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The influence of the meandering Guiana Current on surface conditions near Barbados - temporal variations of Trichodesmium (Cyanophyta) and other plankton¹

by Gary A. Borstad^{2,8}

ABSTRACT

The temporal fluctuations of the surface layer *Trichodesmium* (Cyanophyta) populations off Barbados which occur at roughly three-month intervals are shown to be accompanied by in-phase fluctuations of both the numbers and species composition of other phytoplankton and surface dwelling zooplankton. These periodic *Trichodesmium* and diatom 'blooms' are actually patches advected to Barbados in low salinity, more neritic surface water from the productive regions off the Guiana Shelf. The complex movements of the Guiana Current appear to control the timing of events at Barbados and the distribution of surface plankton over a large portion of the western tropical Atlantic.

1. Introduction

The phytoplankton biomass of most tropical oceanic areas is low and limited by the availability of plant nutrients. In these areas where aseasonal fluctuations of the physical environment are small and the water column is permanently stratified there are not usually large seasonal changes in the abundance or productivity of phytoplankton stocks either in space or time.

Such is also the case in the western tropical Atlantic away from the South American continental shelf; however, in the late 1960's Steven *et al.* (1970) detected regularly occurring fluctuations of near surface total chlorophyll a (chlorophyll a + phaeopigment) concentrations at an oceanic station 8 km west of Barbados (Fig. 1). These increases did not relate to the annual solar cycle or other measured physical or chemical parameters and seemed to them to be due largely to variations of the abundance of the planktonic cyanophyte *Trichodesmium*.

Mathematical analysis confirmed that both parameters fluctuated with a period

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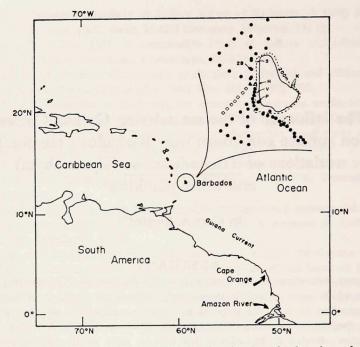


Figure 1. Barbados and the western tropical Atlantic, showing the location of stations and occasional samples mentioned in text. This study: 8 km station (▲); 4 km station (△); May 21, 1975 (○); July 21-23, 1975 (●); January 21, 1976 (◇). Steven et al., 1970 (2B); Sander, 1971 (S.H.); Vezina, 1974 (V,P); Partlo, 1975 (P); Sander, 1976 (H); Kidd, 1978 (K,H); Hawkins, 1980 (H).

of between 93 and 120 days (Steven and Glombitza, 1972) quite unlike any other biological system. Steven and Glombitza hypothesized the oscillations were growth and decay cycles of *Trichodesmium*, and suggested that the periodic increases in abundance might be the result of growth from a 'seed' population in deep water where nutrients were available, with waning of the surface populations occurring when internal cellular reserves were depleted.

This paper reports the results of part of a study of *Trichodesmium* at Barbados which arose from Steven's work. Of concern here are the temporal variations of *Trichodesmium* and the other plankton of the surface layer, and the relationship between fluctuations in plankton abundance and species composition and physical conditions.

Trichodesmium is closely related to freshwater genus Oscillatoria, and in fact some authors prefer to combine the two genera under the latter name (Drouet, 1968; Sournia, 1968; Carpenter and Price, 1976). I prefer the label Trichodesmium because of its historical precedence and because of the as yet unresolved taxonomic problems with blue-greens in general and this genus in particular. In this regard I agree with Japanese (Marumo, 1975) and Indian workers (Ramamurthy, 1970) studying this particular genus and several important recent publications concerning the biology and ecology of cyanophytes as a group (Fogg *et al.*, 1973; Carr and Whitton, 1973; Mague *et al.*, 1977; Hardy and Gibson, 1977). Three *Trichodesmi-um* species are present at Barbados: *T. thiebautii* Gomont, *T. hildenbrandtii* Gomont and more rarely *T. erythraeum* Ehrenberg. For the purposes of this paper they are not differentiated.

2. Materials and methods

Two stations were established off the west coast of Barbados, directly off the Bellairs Research Institute of McGill University, St. James at approximately $13^{\circ}12'N$, $59^{\circ}42'W$ (8 km from shore in 400 m water) and $13^{\circ}12'N$, $59^{\circ}40'W$ (4 km from shore in 200 m water) and visited at intervals of between one week and one month between July 1974 and May 1976 (Fig. 1). At each station a bathythermograph cast was made to 250 m (8 km) or 150 m (4 km) using a Mark IV Thermoline recorder. Water samples were collected at several depths for analysis of chlorophyll *a* and phaeopigment concentrations, *Trichodesmium* cell counts and salinity. Other observations included sea surface temperature, air temperature, wind speed, sea state, Secchi transparency and water color, and general meteorological observations. Qualitative plankton tows were taken regularly at the surface and irregularly at various depths to 50 m using nets of 0.24 mm mesh.

Data from other locations around the island provided nearly synoptic data on the small scale (\sim 30 km) variations of surface temperature, salinity, chlorophyll *a* concentration, and *Trichodesmium* numbers in the vicinity of the island.

At most stations the entire 7 L contents of the Van Dorn bottles were transferred to large Nalgene bottles and stowed in wooden boxes where they could be kept cool and dark for the return to the laboratory. Immediately upon return to shore (usually between 1 and 2 hours after the hydrocast) the samples were mixed gently by inversion several times, and subsampled for salinity, chlorophyll *a* and *Trichodesmium* analysis. Salinity was measured using an inductively coupled Autolab Industries Model 601 Mark III salinometer. Chlorophyll *a* and phaeopigment concentrations were measured by the acidification fluorescence technique given by Strickland and Parsons (1968) using a Turner Model 110 fluorometer.

The cyanophyte *Trichodesmium* from 1 L subsamples was concentrated by gentle filtration through a sintered glass extraction funnel, transferred to 25 mL Utermohl counting chambers with thorough rinsing of the funnel and preserved with Lugol's iodine (the more familiar settling method caused most *Trichodesmium* colonies to disintegrate during the three or four transfers that were necessary from one settling chamber to the next). Lugol's iodine was preferable as preservative since the

gas vacuoles of *Trichodesmium* were not always collapsed by 2% formaldehyde and the cells therefore possessed residual buoyancy. The filtration technique was much more rapid and insured collection of all the *Trichodesmium* in a water sample. Frequent checks of the filtrate showed that less than 1% of the blue-green passed through.

The more accepted technique of counting filaments encountered in 1 percent of the field is much faster and is the obvious choice for studies where the other plankton are also enumerated, but it will not be accurate unless colonies are completely disrupted. Intact *Trichodesmium* colonies were usually present in my samples and during blooms they contributed as much as half the cyanophyte biomass. 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 colonies (Borstad and Brinckmann-Voss, 1979).

Only *Trichodesmium* was enumerated, but qualitative notes were made regarding the most common and unusually large or abundant other species. Because part of the study involved monitoring the size, form and percent contribution of the two main *Trichodesmium* colony types, all of the blue-green in 1 L settled volumes was counted. Both single filaments and those in intact colonies were counted in three size classes, and their total length converted to numbers of cells (the approximate number of filaments in intact colonies was obtained by counting filaments protruding out one end or side of the colony while focussing up and down). Comparison with more conventional cell counts of disrupted colonies showed that this technique was accurate to about $\pm 15\%$.

3. Results

Chlorophyll *a* concentrations in the near surface layer (5 m) were between 0.05 and 0.1 μ g/L during much of the year (Fig. 2) similar to other stable systems of low fertility such as the Sargasso Sea and open Caribbean Seas. Periodic increases were observed in January-February, May, August and October to between 0.25 and 0.35 μ g/L - levels more characteristic of fertile ascending system (Margalef, 1971). These events were temporary - usually only encountered at one or two consecutive hydrographic stations which were two weeks apart. Surveys around the island made in July 1975 showed a small region of elevated 5 m chlorophyll *a* concentrations in the 'wake' of the island along the northwest coast. This did not extend to the location of the serial stations, but may have done so during the last quarter of the year when surface currents are directed more westward. There was no statistical difference between the 5 m chlorophyll *a* concentrations at the 4 and 8 km stations.

The temporal variation of the Trichodesmium population at Barbados is sum-

marized by Figure 3 (vertical distribution discussed in Borstad (1978)). It is evident that the oscillatory variations described by Steven and Glombitza (1972) were still occuring during 1974-1976. There were "pulses" of *Trichodesmium* (predominantly *T. thiebautii*) in January-February, May, August and 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, principally because of differences in technique. The absence of a large increase in cell numbers at 5 m in January 1976 is a reflection of a more or less homogeneous distribution to 175 m at that time. Microscopic observations of material from this station showed *Trichodesmium* from all depths was unhealthy and disintegrating - evidence of waning population.

The variations of chlorophyll *a* concentrations at 5 m closely approximated those of the *Trichodesmium* population at this depth. The coefficient of variation indicated that 49% of the variation of chlorophyll *a* was associated with variations of the *Trichodesmium* population, and this was almost exactly the percentage contribution by calculating the μ g chlorophyll *a*/mm filament (0.00012) from measurements of isolated colonies and multiplying this by the average standing crop (52.3 × 10⁶ cells/m³). By these calculations *Trichodesmium* contributes on the average 0.06 μ g chlorophyll *a*/L or 50% of the annual mean chlorophyll *a* concentration.

4. Discussion

The hypotheses concerning the cause of the cyclical appearance of Trichodesmium off Barbados put forward to Steven and his co-workers (Steven et al., 1970; Steven and Glombitza, 1972) have already been outlined. Carpenter and Price (1976) are the only other authors to have considered the cause of the cycles. 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 (Brongersma-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 at Barbados and found a significant correlation beween 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. These may indeed be factors affecting growth by the alga, however, there was no significant relationship between Trichodesmium abundance and the same meteorological parameters during the current study.

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.

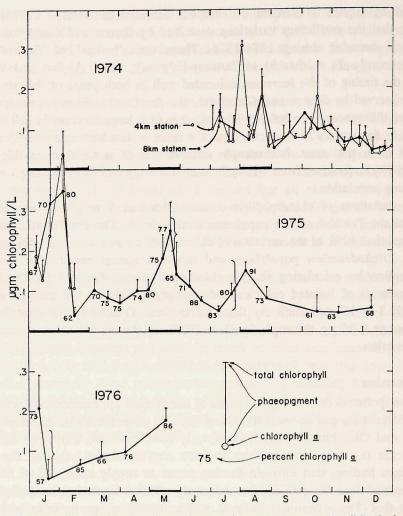


Figure 2. Concentration of chlorophyll *a* and phaeopigment at 5 m depth off Barbados, 1974-1976. 8 km station (●), 4 km station (○). Brackets indicate range of values for stations visited on the same day. Curve drawn for serial stations only. Black bars along abscissa indicate months of recurring maxima in the data of Steven *et al.* (1970).

Very large *Trichodesmium* populations, sometimes already morphologically disintegrating can appear off Barbados overnight. Their equally rapid disappearance suggests that horizontal advection of discrete patches of *Trichodesmium* is important in regulating the populations encountered at Barbados. I have discussed the heterogeneity, origin and general movements of the surface water masses in a companion paper (Borstad, 1982). That paper also describes the intermittent appearance of 'pools' of slightly fresher water and a comparison of surface *Trichodesmium* and salinities is therefore interesting here.

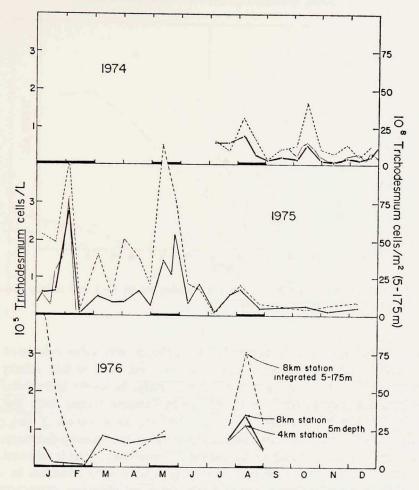


Figure 3. Variations of *Trichodesmium* standing stock at two stations off the west coast of Barbados during 1974-1976. Black bars on the abscissa indicate approximate times of recurring *Trichodesmium* maxima observed by Steven *et al.* (1970).

The alga could always be found in surface waters, both inshore and offshore. While there was no apparent relation between *Trichodesmium* abundance or chlorophyll *a* concentration and salinity, a plot of surface salinity and *Trichodesmium* versus time (Fig. 4) shows that the alga was much more abundant near Barbados in the first eight months of the year and that, the rapid changes in *Trichodesmium* abundance from one station to another were associated with slight changes of surface salinity. A similar inverse relationship between *Trichodesmium* numbers and salinity can also be seen in the data of Steven *et al.*, 1970. It is evident that there is a relationship between algal abundance and deviations from the running mean salinity. Figure 5 illustrates an increase in chlorophyll *a* concentrations at 5

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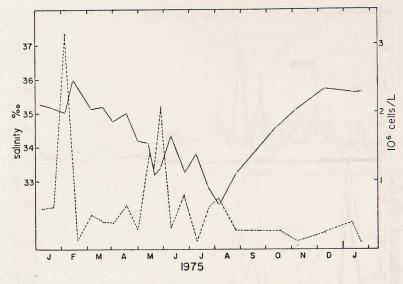


Figure 4. Relationship between *Trichodesmium* standing stocks (---) and salinity (----) at 5 m depth at the 8 km station during 1975.

and 15 m when salinity at 5 m was less than the median value calculated from the 1974-1976 data and the envelope of previously recorded surface salinity (Fig. 2, Borstad, 1982), that is a negative salinity anomaly. In waters more saline than that expected at any particular time, chlorophyll concentrations were low. The relationship is significant at the 9% level, according to a student T test of the correlation coefficient. If the two points representing the January-February 1975 pulse are omitted, statistical significance at the 2% confidence level is achieved.

The fact that *Trichodesmium* and chlorophyll *a* were 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 apear to be, then it is logical to expect evidence of rhythmicity in data concerning other plankton.

Cell counts for phytoplankton other than *Trichodesmium* were not a part of the 1974-76 study, but qualitative notes made of the other plankton 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 abundant in samples containing large numbers of the cyanophyte and in the May 1975 'bloom' fish eggs and larvae were also numerous.

Steven et al. (1970) regarded the offshore phytoplankton excluding Trichodesmium as being rather stable numerically; however they point out that the range of 1982]

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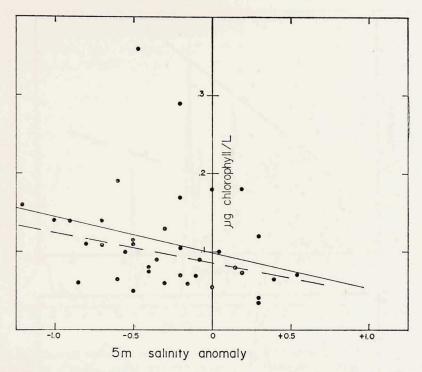
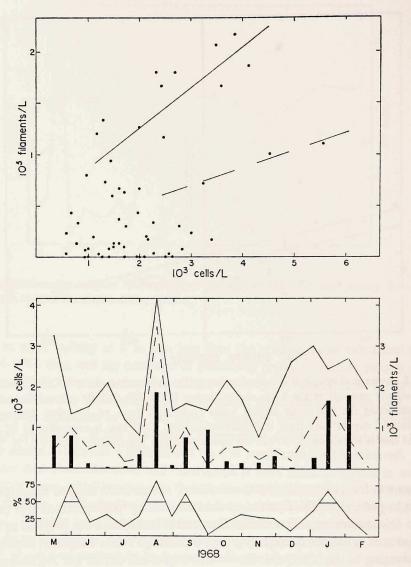


Figure 5. Average chlorophyll a concentration in the near surface layer (5-15 m) versus the 5 m salinity anomaly at the 8 km station during 1974-1976. Salinity anomaly is calculated by subtracting the mid-range salinity value (calculated from all historical data available for each 15 day period) from the observed salinity. Solid line is regression of all points, dashed line is regression of all but the two high points representing January 1975 'bloom'.

variation was from about 500-5000 cells/liter⁴, and mention marked fluctuations of diatoms in particular. Their published data concerning 'phytoplankton cell counts', include *Trichodesmium* cells and filaments and it is therefore not possible to examine the annual variations of the two groups separately. I have examined unpublished data belonging to the late D. M. Steven which give 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 6 and 7. The 'phytoplankton excluding *Trichodesmium*' show marked oscillation in phase with the blue-green, with a linear relation between the two groups at 5 and 50 m for most stations (Fig. 6). In every case the peaks agree to within one interval on the sampling schedule (two weeks). Further, the increases in 'other phytoplankton' are largely due to increases in numbers of

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^{4.} Corrected value: the original cell counts were $6 \times too$ high, and have been corrected by Sander (1971) and Sander and Steven (1973) (F. Sander, personal communication, Bellairs Research Institute, St. James, Barbados.)



- Figure 6. Relation between *Trichodesmium* and phytoplankton excluding *Trichodesmium* at 5 m depth during 1968-1970. Three points along the lower dashed line are all from stations where the increase in other phytoplankton followed that of *Trichodesmium* by one sampling interval (2 weeks) (D. M. Steven, unpublished data).
- Figure 7. Temporal variations of *Trichodesmium* (filaments/L; bars), total other phytoplankton (cells/L; ----), diatoms (cells/L; ---) and percent contribution to total other phytoplankton by diatoms (below) (D. M. Steven, unpublished data).

diatoms which appear with the same periodicity as *Trichodesmium* (Fig. 7) confirming the observations made during the current study. 1982]

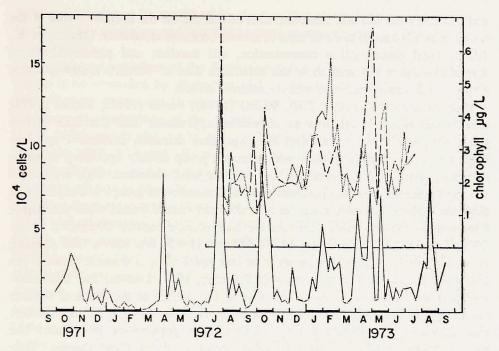


Figure 8. Temporal variations of surface layer (1 m) total chlorophyll concentration (interrupted lines - Vezina, 1974) and phytoplankton cell numbers (continuous line - Sander, 1976) at three inshore stations along the southern half of Barbados' west coast. Vezina's stations are indicated in Figure 1 by V and P, Sander's by 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).

All of the other phytoplankton studies at Barbados with sampling twice a month or more have been conducted close to the island. Work by Partlo (1975) and Kidd (1978) both show sharp temporary pulses of chlorophyll a concentration and cell numbers in the surface layers close inshore during 1974-1976. This is further illustrated by a longer time series prepared from data of Vezina (1974) and Sander (1976) for three inshore stations in shallow (5-10 m) water along the island's west coast (Fig. 8). Cell numbers at 1 m depth at Sander's station (Fig. 1) off Bellairs Research Institute coincided well with 1 m chlorophyll a (+ phaeophytin) concentration at Vezina's stations 5 and 10 km south (V and P in Fig. 1). Sander (1976) points out that the increases in total chlorophyll a measured by Vezina were primarily due to increases in numbers of diatoms and not of dinoflagellates or coccolithophorids which dominated the population during the periods of low cell numbers.

Examination of the data from Sander's earlier study (Sander, 1971) reveals that the synchrony of phytoplankton events which is evident for the southern west coast Journal of Marine Research

and the east coast did not, however, exist at stations off the northwest side of the island, which is known to be an area of slower, confused circulation (Murray *et al.*, 1977). Total chlorophyll a concentration, cell numbers and photosynthesis at several stations in this area show less coherence than at Vezina's southwest coast stations, and poorer synchrony with the offshore station.

Data from Steven et al. (1970), Vezina (1974); Partlo (1975), Sander (1976) and the current study all show an alternating appearance near 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 is 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 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, nitrate and phosphate than do other 'oceanic' species (Carpenter and McCarthy, 1975; Wada and Hasumoto, 1975; McCarthy and Carpenter, 1979). 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 which in turn receives them from the Amazon River. Amazon River water has been recently shown to contain large amounts of natural suspended sediments which release substantial quantities of soluble phosphorus over a period of several days (Chase and Sayles, 1980). This may explain the observation by Kidd and Sander (1979) of slightly elevated phosphate concentrations in the low salinity waters arriving at Barbados. The earlier observation by Carpenter and Price (1976) of large and actively N-fixing Trichodesmium populations in the eastern Caribbean where phosphate concentrations are also

slightly elevated may be explained by the fact that nitrogen fixation is limited by the availability of energy and metabolites from photosynthesis which is affected by nutrient supply.

The temporal variations of the Trichodesmium and other surface phytoplankton appear to be controlled by alternation of Guiana Current water and North Equatorial Current water, and it might therefore be reasonable to expect temporal variations of zooplankton stocks at stations near Barbados. Moore and Sander (1976, 1977), and Sander and Moore (1978) have studied the zooplankton collected during the 1968-1970 study (Steven et al., 1970) 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. Since most representatives of the Barbados zooplankton migrate appreciable vertical distances, they 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 layers. There are, however, many mixed-layer dwellers with only feeble migrations, such as the euthecosomatous pteropods. These herbivorous holoplanktonic molluscs, while they constitute an insignificant fraction of the Barbados zooplankton (Sander, 1971), are often used as water-mass indicators (Myers, 1968; Chen and Hillman, 1970). An intensive study of this group in Barbados waters was conducted by Wells (1974) and was coincident with Sander's (1976) phytoplankton study. Temporal variations of four species recorded by Wells, replotted in Figure 15 show remarkable agreement between members of the group and their periodic nature. Wells did not enumerate phytoplankton but did note an inverse correlation between Trichodesmium and pteropod abundance, which can be confirmed by comparing the timing of phytoplankton pulses at Sander's (1976) inshore station (stippled bars in Figure 9, and Figure 8). Pteropods represent oceanic waters (Bjornberg, 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. The only available salinity data for 1972 and 1973 (Powles, 1975) are for widely spaced intervals and the passage of freshwater pools cannot be detected. Probably for this reason Wells (1976) was only able to see the annual change between the two water types. Like most authors to date, he only considered 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 and diatoms, but in the reverse sense.

5. Conclusions

I have shown in a companion paper (Borstad, 1982) that the wavelike nature of the

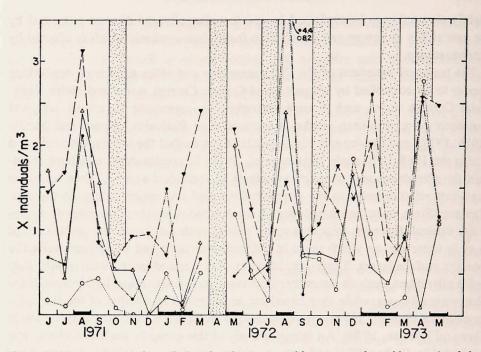


Figure 9. Temporal variation of the abundance (monthly means of weekly tows) of four species of euthecosomatous pteropods in 0-400 m oblique plankton tows off Barbados during 1971-1973 (Wells 1974). Stippled bars indicate months of phytoplankton maxima recorded by Sander (1976) at an inshore station also sampled during this time. Bars along the abscissa represent approximate timing of *Trichodesmium* and/or phytoplankton events during 1968-1970 (Steven et al., 1970) and 1974-1976 (this study). Spiratella inflata × 2 × 10^s individuals/m^s; S. lesueuri × 10 individuals/m^s; Creseis virgula conica × 10^s individuals/m^s.

Guiana Current and the alternate appearance of these waters with higher salinity North Equatorial waters are responsible for the erratic surface salinity regime off Barbados. It has been demonstrated here that this alternation of water types is related to marked in-phase variations of the stocks of *Trichodesmium* and other phytoplankton. Diatoms are much more abundant in the surface water 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 can be detected in many 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 deep waters offshore and in very shallow waters near the beach. There is also evidence that the seasonal distribution of some surface-dwelling zooplankton is controlled in this manner.

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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 (Chase and Sayles, 1980) and dissolved organic compounds brought down by the Amazon River and from local upwelling (Van Bennekom and Tijssen, 1978) and supports prolific diatom growth (Cadee, 1975). 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. By the time the pools reach Barbados (two to four weeks), compounds such as nitrate and orthophosphate will be nearly undetectable. The onset of oligotrophy will not necessarily bring about an immediate decrease in phytoplankton numbers however, since most phytoplankton are capable of storing carbon, nitrogen and phosphorus. 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 phenomena reported here will be of fundamental importance in the entire western tropical Atlantic, especially around Barbados and the southern Leeward Islands. The differences between the physical, chemical and biological properties of the two water masses are exhibited as horizontal heterogenity across the whole region and will be very important to recruitment, production, reproduction and growth in many Barbados marine populations. This should be the subject of further research. It seems likely that improvements in the local fishery are possible based on a better understanding of the oceanographic and planktonic regimes of the area. Barbados is an excellent platform from which to study the oceanic North Equatorial waters and the more neritic waters of the Guiana Current.

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REFERENCES

Bjornberg, T. K. S. 1971. Distribution of plankton relative to the general circulation system in the area of the Caribbean Sea and adjacent regions, *in* Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions, (CICAR-I). UNESCO, Paris, 343-357.

Borstad, G. A. 1978. Some aspects of the occurrence and biology of Trichodesmium (Cyano-

phyta) in the Western Tropical Atlantic near Barbados, West Indies, Ph.D. thesis, McGill University, Montreal, Canada, 234 pp.

---- 1982. The influence of the meandering Guiana Current and Amazon River discharge on surface salinity near Barbados, J. Mar. Res., 40, 421-434.

Borstad, G. A. and A. Brinckmann-Voss. 1979. *Pelagiana trichodesmiae* n. gen., n. sp., family Pandeidae, (Anthomedusae/Athecatae, Cnidaria), a new hydrozoan associated with the planktonic cyanophyte *Trichodesmium thiebautii*. Can. J. Zool., 52, 1232-1237.

Brongersma-Sanders, M. 1957. Mass mortality in the sea. Mem. Geol. Soc. Am., 67, 941-1010.

Cadee, G. C. 1975. Primary production off the Guyana Coast. Neth. J. Sea. Res., 9, 128-143.

- Carpenter, E. J. and J. J. McCarthy. 1975. Nitrogen fixation and uptake of combined nitrogenous nutrients by Oscillatoria (Trichodesmium) thiebautii in the western Sargasso Sea. Limnol. Oceanogr., 20, 389-401.
- Carpenter, E. J. and C. C. Price. 1976. Marine Oscillatoria (Trichodesmium): Explanation for aerobic nitrogen fixation without heterocysts. Science, 191, 1278-1280.
- Carr, N. G. and B. A. Whitton, Eds. 1973. The Biology of the Blue-Green Algae. Bot. Monogr., 9, Univ. Calif. Press, Berkeley, 676 pp.
- Chase, E. M. and F. L. Sayles. 1980. Phosphorus in suspended sediments of the Amazon River. Est. Coast. Mar. Sci., 11, 383-391.
- Chen, C. and N. S. Hillman. 1970. Shell-bearing pteropods as indicators of water masses off Cape Hatteras, North Carolina. Bull. Mar. Sci., 20, 350-367.
- Dodson, A. N. and W. H. Thomas. 1977. Marine phytoplankton growth and survival under simulated upwelling and oligotrophic conditions. J. Exp. Mar. Biol. Ecol., 26, 153-161.
- Drouet, F. 1968. Revision of the Classification of the Oscillatoriaceae. Monogr. Acad. Nat. Sci. Philadelphia, 15, 370 pp.
- Eppley, R. W., J. N. Rogers and J. J. McCarthy. 1969. Half-saturation constants for uptake of nitrate and ammonia by marine phytoplankton. Limnol. Oceanogr., 14, 912-920.
- Fogg, G. E., W. D. P. Stewart, P. Fay and A. E. Walsby. 1973. The Blue-green Algae. Academic Press, London, England, 459 pp.
- Hardy, R. W. F. and A. H. Gibson, Eds. 1977. A Treatise on Dinitrogen Fixation. Wiley-Interscience, New York, 4, 527 pp.
- Hargraves, P. E., R. W. Brody and P. R. Burkholder. 1970. A study of phytoplankton in the Lesser Antilles region. Bull. Mar. Sci., 20, 331-349.
- Hawkins, C. M. 1980. Ecological energetics of the tropical sea urchins *Diadema antillarum* Philippi in Barbados, West Indies. Ph.D. thesis, McGill University, Montreal, Canada, 179 pp.
- Hulbert, E. M. 1962. Phytoplankton in the southwestern Sargasso Sea and North Equatorial Current, February 1961. Limnol. Oceanogr., 7, 307-315.
- Hulbert, E. M. and N. Corwin. 1969. Influence of the Amazon River outflow on the ecology of the western tropical Atlantic. III. The planktonic flora between the Amazon River and the Windward Islands. J. Mar. Res., 27, 55-72.
- Kidd, R. J. 1978. The influence of Amazon River discharge and the island mass effect on distribution, species diversity and numbers of zooplankton near Barbados, West Indies. M.Sc. thesis, McGill University, Montreal, Canada, 210 pp.
- Kidd, R. and F. Sander. 1979. Influence of Amazon River discharge on the marine production system off Barbados, West Indies. J. Mar. Res., 37, 669-681.
- Mague, T. H., F. C. Mague and O. Holm-Hansen. 1977. Physiology and chemical composition of nitrogen-fixing phytoplankton in the central North Pacific Ocean. Mar. Biol., 41, 213-227.

- Margalef, R. 1971. The pelagic ecosystem of the Caribbean Sea, in Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions, UNESCO, Paris, 483-498.
- Marumo, R. 1975. An outline of studies on the community of marine pelagic blue-green algae, *in* Studies on the Community of Marine Pelagic Blue-Green Algae, R. Marumo, ed. Ocean Res. Inst. Univ. Tokyo, 1-16, (in Japanese).
- McCarthy, J. J. and E. J. Carpenter. 1979. Oscillatoria (Trichodesmium) thiebautii (Cyanophyta) in the central North Atlantic Ocean. J. Phycol., 15, 75-82.
- Moore, E. and F. Sander. 1976. Quantitative and qualitative aspects of the zooplankton and breeding patterns of copepods at two Caribbean coral reef stations. Est. Coast. Mar. Sci., 4, 589-607.
- Moore, E. and F. Sander. 1977. A study of the offshore zooplankton of the tropical western Atlantic near Barbados. Ophelia, 16, 77–96.
- Murray, S. P., H. H. Roberts, D. Conlon and G. M. Rudder. 1977. Nearshore current fields around coral islands: control of sediment accumulation and reef growth. Proceedings of the Third International Coral Reef Symposium, Univ. Miami, Miami, 2 - Geology 53-59.
- Myers, T. D. 1968. Horizontal and vertical distribution of euthecosomatous pteropods off Cape Hatteras. Ph.D. thesis, Duke University, 224 pp.
- Partlo, K. 1975. Ecological aspects of a semi-enclosed eutrophic tropical marine environment. M.Sc. thesis, McGill University, Montreal, Quebec, 81 pp.
- Powles, H. 1975. Abundance, seasonality, distribution and aspects of the ecology of some larval fishes off Barbados. Ph.D. thesis, McGill University, Montreal, Canada, 227 pp.
- Ramamurthy, V. D. 1970. Experimental study relating to red tide. Mar. Biol., 5, 203-204.
- Sander, F. 1971. Organic productivity of inshore waters of Barbados. A study of the island mass effect and its causes. Ph.D. thesis, McGill University, Montreal, 151 pp.

- Sander, F. and E. Moore. 1978. A comparative study of inshore and offshore copepod populations at Barbados, West Indies. Crustaceana, 35, 226-240.
- Sander, F. and D. M. Steven. 1973. Organic productivity of inshore and offshore waters of Barbados: a study of the Island Mass Effect. Bull. Mar. Sci., 23, 771-792.
- Sournia, A. 1968. La cyanophycee Oscillatoria (= Trichodesmium) dans le plancton marin: Taxinomie, et observations dans le Canal de Mozambique. Nova Hedwigia, 15, 1-12.
- Steidinger, K. A. 1973. Phytoplankton ecology: a conceptual review based on eastern Gulf of Mexico research. Crit. Rev. Microbiol., 3, 49-68.
- Steven, D. M., A. L. Brooks and E. A. Moore. 1970. Primary and secondary production in the tropical Atlantic. ONR report contract NOOO14-67-A-10432-0001. Bermuda Biol. Stn. Spec. Publ. 124 pp.
- Steven, D. M. and R. Glombitza. 1972. Oscillatory variation of a phytoplankton population in a tropical ocean. Nature (London), 237, 105-107.
- Strickland, J. D. H. and T. R. Parsons. 1968. A practical handbook of seawater analysis. Fish. Res. Board Can., Bull. 167, 311 pp.
- Van Bennekom, A. J., and S. B. Tijssen. 1978. Nutrients on and off the Guyana shelf related to upwelling and Amazon outflow, in CICAR-II. Progress in Marine Research in the Caribbean and Adjacent Regions, H. B. Stewart, Jr., ed., FAO Fisheries Rep. 200, suppl., 233-253.
- Vezina, R. 1974. Seawater quality and phytoplankton of inshore waters of Barbados: a study of the effects of organic production in a tropical environment. M.Sc. thesis, McGill University, Montreal, 95 pp.
- Wada, E. and H. Hasumoto. 1975. Ammonium uptake in Trichodesmium colonies, in Studies

^{— 1976.} Quantitative and qualitative aspects of inshore phytoplankton off Barbados. Can. J. Bot., 54, 2306-2314.

on the Community of Marine Pelagic Blue-Green Algae, R. Marumo, ed., Ocean Res. Inst. Univ. Tokyo, 62-64 (in Japanese).

Wells, F. E. 1974. Biology and ecology of euthecosomatous pteropods off Barbados, West Indies. Ph.D. thesis, McGill University, Montreal, 146 pp.

----- 1976. Seasonal patterns of abundance and reproduction of euthecosomatous pteropods off Barbados, West Indies, Veliger, 18, 241-248.

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