71 STATION 11 3 SEP. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.5	33.180	20.89	.03	.06	169
5	28.5	33.212	20.91	.03	.07	116
10	28.4	33.221	20.95	.03	.06	88
15	28.3	33.259	21.01	.02	.07	74
25	28.0	33.334	21.17	.04	.10	410
50	26.0	36.037	23.84	.16	.11	ND

DAY 78 STATION 12 10 SEP. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.7	33.364	20.96	.01	.08	179
5	ND	33.375	ND	.02	.08	180
10	ND	33.389	ND	.03	.08	191
15	ND	33.432	ND	.04	.07	237
25	ND	35.026	ND	.11	.15	240

DAY 85 STATION 13 17 SEP. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.5	33.495	21.12	.03	.08	91
5	28.5	33.498	21.12	.05	.09	105
10	28.5	33.502	21.13	.06	.08	ND
15	28.5	33.538	21.15	.05	.09	157
25	28.0	34.091	21.73	.09	.22	228

DAY 92 STATION 14 24 SEP. 1974 SECCHI: 22M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	33.223	20.89	.01	.07	45
5	ND	33.266	ND	.02	.08	463
10	ND	33.281	ND	.02	.08	344
15	ND	33.615	ND	.11	.10	443
25	ND	35.014	ND	.11	.22	72
50	ND	36.088	ND	.10	.24	83

DAY 101 STATION 15 3 OCT. 1974 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.0	33.446	21.25	.3	.10	150
5	28.0	33.536	21.32	.04	.08	226
10	28.0	33.522	21.35	.03	.08	228
15	28.0	33.601	21.37	.03	.09	170
25	28.1	33.619	21.35	.03	.10	139
50	26.0	36.240	23.99	.12	.15	9

DAY 106 STATION 16 8 OCT. 1974 SECCHI: 21M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.3	34.536	21.97	.03	.10	614
5	ND	34.540	ND	.04	.10	529
10	ND	34.542	ND	.05	.12	718
15	ND	34.571	ND	.03	.10	501
25	ND	34.536	ND	.08	.13	904
50	ND	36.290	ND	.18	.17	64

DAY 113 STATION 17 15 OCT. 1974 SECCHI: 24M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
0	28.3	34.342	21.82	.05	.15	239
5	28.3	34.345	21.83	.09	.18	599
10	28.3	34.350	21.83	.06	.17	391
15	28.4	34.426	21.85	.04	.14	457
25	28.2	34.819	22.21	.06	.13	288
35	27.7	35.464	22.86	.07	.25	ND
50	27.1	36.035	23.49	.03	.08	75

DAY 120 STATION 18 22 OCT. 1974 SECCHI: 21M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.1	34.575	22.06	.03	.10	439
25	ND	34.719	ND	.05	.15	423
35	ND	34.871	ND	.08	.11	222
50	ND	36.180	ND	.07	.07	62

DAY 127 STATION 19 29 OCT. 1974 SECCHI: 32M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.2	34.579	22.03	.02	.08	241
25	28.2	34.603	22.05	.04	.07	130
35	27.5	34.603	22.18	.03	.09	162
50	27.1	35.928	23.41	.16	.16	89

DAY 134 STATION 20 5 NOV. 1974 SECCHI: 31M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.4	34.509	21.92	.03	.07	124
25	ND	34.509	ND	.02	.08	193
35	ND	35.683	ND	.11	.13	106
50	ND	36.507	ND	.18	.19	226

DAY 141 STATION 21 12 NOV. 1974 SECCHI: 31M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	28.1	34.051	21.67	.02	.05	85
25	28.1	34.127	21.73	.02	.06	24
35	27.7	34.937	22.47	.06	.11	70
50	27.0	36.050	23.53	.07	.11	93

DAY 148 STATION 22 19 NOV. 1974

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.9	34.485	22.06	.04	.08	72
15	ND	34.542	ND	.04	.08	93
24	ND	34.552	ND	.06	.12	76
33	ND	34.554	ND	.06	.16	252
47	ND	36.459	ND	.13	.18	19

DAY 158 STATION 23 29 NOV. 1974 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.7	34.402	22.06	.03	.06	235
15	27.7	34.421	22.08	.03	.05	64
25	27.7	34.433	22.09	.04	.07	155
35	27.7	34.458	22.11	.03	.07	91
50	27.6	35.228	22.72	.24	.08	182

DAY 162 STATION 24 3 DEC. 1974 SECCHI: 20M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.6	34.529	22.19	.02	.09	190
15	ND	34.545	ND	.02	.09	520
25	ND	34.544	ND	.02	.09	159
35	ND	35.469	ND	.05	.12	249
50	ND	36.513	ND	.04	.01	73

DAY 169 STATION 25 10 DEC. 1974 SECCHI: 34M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.6	34.544	22.20	.02	.04	342
15	27.6	34.552	22.21	.03	.06	143
25	27.6	34.572	22.22	.02	.05	68
35	27.6	34.624	22.26	.03	.08	99
50	27.5	34.824	22.45	.05	.10	63

DAY 176 STATION 26 17 DEC. 1974 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.2	34.555	22.34	.02	.04	50
15	ND	34.609	ND	.02	.04	18
25	ND	34.609	ND	.02	.05	20
35	ND	34.827	ND	.02	.06	93
50	ND	36.804	ND	.19	.15	4

DAY 182 STATION 27 23 DEC. 1974 SECCHI: 31M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	27.1	34.845	22.59	.02	.05	386
14	27.1	35.007	22.71	.02	.05	19
24	27.2	35.308	22.91	.02	.08	55
33	27.3	35.402	22.95	.04	.10	78
47	27.4	35.747	23.17	.04	.12	61

DAY 189 STATION 28 30 DEC. 1974 SECCHI: 34M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.8	35.490	23.17	.03	.06	113
15	ND	35.538	ND	.08	.11	320
25	ND	35.618	ND	.08	.09	353
35	ND	35.641	ND	.08	.08	277
50	ND	35.839	ND	.09	.15	377

DAY 197 STATION 29 7 JAN. 1975 SECCHI: 21M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.5	35.233	23.07	.04	.19	588
15	26.6	35.223	23.03	.06	.20	986
25	26.7	35.335	23.09	.09	.21	706
35	26.6	35.438	23.20	.10	.32	972
50	26.6	35.483	23.23	.17	.26	529

DAY 204 STATION 30 14 JAN. 1975 SECCHI: 26M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.4	35.274	23.14	.05	.13	298
15	ND	35.483	ND	.10	.14	28
25	ND	35.565	ND	.08	.23	147
35	ND	35.655	ND	.07	.23	866
50	ND	35.896	ND	.09	.21	359

DAY 211 STATION 31 21 JAN. 1975 SECCHI: 22M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	TRICHO
5	26.4	35.143	23.04	.10	.24	177
15	26.4	35.175	23.06	.10	.31	913
25	26.4	35.181	23.07	.10	.27	1435
35	26.4	35.181	23.07	.10	.26	1712
50	26.6	35.578	23.30	.29	.27	273

DAY 221 STATION 32 31 JAN. 1975 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
5	26.3	35.283	23.17	.07	.28	1577
15	ND	35.301	ND	.10	.31	2188
25	ND	35.305	ND	.14	.26	1429
35	ND	35.301	ND	.12	.33	1111
50	ND	35.392	ND	.08	.31	1653

DAY 225 STATION 33 4 FEB. 1975 SECCHI: 22M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
5	26.2	35.024	23.01	.06	.44	3702
15	26.2	35.041	23.02	.07	.45	3655
25	26.2	35.122	23.08	.13	.48	3031
35	26.2	35.130	23.09	.20	.50	1184
50	26.2	35.186	23.13	.10	.39	10

DAY 232 STATION 34 11 FEB. 1975 SECCHI: 27M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
5	26.2	35.958	23.71	.06	.11	158
15	ND	35.960	ND	.06	.14	20
25	ND	35.977	ND	.08	.15	10
35	ND	36.000	ND	.07	.21	137
50	ND	36.003	ND	.09	.25	66

DAY 236 STATION 35 15 FEB. 1975 SECCHI: 19M

DEPTH	TEMP	SALINITY	SIGMA-T	PHAEO-PIG.	CHL-A	IRICHO
5	25.4	35.810	23.85	.06	.11	ND
15	25.4	35.989	23.99	.06	.11	ND
25	25.4	36.009	24.00	.08	.13	ND
35	25.4	36.019	24.01	.08	.14	ND
50	25.4	36.080	24.05	.10	.16	ND