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The microbial ecology of colonial radiolaria

Angel, Dror L., Ph.D.

City University of New York, 1989

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THE MICROBIAL ECOLOGY OF COLONIAL RADIOLARIA

b y

Dror L. Angel

**A dissertation submitted to the Graduate Faculty in
Biology in partial fulfillment of the requirements for
the degree of Doctor of Philosophy, The City
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Jane C. Gallagher
Chairman of Examining Committee
Prof. Jane C. Gallagher
John C. Chalman
Executive Officer

Neil R. Swanberg
Prof. Neil Swanberg, University
of Bergen
O. R. Anderson
Prof. O. Roger Anderson, Lamont
Doherty Geological Obs. of Columbia
University Linda Mantel
Prof. Linda Mantel, City College
David A. Caron
Prof. David Caron, Woods Hole
Oceanographic Institute

Supervisory Committee

The City University of New York

Abstract

THE MICROBIAL ECOLOGY OF COLONIAL RADIOLARIA

by

Dror L. Angel

Adviser: Professor Neil R. Swanberg

Colonial radiolaria (CR) are distributed throughout most of the world's oceans and it is likely that specific CR assemblages are associated with the different water masses. In this study, cluster analysis of radiolarian assemblages collected in the eastern waters of the North Atlantic Ocean revealed that they were substantially different in composition from CR collected in the waters on the western side of the ocean. Radiolarian colonies are macroscopic and often harbor communities of small organisms including heterotrophic bacteria, a Cryptobia-like bodonid flagellate, Gyrodinium sp. (dinoflagellate), dysterid ciliates and parasitic hyperiid amphipods. Other planktonic organisms have been observed in association with the colonies, however this study was devoted to the description of the five groups mentioned above and to the flow of carbon within the radiolarian microcosm. Gyrodinium sp. and the Cryptobia-like bodonid flagellate were the most common microorganisms associated with the colonies and often occurred in very high abundances, e.g. 10^2 to 10^4 /CR; the dysterid ciliates and hyperiid amphipods were less frequently associated with the colonies and their abundances were much lower, generally between 1 and 40/CR. Bacteria were observed on all of the radiolaria that were examined and their abundances ranged from 1.75×10^4 to 5.00×10^6 cells/CR. Carbon flow within the radiolarian microcommunity was examined by calculating the production of bacteria, Gyrodinium sp. and hyperiid amphipods. Both bacteria and Gyrodinium sp. may reach production rates equivalent to the primary production rates of the radiolarian endosymbiotic algae. Production rate estimates for bacteria associated with CR ranged from 0.04 to 10 ng carbon/hr and Gyrodinium sp. associated with CR fixed between 0.002 and 30 ng inorganic carbon/hr. It is not clear, however, whether the bacteria and the various associated protozoa are beneficial or detrimental to the host colonies. Parasitic hyperiid amphipods often feed on the radiolarian host and may even lead to the demise of the colony. Although the contribution of colonial radiolaria to total planktonic

production is relatively small, the dynamic microbial communities they support may play an essential role in nutrient recycling and regeneration in the epipelagic oceanic waters that they occupy.

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insight into various issues that arose during the formative stages of my dissertation has been an inspiration to me. I owe many thanks also to Linda Mantel for her support (both moral and financial) as Department Chair; her friendship, and her interesting scientific perspective she brought as a non-plankton biologist.

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General Introduction

Some of the most widely encountered macroscopic organisms in the surface waters of the tropical Atlantic Ocean are the colonial radiolaria (CR) (Swanberg, 1979). Abundances of this group of radiolaria are generally between 0.01 and 10 colonies per m³ in the top 30 m of the water column (Swanberg, 1983; Angel, unpublished; McGillivray, 1988). However, much higher abundances, on the order of hundreds (Swanberg, 1983) and thousands of colonies per m³, have been reported in the surface waters (probably the top meter) of the Davis Straits (Pavshitski and Pan'kova, 1966), in the Gulf of Aden (Khmeleva, 1967), and in the eastern North Atlantic Ocean, near Mauritania, Africa (Rico, 1977).

Radiolarian colonies consist of a few to several hundreds or thousands of cells that are identified by the cytoplasm-rich "central capsules" (cc) interconnected within a complex network of rhizopodia. These are often surrounded by a gelatinous matrix of sulfated mucopolysaccharides (Hollande and Hollande, 1975). Each of the central capsules maintains one or more algal symbionts which are enclosed within special rhizopodia and provide organic photosynthates to the host (Anderson, 1978). In addition to the photosynthates provided by the algal endosymbionts, the colonial radiolaria consume endosymbionts at a steady rate (Anderson, 1976a) and opportunistically feed on the planktonic prey which become entangled in the radiolarian rhizopodia (Swanberg, 1979). Thus, considerable trophic autonomy is available which may account for the widespread occurrence of CR in oligotrophic regions (Anderson, 1983; Swanberg, 1983).

Numerous workers have studied colonial radiolarian fine structure (e.g. Hollande et al., 1970; Hollande, 1974; Anderson, 1976a, 1976b, 1978; Swanberg, 1979; Swanberg and Anderson, 1981) and cell physiology (e.g. Haeckel, 1887; Brandt, 1885; Hollande and Enjumeat, 1953; Anderson, 1976c, 1978, 1980; Cachon and Cachon, 1976; Swanberg, 1979; Swanberg and Harbison, 1980). However, relatively little attention has been directed toward the ecology of these colonial sarcodines and their role in planktonic communities. Some of the major ecological issues concerning the colonial radiolaria include a) determining their role as primary,

secondary and tertiary producers, and b) the contribution of CR to the flux of carbon and opal in the ocean.

The primary production rates of CR were measured by Khmeleva (1967), and by Swanberg (1979). During a bloom of Collozoum inerme, in the Gulf of Aden, Khmeleva (1967) reported that the radiolarian photosynthesis was three times greater than the primary production by phytoplankton in the surrounding waters. In a recent review of colonial radiolarian ecology, Swanberg (1983) noted that Khmeleva's conclusions may be misleading, because although the radiolarian primary production is probably quite high within the dense patches of CR, radiolarian colonies are not uniformly distributed throughout the euphotic zone. Swanberg (1979) measured the photosynthetic rates of CR collected in the Atlantic Ocean and concluded that when the radiolarian primary production was integrated over a 100 m water column, CR contribution to total primary production is insignificant. Swanberg (1983) used his CR primary production rates and CR abundance data and the flux rates of CR shells (Takahashi and Honjo, 1981) to calculate the tertiary production of CR in the western tropical Atlantic. He concluded that the contribution of colonial radiolaria to the pelagic food web is at least 1 to 2% of total tertiary production.

It is not known what fraction of the CR production is exported from the euphotic zone to the benthos and what portion enters pelagic food webs. Flux rates have been calculated for the shells of CR (e.g. Takahashi, 1981; Takahashi and Honjo, 1981) and from these rates, the role of CR in the global opal flux may be established. However, it is difficult to calculate colony production rates from flux values since CR are multi-cell entities and it is impossible to determine how many CR are represented by the shells in a sediment trap. Furthermore, flux data underestimate CR production because the genera Collozoum and Sphaerouzoum do not form siliceous shells and are therefore not included in the sediment trap data. In addition to sinking out of the euphotic zone, CR carbon may enter pelagic food webs by a) predation on CR, b) radiolarian death, c) CR excretion and secretion. Although there have been no reports of large predators of colonial radiolaria (aside from an anecdotal observation of flying fish consuming CR in the Florida Keys), a distinct microbial community has been observed among the colonies which may mediate the exchange of carbon with the surrounding water. This microcommunity includes hyperiid amphipods, dysterid ciliates, gyrodinoid dinoflagellates, Cryptobia-like bodonid flagellates and

bacteria. In this research, I have concentrated on the organisms associated with CR and their role in the flow of carbon through the colonial radiolaria.

The association of microorganisms with colonial radiolarian provides a unique opportunity to study the flow of carbon through a pelagic microcosm. Although numerous studies have focussed on the microbial ecology and the production of amorphous organic aggregates (marine snow) (Kane, 1967; Seki, 1972; Wiebe and Pomeroy, 1972; Trent et al., 1978; Alldredge and Cox, 1982; Caron et al., 1982; Prezelin and Alldredge, 1983; Silver et al., 1984), these have generally involved particles of uncertain origin (Gordon, 1970) with extremely diverse and continuously-changing microbial assemblages (e.g. Davoll, 1984). In comparison, it is possible to identify many of the CR to genus or species, thereby reducing the number of unknown variables in the system. Furthermore, the radiolaria are living units which deposit new material as they grow and have the ability to regenerate portions of the colony (Anderson, 1988), thereby exerting a homeostatic influence within this microcosm. This dissertation includes a description of the microorganisms that are commonly associated with the CR and some aspects of the ecology of this microenvironment.

Chapter 1 deals with the abundances and distribution of the colonial radiolaria that were collected during 6 field trips in the North Atlantic Ocean. This demonstrates the ubiquity of CR and their variability among different populations. Cluster analysis and ordination of the data suggest that there are distinct CR assemblages associated with well defined oceanic water masses. One of the problems I encountered in this study was the presence of numerous radiolaria with ambiguous morphological features. These were placed in a category, "unidentified colonies", thereby underscoring the current unsatisfactory status of radiolarian taxonomy.

In the second chapter, I have described the gross morphology and fine structure of the organisms associated with the CR. The fine structure study serves not only to describe possible new species, but also to clarify some functional fine structure features such as contents of food vacuoles and presence or absence of endosymbionts. The third chapter bridges between the previous two chapters and describes the abundances and infestation rates of the associated organisms upon and within the host colonies. This is followed by

three chapters, each dealing with a different infesting organism and its role in the flow of carbon through the CR microcosm.

After these quantitative chapters, a summative discussion is presented on the salient points emerging from this dissertation and a model is presented showing our current knowledge of carbon flow through the colonial radiolarian microcosm.

Chapter 1

Distribution and Abundances of Colonial Radiolaria

INTRODUCTION

One of the greatest difficulties in oceanic biogeography involves sampling the plankton to determine a) which species are present and b) what are their abundances (McGowan, 1971). Sampling is a problem because most plankton are not evenly distributed spatially or temporally throughout the oceans (Haeckel, 1890; Hardy, 1936). Thus, without information on the size of patches and the distances between patches, it is difficult to predict the volume of water that must be sampled to yield a representative assemblage of the organisms of interest (Valiela, 1984). Colonial radiolaria (CR) are strongly stratified in their distribution and are found mostly in the upper 30 meters of the water column (Swanberg, 1979). Although CR may be found in most warm oceanic waters (Swanberg, 1983; Strelkov and Reshetnyak, 1971), their distribution is patchy and there is considerable variation among the sizes of patches and the distances between adjacent CR patches. In order to obtain complete and reliable species lists for each area, it is probably necessary to sample several hundreds or possibly thousands of cubic meters of seawater (McGowan, 1971); however that was not a practical alternative. Assuming that the CR taken by SCUBA divers were randomly collected, I have used the taxonomic composition of CR sampled during 6 field excursions to compile CR assemblages for each dive station. Although it is possible to measure radiolarian abundances by direct underwater methods (Swanberg, 1979), CR were collected by gentle, quantitative plankton tows (Anderson, 1980) during 5 of the 6 field excursions.

MATERIALS and METHODS

A. CR Collections

Colonial radiolaria were hand-collected by SCUBA divers using 125 ml glass jars (for detailed diving protocol, see Hamner et al., 1975) during three oceanic cruises (R.V. Oceanus 176 (OC 176), R.V. Oceanus 177 (OC 177), and R.V. Oceanus 191 (OC 191) and three field excursions (Barbados 1986, Barbados 1987, and Curacao 1988) from 1986 to 1988 (see Figure 1). Most samples were collected during the spring and summer months (March - August). Radiolarian colonies were generally collected within the top 10 meters of the water column, although at some of the oceanic locations, colonies were collected at 20 and 30 m below the surface. The CR were collected individually as they were encountered, thus minimizing bias. Although CR were generally collected in an unbiased fashion (i.e. regardless of colony morphology or dimensions), some constraints imposed by conditions at certain sampling sites required deviations from this practice. On several occasions during OC 177 and OC 191, when large CR (mostly Collozoum caudatum and Rhaphidozoum spp.) were highly abundant, I did not collect colonies in a random fashion, but instead selected a variety of CR, representing the range of colony sizes and shapes present in the surface layers of the water column. Sampling was non-random only with respect to the large CR and was carried out in order to compare infestation rates across several CR taxa.

I did not identify CR with siliceous spicules or skeletons to the species level because this often involves procedures which destroy the colony. Therefore, I have referred to CR with siliceous parts as "Genus" spp. to denote that more than one species may be included in this category.

Collecting colonial radiolaria in oceanic waters is difficult because many colonies are translucent. During the field excursions in the Caribbean (Barbados 1986, 1987, and Curacao 1988) this problem was alleviated by using the background provided by the dark hull of the diving boat (Anderson, 1980) to enhance the image of CR. This procedure was not employed during the three oceanic cruises OC 176, OC 177, and OC 191 because it was not compatible with the "blue water" diving protocol (Hamner et al., 1975) used at sea. "Oceanic" CR were collected without the aid of a dark background and this may have affected the ability of SCUBA divers to obtain

representative random samples from the CR assemblages because some colonies are more visible than others. Numerous factors contribute to the visibility of a colony, e.g. abundance and distribution of symbionts, pigments, growth phase (pre-reproductive ccs are often very opaque), etc., i.e. the visibility of a colony may be environmentally or physiologically controlled. Thus, differences in optical properties are not necessarily indicative of taxonomic differences.

Colonial radiolaria were examined within one to three hours of collection using a Nikon Diaphot inverted microscope (range of magnifications = 40x to 400x). Colonies were assigned to genus or species following the descriptions of Swanberg (1979) and all microbial infestations on or in the colony were recorded. Many of the CR did not match his descriptions, nor other descriptions in the radiolarian literature (e.g. Haeckel, 1887; Strelkov and Reshetnyak, 1971), therefore they were placed in the "unidentified colonies" category. It is impossible, on the basis of gross morphology, to distinguish among several of the Collozoum spp. and the pre-skeletal stages of Collosphaera spp. (Swanberg, pers. comm.).

B. Determining CR Abundance

The abundance of CR was determined at each dive station by quantitative net collections. Plankton tows were taken by towing a 202 μ m-size mesh net suspended on a metal frame with an 0.25, 0.56 or 1.00 m² opening. Ten to twenty minute drift tows at depths ranging from one to 5 m were taken from a boat drifting with the wind. Drift tows were employed to minimize mechanical damage to the CR (Anderson, 1980). The volume of water sampled by the net was determined by multiplying the distance travelled by the net (measured by a calibrated TSK or General Oceanics flow-meter secured in the center of the opening of the plankton net) by the surface area of the net opening. Contents of the net samples were recorded by silhouette photography (Ortner et al., 1979) as soon as possible (generally between 10 and 20 minutes) following collection since many CR would rapidly shrink or sometimes fragment and become unrecognizable if left for longer periods of time in the concentrated seawater samples (Anderson, 1980; Angel, unpublished). After the contents were documented, net tows were preserved in 4% buffered formaldehyde or in Bouin's preservative (Swanberg, 1979).

Silhouette photography equipment was not available for use during the Curacao 1988 field excursion, therefore, estimates of CR abundance were recorded by SCUBA divers. Underwater CR abundance estimates were carried out by swimming approximately three m from the hull of the boat and counting all CR visible within a roughly one m³ (estimated) volume of water between the diver and the boat. Several underwater estimates were carried out during the course of each dive and the average values are presented in Table 1.

C. Measurement of Seawater Temperature and Salinity

Surface seawater temperatures were measured at each location by standard mercury thermometer at depths ranging between one and three meters below the surface. Seawater samples were collected in situ (underwater) during each of the dives in Barbados 1987, Curacao 1988 and during OC 191. Subsamples of the seawater were placed in sealed bottles and salinities were measured using an AGE Minisal salinometer at Lamont Doherty Geological Observatory of Columbia University (LDGO).

D. Identification of *Collozoum pelagicum* and *Collozoum stellatum*

In order to avoid confusion regarding two species of Collozoum that are mentioned in this chapter, I have presented photomicrographs of Collozoum stellatum (Figure 2). Haeckel (1887), described this species, but he did not sketch the colony or the shape of the central capsules. Strelkov and Reshetnyak (1971) presented sketches of C. stellatum, but they named this radiolarian Collozoum pelagicum, in contrast to the descriptions of C. pelagicum presented in Haeckel (1887). Swanberg (1979) did not comment about the Russians' redescription of C. pelagicum and his descriptions and micrographs conform with those of Haeckel (1887). In this study, I have adopted the descriptions of C. pelagicum following Haeckel (1887) and Swanberg (1979) and all references to this species are restricted to the morphotype they have described. It is also possible that both species, *C. stellatum* and *C. pelagicum* are actually the same, but until shown otherwise, these will be considered separate species. Although Collozoum serpentinum has been recognized as a developmental stage of the solitary collodarian, Thalassophysa sanguinolenta and synonymized with C. pelagicum (Brandt, 1902), I have also chosen to distinguish between these morphologically different radiolaria in my descriptions below and in subsequent chapters.

E. Cluster and Correspondence Analysis of CR Assemblages

Distribution and species abundance data from 6 field excursions: OC 176, OC 177, OC 191, Barbados 1986, Barbados 1987, Curacao 1988 were analyzed by an agglomerative hierarchical clustering method (Boesch, 1977) and also by detrended correspondence analysis (Hill and Gauch, 1980), an ordination technique that corrects some of the faults of reciprocal averaging (Gauch, 1983).

RESULTS

A summary of the distributions and abundances of CR collected during 3 oceanic cruises and 3 field excursions in the Caribbean is presented in Table 1. The taxonomic composition of CR assemblages at each location is presented as percentage of total number of CR collected at that location. The average number of CR collected at oceanic locations (16.9 ± 3.4 (st.err.) CR/station) was generally lower than at the Caribbean stations (32.7 ± 2.6 (st.err.) CR/station).

I. Spatial and Temporal Distribution of Colonial Radiolaria

The geographical distribution of CR collected during the 3 oceanic cruises is illustrated in Figures 38 to 57 in Appendix A. In order to provide greater detail of the sampling areas, CR distributions determined during OC 191 and OC 177 were plotted separately from the distributions determined during OC 176. Appendix B consists of pie graphs representing the relative abundances of each of the radiolarian taxa collected at two stations in the Caribbean, 1) during Barbados 1986, 1987, and 2) during Curacao 1988. The data were presented in this manner to illustrate the temporal changes in composition of collected CR. The position and surface seawater temperature measured at each of the dive stations during the 3 oceanic cruises are presented in Appendix C.

A. OC 177 and OC 191

There was considerable overlap in the cruise tracks of OC 177 and OC 191. Most dive stations were located in the Gulf Stream and on the eastern and western boundaries of the Stream. The distribution of each of the 10 CR taxa listed in Table 1 was plotted on

a Mercator projection (station positions were plotted on charts by a UNIX program written by Pal Wessel, LDGO) and is presented in Appendix A, Figures 38 to 57. Although most taxa were fairly well distributed among the dive stations, Collosphaera spp., Siphonosphaera spp., Collozoum serpentinum and Collozoum stellatum were found mostly among offshore stations. The most widely distributed CR taxa (i.e. taxa that were found at the greatest number of stations) were Collozoum caudatum, Sphaerozoum spp., and Collozoum inerme, by descending order of distribution. C. stellatum was found in only 3 stations during OC 177, and was not observed at all during either OC 191 or OC 176.

B. OC 176

The following taxa were distributed fairly evenly along the cruise track of OC 176 : Acrosphaera spp., Collosphaera spp., Siphonosphaera spp., Sphaerozoum spp., Rhaphidozoum spp., Collozoum pelagicum (Appendix A). Whereas Collozoum caudatum was the most widespread CR collected during OC 177 and OC 191, only two colonies of this species were collected off the southwestern coast of Spain, during OC 176. Collozoum inerme and Collozoum serpentinum were also fairly widespread among stations on the western side of the Atlantic (OC 177 and OC 191), however these species appeared in only a handful of stations during OC 176. Surface seawater temperatures may have influenced distributions of CR. The mean surface seawater temperature was 9.0°C higher during OC 177 and OC 191 (mean temperature = 28.0°C) than during OC 176 (mean temperature = 18.8°C). Although I did not present data regarding the distribution of Thalassophysa spp., these radiolaria were found only during OC 176, in the waters surrounding the Canary Islands where Haeckel (1887) first described this genus.

C. Barbados 1986

The genus Sphaerozoum was found at all 18 stations near Barbados. Acrosphaera spp. and Collosphaera spp. were collected at 17 and 16 stations, respectively, whereas Collozoum serpentinum and Collozoum pelagicum were found at only three stations each. In many of the stations, a large proportion of the CR were unidentified colonies (mean = 45.7% of total number CR collected; range = 14 to 69%).

D. Barbados 1987

Collosphaera spp. and Sphaerozoum spp. were collected in 16 of the 17 stations, while Acrosphaera spp. were found in 15 stations. The lack of species richness evident in the March 16, April 4 and April 6 pie graphs (Appendix B) may be related to the small numbers of CR that were collected on these occasions. Few CR were collected on these dates because the abundance of CR in the water was very low (see Table 1). Unidentified colonies (colonial radiolaria which did not sufficiently match any of the previously described CR) were encountered at all stations (mean = 35.3% of the total number of CR collected; range = 9 to 83%) and were highest when CR abundances were low.

E. Comparisons Among CR Assemblages: Barbados 1986 and 1987

The 3 genera, Acrosphaera, Collosphaera and Sphaerozoum were consistently found among CR collected at both Barbados sampling periods : 1986 and 1987. The genera Rhaphidozoum and Siphonosphaera were also common constituents of the CR assemblages though their occurrence was not as consistent as Acrosphaera spp., Collosphaera spp. and Sphaerozoum spp. Both Rhaphidozoum spp. and Siphonosphaera spp. were collected at 23/35 stations whereas Acrosphaera spp., Collosphaera spp. and Sphaerozoum spp. were collected at 32/35, 31/35 and 34/35 stations, respectively (Table 1; see also Appendix B).

Collozoum inerme was the most common Collozoum species encountered in Barbados; its relative abundances (% of total CR collected/station) were higher in 1986 than in 1987. The 3 species Collozoum serpentinum, Collozoum pelagicum and Collozoum stellatum were absent from most CR collections and the only recurring pattern was the appearance of C. stellatum toward the middle or end of April in both years. Collozoum caudatum was collected at 10 of the 18 stations during Barbados 1986, but only two colonies of this species were found among the CR collected during the following spring. Temporal changes in composition of the CR assemblages may be related to changes in the water mass around Barbados. However, surface seawater temperature, the only hydrographic variable that was measured during both years was fairly constant (mean temp (1986) = 26.7°C (st.err. = 0.1); mean temp (1987) = 27.0°C (st.err. = 0.1)) and was not correlated with changes in CR composition. Although there were clear shifts in surface seawater

salinity during March and April, 1987 (Figure 3), the composition of the CR assemblage did not vary in response to this environmental factor. In the only example that may have indicated a response to seawater salinity, C. stellatum was collected on three different dives in April, corresponding to an increase in salinity.

F. Curacao 1988

The field excursion to Curacao included 7 collecting dives during a period of 15 days. Acrosphaera spp., Siphonosphaera spp. and Sphaerozoum spp. were found on all 7 dives. Collosphaera spp., Rhaphidozoum spp. and Collozoum stellatum were collected on 6 of the 7 dives. This is the only area wherein C. stellatum was collected on a regular basis. Collozoum pelagicum was the only CR taxon which was not observed at any of the 7 stations. Mean proportion of unidentified CR among collected colonies = 35.6% (st.err. = 3.6, range = 18 to 45%).

II. Abundances of Colonial Radiolaria

Abundances of CR at each of the Caribbean dive stations are presented in Figure 4. CR abundances were lowest during Barbados 1986 (mean abundance = 0.44 ± 0.08 CR/m³) and were considerably higher during the following spring, Barbados 1987 (mean abundance = 1.31 ± 0.22 CR/m³) and during Curacao 1988 (mean abundance = 1.86 ± 0.29 CR/m³).

Radiolarian abundances were plotted for each of the oceanic cruises and are presented in Figures 5 to 7. The highest abundance at a single station, 7.5 CR/m³, was recorded during OC 176. Mean CR abundances for the three cruises were : 2.76 CR/m³ ± 0.49 for OC 176, 0.96 CR/m³ ± 0.22 for OC 191, and 0.45 CR/m³ ± 0.08 for OC 177. In general, colonial radiolaria were most abundant in open ocean waters, i.e. the areas that were farthest from islands and continents.

III. Cluster Analysis and Ordination of the CR Species Abundances

Figures 8 and 9 are dendrograms (constructed from species abundances) which summarize clusters of samples taken during 3 oceanic cruises and 3 Caribbean field excursions. On the average, there was a greater degree of similarity both within and among the 5 major Caribbean clusters than within or among the 7 cruise clusters.

Clusters 1 through 5 in Figure 8 contained samples from both OC 177 and OC 191, whereas cluster 7 was composed exclusively of samples from OC 176. The colonial radiolarian assemblages collected during OC 176 were quite different from those taken during OC 177 since none of the clusters contained samples from both of these cruises. There was, however, some similarity between samples taken during OC 191 and during OC 176 since cluster 6 consists of representatives from both cruises.

Table 2 summarizes the taxonomic composition and the relative abundances of the taxa in each of the clusters for the three cruises; each cluster is characterized by one or more numerically dominant taxa.

Figure 10 presents the results of detrended correspondence analysis of the oceanic cruise samples and species in a 3-dimensional plot. Although most of the species are located along the periphery of the hyperspace occupied by the samples, the three taxa, Collozoum inerme, C. caudatum and Sphaerozoum spp. occupy central locations among the samples. Table 2 shows that these are also the most abundant species among the 7 clusters.

The distribution of the Caribbean field samples, following detrended correspondence analysis (Figure 11), was much tighter than that of the oceanic cruise samples (Figure 10). Samples were clustered mostly around Acrosphaera spp. which were the dominant CR in most of these clusters (see Table 3), while the other species were scattered along the borders of the hyperspace occupied by the CR samples.

The proportion of unidentified CR among the Caribbean samples (average = 43%) was substantially higher than among the oceanic cruise samples (average = 20%). It is also noteworthy that the clusters formed from the Caribbean field samples were best characterized by 7 CR taxa (see Table 2), whereas the oceanic cruise clusters were best described by 9 CR taxa (see Table 3).

DISCUSSION

At most of the stations where CR were collected, one or more unidentified colonies were reported. The unidentified colonies were not similar to any of the easily-recognized Collozoum spp. (CR genus

with naked central capsules; see Swanberg, 1979) and they lacked siliceous structures, such as spicules and shells around central capsules (cc), which are the key features used to classify the Collosphaerid and Sphaeroid radiolaria. Although some unidentified colonies had intra-colony organization similar to well-recognized Collosphaerids (e.g. Collosphaera huxleyi), it was not possible to make a positive identification in the absence of siliceous structures. Among some CR, silica deposition may occur in the advanced stages of colony formation. This would explain numerous observations of "mosaic" colonies which contained central capsules both with and without shells (Haeckel, 1862; Anderson and Swanberg, 1981). On a number of occasions, I found that colonies which were classified as unidentified species because they lacked obvious siliceous structures when initially examined, formed shells or spicules in vitro. These were actually "naked" forms of Collosphaerids or Sphaeroids which only became recognizable in the lab. Thus, it is possible that many of the unidentified colonies were early developmental stages of known, silica-depositing taxa. This problem might be solved in future studies by maintaining the unidentified colonies in aquaria to allow them to develop identifiable features.

I. Distribution of CR

Colonial radiolaria occur mostly in the top 30 m of the water column, though colonies have also been found between 30 and 50 m below the surface (Strelkov and Reshetnyak, 1971). The CR are capable of limited vertical motility and their presence in the upper portion of the euphotic zone is probably motivated by the light requirements of endosymbiotic algae (Swanberg, 1979; Anderson, 1983) and by the presence of potential prey (Swanberg, 1983). Their proximity to the surface enabled SCUBA divers to collect the gelatinous CR by hand (Hamner et al., 1975), thereby minimizing perturbation of the associated microorganisms which were the focus of this study. The sampling protocol was not oriented toward a biogeographic study of CR, however, colonies were randomly collected, and the data represent the major CR taxa and their relative abundances at each location.

A) CR Distribution in Oceanic Areas

Swanberg (1979) collected CR from both sides of the northern Atlantic Ocean and considerable overlap exists between the areas

that he studied and those reported here. The distribution patterns described for the various CR taxa (Swanberg, 1979) were almost identical to those that I found. Whereas Collosphaera spp., Acrosphaera spp. and Sphaerozoum spp. were abundant on both sides of the Atlantic, Collozoum caudatum and Collozoum inerme were mostly restricted to waters near the east coast of the United States. Regarding the distribution of C. inerme, Haeckel (1887) described this radiolarian as a cosmopolitan CR found throughout the tropical oceans, but he did not indicate where in the Atlantic his specimens were collected. Another radiolarian with limited distribution was Thalassophysa which was observed only during OC 176. It is possible that this genus is a native of the Mediterranean Sea (Brandt, 1885; Hollande and Enjume, 1953) which is occasionally exported to the nearby Atlantic waters.

Rhaphidozoum spp. were the most widely distributed CR observed along the cruise track of OC 176, and were found at 20 of the 21 stations. Swanberg (1979) sampled the same waters, but Rhaphidozoum spp. were not widely distributed there at that time.

The taxa Collosphaera spp., Siphonosphaera spp., Collozoum serpentinum and Collozoum stellatum were found exclusively or predominantly among the eastern stations during OC 177 and OC 191 (see Appendix A), i.e. in the Gulf Stream and in the Sargasso Sea. This suggests that these taxa may fare poorly in coastal waters (Swanberg, 1983) whereas other taxa are less sensitive to "coastal" influence. Swanberg (1979) collected CR in this area, but his data suggest these taxa are more evenly distributed and do not have a preference for either Gulf Stream or Slope waters.

Differences between a) clusters and b) samples within clusters were illustrated by plotting the ordinated data in 3-dimensional space and labelling samples according to the cluster they were assigned to (Figure 10). Both Figure 10 and Table 1 show that there is considerable variability in the composition of the oceanic cruise samples within clusters, and this is expressed quantitatively, as percent similarity, in Figure 8. Nevertheless, the influence of "dominant" CR taxa on the location of clusters in the hypervolume was evident in such examples as the "attraction" of cluster 7 toward Rhaphidozoum spp., or the "attraction" of cluster 6 toward Acrosphaera spp. Cluster 7 (samples collected exclusively during OC 176) is clearly different from clusters 1 through 5 (samples from the western part of the North Atlantic) indicating that CR taxa are not

distributed evenly throughout the North Atlantic Ocean. This suggests that it may be possible to identify water masses on the basis of the colonial radiolarian assemblages found therein.

B) CR Distribution : Caribbean Locations

Swanberg (1979) examined CR taken at two stations to the east (windward side) of Barbados. The abundances of CR were moderate to low at these stations and only Collozoum caudatum and Collozoum inerme were reported. These species were also collected at the dive station located one to three km west (leeward side) of the island (this study). However, other CR taxa, e.g. Sphaerouzoum spp. or Acrosphaera spp., were much more common on the leeward side of the island. Because CR were collected at only two stations on the windward side of the island, in comparison to the intensive sampling that was done on the leeward side of the island, it is not possible to draw conclusions about similarities or differences regarding CR from the windward and leeward sides of the island.

In another survey of Caribbean radiolaria, Strelkov and Reshetnyak (1971) identified CR collected from 56 stations near Cuba. The CR assemblages in the vicinity of Cuba were apparently quite different from those I observed near Barbados and Curacao. Whereas Acrosphaera spp. and Siphonosphaera spp. occurred in the majority of the samples taken near Barbados and Curacao, they were totally absent among the CR populations near Cuba. This finding is somewhat surprising since both Acrosphaera and Siphonosphaera are cosmopolitan genera, yet none were collected from stations representing the large water masses adjacent to Cuba i.e. Atlantic Ocean, Caribbean Sea and Gulf of Mexico. On the other hand, all other CR taxa listed in Table 1 were reported near Cuba.

The data from Barbados 1986 and Barbados 1987 reveal that there was considerable consistency from one year to the next in the composition of CR assemblages. This is evident in the rather tight grouping of the samples summarized in the ordination analysis (Figure 11). The only major deviation observed was the almost total absence of Collozoum caudatum in 1987 as compared to 1986. Due to the lack of hydrographic data, it is not possible to suggest whether the absence of C. caudatum was related to environmental factors or other causes.

During Barbados 1987, surface seawater salinity was measured at each of the dive stations. The salinity decreased as a result of fresh water runoff (precipitation) and/or the entrainment of lenses of brackish water (Borstad, 1979; Borstad, 1982) transported into this region by the Guiana Current. CR composition did not change drastically as a result of small fluctuations in salinity, but during April 4 and 6, 1987, when salinity levels were lowest (33.8‰ and 33.6‰, respectively), CR abundances and species richness dropped as well. When the salinity increased, two days later, CR abundances and species richness returned to the levels observed previously, suggesting salinity has a marked influence on the colonial radiolarian population.

Seawater salinities were fairly constant near Curacao during the two weeks of April 1988 and the composition of CR assemblages did not change dramatically (though these two factors are not necessarily the major determinants of CR population composition). It is noteworthy that although Curacao is several hundred miles west of Barbados and much closer to the coast of South America, there is very little difference between these areas in terms of the local CR assemblages (see Figures 9 and 11). Whereas Collozoum pelagicum was totally absent from the Curacao collections, Collozoum stellatum was found in 6 of the 7 samples. This is somewhat surprising since C. stellatum was infrequently encountered in all of the other areas sampled.

II. Abundances of CR

The horizontal distribution of colonial radiolaria is patchy making it difficult to measure population abundances by conventional means, e.g. net tows. Swanberg (1979) measured radiolarian abundances by direct (in situ) counting procedures and generally found less than one colony/m³ on the western side of the North Atlantic Ocean. Several abundances in excess of 100 colonies/m³ were recorded (Swanberg, 1979), yet these high densities were restricted to the top ten or twenty centimeters of the water column where CR often accumulate when the sea is calm. Other workers have reported similar and even higher CR abundances. Khmeleva (1967) reported 20,000 CR/m³ in the Gulf of Aden, and Pavshchik and Pan'Kova (1966) measured swarms of 4000 CR/m³ in the Davis Straits. However, these are extremely high values and it is not clear how the abundances were calculated.

Although net tows often damage fragile gelatinous zooplankton (e.g. CR), non-motorized, drift tows (Anderson, 1980) are sufficiently gentle to collect and quantify CR in the water column. The CR abundances measured by drift tows (Table 1) were comparable to abundances measured by in situ counting procedures (Swanberg, 1979). Swanberg recorded between 0.04 and 1.10 colonies/m³ in 18 stations taken from a number of areas in the Atlantic Ocean and in the Indian Ocean. The abundances that I measured using drift tows rarely exceeded two or three colonies/m³ and were often less than one CR/m³ on the western side of the north Atlantic Ocean. The highest abundances were recorded during OC 176 (Figure 6) at stations where very few metazoan zooplankton were observed. It is not clear whether the high CR abundances encountered during OC 176 were related to the absence of other animals and oligotrophic conditions or whether this pattern was coincidental.

Abundances of CR were generally lower in 1986 than in 1987, for both eastern North Atlantic and Caribbean areas. In Barbados 1986, mean abundance was 0.44 +/- 0.08 CR/m³ and during OC 177, mean abundance was 0.45 +/- 0.08 CR/m³. In comparison, the mean abundance in Barbados 1987 was 1.31 +/- 0.22 CR/m³, and for OC 191, 0.96 +/- 0.22 CR/m³. Since hydrographic and biological variables, e.g. salinity and chlorophyll a concentration were only measured during the 1987 field excursions, it is not possible to determine if any of these were correlated with the change in abundances.

SUMMARY

The distributions of 10 CR taxa among geographic locations in the tropical and subtropical Atlantic Ocean were described in this study. Many taxa, including Sphaerozoum spp., Acrosphaera spp., Collosphaera spp., Siphonosphaera spp. and Rhaphidozoum spp. were found in all the regions studied, though not at all dive stations in these regions. Collozoum caudatum, and Collozoum inerme were widely distributed on the western side of the Atlantic Ocean, but were almost totally absent from the oceanic waters off the northwestern coast of Africa. In these waters, numerous Thalassophysa spp. were observed, but these radiolaria were absent from all other study areas. Collozoum serpentinum and Collozoum stellatum were not widely distributed in general, yet C. stellatum was found in 6 of the 7 stations sampled during Curacao 1988. Field

work in the Caribbean islands included bi-weekly sampling at a constant geographic location and CR distributions were fairly invariable during two 8-week periods in Barbados. The only significant difference noticed from one year to the next was the absence of C. caudatum in 1987. Overall, the composition of CR assemblages at the Caribbean stations were very similar to the assemblages described in the Gulf Stream and Sargasso Sea, off the east coast of the United States. In all areas, there was a fairly large percentage of unidentified colonies among the collected CR; these may have been developmental stages of known taxa. Abundances of CR were measured by drift tows and ranged from 0.001 to 7.5 CR/m³. Mean abundances, measured from one to 3 m below the surface were usually equal to or lower than one CR/m³, although highly dense swarms (hundreds of CR/m²) have been observed in the top few cm of the water column. Lowest mean abundances were measured during OC 177 (0.45 CR/m³) and the highest abundances were recorded during OC 176 (1.35 CR/m³).

Table 1. Summary of the abundances and taxonomic composition of CR assemblages, listed by geographic location. At each station, the number of CR of each species collected was divided by the total # of CR collected and these ratios (%) are presented below. Abundances were measured by net tows at all stations, except Curacao, where abundances were estimated by SCUBA divers. The following abbreviations were used : Acro=Acrosphaera sp., Collos=Collosphaera sp., Siphon=Siphonosphaera sp., Sphaer=Sphaerozoum sp., Raph=Raphidozoum sp., C. Iner=Collozoum Inerme, C. caud=Collozoum caudatum, C. serp=Collozoum serpentinum, C.pel=Collozoum pelagicum, C. stel=Collozoum stellatum, col?=Unidentified Colonies, n.d.=not determined.

Date	Dive Station	CR Abundance (CR/m ³)	Total # CR Examined	Acro (%)	Collos (%)	Siphon (%)	Sphaer (%)	Rhaph (%)	C. iner (%)	C. caud (%)	C. serp (%)	C. pel (%)	C. stel (%)	col? (%)
OC 176														
5/23/86	1533	6.100	32	21.8	9.4	9.4	9.4	15.6	0.0	0.0	0.0	21.8	0.0	12.5
5/25/86	1536	5.900	29	6.9	10.3	10.3	13.8	10.3	0.0	0.0	0.0	6.9	0.0	34.5
5/26/86	1538	4.900	23	4.3	8.7	13.0	17.4	30.4	4.3	0.0	0.0	17.4	0.0	4.3
5/27/86	1542	0.800	10	27.3	0.0	0.0	9.1	54.5	0.0	0.0	0.0	0.0	0.0	0.0
5/28/86	1545	0.800	25	28.0	4.0	20.0	4.0	20.0	0.0	0.0	8.0	12.0	0.0	4.0
5/29/86	1547	0.500	26	7.7	3.8	19.2	0.0	30.8	0.0	0.0	0.0	23.1	0.0	15.4
5/31/86	1553	2.400	26	0.0	15.4	3.8	0.0	3.8	0.0	0.0	7.7	19.2	0.0	15.4
6/1/86	1557	0.800	45	6.7	8.9	6.7	15.5	4.4	0.0	0.0	6.7	22.2	0.0	11.1
6/2/86	1560	2.900	13	7.7	0.0	0.0	30.8	46.2	0.0	0.0	0.0	7.7	0.0	0.0
6/3/86	1562	4.000	38	2.6	18.4	5.3	13.2	10.5	0.0	0.0	0.0	23.7	0.0	15.8
6/4/86	1566	2.100	25	0.0	0.0	4.0	12.0	44.0	0.0	0.0	8.0	12.0	0.0	8.0
6/5/86	1568	3.600	13	0.0	23.1	15.4	7.7	15.4	0.0	0.0	0.0	15.4	0.0	7.7
6/6/86	1572	1.700	11	0.0	9.1	0.0	9.1	27.3	0.0	0.0	9.1	18.2	0.0	27.3
6/9/86	1574	2.600	8	0.0	12.5	0.0	0.0	37.5	0.0	0.0	12.5	25.0	0.0	12.5
6/10/86	1577	7.500	16	6.2	6.2	18.7	18.7	18.7	0.0	0.0	0.0	12.5	0.0	6.2
6/11/86	1579	0.001	2	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	50.0
6/12/86	1582	0.700	39	23.1	10.2	15.4	0.0	10.2	0.0	0.0	0.0	25.6	0.0	15.4
6/13/86	1586	0.100	19	26.3	47.4	5.3	0.0	10.5	0.0	0.0	0.0	0.0	0.0	10.5
6/14/86	1588	7.200	57	5.3	14.0	10.5	3.5	26.3	22.8	3.5	0.0	3.5	0.0	10.5

Table 1. (cont.)

Date	Dive Station	CR Abundance (CR/m3)	Total # CR Examined	Acro	Collos	Siphon	Sphaer	Rhaph	C. iner	C. caud	C. serp	C. pel	C. stel	col?
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OC 176 (cont.)														
6/15/86	1590	3.000	33	3.0	3.0	21.2	3.0	42.4	0.0	0.0	6.1	15.1	0.0	0.0
6/16/86	1593	2.700	8	25.0	0.0	12.5	0.0	12.5	12.5	0.0	0.0	0.0	0.0	25.0
OC 177														
7/29/86	1600	0.030	6	0	16.7	0	0	0	0	33.3	0	16.7	0	33.3
7/30/86	1602	0.100	16	0	6.3	0	6.3	6.3	12.6	37.5	12.6	0	0	12.6
"	1604	0.100	9	11.1	0	0	0	11.1	0	55.5	0	11.1	0	11.1
7/31/86	1605	0.080	7	0	14.3	0	14.3	0	0	28.6	28.6	0	0	14.3
"	1607	0.700	20	5	0	0	20	0	0	40	0	20	0	10
"	1608	0.500	11	9.1	18.2	9.1	18.2	0	27.3	9.1	0	9.1	0	0
8/1/86	1610	0.050	7	0	0	0	0	0	0	28.6	42.8	0	0	14.3
"	1612	0.100	21	0	23.8	4.8	9.5	0	9.5	38.1	0	9.5	0	4.8
8/2/86	1614	0.000	2	0	0	0	0	0	0	0	50	0	0	50
"	1615	0.850	12	0	0	8.3	8.3	8.3	16.6	33.3	0	16.6	0	0
8/4/86	1617	0.100	5	0	0	0	0	0	0	40	20	0	0	40
"	1618	0.070	17	0	0	5.9	17.6	0	17.6	11.8	0	5.9	0	41.2
8/5/86	1620	0.730	19	5.3	5.3	10.6	0	5.3	0	36.8	5.3	0	0	31.6
"	1621	2.000	15	0	6.7	0	6.7	0	13.4	53.3	0	0	0	20
8/6/86	1623	0.650	26	3.8	0	0	0	3.8	3.8	53.8	0	3.8	0	30.8
8/7/86	1627	0.250	16	0	0	0	6.3	0	0	68.7	0	0	0	25
8/8/86	1629	0.080	5	0	0	0	40	0	20	0	0	20	0	20
"	1630	0.200	5	0	0	0	20	0	0	0	0	20	0	60
8/9/86	1632	0.520	12	25	0	0	0	0	25	16.7	0	16.7	0	16.7
"	1633	0.300	10	0	10	0	10	0	10	50	0	0	0	20
8/10/86	1635	0.100	8	0	0	0	0	12.5	0	12.5	25	37.5	0	12.5
8/13/86	1638	0.180	9	0	0	0	11.1	11.1	22.2	33.3	0	11.1	0	0
"	1639	0.500	10	10	0	0	40	10	20	20	0	0	0	0
8/14/86	1641	0.100	6	0	16.7	0	16.7	0	16.7	16.7	0	16.7	0	16.7
"	1642	0.200	7	0	14.3	0	0	0	42.8	0	0	0	0	42.8

Table 1. (cont.)

Date	Dive Station	CR Abundance (CR/m3)	Total # CR Examined	Acro	Collos	Siphon	Sphaer	Rhaph	C. iner	C. caud	C. serp	C. pel	C. stel	col?
OC 177 (cont.)														
8/15/86	1643	0.100	9	0	0	0	11.1	0	33.3	0	11.1	22.2	0	22.2
"	1644	0.020	7	0	0	0	57.1	0	28.6	0	14.3	0	0	0
"	1645	0.020	5	0	0	0	60	0	20	0	0	0	0	20
8/16/86	1646	0.001	15	6.7	0	6.7	0	0	20	6.7	0	13.4	6.7	40
"	1647	2.000	28	7.1	0	0	0	7.1	35.7	3.6	0	3.6	3.6	39.3
"	1648	0.800	17	11.8	17.6	0	17.6	0	23.5	17.6	0	0	0	11.8
8/17/86	1650	0.350	16	0	0	0	68.7	0	25	6.3	0	0	0	6.3
"	1651	0.400	9	0	0	0	11.1	0	11.1	11.1	0	66.6	0	0
8/19/86	1652	0.001	11	0	0	0	9.1	9.1	36.4	0	0	9.1	0	9.1
"	1653	1.570	29	6.9	6.9	6.9	13.8	0	34.5	6.9	3.4	3.4	0	17.2
"	1654	1.200	20	0	50	0	0	0	40	0	0	0	0	5
8/20/86	1656	0.010	8	0	12.5	0	0	0	12.5	0	12.5	0	0	62.5
8/21/86	1659	0.550	14	0	14.3	0	0	0	7.1	0	28.6	0	0	42.8
"	1660	0.840	26	15.4	3.8	3.8	15.4	0	19.2	7.7	3.8	3.8	0	23.1
8/23/86	1661	0.310	9	0	0	0	11.1	0	11.1	0	0	0	0	77.7
"	1662	0.001	6	0	16.7	0	0	0	16.7	0	0	0	0	66.7
"	1663	1.000	18	0	27.8	5.5	5.5	0	11.1	0	0	0	5.5	44.4
OC 191														
7/15/87	1713	0.050	6	0	0	0	0	0	16.7	16.7	16.7	16.7	0	33.3
7/16/87	1715	2.000	20	20	4	4	4	4	0	4	0	0	0	0
7/16/87	1717	1.000	16	12.5	43.7	0	0	0	25	6.2	0	0	0	6.2
7/17/87	1719	2.000	15	33.3	0	6.7	6.7	0	40	6.7	0	0	0	6.7
7/18/87	1722	1.500	19	10.5	10.5	0	0	5.3	26.3	0	10.5	0	0	31.6
7/19/87	1725	0.001	6	16.7	0	0	33.3	0	0	33.3	0	0	0	16.7
7/19/87	1726	0.200	11	0	0	9.1	18.2	0	0	18.2	0	0	0	54.5
7/20/87	1728	1.000	16	6.2	6.2	0	18.7	6.2	6.2	0	0	0	0	68.8
7/21/87	1731	3.000	15	66.7	0	0	6.7	6.7	0	0	0	0	0	13.3
7/22/87	1733	0.001	9	0	0	0	0	11.1	0	11.1	0	0	0	77.7

Table 1. (cont.)														
Date	Dive Station	CR Abundance (CR/m3)	Total # CR Examined	Acro	Collos	Siphon	Sphaer	Rhaph	C. iner	C. caud	C. serp	C. pel	C. stel	col?
OC 191 (cont.)														
-	1734	0.001	6	50	0	0	0	0	0	33.3	0	0	0	16.7
7/23/87	1736	2.000	27	14.8	11.1	3.7	37	0	0	7.4	0	0	0	25.9
-	1737	2.000	16	0	6.2	6.2	25	0	6.2	18.8	6.2	0	0	25
7/24/87	1740	1.200	20	5	10	0	15	0	0	25	0	0	0	45
-	1741	0.300	9	11.1	0	0	22.2	0	0	11.1	0	0	0	55.5
7/25/87	1743	0.400	21	9.5	19	0	9.5	9.5	9.5	14.3	0	0	0	28.6
7/26/87	1746	0.500	19	10.5	5.3	0	15.8	0	5.3	15.8	0	0	0	47.4
7/27/87	1750	0.200	18	0	0	0	16.7	0	27.8	11.1	5.5	0	0	38.9
7/28/87	1753	0.005	8	0	0	0	62.5	0	0	12.5	0	0	0	12.5
Barbados 1986														
3/10	Bel-1	n.d.	7	28.6	14.3	0	14.3	0	0	28.6	0	0	0	14.3
3/12	Bel-2	0.530	32	21.8	0	6.3	12.5	6.3	15.6	15.6	0	0	0	21.8
3/17	Bel-3	0.250	7	28.6	14.3	0	28.6	0	14.3	0	0	0	0	14.3
3/19	Bel-4	0.230	9	11.1	11.1	0	11.1	11.1	11.1	11.1	0	0	0	33.3
3/20	Bel-5	0.010	17	11.8	17.6	0	5.9	0	5.9	0	0	0	0	58.8
3/24	Bel-6	0.610	32	12.5	0	0	21.8	0	6.3	3.1	0	0	0	59.4
3/26	Bel-7	0.200	26	11.5	3.8	3.8	23.1	7.6	0	3.8	7.7	3.8	0	38.4
4/1	Bel-8	0.570	30	20	6.7	10	20	0	6.7	0	0	0	0	40
4/3	Bel-9	0.830	35	17.1	2.8	8.6	22.8	8.6	2.8	2.8	0	0	0	40
4/8	Bel-10	1.060	43	11.6	2.3	2.3	11.6	4.6	6.9	6.9	0	4.6	4.6	44.2
4/10	Bel-11	0.380	48	16.7	6.3	8.3	2.1	8.3	0	2.1	4.2	0	0	54.2
4/14	Bel-12	0.090	25	12	12	8	4	4	4	0	4	0	0	56
4/16	Bel-13	0.100	26	0	3.8	3.8	26.9	0	7.7	1	0	0	0	57.7
4/21	Bel-14	0.450	39	15.4	2.6	10.2	2.6	10.2	2.6	0	0	0	2.6	56.4
4/23	Bel-15	0.010	13	7.7	7.7	0	30.8	7.7	0	0	0	0	0	53.8
4/26	Bel-16	0.800	42	7.1	4.8	7.1	7.1	7.1	4.8	4.8	0	0	2.4	57.1
4/28	Bel-17	0.880	33	18.2	3	9.1	6.1	3	0	0	0	3	3	54.5
4/30	Bel-18	0.490	32	15.6	6.3	3.1	9.4	0	0	0	0	0	0	68.8

Table 1. (cont.)

Date	Dive Station	CR Abundance (CR/m3)	Total # CR Examined	Acro	Collos	Siphon	Sphaer	Rhaph	C. iner	C. caud	C. serp	C. pel	C. stel	col?
Barbados 1987														
2/24	Bel-21	3.000	42	19	19	2.4	9.5	7.1	4.8	0	0	4.8	0	30.9
3/1	Bel-22	1.000	28	21.4	3.6	7.1	17.8	10.4	3.6	0	7.1	0	0	28.6
3/3	Bel-23	0.600	25	12	24	0	32	4	0	0	0	0	0	24
3/6	Bel-24	2.000	41	7.3	4.8	2.4	26.8	7.3	2.4	0	0	0	0	43.9
3/9	Bel-25	0.500	39	10.2	38.5	2.6	2.6	5.1	7.7	0	2.6	0	0	33.3
3/13	Bel-26	1.000	53	32.1	24.5	5.7	11.3	11.3	1.9	0	0	0	1.9	11.3
3/16	Bel-27	0.010	6	16.7	16.7	0	16.7	0	0	0	0	0	0	50
3/19	Bel-28	1.000	44	27.3	15.9	6.8	20.4	9.1	2.3	0	0	0	0	20.4
3/21	Bel-29	3.000	44	25	15.9	6.8	20.4	11.4	0	0	0	0	0	15.9
3/25	Bel-30	2.000	61	27.9	16.4	3.2	16.4	1.6	1.6	0	0	0	0	31.1
3/31	Bel-31	1.500	41	26.8	14.6	0	12.2	4.9	4.9	4.9	0	0	0	31.7
4/4	Bel-32	0.001	10	0	22.2	0	0	0	0	0	0	0	0	77.7
4/6	Bel-33	0.001	6	0	0	0	16.7	0	0	0	0	0	0	83.3
4/8	Bel-34	0.300	41	14.6	29.3	0	19.5	0	0	0	0	0	2.4	31.7
4/11	Bel-35	1.500	52	11.5	15.4	5.7	25	0	0	0	0	0	1.9	40.4
4/13	Bel-36	2.000	45	17.8	8.9	4.4	24.4	4.4	0	0	0	0	0	37.8
4/16	Bel-37	1.500	33	21.2	27.3	3	30.3	3	3	0	0	0	3	9.1
Curacao 1988														
3/28	Car-1	1.000	25	16.0	4.0	4.0	16.0	8.0	0.0	4.0	8.0	0.0	8.0	28.0
3/30	Car-2	2.000	20	30.0	0.0	5.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	45.0
4/1	Car-3	1.500	43	18.6	9.3	6.9	11.6	6.9	0.0	0.0	0.0	0.0	2.3	41.8
4/4	Car-4	1.500	26	11.5	7.7	11.5	3.8	11.5	3.8	3.8	0.0	0.0	3.8	42.3
4/6	Car-5	3.000	39	5.1	17.9	12.8	2.6	35.9	2.6	0.0	0.0	0.0	2.6	17.9
4/8	Car-6	1.000	47	14.9	19.1	8.5	6.4	17.0	0.0	2.1	0.0	0.0	2.1	29.8
4/11	Car-7	3.000	43	9.3	13.9	2.3	13.9	6.9	0.0	4.6	0.0	0.0	4.6	44.2

Table 2. Summary of species in clusters derived from hierarchial classification analysis for three oceanic cruises : R.V. Oceanus (OC) 176, OC 177 and OC 191. Tabular values are the proportion (%) of each cluster represented by that species; dashed lines (-) indicate the absence of that species in the cluster. The sum of all species (see bottom row) should be 100% for each cluster, however, Collozoum stellatum and the "unidentified" CR have been omitted from this table, thereby resulting in lower sums.

CLUSTER (# stations/cluster)	1 (17)	2 (5)	3 (14)	4 (13)	5 (9)	6 (6)	7 (18)
Cruise(s)	OC 177 + OC 191	OC 177 + OC 191	OC 177 + OC 191	OC 177 + OC 191	OC 177 + OC 191	OC 176 + OC 191	OC 176
<i>Collozoum</i> <i>caudatum</i>	38.47	8.06	10.24	9.92	0.69	6.22	0.19
<i>Collozoum</i> <i>serpentinum</i>	15.23	10.56	1.46	0.98	11.29	-	3.23
<i>Collozoum</i> <i>pelagicum</i>	0.63	32.60	1.43	6.28	-	-	15.63
<i>Sphaerozoum</i> sp.	3.43	8.44	36.40	10.87	0.61	1.78	9.29
<i>Collozoum</i> <i>inermè</i>	0.63	12.22	10.17	25.63	20.17	2.08	1.51
<i>Collosphaera</i> sp.	2.38	-	2.06	6.32	21.09	8.57	8.72
<i>Acrosphaera</i> sp.	0.63	-	4.95	9.60	2.56	39.67	8.37
<i>Rhaphidozoum</i> sp.	2.48	2.50	1.16	1.98	0.59	5.62	24.91
<i>Siphonosphaera</i> sp.	-	-	1.36	3.01	0.61	3.63	9.61
Sum	63.88	74.38	69.23	74.59	57.61	67.57	81.46

Table 3. Summary of species in clusters derived from hierarchical classification analysis for three Caribbean field excursions : Barbados (Bdos) 1986, Bdos1987 and Curacao (Cur) 1988. Tabular values are the proportion (%) of each cluster represented by that species; dashed lines (-) indicate the absence of that species in the cluster. The sum of all species (see bottom row) should be 100% for each cluster, however, Collozoum stellatum, C. serpentinum, C. pelagicum and the "unidentified" CR have been omitted from this table (because they were relatively rare and did not contribute substantially to the cluster analysis), thereby resulting in lower sums.

CLUSTER (# stations per cluster)	1 (8)	2 (4)	3 a (4)	3 b (4)	3 c (15)	4 (2)	5 (4)
Location and Year	Bdos 1986 Cur 1988	Bdos 1986	Bdos 1986 Bdos 1987 Cur 1988	Bdos 1986 Cur 1988	Bdos 1986 Bdos 1987 Cur 1988	Bdos 1986 Bdos 1987	Bdos 1986 Bdos 1987
<i>Siphonosphaera</i> sp.	9.44	2.15	5.88	3.75	2.95	1.30	1.55
<i>Rhaphidozoum</i> sp.	12.13	5.50	8.65	-	3.88	2.55	3.75
<i>Collozoum</i> <i>caudatum</i>	1.60	15.55	2.65	0.78	0.48	-	0.25
<i>Acrosphaera</i> sp.	12.61	18.28	16.50	22.78	18.57	11.00	3.75
<i>Sphaerouzoum</i> sp.	4.34	12.38	19.93	22.60	19.82	4.25	25.30
<i>Collosphaera</i> sp.	9.18	6.93	3.55	5.25	18.50	28.05	4.08
<i>Collozoum</i> <i>inerm</i>	2.23	8.40	1.60	6.83	1.07	6.80	2.53
Sum	51.53	69.19	58.76	61.99	65.31	53.95	41.21

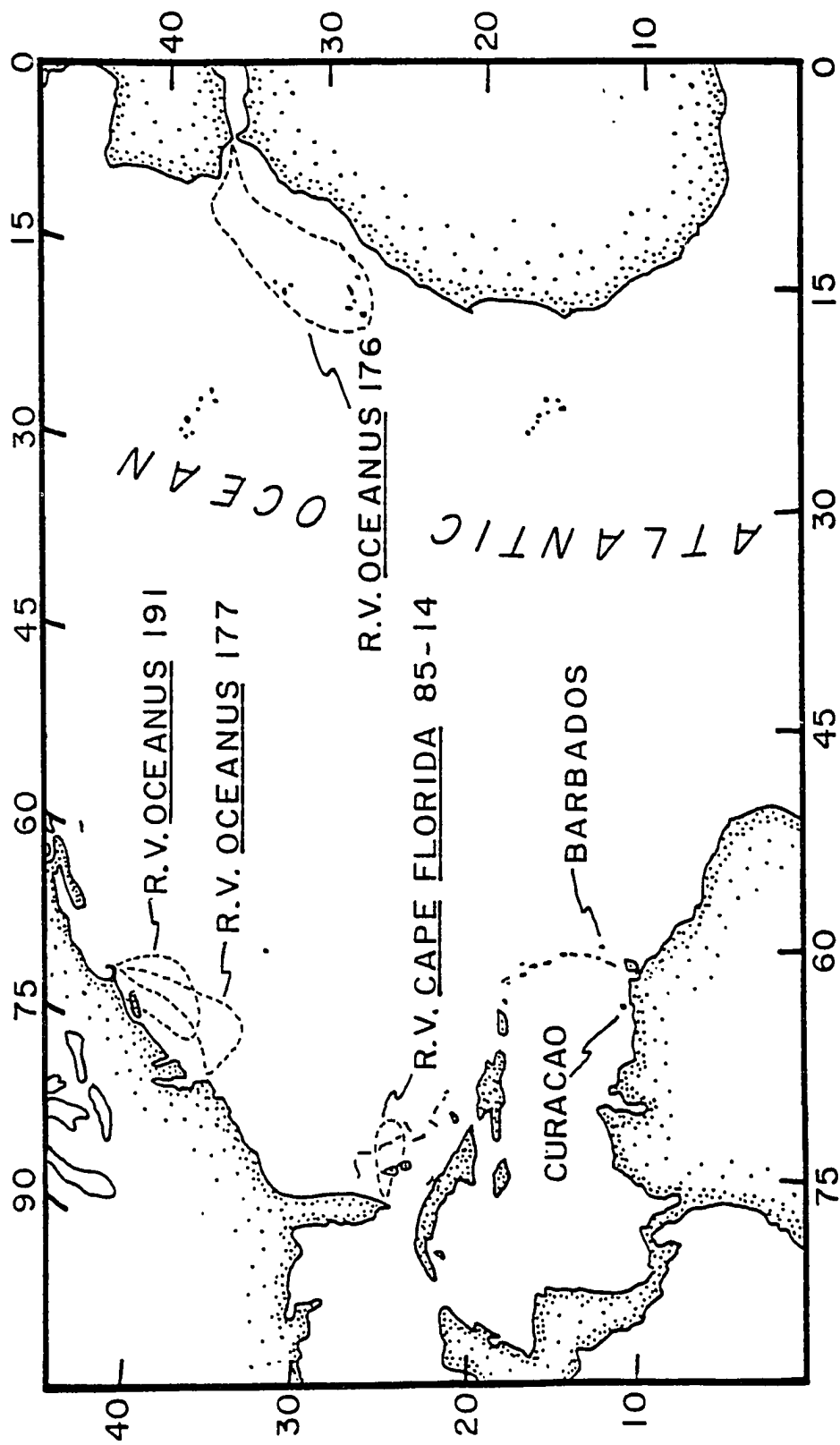


Figure 1. Locations of oceanic cruises and field stations in the North Atlantic Ocean. Positions and surface seawater temperature at each of the dive stations are listed in Appendix C.

Figure 2. Light micrographs showing the central capsules of Collozoum stellatum. Central capsules have one large lipid droplet in the center of the cell and usually between 10 and 20 endosymbionts per cell. Both spherical and cylindrical colonies ahve been observed. Scale : fig. 2a = 200 um.; figs. 2b,2c = 100 um.

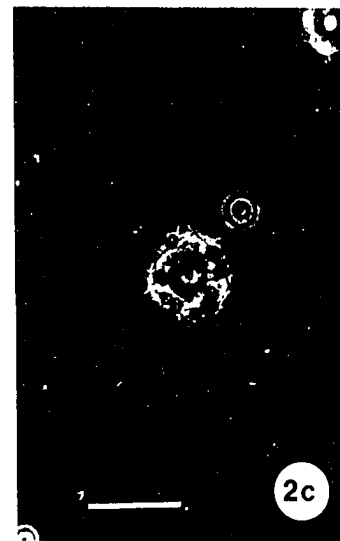
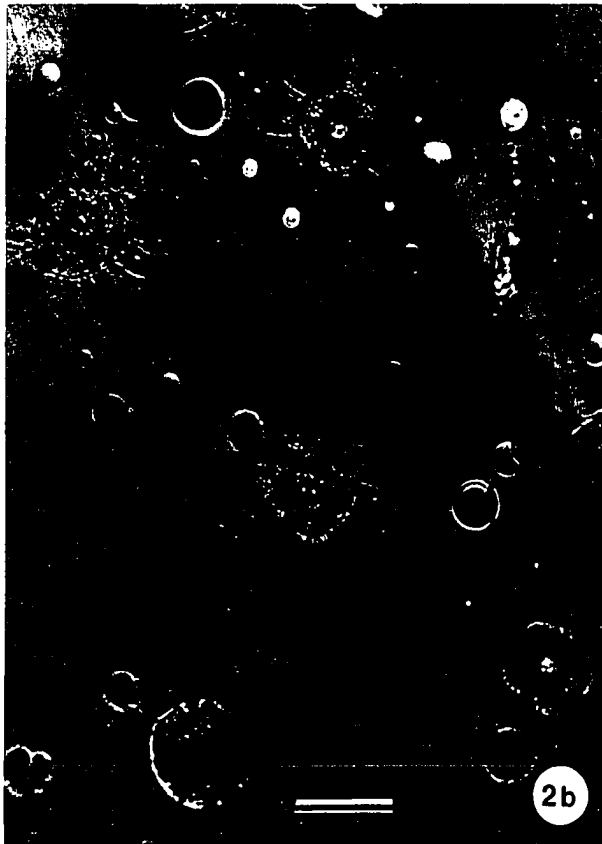
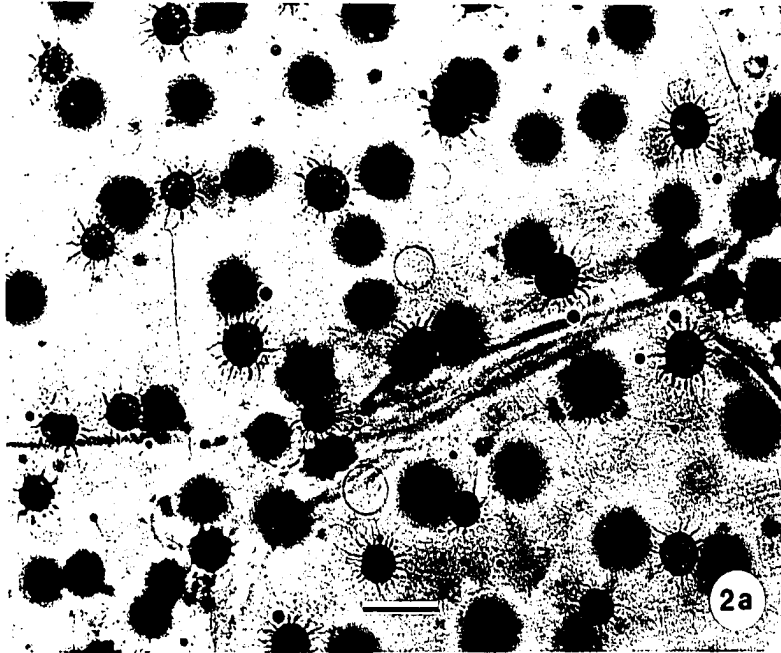


Figure 3. Surface seawater salinities (‰) measured during OC 191, Barbados 1987 and Curacao 1988.

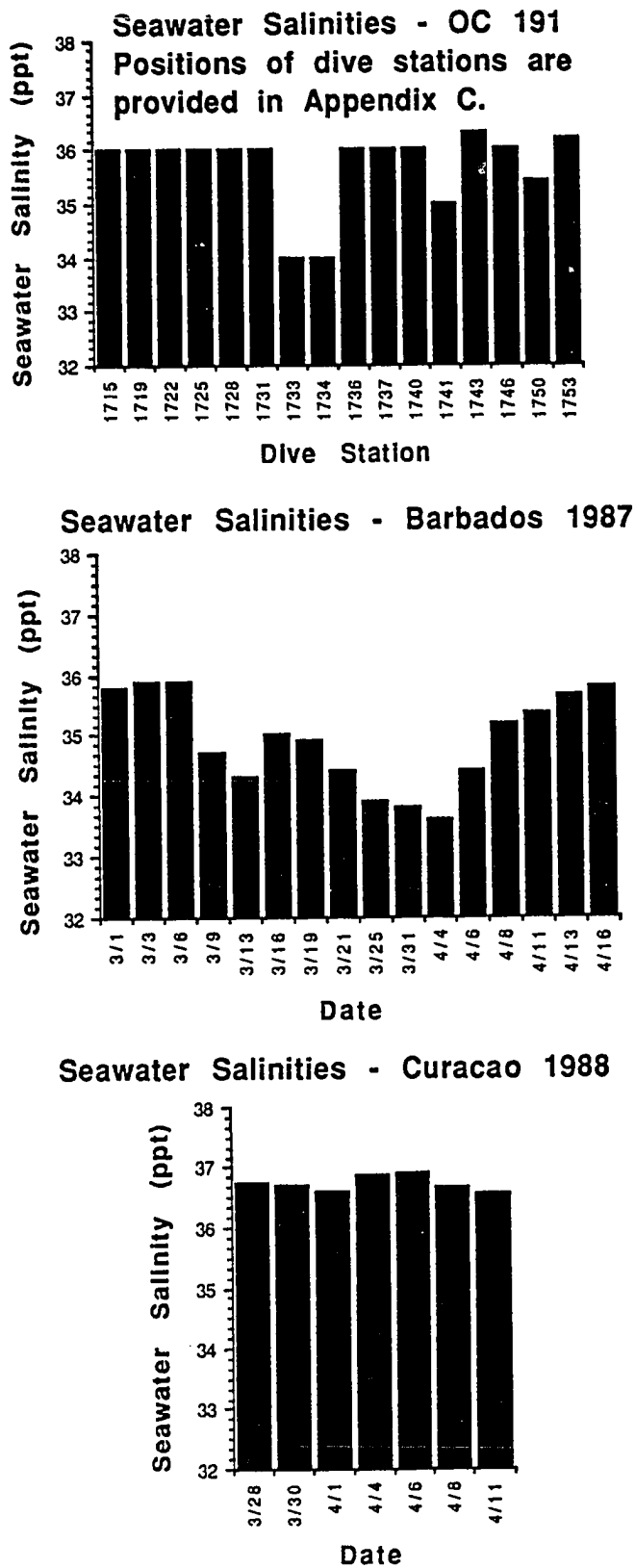
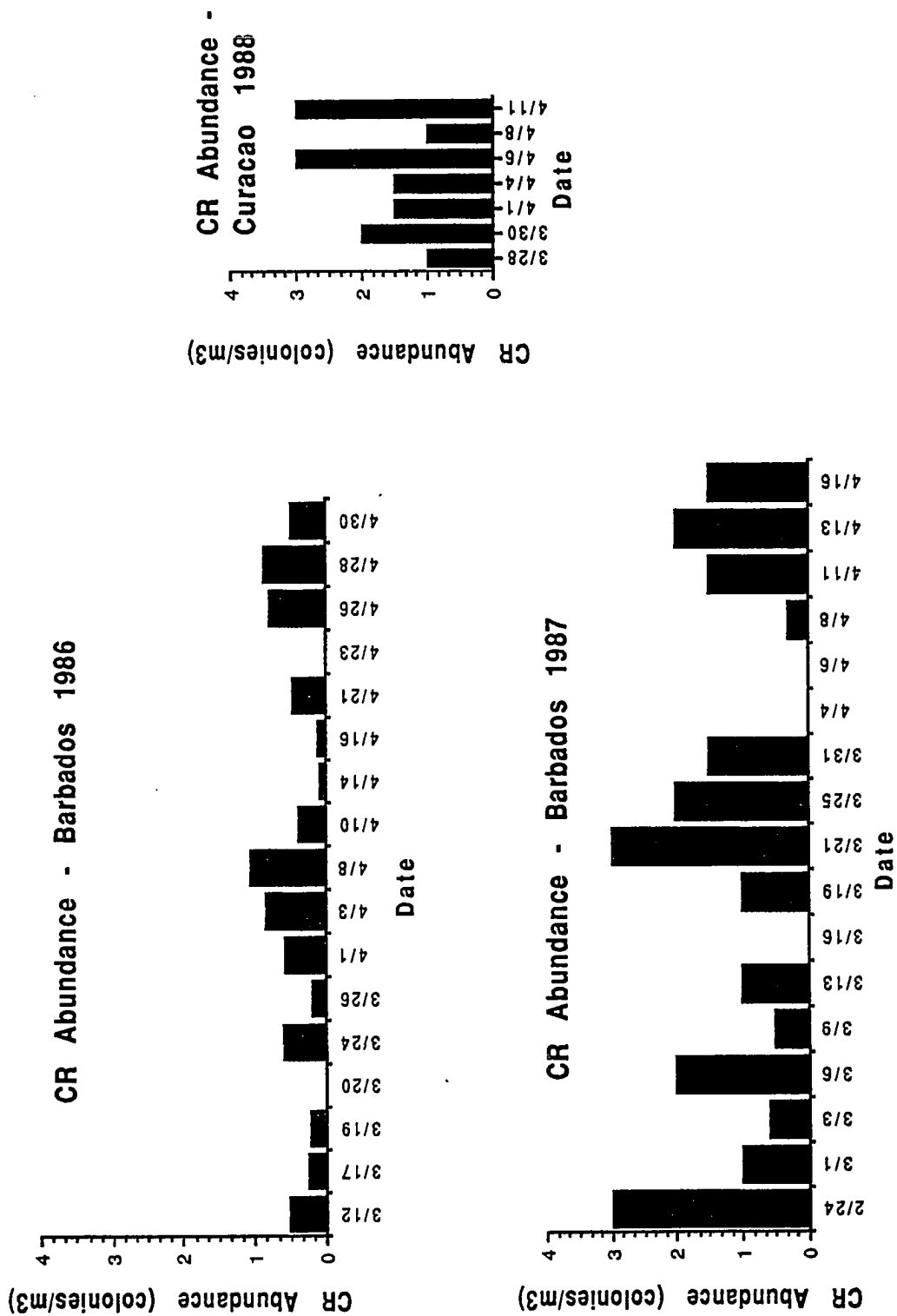


Figure 4. Abundances of colonial radiolaria (# CR/m³) at Caribbean locations: Barbados 1986, Barbados 1987 and Curacao 1988.



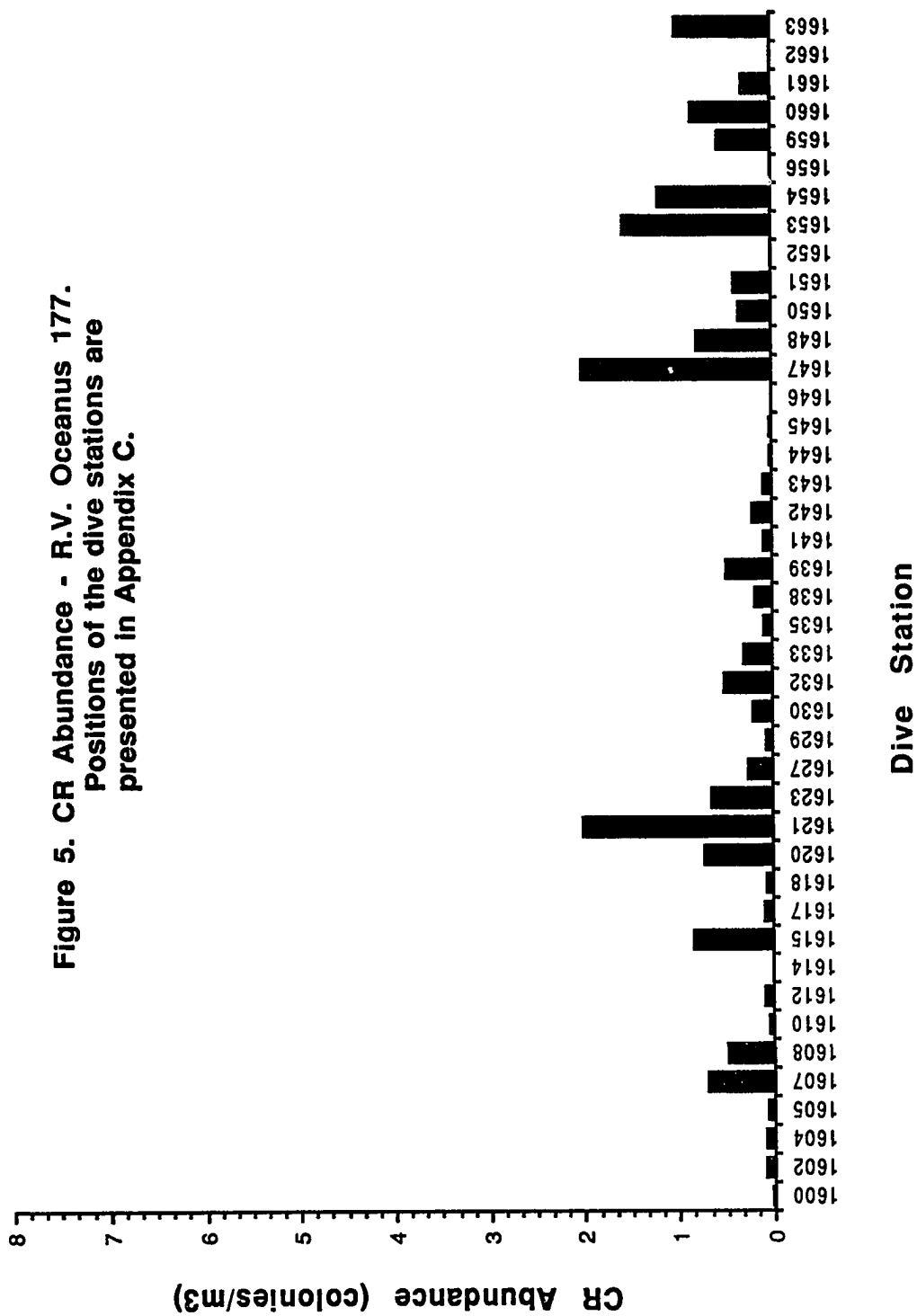


**Figure 5. CR Abundance - R.V. Oceanus 177.
Positions of the dive stations are
presented in Appendix C.**

Figure 6. CR Abundance - R.V. Oceanus 176.
Positions of the dive stations are
provided in Appendix C.

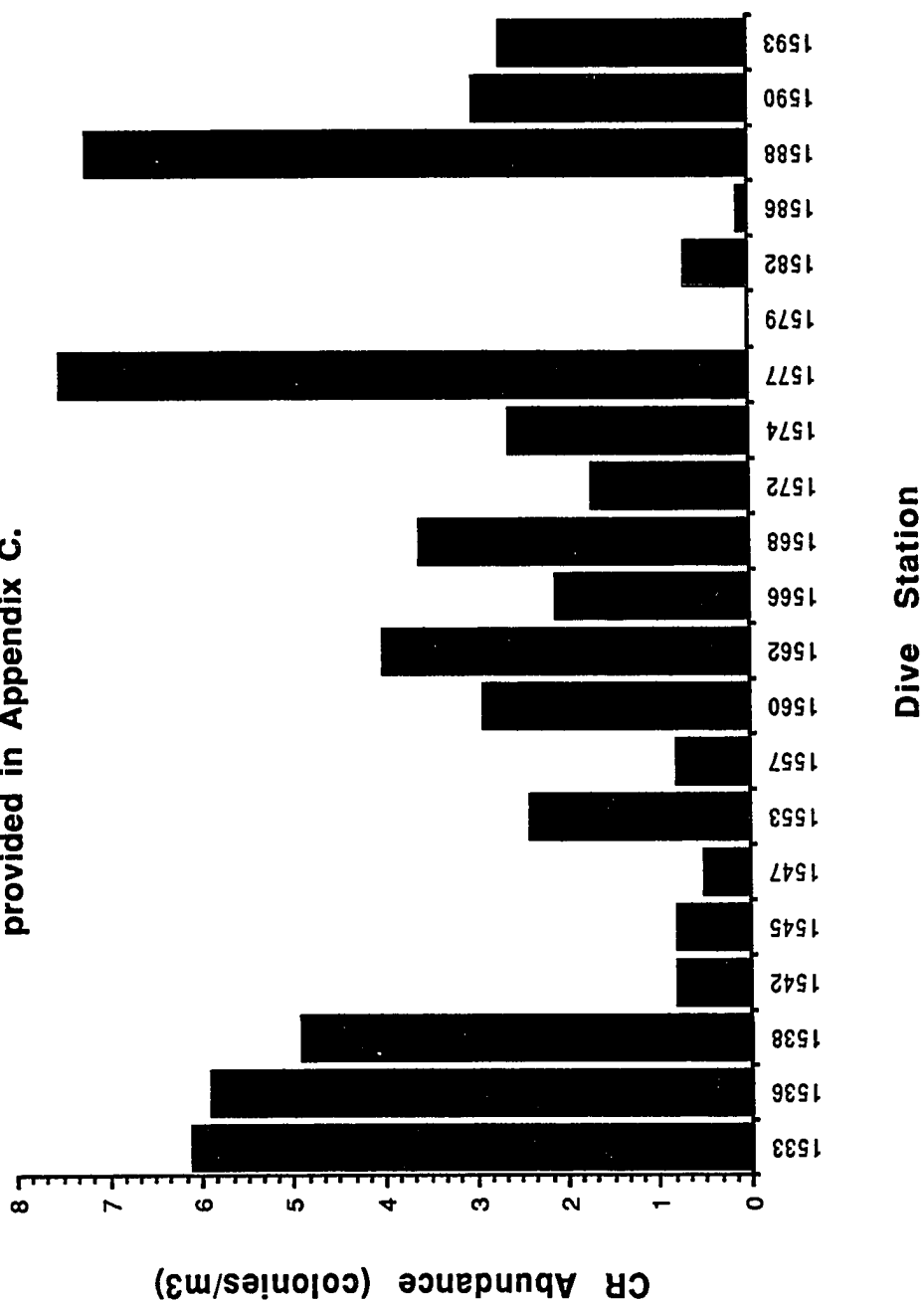


Figure 7. CR Abundance - R.V. Oceanus 191.
Positions of the dive stations are
provided in Appendix C.

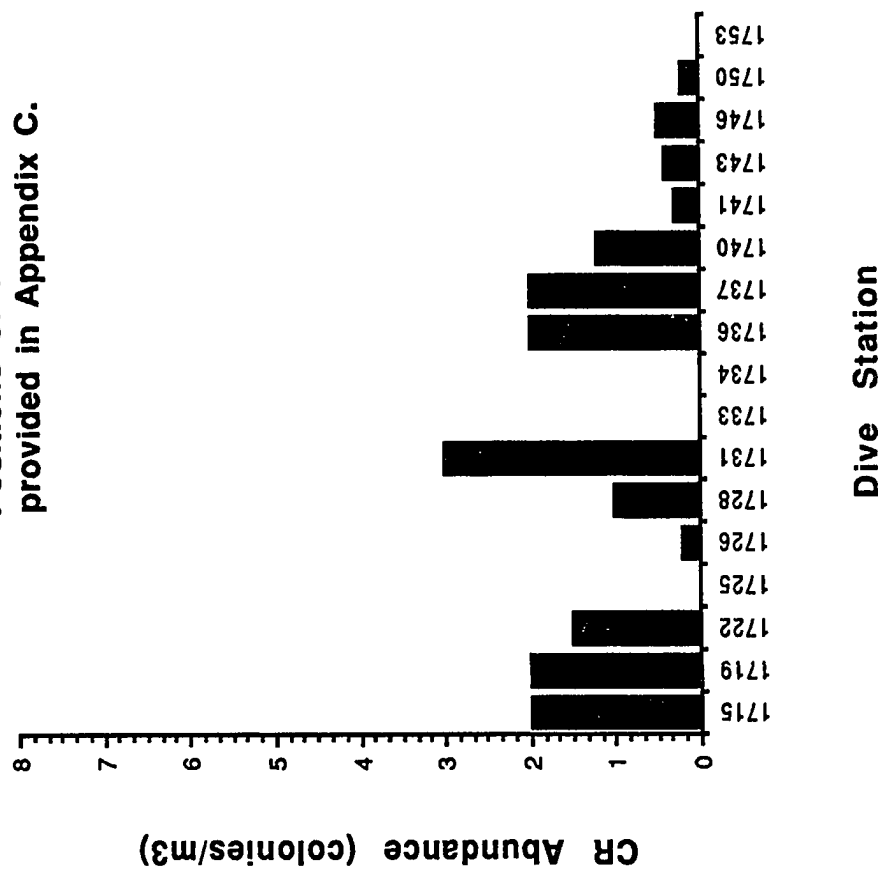


Figure 8. Hierarchical classification of samples collected during three cruises, R.V. Oceanus (OC) 176, OC 177 and OC 191. Circled numbers represent major clusters and the species represent numerical dominants within each of the clusters. The number in parentheses is the number of samples represented by each leg of the dendrogram.

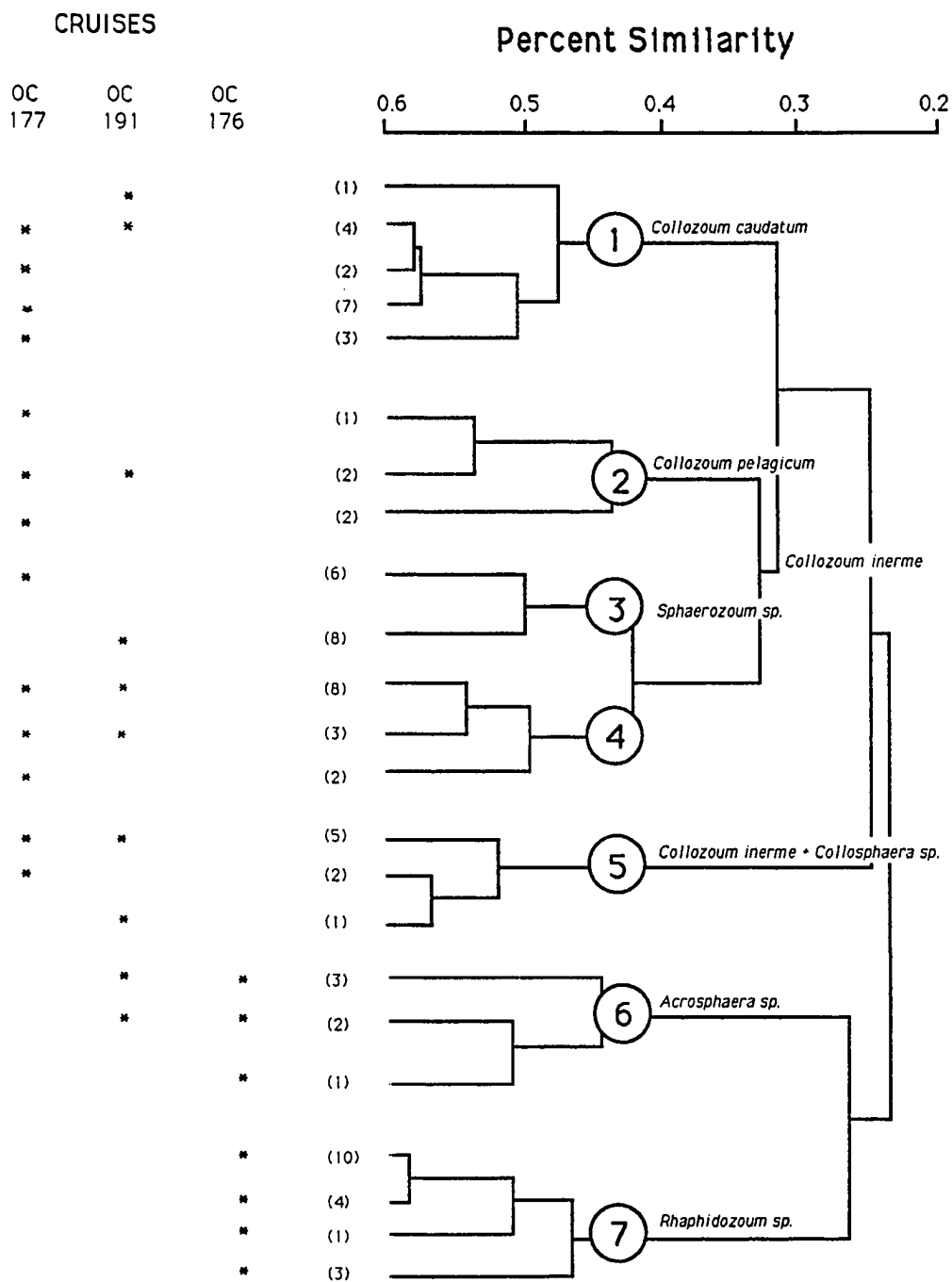


Figure 9. Hierarchical classification of samples collected during three Caribbean field excursions, Barbados 1986, 1987 and Curacao 1988. Circled numbers represent major clusters and the species represent numerical dominants within each of the clusters. The number in parentheses is the number of samples represented by each leg of the dendrogram.

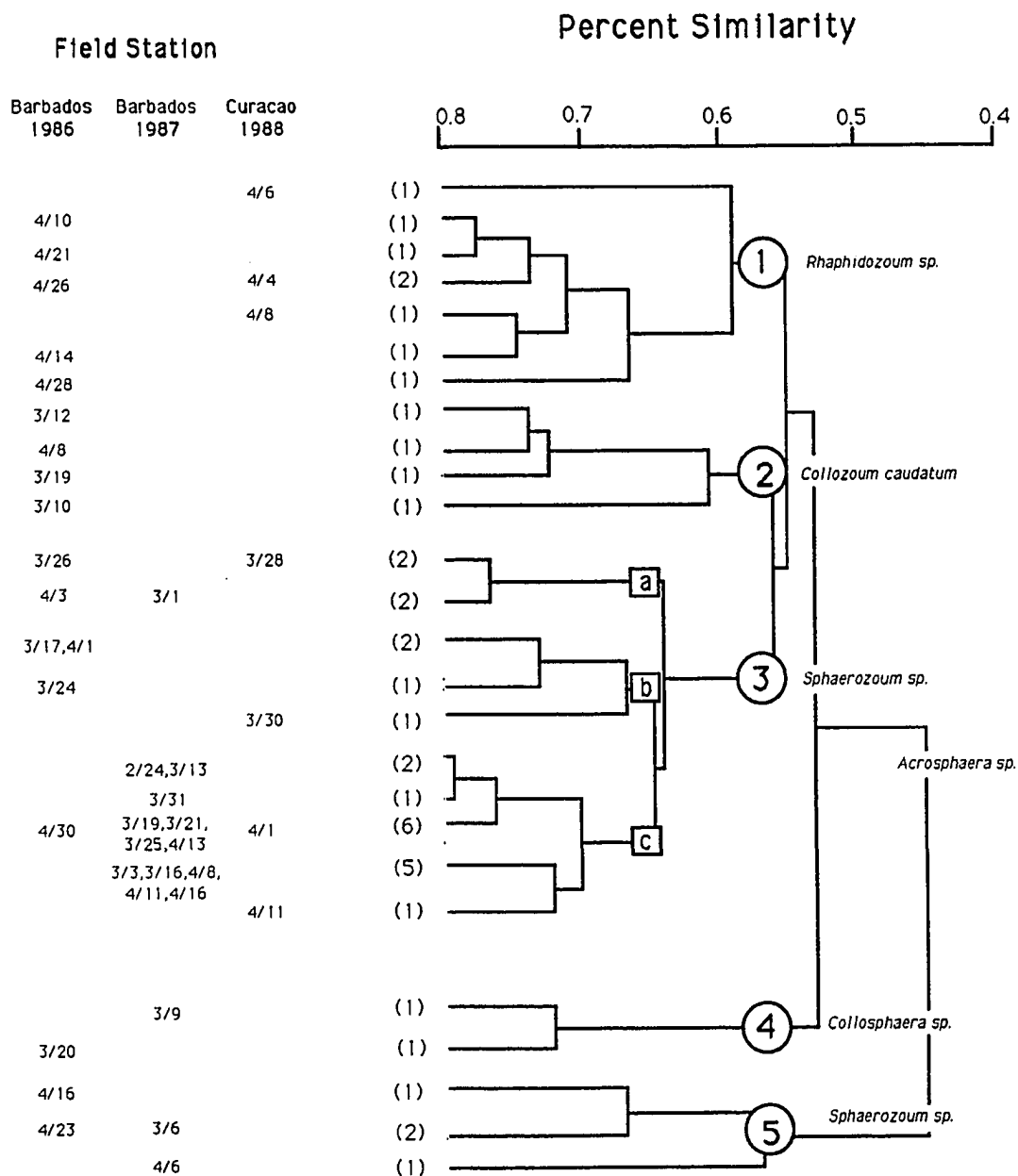


Figure 10. Ordination of the radiolarian taxa and samples on the first three axes defined by detrended correspondence analysis. Symbols represent clusters of radiolarian taxa defined by classification analysis. Data from the three oceanic cruises, R.V. Oceanus (OC) 176, OC 177 and OC 191 are summarized herein.

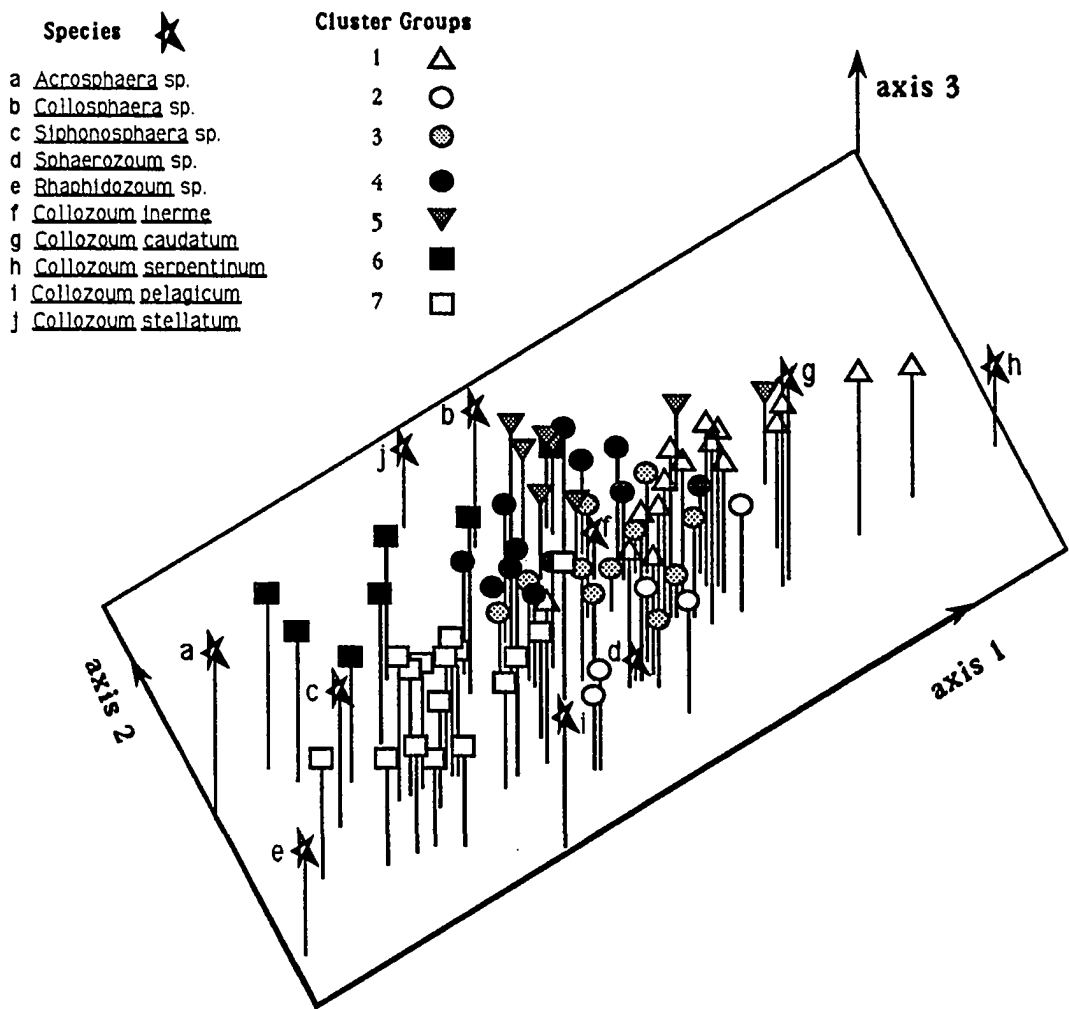
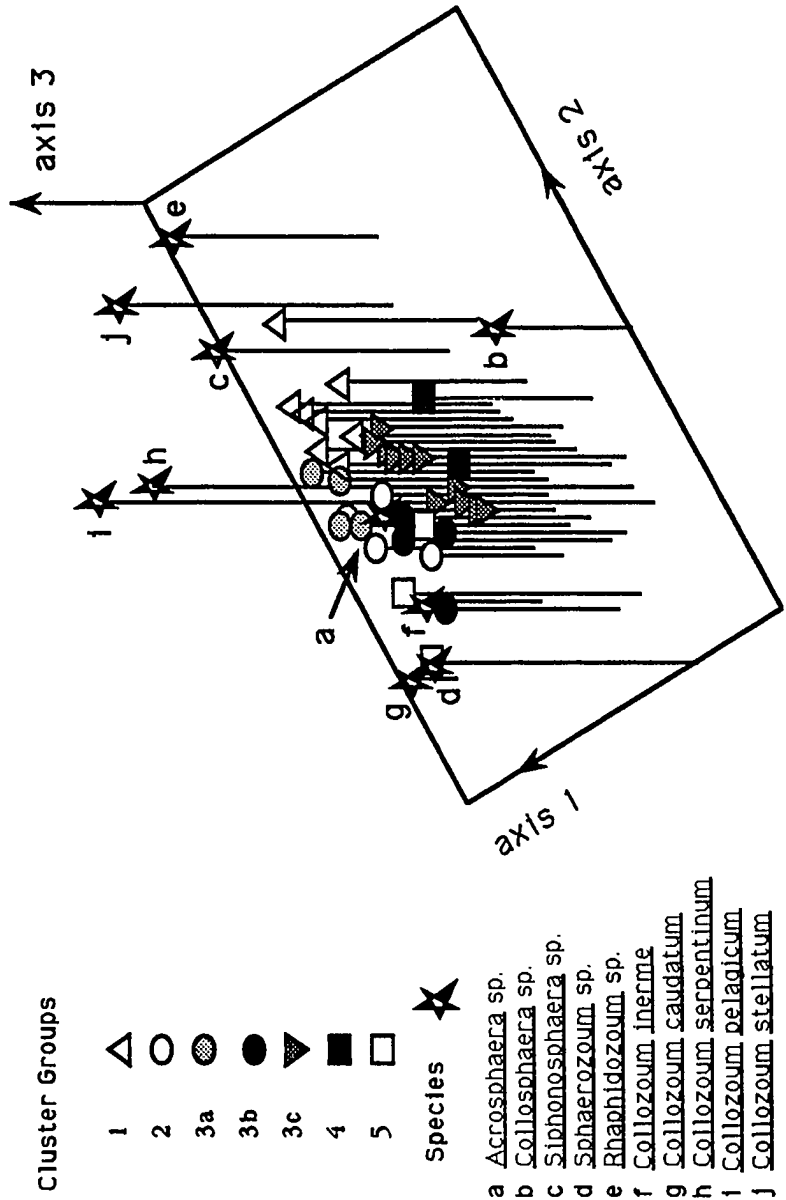


Figure 11. Ordination of the radiolarian taxa and samples on the first three axes defined by detrended correspondence analysis. Symbols represent clusters of radiolarian taxa defined by classification analysis. Data from the three Caribbean stations, Barbados 1986, 1987 and Curacao 1988 are summarized herein.



Chapter 2

Gross Morphology and Fine Structure of Organisms Associated with Colonial Radiolaria

INTRODUCTION

Many zooplankton harbor symbiotic microorganisms (Droop, 1963) which may supplement their normal diets and simultaneously supply the symbionts with necessary nutrients (e.g. Mews, 1980; Thorington and Margulis, 1981). Although symbiosis has often been used to describe such mutualistic associations, it is a much broader term which may be used to describe a wide range of interactions that are not necessarily based on the mutual benefit or harm derived from the association. Therefore, Smith and Douglas (1987) have defined symbiosis as an association where there is "intimate contact" between the partners for an "appreciable length of time" relative to their life span.

Colonial radiolaria (CR) harbor endosymbiotic algae (i.e. intracellular symbionts) which were first described by Huxley (1851). In addition to the algal endosymbionts, several other microscopic organisms are intimately associated with radiolarian colonies, however, they are extracellular and should, therefore, be considered as "ectosymbionts" (Smith and Douglas, 1987). The radiolarian ectosymbionts observed in the current study include bacteria, a bodonid flagellate that bears a strong morphological resemblance to certain members of the genus Cryptobia (Vickerman, 1976), Gyrodinium sp. (a gymnodinioid dinoflagellate), a dysterid ciliate, and several different species of small hyperiid amphipods (Brandt, 1885; Harbison et al., 1977; Swanberg, 1979). In addition to these groups of ectosymbionts, Hollande and Enjumet (1953) found Bodo insidiosus (a bodonid flagellate) within Collozoum colonies taken from the Mediterranean Sea and Swanberg (1979) described Miracia efferata (harpacticoid copepod) on the surfaces of CR in the Atlantic Ocean.

The gross morphologies of the radiolarian ectosymbionts (excluding Bodo insidiosus and Miracia efferata) are described below.

In addition, I have presented the fine structure of the protozoan ectosymbionts because the association of these organisms with colonial radiolaria has not been described previously and they may be new species. Furthermore, ultrastructural details shown here help to clarify the nature of the association between the CR and the protozoan ectosymbionts.

In this and the following chapters, the ectosymbiotic organisms have also been referred to as "associated" and "infesting" organisms. These names are used without reference to the beneficial or harmful effect of the ectosymbionts but more typically with respect to their abundance, where infestation is used for small, more numerous ectosymbionts.

MATERIALS and METHODS

A. Examination of Organisms Associated with CR

Colonial radiolaria collected by SCUBA divers (see Chapter 1) were examined as soon as possible following each dive (generally one to three hrs.) with a Nikon Diaphot inverted microscope to determine if CR had microbial infestations. Radiolarian colonies were initially scanned using a 10x objective (total magnification = 100x). This magnification was sufficient to detect the three major types of protozoan infestations : Cryptobia-like bodonid flagellate, Gyrodinium sp. and dysterid ciliate. The protozoan cell size, cell shape, swimming behavior and its location on or in the CR were used to assign it to one of the three protozoan categories. In order to verify the protozoan identifications, higher microscope magnifications (total magnification = 200x or 400x) were used. Hyperiid amphipods associated with CR were always larger than 500 μ m (length) and were easily distinguished from other microcrustaceans at low microscope magnifications (40x or 100x). Amphipods were identified to species using the keys and descriptions of Bowman (1973). Whenever possible, protozoans and amphipods were photographed in vivo using a Nikon FG 35 mm camera mounted on the Nikon Diaphot inverted microscope.

Although many of the bacteria associated with CR were large (up to several micrometers in length), they were not visible with the inverted microscope. Bacteria on the surfaces of CR were studied by staining radiolarian colonies with 4'6-diamidino-2-phenylindole

(DAPI; Porter and Feig, 1980) and examining stained colonies with an epifluorescent microscope (see Chapter 4).

B. Fine Structure of Protozoan Infestors

Colonial radiolarians with protozoan infestations were fixed in 4% buffered glutaraldehyde using 0.05M cacodylate in filtered seawater, pH=7.0 at 4°C for 30 min. and post-fixed for 4 hrs. in 2% cacodylate-buffered (0.05M, pH=7.0) osmium tetroxide. Fixed specimens were dehydrated in the following series of acetone solutions 10%, 30%, 50%, 75%, and 95%; using 15 min. immersions in each, followed by 3 transfers through fresh solutions of 100% acetone (15 min. in each). Specimens were infiltrated overnight in a 1:1 mixture of acetone and Polaron "One-Shot" epon embedding medium, transferred to flat embedding molds with fresh catalyzed embedding resin and placed in a 45°C oven for 36 hrs.

Ultra-thin sections were obtained with a diamond knife using a Porter-Blum MT-2 ultramicrotome, collected on 200 mesh copper grids, stained with Reynold's lead citrate and examined using a Philips EM 201 transmission electron microscope.

C. SEM Examination of Gyrodinium sp.

Gyrodinium sp. were removed from infested colonies and immersed in a chilled (4°C) solution of osmium tetroxide (final concentration = 2%) prepared in cacodylate buffered seawater (0.05M, pH=7.0) for 15 min. The dinoflagellates were then gently filtered onto 1 μ m pore size nucleopore filters, dehydrated in a graded ethanol series, critical-point dried, attached to an aluminum stub and coated with gold-palladium following the procedure described by Spero (1987). Specimens were viewed using a Cambridge 250 Mk2 scanning electron microscope at 20 KV.

D. Protargol Staining of Dysterid Ciliates

Colonial radiolaria with dysterid ciliate infestations were fixed in a modified Bouin's fluid (Small, unpublished). This fixative was prepared in the following manner. 1) A saturated solution of calcium carbonate in full strength formalin (37% formaldehyde) was prepared (solution A). 2) picric acid was added to the supernatant from solution A to produce a solution saturated in picric acid (solution B). 3) Solution B was diluted 1:15 with filtered seawater

and just prior to fixation, glacial acetic acid was added to produce a final concentration of 1.3% acetic acid (solution C). 4) Samples were fixed by adding three parts solution C to one part sample volume, and stored at room temperature in a tightly sealed vessel until examination

Colonial radiolaria fixed in Bouin's fluid were gently washed in distilled water to eliminate the fixative because picric acid may interfere with the Protargol stain. In some CR, the distilled water rinses were not sufficient to remove the picric acid and it was necessary to transfer the colony and associated ciliates through several saturated solutions of sodium bicarbonate to prepare them for staining. After eliminating the picric acid, colonial radiolaria were attached to cover glasses and stained by the Protargol procedure. The Protargol stain is one of the most widely accepted silver-stains used for morphological preparations of ciliates (Lee et al., 1985).

RESULTS

A. Bacteria Associated with CR Surfaces

Bacteria were found on the surfaces of radiolarian rhizopodia and on the CR gelatin. The morphologies of bacteria associated with CR surfaces included spherical cells, rods, curved rods and filamentous forms. Although many of the free living bacteria in the surrounding waters had shapes that were similar to the cells on CR, the radiolarian-associated bacteria were generally larger. Furthermore, filamentous bacteria were found almost exclusively on CR surfaces. Further information, including the ranges of bacterial cell volumes and abundances of bacteria on CR, is presented in Chapter 4.

B. Description of the Cryptobia-like Bodonid Flagellate

The gross morphology of the bodonid flagellate is shown in a hand-drawn sketch (Figure 12). Several attempts to photograph the flagellate in situ were unsuccessful because the cell is small (2 to 3 μm x 7 to 20 μm), highly motile and almost translucent. Furthermore, this bodonid was always found swimming within the radiolarian gelatin and therefore was not readily pipetted off the colony.

The flagellate generally moved in a forward direction (the point at which the flagella insert into the body is considered the anterior end), and was propelled by the posterior (recurrent) flagellum and an undulating or spiral motion of the body, beginning at the anterior end and progressing posteriorly. Because the posterior flagellum was constantly in motion, I could not determine its degree of attachment to the body; therefore part of its length is represented by a dotted line in Figure 12. As it swam, the flagellate probed the surrounding environment with the anterior flagellum, occasionally stopping and contracting the anterior portion of its body before proceeding in a new direction. As indicated above, the bodonid was variable in length but did not exceed three μm in diameter.

Cross sections of the anterior region of the Cryptobia-like bodonid were photographed by TEM and are presented in Figures 13 and 14. The ultrastructural features are described and discussed further in the discussion section of this chapter.

C. Gyrodinium sp.

Gyrodinium sp. cells measured in situ, by light microscope, ranged from 16 to 22 μm long and 7 to 10 μm wide. The dimensions of dinoflagellates that were fixed and dehydrated for electron microscope examination were reduced, sometimes by 30% of their true size. The non-thecate dinoflagellate swam among the radiolarian rhizopodia (Figure 15), and occasionally adhered to a rhizopodium for an indefinite period of time, ranging from seconds to minutes. All of the dinoflagellates observed were able to detach from the rhizopodium and resume their swimming behavior, i.e. they were not captured as prey by the radiolarian. Upon removal from the surface of the host CR, Gyrodinium sp. almost invariably swam to the bottom of the dish and remained there, immotile, for periods of time ranging from minutes to tens of minutes and possibly even hours.

Gyrodinium sp. has a complete girdle (i.e. it completes one turn around the body) which is displaced approximately one times its width (Figure 16). The epicone is smaller than the hypocone and the sulcus (the groove in which the longitudinal flagellum lies) is shallow and does not occupy the full length of the hypocone. Although the longitudinal flagellum is not shown, its length was approximately 15 μm .

Longitudinal thin sections of Gyrodinium sp. (Figures 17 and 18) show the deep girdle and the prominent girdle lists (the upper lips over the girdle). The large hypocone, relative to the epicone, and the displacement of the girdle are prominent features of Gyrodinium sp. that are clearly shown in Figures 16 and 17. The nucleus which is always located in the hypocone (Figures 17 and 18) contains chromosomes with lightly condensed chromatin (Figure 18).

Mitochondria, and large numbers of ejectosomes in various stages of development are found throughout the cell (Figures 19 and 20). As they develop, ejectosomes migrate toward the cell surface, so that mature ejectosomes are located along the periphery of the dinoflagellate (arrows in Figure 17). Longitudinal and cross sections of ejectosomes (Figure 19) reveal two major types, ejectosomes with amorphous contents and ejectosomes with fibrillar contents. Several intracellular bacteria which are not surrounded by host membrane are often found near the nucleus (Figure 20).

Numerous chloroplast lobes are distributed along the periphery of the cell (Figures 17 and 18). Single stalked pyrenoids are penetrated by several thylakoid lamellae (Figure 20) and storage material is almost exclusively restricted to the starch caps of Gyrodinium sp. A triangular ribosomal array is found next to many of the chloroplasts (Figure 22), but its function is not known. Chloroplast thylakoids are arranged in 3-thylakoid bands within the chloroplasts (Figure 24).

The cross section in Figure 21 shows a putative pinocytotic invagination near the insertion point. The actual insertion point is presented in Figure 23 and at the base of the flagellar groove, a coated pinocytotic vesicle is shown in the process of formation. Adjacent to this nascent vesicle is another previously formed pinocytotic vesicle with a double membrane which has shed the coat.

D. Description of Dysterid Ciliates

A light micrograph of dysterid ciliates crawling along the external rhizopodia of a colonial radiolarian is presented in Figure 25. The dark shadows in the background are the radiolarian central capsules which are several focal planes below the ciliates.

Dysterid ciliates (measured in vivo by light microscope) were 40 to 60 μm long by 15 to 20 μm wide. The generally oval, laterally

compressed shape of Protargol-stained dysterids is shown in Figures 26 and 27. Also visible are the left ventral body kinetics and the podite which help to distinguish the Dysteriidae from other similar ciliates (Lee et al., 1985).

The fine structure of the dysterid ciliate is shown in Figure 28. The ciliate is surrounded by a loose pellicle with large alveolar spaces and a layer of small microtubules, providing structural support, is visible along the cell periphery, just below the pellicle. Somatic cilia are concentrated on one side of the cell, as seen in the light micrographs above. The macronucleus has regions of condensed and diffuse chromatin and is located on the dorsal side of the cell. A large number of electron-dense bodies are scattered throughout the cell.

A cluster of intracellular bacteria is located near the macronucleus (Figure 28). At high magnification, numerous mitochondria may be seen scattered among the intracellular bacteria (Figure 29). The ciliate also has one or more contractile vacuole and Golgi body; both organelles are shown on the ventral side of the ciliate (Figures 28 and 30). Many food vacuoles contain amorphous matter, but in some, the semi-digested remains of chloroplasts may be seen (Figure 31).

E. Description of Hyperiid Amphipods

Hyperiid amphipods associated with CR generally ranged between 0.5 to 2.0 mm in length. Although most amphipods were not identified to species, careful observations were made regarding the general body shape and gross features such as length, shape, and number of antennae (a morphological feature used to distinguish males from females). Amphipods were generally found embedded within the radiolarian gelatin and used pereopods 4 to 7 to move within the colony and to anchor themselves in place (Figure 32). A few large hyperiid amphipods were found on the outside of colonies and often swam off when captured in a glass jar. The amphipod in Figure 32 was feeding on a radiolarian central capsule (cc) and pereopods 1 to 3 were used to rotate the central capsule and to bring it to the mouthparts.

DISCUSSION

A. Bacteria on CR

Although many of the colonial radiolaria did not have protozoan or amphipod infestations, all of the DAPI-stained CR that were examined had bacteria on their surfaces. The CR-associated bacteria included large filamentous forms that are not generally found among planktonic bacterial assemblages, but the morphologies of other bacteria on radiolarian surfaces were similar to the free living forms observed in the surrounding waters. Morphological descriptions of CR-associated bacteria were limited to the resolving power of the epifluorescent microscope because several attempts to examine the CR microbial community by SEM proved unsuccessful. The bacterial ectosymbionts associated with the CR and their carbon demands are described further in chapter 4 of this thesis.

B. The Cryptobia-like Bodonid Flagellate

The decision to place this unidentified flagellate in the order Bodonidae was based upon its gross morphology (similar to several of the Cryptobia species) and the presence of a kinetoplast and a recurring flagellum. Although only a few specimens have been examined by TEM, the absence of bacteria or other solid food in its digestive suggest that it is neither a phagotrophic Bodo sp., nor a Procryptobia sp. and is therefore, probably a Cryptobia sp. (Vickerman, 1978; Vickerman, pers. comm.). The flagellates observed within infested colonies had strikingly similar morphology and swimming behavior, however, it is possible that these flagellates were actually represented by more than one species.

Figures 13 and 14 are different thin sections of the same flagellate. In Figure 14, three different flagella are shown. The two flagella marked anterior and posterior flagellum may belong to the same flagellate or to two different organisms situated in different planes of section. If the two flagella belong to the same flagellate, it is possible that the cell is dividing (Vickerman, pers. comm.).

Hollande and Enjume (1953) described another bodonid flagellate, Bodo insidiosus, embedded in the gelatin of many of the Collozoum colonies that were collected in the Bay of Algiers. I have observed Bodo insidiosus infestations in various CR collected from the eastern North Atlantic Ocean (Chapter 3), but these flagellates

were easily distinguished from the Cryptobia-like bodonid by differences in size, shape and swimming behavior.

Because the bodonid flagellates observed in the CR were very small, and were identified solely on the basis of their morphology and swimming behavior, it is possible that colonial radiolaria serve as hosts to other small, morphologically similar bodonids in addition to B. insidiosus and the Cryptobia-like bodonid. The same comment applies to the other protozoans observed in or on the CR. It is possible that more than one morphologically similar (yet taxonomically distinct) organism was involved in each of the associations that I have described below. Therefore, in each of the described associations it is possible that there may be more than one species involved.

C. The Ectosymbiotic Dinoflagellate, Gyrodinium sp.

One of the unresolved questions regarding the association of small organisms with colonial radiolaria is : how do they avoid predation? The ejectosomes of Gyrodinium sp. may provide the dinoflagellate with the necessary protection against radiolarian predation. Mucocysts are ejectosomes with homogeneous, finely granular contents (Cachon et al., 1976) which are apparently secreted on the cell surface. The Gyrodinium sp. ejectosomes with amorphous contents match this description and may coat the cell surface with a protective substance that counters the adhesive action of the radiolarian rhizopodia. In addition to the mucocyst-like organelles, Gyrodinium sp. has ejectosomes with fibrillar contents which correspond to the description of trichocysts (Dodge and Greuet, 1987). Many of the ejectosomes observed in the thin sections of Gyrodinium sp. have an appearance that is intermediate between the mucocysts and the trichocysts. In such cases, where it is difficult to distinguish between the two types of organelles, Cachon et al. (1976) suggested they be considered as homologous structures.

There are additional structures within the cytoplasm of Gyrodinium sp. whose function is not fully understood e.g. intracellular bacteria which are not surrounded by host membrane. Gold and Pollinger (1971) observed large numbers of bacteria within the cells of several other dinoflagellates : Gymnodinium splendens, Crypthecodinium cohnii, Ceratium tripos, Amphidinium carterae, and Prorocentrum micans, but it is not clear whether these bacteria were enclosed within host membranes.

Intracellular bacteria that closely matched the appearance of bacteria observed inside Gyrodinium sp. were described in thin sections of several different ciliates (Matthes and Graf, 1967; Soldo, 1987; Soldo, 1983). The intracellular bacteria, also known as "xenosomes" (Soldo and Brickson, 1978), are not surrounded by host membranes, yet their existence relies heavily on nutrition from the host ciliate. The interaction between xenosomes and host cells is complex and may include either a harmonious type of co-existence or a parasitic interaction whereby the bacterium kills the host cell (Soldo et al., 1986). On the other hand, the host is not dependent on the intracellular bacteria in any way (excluding one exceptional case; see Soldo, 1973) and if xenosomes are artificially removed from the host cell, this does not interfere with the completion of its life cycle (Soldo, 1987). At this time, it is not known whether a) intracellular bacteria in Gyrodinium sp. are essential to the existence of the dinoflagellate, or b) the bacteria are capable of killing the host dinoflagellate. It is also possible that Gyrodinium sp. consumes intracellular bacteria, however, none of the thin sections of the dinoflagellate examined by TEM contained the remains of solid food.

Transmission electron micrographs of Gyrodinium sp. reveal a large number of chloroplast lobes within the cell which autofluoresce brightly when examined by epifluorescent microscope. Brightly autofluorescing chloroplasts are often associated with healthy photosynthetic cells, however, there is a strange paucity of storage materials inside the Gyrodinium sp. cytoplasm when comparing these to thin sections of other autofluorescing dinoflagellates.

A triangular ribosomal array is often found near the chloroplasts of Gyrodinium sp. (Figure 22). The function of this structure is not known although its consistent proximity to chloroplasts suggests it may be involved in biosynthetic activities.

D. Dysterid Ciliates Associated with the Colonies

Most of the dysterid ciliates that were previously described in marine waters were collected from littoral and benthic environments (Wilbert, 1971; Deroux and Dragesco, 1968; Dragesco, 1966), or from the surfaces of fish, which they parasitized (Lom and Nigrelli, 1970). In contrast, dysterid ciliates associated with CR were collected in oceanic waters, usually several hundred miles offshore. Furthermore, dysterid ciliates have been observed among the microbial communities associated with marine snow collected from the Gulf

Stream and the Sargasso Sea (Small, pers. comm.). Thus, it appears that dysterid ciliates are more widely distributed than previously believed.

Dysterid ciliates are weak swimmers (Huxley, 1857) which utilize a podite to maintain contact with their substrate. The somatic cilia, arranged in parallel rows (kineties), are found exclusively on the ventral side of the cell and are used to crawl along surfaces, and possibly to aid in the feeding process.

The dysterid ciliates maintained close contact with the radiolarian colonies during several lengthy observation periods, and appeared immune to the host rhizopodia. Unlike Gyrodinium sp., these ciliates do not have mucocyst-like ejectosomes, however, dysterids are surrounded by a loose pellicle which may provide the necessary protection against the sticky radiolarian rhizopodia.

Numerous electron dense bodies which probably contain reserve products (e.g. lipids) are found within the cytoplasm of the dysterids. The abundance of storage products suggests that these protozoa are well-fed, but the diet of the dysterid ciliates is only partially defined. Digested plastids with the stacked thylakoid arrangement that is characteristic of algal chloroplasts were observed in several of the ciliate food vacuoles. This raises the possibility that dysterids use the radiolarian host as a platform from which to feed on phytoplankton from the surrounding water. It is also possible that the dysterids graze Gyrodinium sp. from the surface of the CR since both protists have been observed together on at least 30 of the colonies examined in this study (see chapter 3).

A cluster of intracellular bacteria, interspersed with many mitochondria, was observed near the macronucleus. The high concentration of mitochondria in this region suggests this is a metabolically active area, but it is not clear how this is related to the intracellular bacteria. The fine structure of the bacteria strongly resembles the fine structure of xenosomes (described above), however, it is not known whether the bacteria are a benefit or a detriment to the host. It is fairly certain that the dysterid ciliate does not feed on these bacteria since they are not enclosed within food vacuoles.

An additional organelle observed inside dysterid ciliates was the contractile vacuole. This regulatory organelle is frequently found

among protozoa in fresh or brackish waters where there is a constant need to eliminate excess water from the hypertonic cell cytoplasm, but is much less common among marine protozoa because the protozoan cytoplasm is nearly isotonic to the surrounding seawater (Anderson, 1988). The presence of this regulatory organelle in dysterid ciliates associated with CR suggests that the ciliates may have been exported from coastal, low-salinity waters to the oceanic environment.

E. Protozoan Bacterivory

Examination of the protozoa by transmission electron microscopy did not show evidence of bacterivory in the three protozoans associated with CR. However, it is often necessary to search exhaustively through thin sections of the protozoan digestive vacuoles before finding solid proof of bacterial food (Anderson, pers. comm.). I have not done so and until this is done, bacterivory may not be ruled out as a possible source of nutrition. In addition, both gyrodinoid dinoflagellates and dysterid ciliates contain large intracellular bacteria which may be digested by the host.

F. Hyperiid Amphipods

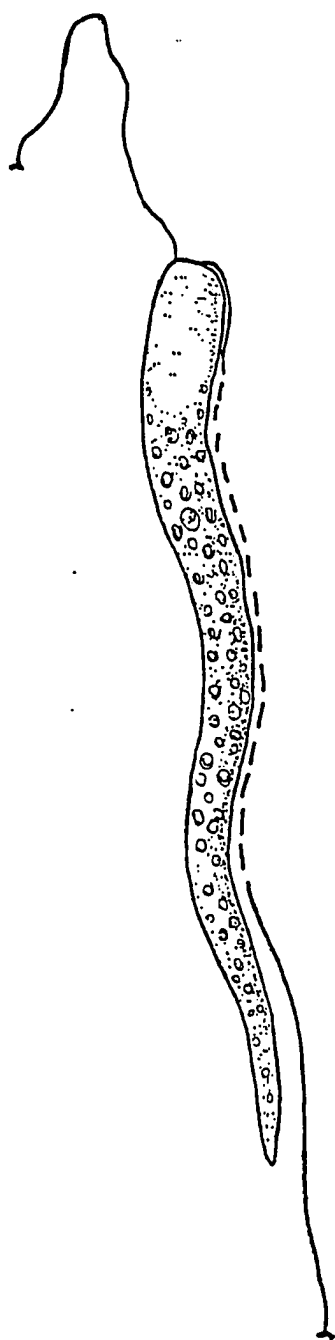
Hyperiid amphipods were the largest infesting organisms that I studied in the radiolarian microcosm. Their large size and translucent bodies permitted observation of internal structures by light microscope including peristaltic movements of the gut and the presence of eggs within large (gravid) females. Hyperiid amphipods seemed well adapted to their radiolarian hosts and their behavior within CR has been described by previous workers (Brandt, 1885; Swanberg, 1979). The mechanism that protects hyperiid amphipods against predation by the host has not been determined, however Laval (1980) suggested that the waxy cuticle covering the exoskeleton may be involved.

On several occasions, amphipods were observed feeding on the contents of radiolarian cells (Swanberg, pers. comm.; see also chapter 6) and in some cases, they even destroyed entire colonies. In general, however, amphipods disrupted radiolarian rhizopodia within the CR, but it was not clear what they were feeding on.

SUMMARY

Several different ectosymbionts including heterotrophic bacteria, various protozoans and microcrustaceans have been observed in or on colonial radiolaria (CR). Bacteria were found on the surfaces of all CR that were studied. Although many of the CR-associated bacteria had morphologies that were similar to free-living bacteria in the surrounding water, filamentous bacteria were found only on radiolarian colonies. The eukaryotic ectosymbionts were within the size range of normal radiolarian prey, however they appeared immune to the radiolarian rhizopodia. The protozoans associated with CR include a Cryptobia-like bodonid flagellate, a naked dinoflagellate, Gyrodinium sp. and a dysterid ciliate. Whereas the bodonid was invariably found embedded within the CR gelatin, Gyrodinium sp. and the dysterid ciliate were associated with the external radiolarian rhizopodia. Both Gyrodinium sp. and dysterid ciliates contain intracellular bacteria that are ultrastructurally similar to xenosomes (intracellular bacteria found in a number of different ciliates which have complex interactions with the host cell). In addition to intracellular bacteria, semi-digested chloroplasts and an abundance of storage material have been observed inside the ciliates, suggesting they are well-fed. Although there was not evidence of bacterivory in the TEMicrographs, it is possible that one or more of the protozoans feeds on the radiolarian-associated bacteria. The microcrustacea associated with CR include several genera of hyperiid amphipods. Both juvenile and adult amphipods were found embedded within the radiolarian colony; adults were occasionally also found on the outer surface of CR. Hyperiid amphipods may consume radiolarian central capsules, but this trophic behavior was only observed in a small proportion of the radiolarian colonies that contained amphipods.

Figure 12. Sketch of Cryptobia-like bodonid flagellate, drawn during observation by light microscope. The anterior flagellum is shorter than the posterior flagellum and is oriented forward, in the swimming direction. The posterior flagellum extends backward and is found within the flagellar pocket. The degree of attachment of the posterior flagellum to the body was not observed, therefore, it is represented by a dashed line. Scale = 5 μ m.



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Figure 13. Transmission electron micrograph (TEM) of Cryptobia-like bodonid flagellate. This is a cross section of the anterior region of the flagellate showing both anterior flagellum (Af) and posterior flagellum (Pf) which is located within the flagellar pocket (Fp). A food vacuole (Fv) with amorphous contents is located between the nucleus (N) and the kinetoplast (K). A Golgi body (G) is shown adjacent to the kinetoplast. Scale = 1 um.

Figure 14. Transmission electron micrograph of Cryptobia-like bodonid flagellate. The three flagella shown are : anterior flagellum (Af), posterior flagellum (Pf) and recurrent flagellum (Rf).



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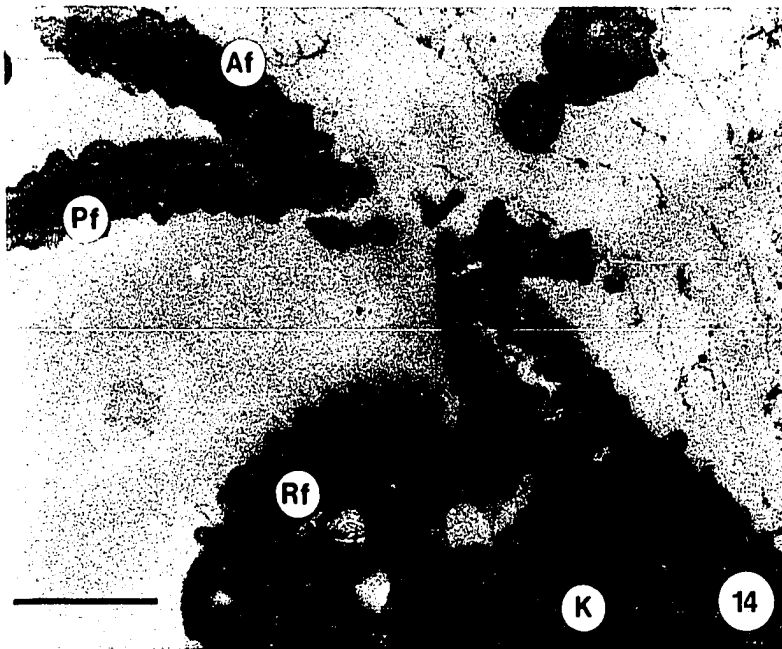


Figure 15. A portion of a colony of Rhaphidozoum sp., showing the dinoflagellate Gyrodinium sp. (arrows) associated with the peripheral rhizopodia. A radiolarian central capsule (cc) with its associated endosymbiotic algae (sy) is shown inside the colony. Scale = 100 um.

Figure 16. A scanning electron micrograph of Gyrodinium sp. showing the relatively large hypocone (H) and the smaller epicone (E). The transverse flagellum (Tf) is located shown within the girdle (Gd).

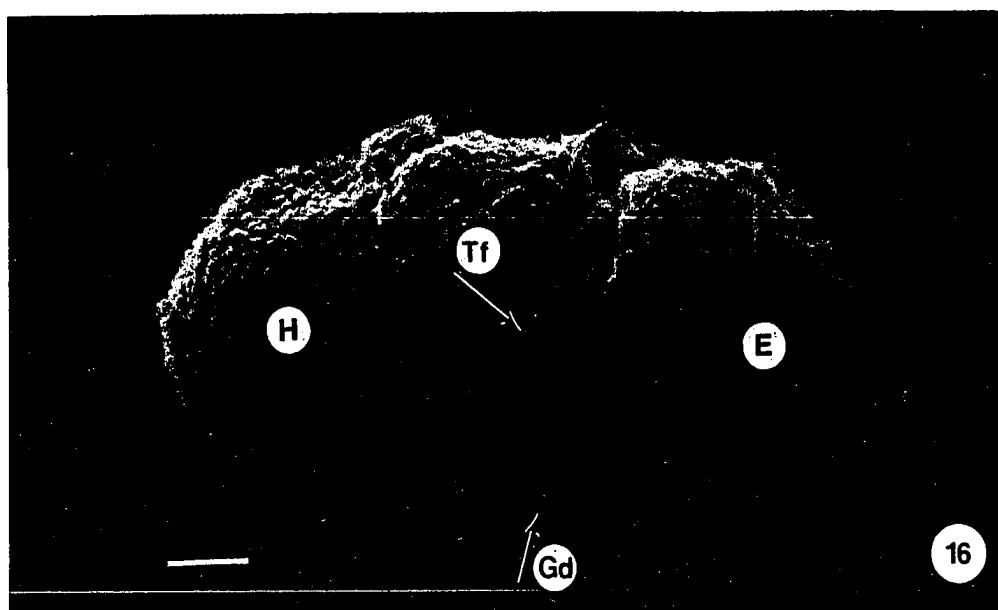


Figure 17. Transmission electron micrograph of Gyrodinium sp. The deep girdle (Gd) which separates between the epicone and the larger hypocone is shown here. Chloroplasts (C) with single stalked pyrenoids (P) are found mostly along the periphery of the cell. Numerous ejectosomes (Ej) are found throughout the cell; mature ejectosomes sometimes protrude from the cell surface (arrows). Scale = 1 μ m.

Figure 18. Transmission electron micrograph of Gyrodinium sp. showing the large nucleus (N), with lightly condensed chromatin, located in the hypocone. Scale = 1 μ m.

Figure 19. High magnification of the periphery of a Gyrodinium sp. cell, showing ejectosomes with fibrillar (fi) and amorphous (am) contents. A longitudinal section through the transverse flagellum (Tf) is shown near the cell surface. Scale = 1 μ m.

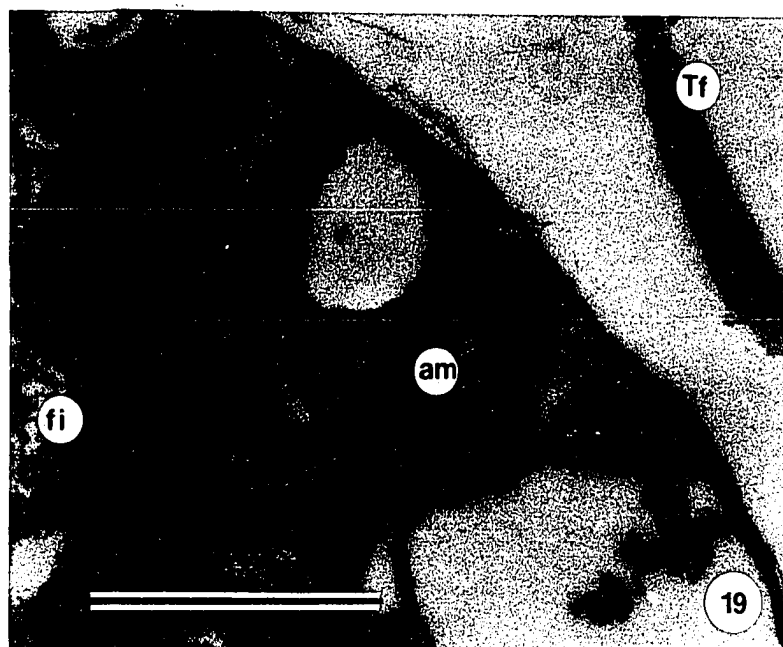
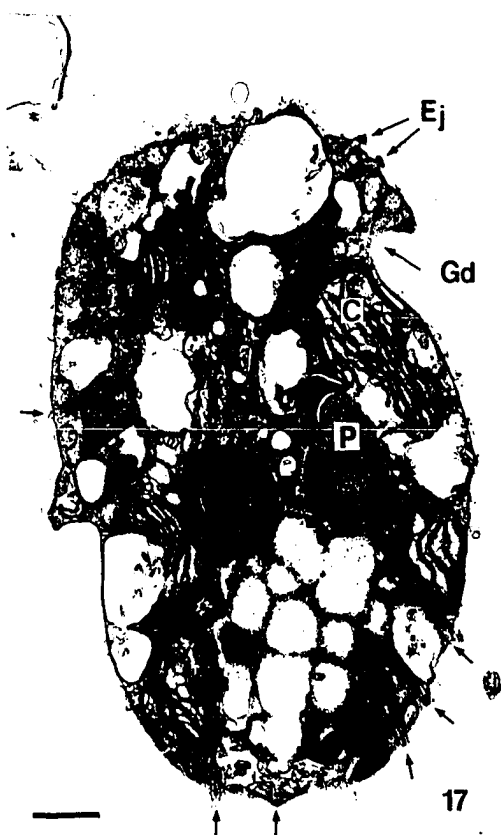


Figure 20. High magnification TEM of Gyrodinium sp. showing the electron-dense starch cap surrounding the pyrenoid (P). Two intracellular bacteria (B) and a portion of the nucleus (N) are also shown. Scale = 1 μ m.

Figure 21. A cross section of the transverse flagellum (Tf) within the girdle of a Gyrodinium sp. An invagination (arrow) on the lower portion of the girdle may be a sign of pinocytotic activity. Scale = 500 nm.

Figure 22. High magnification TEM of a ribosomal array (Ra) adjacent to a chloroplast (C) within Gyrodinium sp. An intracellular bacterium (B) is shown adjacent to the ribosomal array. Scale = 500 nm.

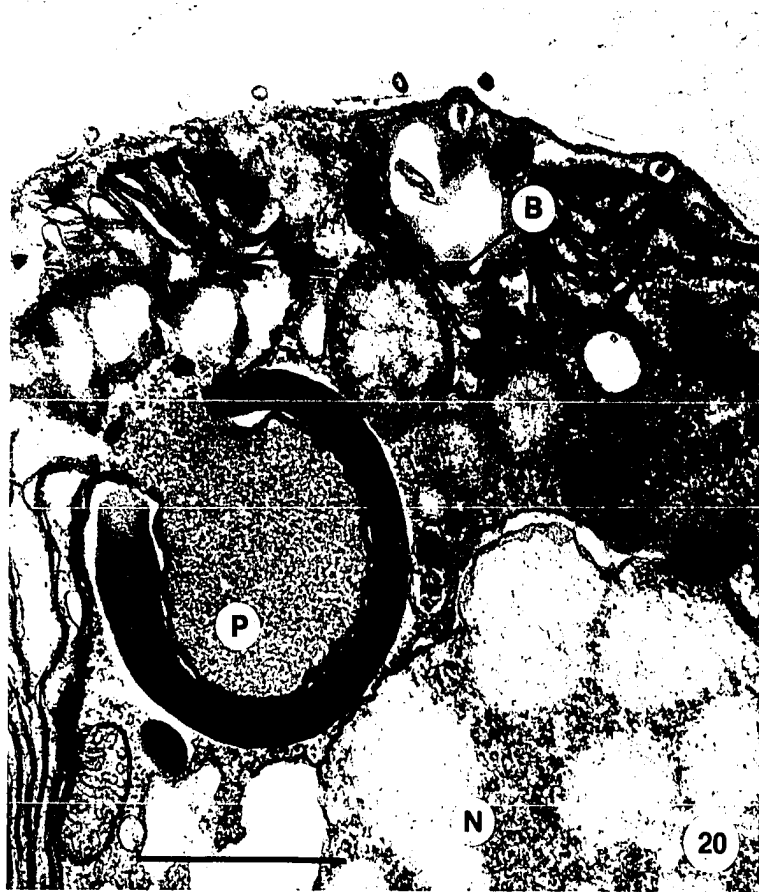


Figure 23. High magnification TEM of Gyrodinium sp. showing the insertion of the transverse flagellum (Tf) into the body. This is probably an area of osmotrophic activity, indicated by the clathrin-coated pinocytotic vesicles (arrows). Scale = 100 nm.

Figure 24. Transmission electron micrograph of Gyrodinium sp. chloroplast. The arrows indicate two areas where the 3-thylakoid bands are clearly visible. Scale = 100 nm.

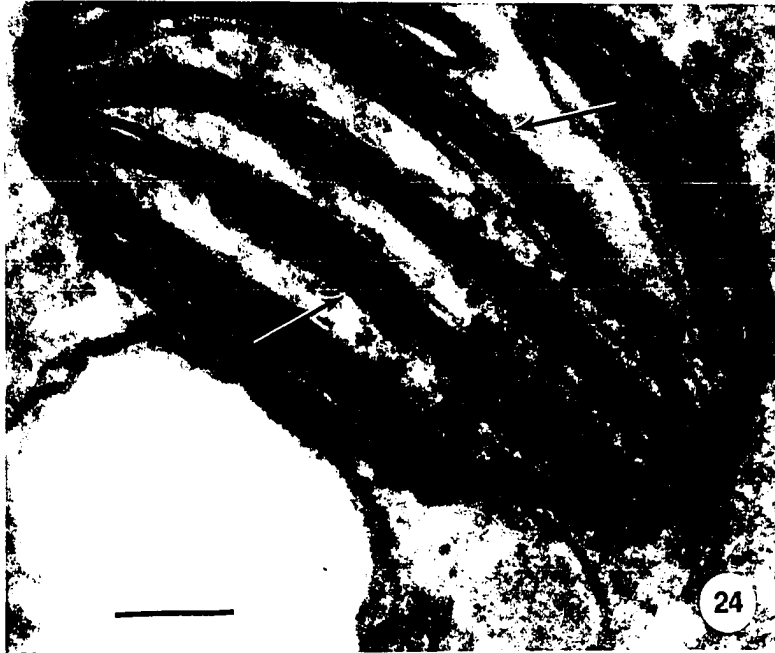
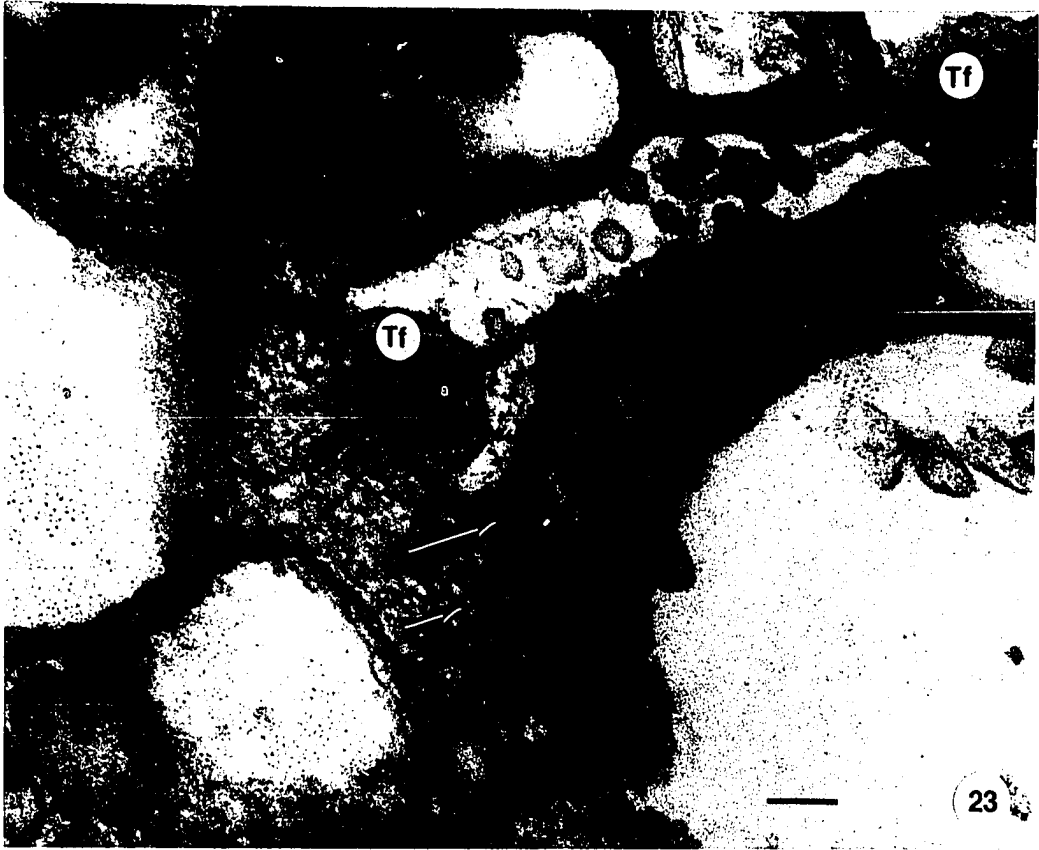


Figure 25. Light micrograph of dysterid ciliates on the external rhizopodia of a radiolarian colony. Scale = 100 μ m.

Figure 26. Light micrograph of Protargol-stained dysterid ciliates, next to a radiolarian central capsule (cc). Left ventral body kinetics (ki) extend posteriorly past the podite (Po), a specialized structure that enables dysterids to adhere to surfaces. Scale = 50 μ m.

Figure 27. Light micrograph of Protargol-stained dysterid ciliate showing the large macronucleus (n) and the podite (Po) surrounded by somatic cilia. Scale = 10 μ m.

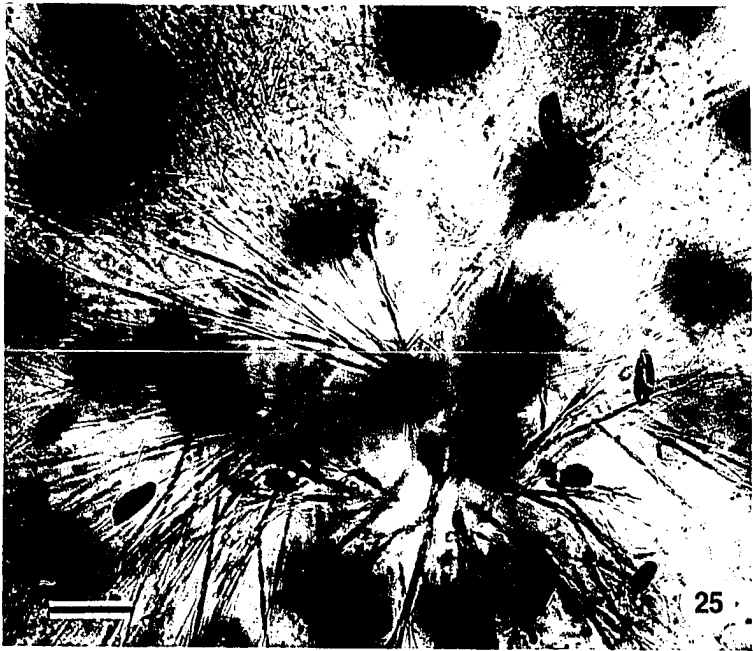
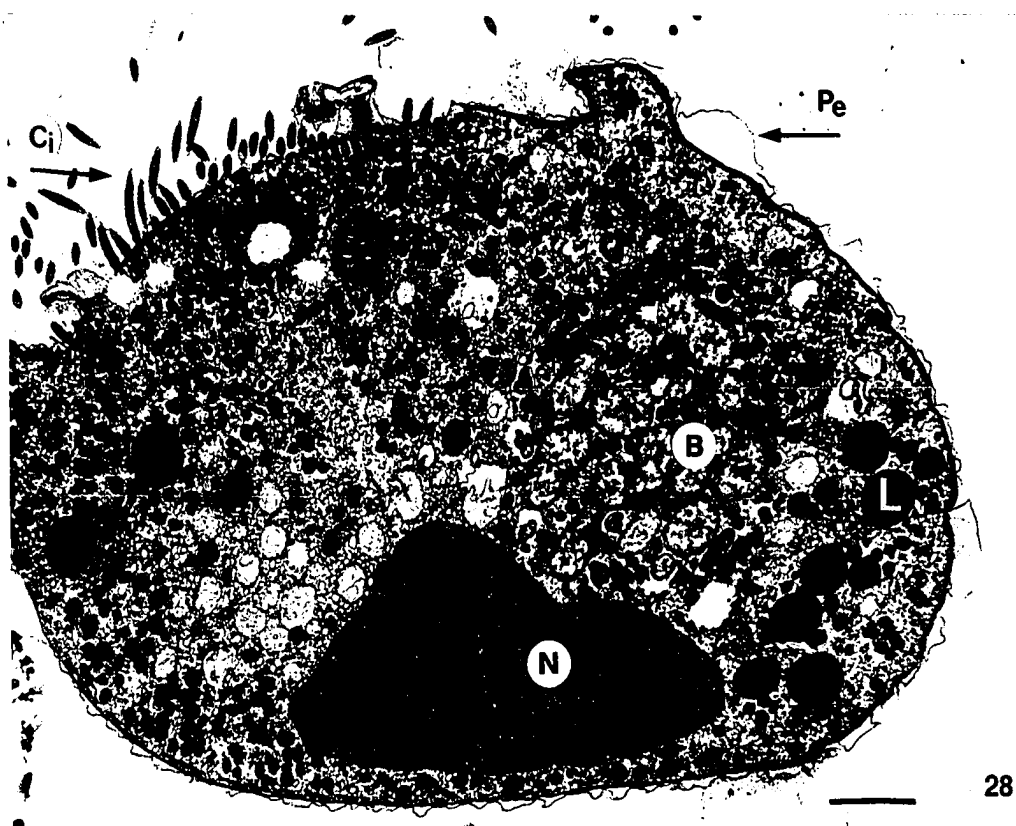
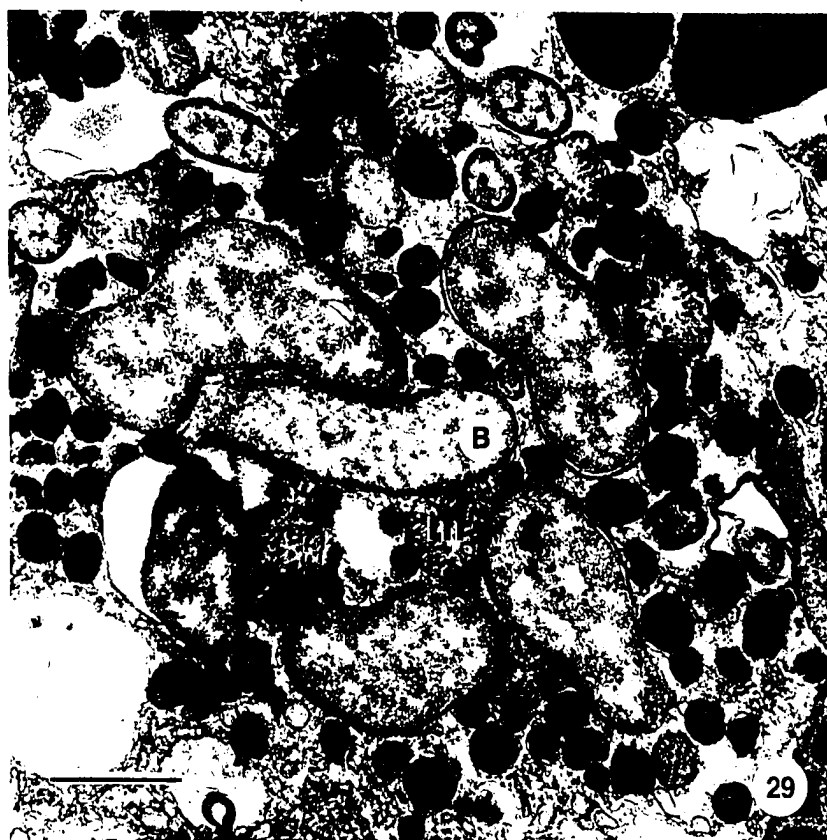


Figure 28. Transmission electron micrograph of dysterid ciliate showing somatic cilia (Ci) concentrated in the ventral region of the body. The ciliate is surrounded by a loose pellicle (Pe) with large alveolar spaces. A large macronucleus (N) is segregated into a region of condensed and a region of diffuse chromatin. Numerous electron-dense bodies (L) with the appearance of unsaturated lipids are scattered throughout the cell and a cluster of intracellular bacteria (B) are shown adjacent to the macronucleus. Scale = 2 μ m.

Figure 29. High magnification TEM of dysterid ciliate showing several intracellular bacteria (B) with intact double membranes. Numerous mitochondria (m) are interspersed among the bacteria. Scale = 1 μ m.



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Figure 30. Transmission electron micrograph of dysterid ciliate showing a golgi body (G) next to a contractile vacuole (cv). Several of the spherical, grey bodies surrounding the contractile vacuole may be microbodies. Scale = 1 um.

Figure 31. Transmission electron micrograph of dysterid ciliate showing semi-digested chloroplasts (C) within food vacuoles and a microbody (Mb). Scale = 1 um.

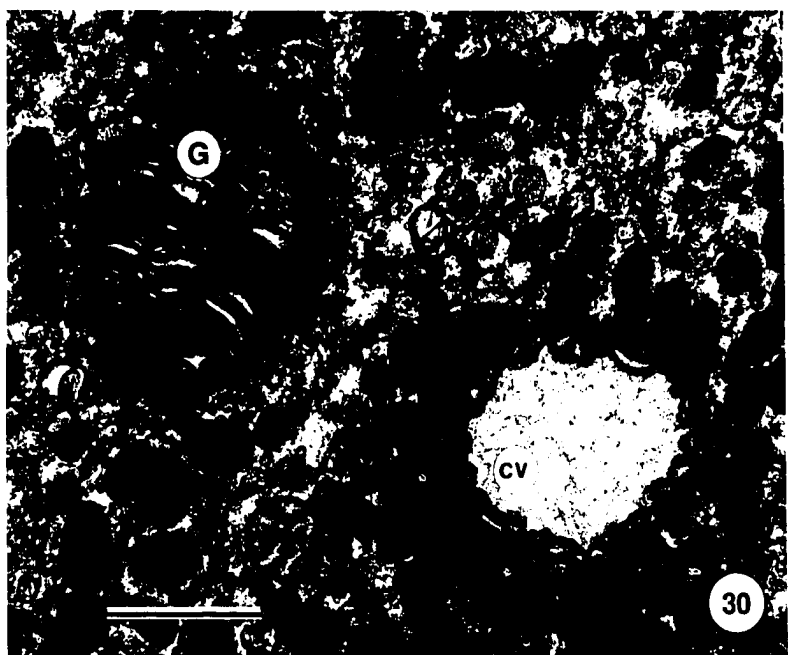
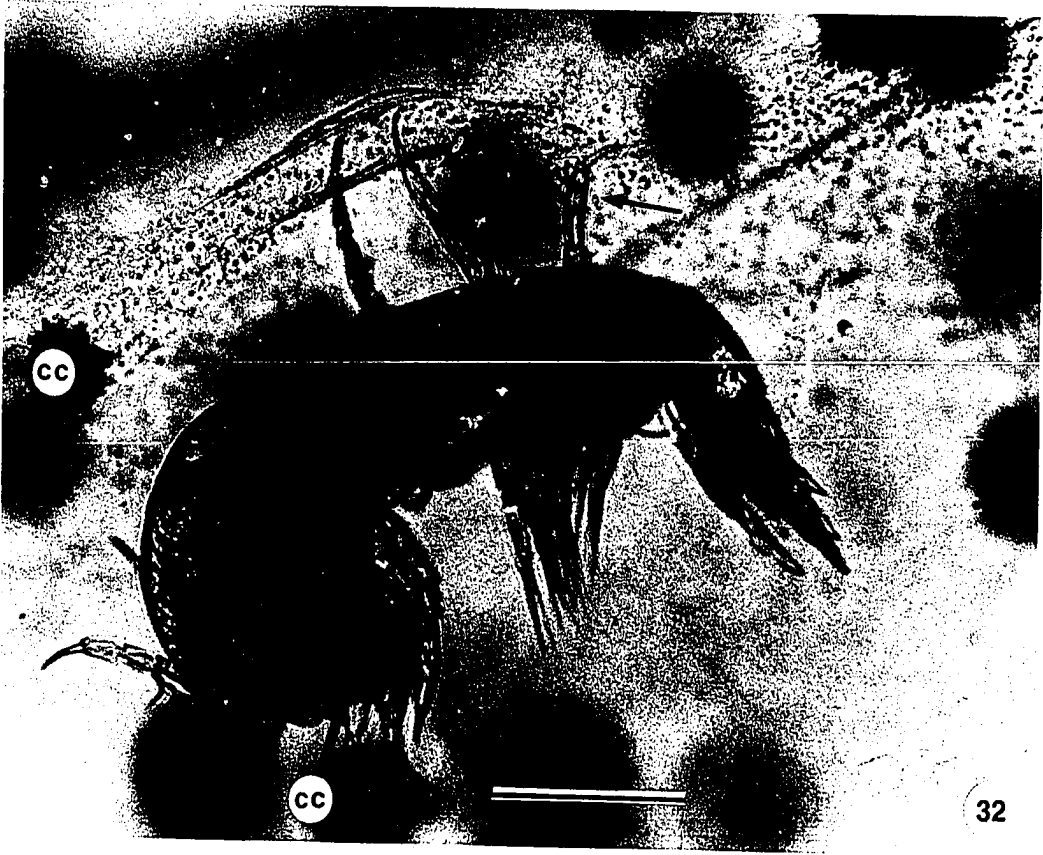


Figure 32. Light micrograph of hyperiid amphipod within an Acrosphaera spinosa colony. The amphipod holds itself in place by embedding pereopods (arrows; generally pereopods 4 through 7 are used for support and for movement) in the radiolarian gelatin. The amphipod is feeding on the cytoplasmic contents of a radiolarian central capsule (cc). Scale = 200 um.



Chapter 3

Infestation Rates and Abundances of Microorganisms Associated with Colonial Radiolaria

INTRODUCTION

The distribution of organisms and nutrients within the water column of both marine and fresh water environments is usually stratified and often horizontally patchy (Goldman, 1984; Parsons et al., 1979). Therefore, many organisms with limited motility among the plankton have established associations with both living and nonliving surfaces in the water column in order to ensure a reliable source of nutrition (Picken, 1937; Sleight, 1973). Examples of such associations include (1) the complex microbial communities found in marine snow (Caron et al., 1982; Caron et al., 1986; Silver et al., 1984), (2) bacterivorous amoebae associated with filaments of the colonial blue-green alga Oscillatoria (Trichodesmium) thiebautii (Anderson, 1977), (3) free living dinoflagellates associated with the spines of planktonic foraminifera (Spindler and Hemleben, 1980; Spero, unpublished) and (4) various protozoa and invertebrates associated with omnivorous colonial radiolaria (CR) (Swanberg, 1979; Angel, 1987). The association of certain protozoa and invertebrates with colonial radiolaria is especially interesting because most plankters that are smaller than the omnivorous sarcodines are consumed following contact with the sticky rhizopodia, yet these organisms have evolved the means to avoid predation.

In the following study, I describe the distributions and abundances of 4 commonly observed infestations among colonial radiolaria collected from the Atlantic Ocean. The infestations include hyperiid amphipods (previously described by Brandt, 1885; Harbison et al, 1977; Swanberg, 1979; Swanberg and Harbison, 1980), a naked dinoflagellate : Gyrodinium sp., an unidentified dysterid ciliate, and a Cryptobia-like bodonid flagellate. In order to clarify some of the terminology that is used in this and the following chapters, I have defined "abundances" of infesting organisms as the numbers of organisms observed per host colony, and "infestation rate" refers to

the proportion of infested radiolaria among the total number of CR examined.

MATERIALS and METHODS

A. Collection and Examination of CR

Colonial radiolaria were hand-collected by SCUBA divers (see chapter 1) during three cruises: R.V. Oceanus (OC) 176, 177, 191; and three field studies in the Caribbean : Barbados 1986, 1987, and Curacao 1988. CR were examined using a Nikon Diaphot inverted microscope equipped with an ocular Whipple grid. Specimens were examined within one to three hours of collection and the following data were recorded for each radiolarian : a) CR species, b) shape and dimensions of CR, c) number of central capsules (ccs) within CR, and d) types and abundances of protozoa and amphipods associated with the CR. Protozoan abundances on the surfaces of CR were determined by calculating the mean number of cells observed in three or more randomly selected Whipple grid fields. The mean abundance was then multiplied by a conversion factor (converting the area of the Whipple grid to total surface area of the CR) to estimate total abundance of protozoa on the CR. Amphipod infestations never exceeded 50 individuals per CR, therefore, amphipod abundances were determined by direct counts using low microscope magnifications. In order to minimize stress to the colonies, glass jars with CR specimens were maintained at a constant temperature (usually within one or two degrees centigrade of the ambient seawater temperature) during the period of time following collection and prior to examination.

The potential effect of jar containment on CR infestations, was examined by recording microbial associations found on randomly selected CR within one hour following collection. These colonies were returned to the collection jars and re-examined after several additional hours to determine whether containment affected the associated protozoan or amphipod populations. Both infested and uninfested colonies were included in these observations, yet there were no detectable changes in either type of colony.

Most of the radiolaria encountered during the 6 field excursions were recognized and accordingly assigned to a category that matched their morphological appearance. Colonies which were

not identifiable on the basis of gross morphology were assigned to the "unidentified colonies" category (see chapter 1).

B. Assignment of Abundance Scores to Infestations

Abundances of organisms associated with CR were recorded as ranges of abundances during the two field excursions, OC 176 and Barbados 1986. Thereafter, the abundances of infestors were determined numerically during the following 4 field excursions (OC 177, Barbados 1987, OC 191 and Curacao 1988). To accomodate the semi-quantitative data from OC 176 and Barbados 1986, a scoring scheme was used whereby all infested CR were assigned scores of 0 to 4 to represent ranges of abundances of CR infestations. Numerical abundances (actual counts) of infestations are summarized separately and presented in Tables 4 and 5. A key to the infestation scores is presented in Table 6. The scoring scales are the same for Gyrodinium sp. and Cryptobia-like bodonid infestations, because the abundances of these protozoa ranged from several to more than 10^4 cells per colony. The abundances of dysterid ciliates and hyperiid amphipods were often only one or several organisms per colony, therefore it was necessary to use different scoring scales to represent their abundances.

An infestation score was assigned to each colony and the following mean scores were calculated. A) Mean infestation score by type of infestation for all infested colonies collected at a specific geographical location (Table 7). B) Mean infestation score by colony type for the two field excursions, Barbados 1986 and OC 176 (Table 8).

Scores represent ranges of abundances, but I have presented mean scores as fractions instead of integers because most of the mean values fall between zero and one. Therefore, a mean score of zero may mean that the specified infestation was not observed at all or that the mean score was less than 0.001. I chose 0.001 as the cutoff point since values smaller than this indicated that these infestations were extremely rare.

C. Measurements of Seawater Temperature, Salinity and Chlorophyll a Concentration

In addition to examination of colonial radiolaria collected at each station, I recorded the surface water temperature, salinity and

chlorophyll a concentration during OC 191, Barbados 1987 and Curacao 1988. Seawater samples were collected in clean 1-liter glass jars during each dive and concentration of chlorophyll a was determined immediately thereafter by a fluorometric method capable of measuring pigment concentrations of <0.05 ug/ml (Parsons et al., 1984). Subsamples of the seawater collected from each station were stored in sealed 100-ml plastic bottles and salinities were determined at Lamont-Doherty Geological Observatory of Columbia University (LDGO) using an AGE Minisal salinometer.

RESULTS

A. Calculation of Mean CR Infestation Rates

CR infestation rates were summarized for the 6 field excursions (Tables 4 and 7) and for the 10 species of CR (Tables 5 and 8) by calculating mean infestation rates and standard errors of the means. Because it is not mathematically correct to calculate means from percent values, the means are presented only for the purpose of comparing infestation rates among spatially and temporally separated populations and among different taxonomic groups of CR.

B. Gyrodinium sp. Infestations

Among the four types of infestations found on CR, the predominant form of infestation was Gyrodinium sp. Dinoflagellate infestations occurred more consistently among Caribbean CR populations (mean infestation rates ranged from 5% to 68% of the colonies collected at any given station during the field excursions Barbados 1986, 1987 and Curacao 1988) than among CR populations that were sampled from the northwestern Atlantic Ocean, during cruises OC 177 and OC 191 (infestation rates ranged from 0 to 83% at any given station). However, not a single colony among the 496 CR that were collected from the northeastern Atlantic Ocean during OC 176 had a Gyrodinium sp. infestation.

C. Cryptobia-like Bodonid Flagellate Infestations

Cryptobia-like bodonid infestations were higher in oceanic locations than at Caribbean sites. The mean bodonid infestation rates were greater than 18% among oceanic CR, whereas mean infestation rates among Caribbean CR ranged from 2.4% to 7%.

D. Dysterid Ciliate and Hyperiid Amphipod Infestations

Dysterid ciliate and hyperiid amphipod infestations occurred among CR at much lower frequencies and in smaller numbers (abundances) than the Gyrodinium sp. and the bodonid flagellate infestations. For example, the abundances of Gyrodinium sp. and Cryptobia-like bodonids often exceeded 10,000 cells per colony, whereas ciliate and amphipod infestations usually included less than 10 individuals per CR. The highest infestation rates and mean abundances of both ciliates and amphipods were observed in Barbados, during two separate field excursions (see Tables 4 and 7). Amphipod infestation rates were generally higher among Caribbean CR than among oceanic CR populations. However, ciliate infestation rates were generally low and did not exhibit a clear spatial trend.

E. The Influence of CR Taxa on Infestation Rates and Abundances

Mean abundances and rates of infestation were summarized for 10 taxonomic groups of CR (Tables 5 and 8). The predominant form of infestation among CR taxa included in this study was Gyrodinium sp. Dinoflagellate infestation rates were especially high among Collozoum pelagicum (65.9%), Rhaphidozoum spp. (57.2%), and Collozoum caudatum (55.4%). Moreover, C. caudatum had the highest abundances of Gyrodinium sp. (mean abundance = 15,964 dinoflagellates/CR), and highest Cryptobia-like bodonid infestation rates (mean infestation rate = 40%) among CR taxa examined. The affinity of both Gyrodinium sp. and Cryptobia-like bodonids for C. caudatum is further exemplified by the large proportion of C. caudatum that have both types of infestations (28% of all C. caudatum colonies examined, Table 10) within the same colony. Cryptobia-like bodonid infestations occurred among all of the CR taxa except for Collozoum stellatum. The absence of bodonid infestations may have been related to the small number of C. stellatum examined (n = 19; Tables 5 and 8).

Dysterid ciliate infestations occurred at relatively low frequencies among all CR taxa, therefore, it is not surprising that none of the 19 Collozoum stellatum colonies collected had ciliates on their surfaces. With the exception of two colonies, dysterid ciliates did not occur among the Collozoum spp. collected during the field excursions Barbados 1986 and OC 176. The only CR species with a dysterid ciliate mean infestation rate larger than 10% was Collozoum pelagicum (mean infestation rate = 12%).

Hyperiid amphipod infestations occurred at relatively low rates (2.4 to 15.6%) and low abundances (mean abundance = 1 to 6 amphipods/CR) among all amphipod-infested CR taxa (Table 5). Although infestation rates sometimes included 50% or more of the colonies at a given dive station (see ranges of infestation rates), only Acrosphaera spp. and Collozoum pelagicum had mean infestation rates in excess of 10%.

F. Co-occurring Infestations

Infestations by more than one species of symbiont were summarized for the 6 field excursions and presented in Table 9. The frequencies of co-occurring infestations were generally low, between zero and 1%, however there were a number of exceptions to the rule. Gyrodinium sp. and Cryptobia-like bodonids co-occurred at mean infestation rates of 10.3% and 11.5% on CR from OC 177 and OC 191, respectively. Gyrodinium sp. co-occurred with hyperiid amphipods in Barbados 1986 and Gyrodinium sp. co-occurred with dysterid ciliates in Barbados 1987; both at mean infestation rates of 7.7%.

The co-occurring infestations are summarized by CR taxa in Table 10. Both absolute numbers of CR with the co-occurring infestations and percentages representing number of infested/total number CR are presented. The most common co-occurring infestation was Gyrodinium sp. and Cryptobia-like bodonids, and was observed among all CR taxa except for Collozoum stellatum and Siphonosphaera spp. Almost 28% of all Collozoum caudatum colonies examined had this combination of infestations. The other combination of infestations found among all CR taxa, excluding C. stellatum and Collozoum serpentinum, was the co-occurrence of Gyrodinium sp. and hyperiid amphipods. All other possible pairwise combinations of the four types of infestation were observed on CR, albeit at different infestation rates. Combinations of 3 types of infestors on the same CR were much less common and only 3 out of 4 possible combinations were observed. I did not observe CR with a combination of hyperiid amphipods, dysterid ciliates and Cryptobia-like bodonids, but it is possible that one of the infestors may have been overlooked. Furthermore, although more than 2500 colonies were examined, I never observed a colony which had all 4 types of infestation.

G. Environmental Conditions and CR Infestation Rates

The relationships between CR infestation rates and three environmental parameters (seawater temperature, salinity and concentration of chlorophyll a in seawater) were examined. Infestation rates, measured during Barbados 1987, OC 191 and Curacao 1988, were not linearly correlated with either seawater temperature or salinity. However, two different trends may be seen in the scatterplots of both Cryptobia-like bodonids and Gyrodinium sp. infestations versus chlorophyll a concentration (Figures 33a and 33b). Gyrodinium sp. infestation rates were highly variable over a narrow range of chlorophyll a concentrations during OC 191, but there was a positive linear relationship between the two variables ($R^2 = 0.32$; $p < 0.1$) at the Caribbean stations during Barbados 1987 and Curacao 1988. The results presented in Figure 33b reinforce the findings of Tables 4 and 7, wherein Cryptobia-like bodonid infestation rates were higher among oceanic CR (found in waters with low chlorophyll a concentrations) than among CR collected near island masses (areas with high chlorophyll a concentration). A Mann-Whitney U-test, a non-parametric test for mean differences, was highly significant ($U_s = 218$, $p < 0.01$; Sokal and Rohlf, 1969).

DISCUSSION

Taylor (1982) studied co-associations of marine organisms and used the location of associated organisms in or on the host to distinguish among different types of symbioses in marine microplankton. He noted that organisms which are in close proximity, but not directly adhered to the host, are parabionts as opposed to epibionts which are in constant contact with the host. Gyrodinium sp. and the dysterid ciliate may be considered parabionts since they are always found on the exterior of the colony. The Cryptobia-like flagellates and the amphipods were almost always found embedded within the radiolarian gelatin and are therefore considered epibionts.

The most common, and often the most abundant type of infestation observed on the surfaces of CR was that of Gyrodinium sp. Dinoflagellate infestations were observed among all groups of CR, yet there was a clear preference for dinoflagellates to dwell upon Collozoum caudatum, Collozoum pelagicum and Rhaphidozoum spp. Gyrodinium sp. infestations were observed in all 5 of the field excursions on the western side of the Atlantic Ocean; during the two

cruises, (OC 177 and OC 191) and during three separate field trips in the Caribbean (Barbados 1986, 1987, and Curacao 1988). However, none of the colonial radiolaria collected and examined during OC 176, in the northeastern waters of the Atlantic, had this infestation. The exclusive occurrence of Gyrodinium sp. infestations among CR on one side of the Atlantic Ocean suggests that although the genus Gyrodinium is widely distributed throughout the oceans (Wood, 1968), the species which infests colonial radiolaria does not occur in the oceanic waters near the northwest coast of Africa. The other three types of infestation, the Cryptobia-like bodonids, dysterid ciliates and hyperiid amphipods were observed among CR on both the western side of the Atlantic and among the CR collected during OC 176, thereby indicating that their distribution is not related to that of Gyrodinium sp.

Gyrodinium sp. infestations were observed in all of the CR populations (range of infestation rates = 5 to 68% CR infested with Gyrodinium sp. per dive) sampled during collections at Barbados 1986, 1987, and Curacao 1988. In comparison, the oceanic CR populations that were sampled during OC 177 and OC 191 did not always have Gyrodinium sp. infestations (range of infestation rates = 0 to 83% CR infested with Gyrodinium sp. per dive). This may indicate that Gyrodinium sp. are endemic to the productive waters of the Caribbean and are more unevenly distributed in oceanic waters. It is important to note that the mean number of colonial radiolaria collected at each dive station was substantially lower during the two oceanic cruises than in the Caribbean and the erratic dinoflagellate infestation rates among oceanic CR may have been the result of sampling error.

The concentration of chlorophyll a was more than ten fold higher in Caribbean waters (range = 1.3 to 5.5 ug/ml) than it was in the oceanic regions studied (range = 0.05 to 0.35 ug/ml). The relationship between Gyrodinium sp. infestations and chlorophyll a follows a linear relationship at chlorophyll a concentrations greater than 1.0 ug/ml (Caribbean stations); dinoflagellate infestation rates increase with the concentration of chlorophyll (Figure 33a). At concentrations of chlorophyll a lower than 0.35 ug/ml, this linear relationship does not exist. Since the concentration of chlorophyll a is related to the abundance of potential radiolarian prey in the surrounding water, it is possible that there is a functional difference in the relationship between Gyrodinium sp. and host CR in the oceanic versus the Caribbean waters.

An alternative possibility is that radiolaria collected in the waters around Curacao and Barbados may have been less healthy than oceanic CR as a result of the high concentrations of particulate matter found in these productive waters (Swanberg, 1983). High concentrations of particulate matter in the surrounding water would probably be hazardous to the CR because considerable energy must be invested to eliminate the foreign matter adhering to the radiolarian rhizopodia (e.g. large quantities of mucus secreted by corals to avoid "suffocation" by settling particulates, Qasim and Sankaranarayanan, 1970). Therefore, the higher frequencies of Gyrodinium sp. infestations observed near Caribbean islands may have been related to the physiological status of the host colonies.

The second most common protozoan associated with CR on both sides of the Atlantic Ocean was the Cryptobia-like bodonid flagellate. The bodonid flagellate infestation rates seem to be more strongly related to geographical locations than to chlorophyll a concentration (Figure 33b). It is possible that Cryptobia-like bodonid infestation rates were influenced by the abundance of particulate matter in the water. CR collection stations near Barbados and Curacao generally had higher abundances of amorphous organic aggregates than the oceanic stations (OC 176, OC 177, OC 191) and these particles may have served as alternative supports for Cryptobia-like flagellates, thereby reducing the proportion of infested CR.

One of the factors contributing toward the high proportion of Cryptobia-like bodonid infestations in oceanic areas is the apparent host affinity of this protozoan for Collozoum caudatum. Collozoum caudatum is an oceanic CR (Swanberg, 1979; Swanberg and Anderson, 1981; Angel, unpublished) that was seldom encountered near Barbados or Curacao. Although C. caudatum was not observed among the colonies collected during OC 176, numerous specimens of Thalassophysa sp. (possibly Thalassophysa sanguinolenta), a collodarian radiolarian which Swanberg and Anderson (1981) considered an "early ontogenetic stage" of C. caudatum, were observed in these waters. Cryptobia-like flagellate infestations were found in 12 of the 26 Thalassophysa sp. specimens examined, suggesting that the solitary form is equally susceptible to infestation by this protozoan.

Dysterid ciliate infestation rates and abundances were generally low in comparison to Gyrodinium sp. and Cryptobia-like bodonid flagellate infestations. There were also major differences

between mean ciliate infestation rates in CR populations collected in the same area from one year to the next. For example, the mean dysterid ciliate infestation rate was 2.9% for Barbados 1986 and 16.2% for Barbados 1987 (CR were collected from March-April in both years). The spatial and temporal variability of ciliate infestations may be the result of a patchy and/or seasonal distribution. Furthermore, dysterid ciliate infestations may be related to the abundance and sources of particulate matter in the surrounding water. Small (pers. comm.) observed diverse assemblages of ciliates, including several dysterids associated with amorphous organic aggregates (marine snow) collected from the northeastern Atlantic Ocean. It is possible, therefore, that ciliates swimming among planktonic particulates may reach colonial radiolaria. Ciliate infestations were observed among all taxa of CR excluding Collozoum stellatum. The absence of both dysterid ciliate and Cryptobia-like flagellate infestations among C. stellatum may have been the result of the small sample size; only 19 C. stellatum were examined whereas sample sizes of the other 9 CR taxa ranged from 47 to 316 colonies per taxon.

Hyperiid amphipod infestation rates were generally higher in the Caribbean stations than among the CR collected in oceanic waters. There was no relationship, however, between chlorophyll a concentration and amphipod infestation rates. There was also temporal variability in infestation rates. Whereas the mean amphipod infestation rate was 17.3% in Barbados 1986, the mean rate dropped to 4.7% for the following year at the same site. It is difficult to interpret these patterns of infestation because very little is known about the biology of the hyperiid amphipods and the host selection process. Mean amphipod infestation rates range from 2.4% to 15.6% among the 10 CR taxa examined. The data suggest that amphipods do not strongly favor any one species of CR over another; i.e., host selection may be opportunistic. Swanberg (1979) identified the amphipods associated with specific CR taxa and found that certain hyperiids are preferentially found on specific CR taxa, thereby suggesting there is a certain degree of host selection.

Although CR infestations usually involved only one type of infesting organism, there were many infested colonies that had two co-occurring infestations and a few colonies were host to three infestations. Several amphipod infested CR had dysterid ciliate infestations wherein the ciliates aggregated on the surface of the colony, adjacent to the amphipods. This may suggest a cause and

effect relationship whereby ciliates may have been attracted to the CR as a result of amphipod activities. The feeding activity of hyperiid amphipods within CR also appeared to attract Gyrodinium sp. though most of the colonies with this combination of infestations were not identified. The co-occurring infestation involving Gyrodinium sp. and Cryptobia-like bodonids was very common, and was observed among almost all species of radiolaria (28% of all Collozoum caudatum colonies had this combination of infestations) during 4 of the 6 field excursions. The relationship between these protozoa is not clear since the two groups are exposed to different microenvironments within the CR microcosm. Cryptobia-like flagellates are embedded within the radiolarian gelatin whereas Gyrodinium sp. swims among the external rhizopodia.

Other Organisms Associated with CR

Whereas I have observed large numbers, and at times high infestation rates, of the Cryptobia-like bodonid flagellates among populations of colonial radiolaria collected in the Atlantic Ocean, Hollande and Enjume (1953) reported finding a different bodonid, Bodo insidiosus embedded within the gelatin of various species of Collozoum collected in the Bay of Algiers. On a few occasions, I also found flagellates within CR which appeared very similar to B. insidiosus, however most of the bodonid infestations I observed included only Cryptobia-like flagellates.

Although Gyrodinium sp. infestations did not occur among CR collected during OC 176, many of the Thalassophysa specimens that were examined had aggregations of an armored dinoflagellate (sutures between thecate plates were clearly visible) which was invariably found swimming among the "tails" of these collodarian radiolaria. The tails of Thalassophysa often contained undigested remains of radiolarian prey e.g. shells of mollusc larvae and tintinnid loricae and I assumed that the dinoflagellates were scavenging nutrients or particles associated with the radiolarian "wastes".

On several occasions, I recorded extremely high abundances of Nitzschia spp. on CR (estimates of more than 10,000 diatoms on some colonies) collected both in the Caribbean Sea and during cruises in the Atlantic Ocean. The diatoms (see Figure 34) appeared to glide along the outer surface of the CR, generally in a direction that was orthogonal to the rhizopodia. Although some of the algae may have

been captured and digested by the radiolarian (Swanberg, 1979), the majority seemed to move freely along the outer surfaces of the colony. Dense infestations of Nitzschia-type diatoms have also been observed on the outer surfaces of planktonic spinose foraminifera (Bijma, pers. comm.) collected in both Barbados and Curacao. Diatom blooms are not uncommon in the Caribbean waters near islands (Bennett, pers. comm.) and the phytoplankters probably adhere to the sticky surfaces of planktonic sarcodines floating through patches of the blooming algae.

Additional organisms which were observed on the surfaces of CR included turbellarians and Sapphirina sp. (harpacticoid copepods). These associations and the infestation of CR by the harpacticoid copepod Miracia efferata were previously described by Swanberg (1979). Because they were observed very infrequently in my samples, I did not describe their abundances or infestation rates.

SUMMARY

Four types of infestations, three protozoan and one microcrustacean, have been observed with varying degrees of regularity among colonial radiolaria collected in tropical and subtropical waters of the Atlantic Ocean. The nonthecate dinoflagellate, Gyrodinium sp., was found on CR representing all of the taxa that were identified (and also among the unidentified radiolaria), in all of the areas studied on the western side of the Atlantic Ocean. Gyrodinium sp. had especially high infestation rates and abundances among Collozoum pelagicum, Collozoum caudatum and Rhaphidozoum spp. Although this protist was commonly found among CR on the western side of the Atlantic, Gyrodinium sp. did not occur at all among CR collected from eastern Atlantic Ocean waters near the northwestern coast of Africa. The Cryptobia-like bodonid flagellates which occurred within the gelatinous mass of colonial radiolaria, were found among almost all radiolarian taxa in all of the areas that were studied. Infestation rates were highest among oceanic populations of CR, and preferentially among C. caudatum, Collozoum serpentinum, and Rhaphidozoum spp. The Gyrodinium sp. and the Cryptobia-like flagellate infestations were often mutually inclusive, e.g. 28% of all C. caudatum examined had infestations that included both protozoan types.

In comparison to the flagellated protozoan infestations, dysterid ciliates and hyperiid amphipod infestations were considerably less common among radiolarian colonies, but they occurred on and in CR in all of the areas that were studied. Table 11 summarizes the CR infestation rates, comparing infestations in oceanic waters versus the waters around Caribbean island masses. Whereas dinoflagellate and bodonid flagellate infestation rates remained fairly similar in CR populations studied near Barbados in two consecutive years, ciliate and amphipod infestation rates were very different from one year to the next. The reasons for the different infestation patterns are not clear. Additional infestations of unicellular organisms observed among colonial radiolaria include armored dinoflagellates associated with the "tails" of Thalassophysa sp., and Nitzschia sp. on the external rhizopodia of several different CR taxa. The nature of the various CR associations has not been fully determined, however the results described in the following chapters suggest that infested radiolarian colonies are sites of considerable microbial production.

Table 4. Infestation rates and mean abundances of organisms in or on infested colonial radiolaria (number of organisms/CR) collected during 4 field excursions. Infestation rate = (# CR Infested)/(total # CR collected). Mean abundances represent numbers of infesting organisms among infested CR and not the total CR population.

Infestation	OC 177			OC 191			Barbados 1987			Curacao 1988		
	Mean Abundance (#/CR)	Infestation Rate (%)	Mean Abundance (#/CR)	Infestation Rate (%)	Mean Abundance (#/CR)	Infestation Rate (%)	Mean Abundance (#/CR)	Infestation Rate (%)	Mean Abundance (#/CR)	Infestation Rate (%)	Mean Abundance (#/CR)	Infestation Rate (%)
<i>Gyrodinium</i> sp.	Mean	9087.0	37.2	4576.5	31.3	2144.7	44.5	2908.7	15.4			
	St. Err.	1511.9	3.5	1081.4	4.2	369.5	3.1	992.2	3.7			
	n	100		47		85		20				
<i>Cryptobia</i> - like flagellate	Mean	5373.9	19.7	6002.5	25.2	1428.2	7.1	265.5	2.4			
	St. Err.	1573.1	2.9	3047.7	3.1	703.7	2.0	137.3	1.0			
	n	53		44		25		5				
dysterid ciliate	Mean	74.5	2.4	11.0	0.3	26.1	16.2	4.0	0.4			
	St. Err.	39.9	0.7	1.0	0.3	7.3	2.5	/	0.3			
	n	11		2		38		1				
hyperiid amphipod	Mean	5.3	3.6	1.6	2.8	2.6	4.7	3.1	11.8			
	St. Err.	1.4	1.2	0.4	1.2	0.4	1.4	0.9	4.2			
	n	16		7		16		12				
Mean Number of CR Collected per Station (st. err.)	12.7 (1.0)			14.6 (1.3)		37.5 (3.9)		34.7 (3.8)				
# of stations	42			19		17		7				

Table 5. Summary of infestation rates and mean abundances of infesting organisms (number of organisms/CR) among 10 CR taxa collected during the following field excursions : OC 177, OC 191, Barbados 1987, Curacao 1988, Infestation rate = (# CR infested)/(total # CR collected). Mean abundances represent only the infested CR, not the total CR population.

Infesting Organism	<i>Acrosphaera</i> spp.			<i>Collosphaera</i> spp.			<i>Siphonosphaera</i> spp.			<i>Sphaerozoum</i> spp.			<i>Rhaphidozoum</i> spp.		
	Mean Abundance	Infestation Rate (%)		Mean Abundance	Infestation Rate (%)		Mean Abundance	Infestation Rate (%)		Mean Abundance	Infestation Rate (%)		Mean Abundance	Infestation Rate (%)	
<i>Gyrodinium</i> sp.	mean	621.9	26.2	1840.7	20.1		3096.8	17.6		3197.6	28.0		3818.7	57.2	
	st. err.	424.1	3.1	764.3	3.6		1733.5	4.5		998.0	3.9		1618.4	5.2	
	n	20		23			7			32			23		
<i>Cryptobia</i> - like flagellate	mean	10688.1	8.7	1303.8	10.9		198.0	4.9		1798.8	11.9		9264.5	18.2	
	st. err.	9916.9	2.0	1011.6	2.9		/	1.9		633.3	3.3		8680.0	3.7	
	n	13		9			1			15			6		
dysterid ciliate	mean	4.0	3.0	18.2	6.3		6.3	1.8		37.6	6.1		15.0	3.6	
	st. err.	1.1	1.0	7.4	2.1		1.5	0.9		23.9	2.0		5.0	1.9	
	n	4		9			3			8			2		
hyperid amphipod	mean	1.0	15.6	2.0	6.6		2.0	5.6		3.9	8.6		1.2	2.4	
	st. err.	0.1	3.5	0.8	2.3		/	2.4		0.9	2.5		0.2	1.1	
	n	9		4			1			10			3		

Table 5. (cont.)

<i>Collozoum inerne</i>	<i>Collozoum caudatum</i>			<i>Collozoum serpentinum</i>			<i>Collozoum pelagicum</i>			<i>Collozoum stellatum</i>			Unidentified Colonies		
	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance	Infestation Rate (%)	Mean Abundance
6103.6	32.5	55.4	633.0	11.9	9585.7	65.9	700.8	40.6	3526.5	45.4					
1360.2	4.8	5.4	410.3	5.8	3318.5	6.7	391.4	12.3	420.8	3.1					
29			3		16		5		60						
2063.2	10.8	39.9	1417.0	21.9	396.0	11.1	/	0.0	1883.4	16.6					
651.1	3.2	5.4	463.2	6.8	322.0	3.4	/	0.0	552.1	2.6					
11			6		2		0		37						
27.7	2.6	0.3	10.0	3.7	14.3	12.0	/	0.0	64.6	4.8					
23.8	1.7	0.2	/	3.6	5.4	4.3	/	0.0	25.8	1.1					
3			1		3		0		18						
6.7	5.1	3.5	/	4.9	3.0	12.5	3.0	6.7	4.7	9.9					
2.4	2.4	2.1	/	3.7	/	3.6	/	6.5	1.3	2.0					
3			0		1		1		16						

Table 6. Key to infestation scores representing abundances of organisms on CR. Infestation scores were assigned to the semi-quantitative abundance data recorded during the field excursions Barbados 1986 and OC 176. Abundance scores are not equally scaled among different infesting organisms because the abundances of Gyrodinium sp. and Cryptobia sp. were usually one or several orders of magnitude greater than the abundances of dysterid ciliates and hyperiid amphipods.

Infestation (Total Number of Organisms/CR)				
Score	<i>Gyrodinium</i> sp.	<i>Cryptobia</i> - like flagellate	Dysterid ciliate	Hyperiid amphipod
0	0	0	0	0
1	1 - 10	1 - 10	1 - 10	1 - 5
2	11 - 100	11 - 100	11 - 50	6 - 10
3	101 - 1000	101 - 1000	51 - 100	11 - 20
4	> 1000	> 1000	> 100	> 21

Table 7. Summary of infestation rates and abundances (scores) of infesting organisms in or on CR collected during two field excursions : Barbados 1986 and OC 176. Infestation rate = (# CR infested)/(total # CR collected). Abundance scores for organisms follow Table 3. The symbol (/) represents absence of infestation.

		Barbados 1986		OC 176	
		Score	Infestation Rate (%)	Score	Infestation Rate (%)
Infestation					
Gyrodinium sp.	mean	3.4	32.6	/	/
	st. err.	0.1	2.9	/	/
	n	61		/	
Cryptobia - like flagellate	mean	2.7	6.4	3.6	18.5
	st. err.	0.2	1.8	0.1	2.4
	n	23		48	
Dysterid ciliate	mean	1.7	2.9	1.3	5.4
	st. err.	0.4	0.7	0.1	1.6
	n	9		15	
Hyperiid amphipod	mean	1.1	17.3	1.1	9.7
	st. err.	0.1	3.4	0.1	2.8
	n	33		26	
Mean Number of CR Collected per Station (st. err.)		28.8 (2.8)		24.8 (2.9)	
# of stations		17		20	

Table 8. Summary of mean infestation rates and abundances (scores) of infesting organisms in or on 10 CR taxa collected during two field excursions : Barbados 1986 (B'dos 86) and OC 176. Infestation rate = (# CR infested)/(total # CR collected). Abundance scores for organisms follow Table 3. The symbol (/) represents absence of infestation and/or uncalculated standard error.

Infesting Organism	Acroephaera			Acroephaera			Colloephaera			Colloephaera			Siphonophæra			Siphonophæra		
	app.	B'dos 86	Infestation Rate (%)	app.	OC 178	Infestation Rate (%)	app.	B'dos 86	Infestation Rate (%)	app.	OC 176	Infestation Rate (%)	app.	B'dos 86	Infestation Rate (%)	app.	OC 178	Infestation Rate (%)
<i>Gyrodinium</i> sp.	Mean st. err. n	2.7 0.2 6	22.2 3.5 6	/	/	/	3.2 0.4 3	61.1 20.0 3	/	/	/	/	3.2 0.5 4	54.2 15.8 4	/	/	/	/
<i>Cryptobia</i> - like flagellate	Mean st. err. n	2.3 0.4 4	25.0 4.8 4	3.0 0.0 2	32.0 18.0 2	0.0 0.3 4	2.5 0.3 4	70.8 17.2 4	4.0 0.0 7	42.0 15.0 7	33.3 /	4.0 0.0 4	2.0 /	33.3 /	47.0 7.0 4			
<i>Dysterid</i> ciliate	Mean st. err. n	1.0 /	14.3 /	1.0 0.0 2	28.0 6.0 2	1.0 /	1.0 /	50.0 /	2.0 1.0 2	56.0 44.0 2	/	1.0 /	/	/	17.0 /			
<i>Hyperlid</i> amphipod	Mean st. err. n	1.0 0.0 6	26.1 5.4 6	1.0 /	100.0 /	1.0 0.0 4	1.0 0.0 4	66.7 11.8 4	1.0 0.0 2	67.0 33.0 2	58.3 18.0 4	1.0 0.0 4	1.0 /	33.0 /				
Infesting Organism	Sphaerozooum			Sphaerozooum			Rhaphidozooum			Rhaphidozooum			Collozooum			Collozooum		
	app.	B'dos 86	Infestation Rate (%)	app.	OC 178	Infestation Rate (%)	app.	B'dos 86	Infestation Rate (%)	app.	OC 176	Infestation Rate (%)	app.	B'dos 86	Infestation Rate (%)	app.	OC 178	Infestation Rate (%)
<i>Gyrodinium</i> sp.	Mean st. err. n	3.1 0.3 10	40.9 7.2 10	/	/	/	3.9 0.1 8	70.8 11.3 8	/	/	/	/	3.8 0.3 2	50.0 0.0 2	/	/	/	/
<i>Cryptobia</i> - like flagellate	Mean st. err. n	2.8 0.9 3	17.9 3.6 3	4.0 0.0 3	51.0 25.0 3	3.0 1.0 2	41.7 8.4 2	4.0 0.0 14	4.0 0.0 14	42.0 6.0 14	25.0 /	1.0 1	4.0 /	25.0 /	31.0 /			
<i>Dysterid</i> ciliate	Mean st. err. n	1.0 /	50.0 /	1.0 0.0 4	52.0 17.0 4	/	/	/	1.0 1.0 2	42.0 8.0 2	/	/	/	/	/	/	/	/
<i>Hyperlid</i> amphipod	Mean st. err. n	1.5 0.3 3	38.9 5.6 3	1.0 0.0 5	49.0 15.0 5	/	/	/	1.0 0.0 3	30.0 12.0 3	83.3 18.7 3	0.8 0.2 3	0.8 0.2 3	83.3 18.7 3	/	/	/	/

Table 8. (continued)

Infesting Organism	Collozoum caudatum B'dos 86			Collozoum caudatum OC 176			Collozoum serpentinum B'dos 86			Collozoum pelagiolum B'dos 86			Collozoum OC 176			Collozoum OC 176		
	Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)	
<i>Gyrodinium</i> sp.	Mean	3.8	97.5	/	/	/	/	/	/	3.5	100.0	/	/	/	/	/	/	/
	st. err. n	0.1 8	2.5 8	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
<i>Cryptobia</i> - like flagellate	Mean	4.0	100.0	/	/	/	3.0	50.0	4.0	/	/	4.0	42.0	/	/	4.0	26.0	/
	st. err. n	/	/	/	/	/	/	/	0.0 2	/	/	0.0 2	8.0 2	/	/	0.0 7	5.0 7	/
<i>Dysterid</i> oillate	Mean	/	/	/	/	/	/	/	/	/	/	/	/	/	/	1.0	44.0	/
	st. err. n	/	/	/	/	/	/	/	/	/	/	/	/	/	/	0.0 2	8.0 2	/
<i>Hyperiid</i> amphipod	Mean	1.0	50.0	/	/	/	/	/	1.0	/	/	/	67.0	/	/	1.0	42.0	/
	st. err. n	/	/	/	/	/	/	/	0.0 2	/	/	0.0 2	33.0 2	/	/	0.0 8	10.0 8	/
Infesting Organism	Collozoum stellatum B'dos 86			Collozoum stellatum OC 176			Unidentified Colonies B'dos 86			Unidentified Colonies OC 176			Unidentified Colonies OC 176			Unidentified Colonies OC 176		
	Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)		Score	Infestation Rate (%)	
<i>Gyrodinium</i> sp.	Mean	3.8	100.0	/	/	/	3.3	50.4	/	/	/	/	/	/	/	/	/	/
	st. err. n	0.3 2	0.0 2	/	/	/	0.2 17	6.6 17	/	/	/	/	/	/	/	/	/	/
<i>Cryptobia</i> - like flagellate	Mean	/	/	/	/	/	2.7	17.0	3.0	/	/	3.0	57.0	/	/	3.0	20.0	/
	st. err. n	/	/	/	/	/	0.6 6	4.1 6	0.0 8	/	/	0.0 8	13.0 8	/	/	0.0 2	5.0 2	/
<i>Dysterid</i> oillate	Mean	/	/	/	/	/	2.1	10.0	1.0	/	/	1.0	20.0	/	/	1.0	67.0	/
	st. err. n	/	/	/	/	/	0.5 6	2.5 6	0.0 2	/	/	0.0 2	5.0 2	/	/	0.0 4	20.0 4	/
<i>Hyperiid</i> amphipod	Mean	/	/	/	/	/	1.3	7.3	1.0	/	/	1.0	67.0	/	/	1.0	20.0	/
	st. err. n	/	/	/	/	/	0.2 12	29.9 12	0.0 4	/	/	0.0 4	20.0 4	/	/	0.0 8	10.0 8	/

Table 9. Summary of co-occurring infestation rates (i.e. two or more infesting organisms within the same colony) among all CR, collected during six field excursions : Barbados 1986, 1987, Curacao 1988, OC 176, OC 177, OC 191. Co-occurring infestation rate = (# CR with co-occurring infestation)/(total # CR collected). All infestation rates are expressed as %.

Co-Occurring Infestations		Barbados 1986	Barbados 1987	Curacao 1988	OC 176	OC 177	OC 191
G+C	mean	0.5	2.3	0.0	0.0	10.3	11.5
	st. err.	0.3	1.1	0.0	0.0	2.2	2.8
G+H	mean	6.7	0.7	1.9	0.0	1.1	0.5
	st. err.	2.0	0.3	1.0	0.0	0.4	0.5
H+D	mean	0.4	0.3	0.0	0.0	0.0	0.0
	st. err.	0.4	0.2	0.0	0.0	0.0	0.0
G+D	mean	0.7	7.7	0.0	0.0	0.0	0.3
	st. err.	0.3	1.8	0.0	0.0	0.0	0.3
D+C	mean	0.2	7.7	0.0	0.1	0.1	0.0
	st. err.	0.2	1.8	0.0	0.1	0.1	0.0
G+H+D	mean	0.2	0.8	0.0	0.0	0.0	0.0
	st. err.	0.2	0.5	0.0	0.0	0.0	0.0
H+C	mean	0.0	0.0	0.4	1.0	0.2	1.0
	st. err.	0.0	0.0	0.4	0.6	0.2	0.5
G+H+C	mean	0.2	0.0	0.0	0.0	0.5	0.0
	st. err.	0.2	0.0	0.0	0.0	0.3	0.0
G+D+C	mean	0.0	0.0	0.0	0.0	0.1	0.3
	st. err.	0.0	0.0	0.0	0.0	0.1	0.3
# of stations		17	17	7	20	42	19

Key to Symbols : G=Gyrodinium sp.
C=Cryptobia-like bodonid flagellate
H=hyperiid amphipod
D=dysterid ciliate

Table 10. Summary of co-occurring infestations (i.e. two or more infesting organisms within the same colony) among 10 CR taxa, collected during six field excursions : Barbados 1986, 1987, Curacao 1988, OC 176, OC 177, OC 191. Co-occurring infestation rate = (# CR with co-occurring infestation)/(total # CR collected).

Co-Occurring Infestations		<i>Acrosphaera</i> app.	<i>Collosphaera</i> app.	<i>Siphonosphaera</i> app.	<i>Sphaerozoum</i> app.	<i>Rhaphidozoum</i> app.
G+C	# of Infested CR % of Total CR	5 1.7	5 1.8	0	9 2.9	4 2.0
G+H	# of Infested CR % of Total CR	1 0.3	2 0.7	1 0.9	6 1.9	1 0.5
H+D	# of Infested CR % of Total CR	0	0	0	2 0.6	0
G+D	# of Infested CR % of Total CR	2 0.7	2 0.7	2 1.7	9 2.9	3 1.5
D+C	# of Infested CR % of Total CR	0	3 1.1	0	0	0
G+H+D	# of Infested CR % of Total CR	0	0	0	2 0.6	0
H+C	# of Infested CR % of Total CR	4 1.3	1 0.4	0	1 0.3	2 1.0
G+H+C	# of Infested CR % of Total CR	0	0	0	0	0
G+D+C	# of Infested CR % of Total CR	0	0	0	0	0
Total Number of CR Examined		301	272	117	316	203

Key to Symbols : G=Gyrodinium sp. H=hyperiid amphipod
D=dysterid ciliate C=Cryptobia-like bodonid flagellate

Table 10. (cont.)

Co-Occurring Infestations	Collozoum					Collozoum stellatum	Unidentified Colonies
	Inerme	caudatum	serpentinum	pelagicum			
G+C	# of Infested CR % of Total CR	8 5.7	45 28.0	1 2.1	1 0.9	0	23 3.0
G+H	# of Infested CR % of Total CR	3 2.1	2 1.2	0	1 0.9	0	46 6.1
H+D	# of Infested CR % of Total CR	0	0	0	0	0	3 0.4
G+D	# of Infested CR % of Total CR	1 0.7	0	0	1 0.9	0	27 3.6
D+C	# of Infested CR % of Total CR	0	0	0	0	0	0
G+H+D	# of Infested CR % of Total CR	0	0	0	0	0	6 0.8
H+C	# of Infested CR % of Total CR	0	0	1 2.1	0	0	3 0.4
G+H+C	# of Infested CR % of Total CR	0	1 0.6	0	0	0	4 0.5
G+D+C	# of Infested CR % of Total CR	1 0.7	0	0	0	0	1 0.1
Total Number of CR Examined		140	161	47	114	19	760

Key to Symbols : G=Gyrodinium sp. H=hyperiid amphipod
D=dysterid ciliate C=Cryptobia-like bodonid flagellate

Table 11. Comparison between CR infestation rates in oceanic waters and around Caribbean island masses. Radiolaria representing oceanic populations were collected during OC 176, OC 177 and OC 191; Caribbean CR were collected during Barbados 1986, 1987 and Curacao 1988. Infestation rate = (# CR Infested)/(total # CR collected). Values in the table are mean % (+/- standard error). (mean value was calculated only for OC 177 and OC 191)**

Infesting Organism	Infestation Rate on CR Collected in Oceanic Waters	Infestation Rate on CR Collected Near Caribbean Islands
<i>Gyrodinium</i> sp.	34.2 ** (2.1)	30.8 (6.9)
<i>Cryptobia-like</i> bodonid flagellate	21.1 (1.7)	5.3 (1.2)
Dysterid ciliate	2.7 (1.2)	6.5 (2.2)
Hyperiid amphipod	5.4 (1.8)	11.3 (2.9)

Figure 33a. Gyrodinium sp. infestation rates vs concentration of chlorophyll a in surrounding seawater in Curacao, Barbados and OC 191

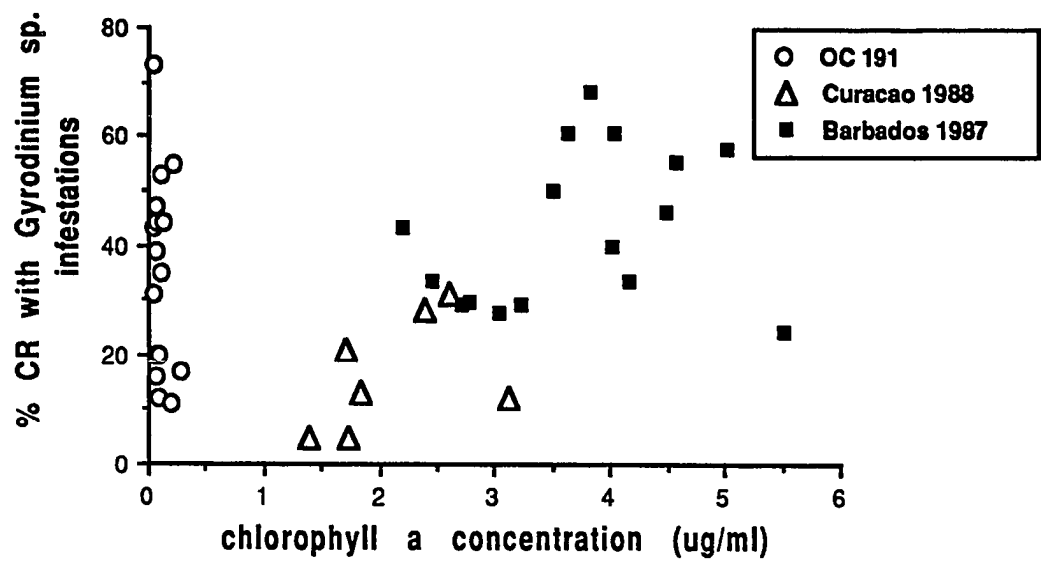


Figure 33b. Cryptobia-like flagellate infestation rates vs concentration of chlorophyll a in surrounding seawater in Curacao, Barbados and OC 191

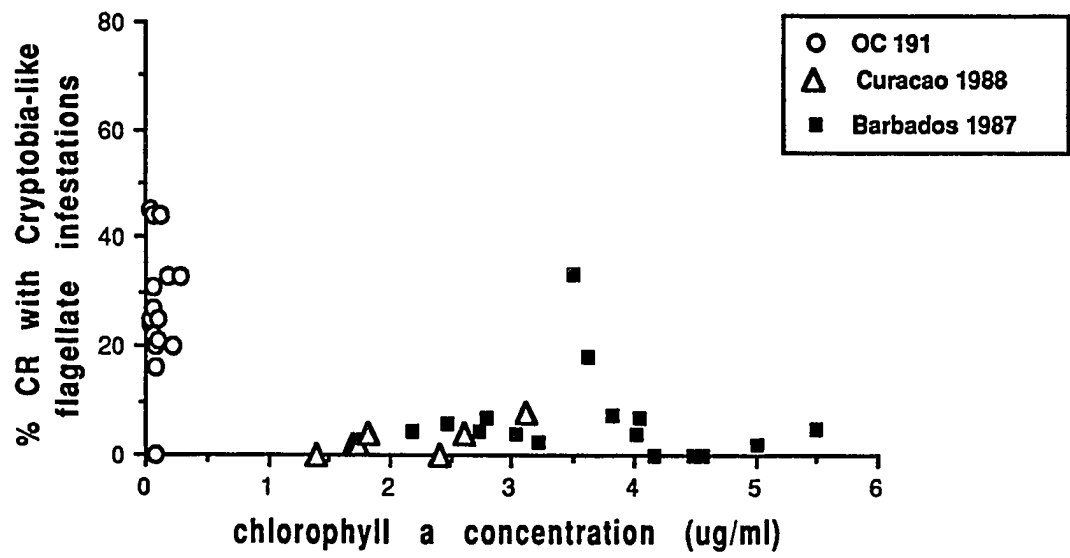
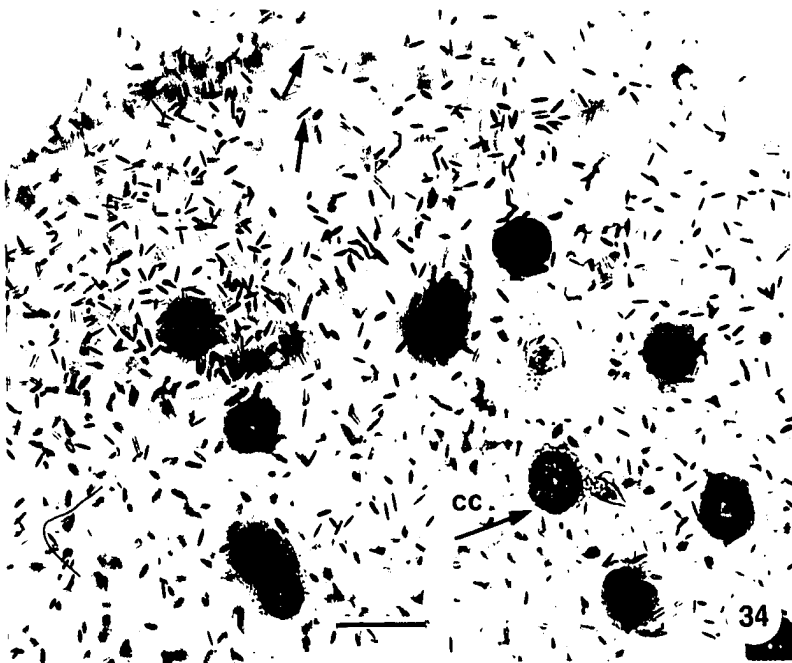


Figure 34. Light micrograph of radiolarian colony with Nitzschia sp. infestation. The dark spheres are radiolarian central capsules (cc) and the thin cells with tapered ends (small arrows) are the infesting diatoms. Scale = 200 um.



Chapter 4

Bacteria on the Surfaces of Colonial Radiolaria

INTRODUCTION

The surfaces of aquatic organisms are frequently colonized by bacteria (Beams and Kessel, 1973; Sieburth, 1975; Fletcher and Marshall, 1982). This is especially true of organisms with biologically inactive surfaces which undergo fouling similar to that found on non-living surfaces (Sieburth, 1979). Nutrients released by the host probably attract and sustain these bacteria (Adler, 1966; Berg and Brown, 1972; Sieburth, 1979), which flourish in the absence of predation or deterrents. Some marine organisms have biologically active surfaces and they secrete chemicals that deter bacterial growth (Sieburth and Conover, 1965; Sieburth, 1968) or cleanse their surfaces by producing mucus (Johannes, 1967) or a cuticle (Hanic and Craigie, 1969) which periodically sloughs off.

Because the surfaces of colonial radiolaria are biologically active (pseudopods), it is surprising to find them covered by large populations of bacteria (see Chapter 2). However, there are other examples of biologically active surfaces in marine environments, including egg masses and larval forms, that are similarly covered by a dense bacterial growth (Johnson et al., 1971). Colonial radiolaria apparently do not possess an antimicrobial strategy and probably do not feed on the associated microflora because bacteria have not been observed inside CR food vacuoles (Anderson, pers. comm.; Angel, unpublished).

The purpose of the present study was twofold : (1) to describe the bacterial populations associated with CR, and (2) to assess the flow of carbon to this microbial community within the colonial radiolarian microcosm. In addition, I examined the influence of two environmental parameters, seawater temperature and productivity (approximated by the concentrations of chlorophyll a, phaeopigment and planktonic bacteria in the surrounding seawater) on the abundance of bacteria on CR.

MATERIALS and METHODS

A. Bacteria on the Surfaces of CR

Colonial radiolaria were hand-collected by SCUBA divers (see Chapter 1) during field trips to Barbados (March - April 1987) and Curacao (April 1988), and during two cruises to the Gulf Stream off the northeastern coast of the United States, R.V. Oceanus (OC) 177, R.V. Oceanus (OC) 191. Colonies were examined as soon as possible following their collection (usually from one to three hrs.) to determine taxonomic identity, number of central capsules per colony, shape and dimensions of CR, and type and abundance of protozoan infestation. During the period of time following collection and prior to their examination, CR were left inside the seawater-filled glass jars in which they were collected; one colony per jar, at room temperature (22°-25°C). Following initial examination, CR were rinsed with filtered seawater (all seawater used in these procedures was filtered through 0.2 μ m Nuclepore filters) and fixed in 2% filtered (0.2 μ m Nuclepore) glutaraldehyde for 20 min. Fixed CR were transferred to pre-stained (Irgalan Black) 0.4 μ m Nuclepore filters in a Millipore filtration unit, flooded with 3 μ g/ml 4'6-diamidino-2-phenylindole (DAPI; Porter and Feig, 1980) for 10 minutes and rinsed twice with 2 ml filtered seawater. The vacuum applied did not exceed 12.5 cm Hg, however this was usually sufficient to cause the colony to collapse and flatten onto the Nuclepore filter. DAPI-stained CR and filters were transferred to microscope slides, immersed in a drop of immersion oil, covered with a glass cover slip, and stored frozen until further examination.

All DAPI-stained samples were examined at Lamont-Doherty Geological Observatory of Columbia University (LDGO) using a Leitz Laborlux 11 microscope equipped with an HBO-50 mercury lamp. An NPL Fluotar 100x objective lens was used because it yields a flat field of vision with minimum distortion at the edges. The total magnification, using 10x eyepieces, was 1000x. The filter set, used for fluorescence observations, consisted of a BP 340-380 excitation filter, an RKP 400 beam splitter, and an LP 430 barrier filter.

Bacterial abundances on CR surfaces were calculated as follows. Ten randomly selected fields on the rhizopodial surfaces of CR were chosen and all bacterial cells in a Whipple grid field (53 μ m x 53 μ m) were counted. When bacterial abundances exceeded 300 cells/grid; only 5 fields were counted.

Several attempts to examine the CR microbial community by SEM proved unsuccessful because specimens were not properly fixed and as a result, the fragile radiolarian rhizopodia contracted and collapsed onto the colony gelatin. Therefore, all descriptions and measurements were based on epifluorescent microscope observations.

B. Estimating the Carbon Demand of CR-Associated Bacteria

The following equation was employed to estimate the "bacterial carbon demand" (BCD) of the populations of bacteria observed on CR surfaces.

$$\text{BCD (g carbon/CR/day)} = V \times N \times C \times \text{GR} \times (\text{GE})^{-1} + (N \times \text{MC})$$

(Equation 1)

V = mean cell volume of single bacterium (μm^3)

N = number of bacteria/CR

C = 0.38 ± 0.05 pg carbon/ μm^3 (conversion factor for cell volume to carbon)

GR = bacterial growth rate (doublings/day)

GE = bacterial growth efficiency (I used 0.5)

MC = bacterial maintenance carbon (1.84 fg carbon/bacterium/day)

For each CR included in this study, dimensions of 20 bacterial cells (of each morphological type) were measured by ocular micrometer (smallest interval : 0.4 μm ; resolution 0.2 μm). Mean dimensions of the bacterial cells were used to calculate cell volumes (V). Volumes of rod-shaped cells were calculated by employing the equation for a cylinder with 2 hemispherical caps (Fuhrman, 1981).

I chose the biovolume to biomass conversion factor (C) determined by Bjornsen (1986) because the bacterial cell volumes he worked with included the range of sizes I measured on colonial radiolaria. Lee and Fuhrman (1987) observed that the biomass to biovolume conversion factor was not constant for all bacteria and decreased with increasing cell size, hence it is important to use an appropriate conversion factor.

The frequency of dividing or recently-divided bacteria (FDDC; Davis and Sieburth, 1984) observed on CR surfaces was recorded. "Dividing" and "recently-divided" bacteria included cells with a clear invagination of the cell wall (Hagstrom et al., 1979), yet not more

than 0.2 μm separating 2 adjacent cells that were oriented in a manner indicating recent division. FDDC values were subsequently converted to bacterial growth rates (GR) by :

$$\text{GR (doublings/day)} = 0.0357 \times \text{FDDC} - 0.4219 \quad (\text{Equation 2})$$
$$R^2 = 0.948 \quad (P < 0.01)$$

(Davis and Sieburth, 1984)

I used the FDDC method which provides an instantaneous estimate of bacterial growth rates because it does not require incubation of the samples. Although various criticisms have been raised regarding the use of FDC or FDDC ratios to estimate bacterial growth rates (van Es and Meyer-Reil, 1982; Newell et al., 1986), for now, this method appears to be at least as good as any other available (van Es and Meyer-Reil, 1982; Li, 1984; Hollibaugh, 1988). In order to apply the FDDC method to CR associated bacteria, I assumed that these bacteria have a similar FDDC to doubling-rate ratio as the Vibrio sp. used by Davis and Sieburth (1984). As noted previously, only CR with relatively rapidly growing bacteria (FDDC greater than 13%) were considered in the BCD calculations (mean FDDC = 26.9% (st. err. = 3.4)), therefore BCD values may represent above-average estimates of bacterial carbon consumption rates. Although this may appear to give a skewed representation of CR associated bacterial production, mean FDDC in a random sample of CR (including colonies with FDDC values below 13%) was 18.2% (st.err. = 1.2; n = 42; Table 13) indicating that most CR associated bacteria were dividing at moderately rapid rates and therefore the calculated BCD values were probably not inflated.

I chose the Davis and Sieburth (1984) modification of the Hagstrom et al. (1979) "frequency of dividing cells" method because the frequencies of dividing cells observed on CR (4 to 34%) were within the 13 to 38% range described by Davis and Sieburth (1984); well above the 0.6 to 6% FDC values reported by Hagstrom et al. (1979), the 2 - 15% FDC observed by Newell and Christian (1981) and the 3 - 5% FDC recorded by Hanson et al. (1983). Davis and Sieburth (1984) calibrated FDDC to bacterial growth rates at 21°C which was several degrees lower than the ambient surface seawater temperatures at which CR were collected. This temperature difference may result in an underestimate of bacterial growth rates (Newell and Christian, 1981).

Bacterial growth efficiencies (GE) estimated by various workers range from 20% (Hobbie et al., 1977; Bjornsen, 1986; Linley et al., 1983) to 50% to 80% (Williams, 1984). Therefore, I have assumed a median value, $GE = 0.5$ which was also used by Azam et al. (1983) for oceanic bacteria.

The bacterial maintenance carbon (MC) used in the BCD equation was 1.84 fg carbon/bacterium/day (1 fg = 10^{-15} g). Marr et al. (1962) found that the specific maintenance of glucose-starved Escherichia coli was 16 ug glucose/mg cells (dry weight) per hour. The maintenance carbon was calculated by assuming the mean cell volume of starved E. coli is 0.164 um^3 , and the biovolume/biomass conversion factor is $0.44 \text{ pg dry weight/um}^3$ (based on the biovolume to biomass conversion factor for E. coli, $0.22 \text{ pg carbon/um}^3$ (Bratback and Dundas, 1984), converted from cell carbon to dry weight by assuming 50% of bacterial dry weight is carbon (Luria, 1960)).

C. Bacteria in the Surrounding Seawater

In order to compare the bacteria on CR surfaces to those in the surrounding seawater, 1-liter water samples were collected in glass jars during the dives. Before samples were taken, jars were flushed several times underwater by inverting the jars and replacing the seawater with air from my SCUBA diving regulator. Seawater samples were stored in the dark at 4°C for one to three hours prior to subsampling, fixation and DAPI staining. Ten to 20 ml seawater were fixed with 1% filtered glutaraldehyde (final concentration) for 20 minutes prior to DAPI staining (Porter and Feig, 1980). Samples were concentrated onto prestained (Irgalan Black) 0.2 um Nuclepore filters using a vacuum of 6 cm Hg or less and stained with 3 ug/ml DAPI following the same procedure as described above for bacteria on radiolarian colonies.

RESULTS

Bacteria were found on all of the CR that were stained with DAPI. These bacteria were usually larger than the majority of free-living bacteria that were examined in the same waters (Table 12). Most of the CR-associated bacteria were either straight or slightly curved rods with cell volumes in excess of 0.200 um^3 . On many colonies, there was more than one morphologically distinct type of

bacterium. Some of the CR-associated bacteria that were morphologically distinct from the free living forms included streptobacilli (chains of rods) and extremely long filamentous forms. Planktonic bacteria in the surrounding waters consisted mostly of small cocci and rods, generally less than $0.100 \mu\text{m}^3$.

The abundances of bacteria on the surfaces of CR were compared to the abundances of planktonic free-living bacteria found in an equivalent volume of surrounding seawater. The volumes of colonial radiolaria that were stained with DAPI and examined for bacteria ranged between 0.025 and 0.147 ml. Most of the colonies examined were either spherical or oval in shape. The total abundances of bacteria on CR surfaces ranged between 0.22 and 9.60×10^7 bacteria/ml CR for the Caribbean stations located near Barbados and Curacao, and between 0.33 and 14.10×10^7 bacteria/ml CR for the stations taken during the cruises in the northwestern Atlantic Ocean (OC 177 and OC 191). In comparison, abundances of free-living bacteria in the surrounding seawater ranged between 0.28 and 13.10×10^5 bacteria/ml seawater for the Caribbean stations located near Barbados and Curacao and between 1.90 and 13.20×10^5 bacteria/ml seawater for all the stations taken during the cruises in the northwestern Atlantic Ocean. Therefore, the bacteria on CR were not only larger than the free living bacteria; they were also more abundant when compared with the numbers of bacteria in an equivalent volume of surrounding seawater.

A summary of mean bacterial abundances and FDDCs measured on 43 different radiolarian hosts is presented in Table 13. The data are arranged by genus of host colonies to facilitate comparison between the CR-associated bacteria and such variables as seawater temperature or CR surface area which may influence the associated bacterial populations. The group of unidentified colonies included in Table 13 consisted of several morphologically different types of CR which I could not assign to one of the known species. Among the identifiable CR, Collozoum caudatum colonies had the largest surface areas and, as a result, they had the largest populations of associated bacteria. Abundances of associated bacteria on the other four CR categories are also related to the mean CR surface area.

Mean bacterial cell volume, the abundance of associated bacteria/CR and FDDC were measured in 20 different CR (Table 14). These measurements were used in conjunction with an estimated bacterial growth efficiency, a bacterial cell volume-to-biomass

conversion factor, an FDDC to bacterial growth rate conversion equation (equation 2), and an estimated bacterial maintenance requirement to calculate the CR associated bacterial carbon demand (BCD, equation 1). The mean BCD value was 132 ng carbon/day (range = 1 to 523 ng carbon/day) for a mean CR-associated bacterial population of 1.49×10^6 cells/CR (range = 1.75×10^4 to 5.00×10^6 cells/CR). There was a bias in the choice of CR for inclusion in the BCD calculations. Because I selected the Davis and Sieburth (1984) FDDC, only bacterial populations with FDDC values greater than 14% were appropriate for use in the FDDC to growth rate conversion equation (equation 2), therefore, the calculated BCD values represent bacterial carbon demands for CR with relatively rapidly growing bacterial populations. In all of the FDDC counts, the majority of bacteria included under the category "dividing or recently divided" were cells that were physically joined, i.e. "dividing". CR protozoan infestations were presented in Table 14 to examine their influence on the populations of CR associated bacteria, however the data do not demonstrate a clear relationship between these two groups.

In order to examine some of the environmental variables that may contribute to the large populations of bacteria on CR surfaces, I plotted them against bacterial abundances and calculated their correlation coefficients (Table 15). Although the initial inoculum of CR-associated bacteria probably originates in planktonic prokaryotes from the surrounding seawater, the concentration of free living bacteria was not significantly correlated with either abundances or FDDCs of CR associated bacteria. The total number of bacteria/CR and the FDDC were related to concentration of chlorophyll a and phaeopigment in the surrounding seawater. Bacterial abundances expressed on a per mm² CR basis were not significantly correlated with any of the independent variables. I also plotted the cell volume of CR associated bacteria against each of the independent variables listed in Table 15, but the relationships were not statistically significant.

After calculating the correlation coefficients, the data were arranged in a matrix for analysis by multiple regression. The concentration of phaeopigment in the seawater was highly correlated ($R^2 = 0.91$) with concentration of chlorophyll a, therefore, I excluded phaeopigment from the data matrix. There were missing values for several of the samples (i.e. not all of the variables were measured during each of the sampling dates), therefore the multiple regression matrix (32 x 6) included fewer data than were used to calculate each

of the bivariate correlation coefficients. The correlation coefficients calculated for the same pairs of variables (see Table 15) from this data matrix were not significant at the $p = 0.05$ level. Furthermore, scatter diagrams of dependent versus independent variables did not suggest either linear or curvilinear relationships between the variables. Nevertheless, numerous combinations (additive, interactive and second order) of the three independent variables in the matrix (seawater temperature, chlorophyll a concentration and concentration of bacteria in the surrounding seawater) were used in multiple regression models to examine the possibility that a) the dependent variables are influenced by more than one independent variable and b) the interaction is non-linear. A backward selection process (Dillon and Goldstein, 1984) was used to test the fit of the data to the regression model. In this method, the initial regression equation includes all independent variables and at each successive step, one of the randomly chosen variables is eliminated until the "best" regression model is produced. At each backward selection step, the regression model is appraised by comparing the coefficient of determination (R^2) and the partial F test value to previous values. The multiple coefficients of determination for the regression equations calculated from my data were very low and did not explain more than 45% of the variance.

In an effort to reduce the variance among the data, I split the multiple regression matrix (above) into two separate matrices on the basis of geographic area in which the host colonies and measurements were taken. All measurements from OC 177 and OC 191 were included in the "oceanic" matrix (11 x 6) and measurements from Barbados 1987 and Curacao 1988 were assigned to the "Caribbean" matrix (21 x 6). Scatter diagrams of the dependent versus independent variables in each of these small matrices did not reveal significant linear or curvilinear relationships to warrant further multi-variate analysis of the data.

DISCUSSION

The abundances of CR-associated bacteria, 2.2×10^6 to 1.4×10^8 bacteria per ml of radiolarian colony, are rather high, considering that most of the associated bacteria are found on external CR surfaces. In addition to being very abundant, the associated bacteria are often larger than the average free living bacterium found in the surrounding water.

The combination of highly abundant, large bacteria which are actively growing on the surfaces of CR raises the question, where do the bacteria acquire the nutrients to support this biomass? A notable mechanism which could supply organic substrates to associated bacteria is the radiolarian's sloppy feeding; in particular, the consumption of macroscopic prey e.g. copepods. Radiolarian feeding rhizopodia rupture the carapace of such crustaceans to expose the soft, digestable tissue which is subsequently phagocytosed (Anderson, 1983). In the tearing process, tissue is ruptured, thereby releasing the rich cytoplasmic constituents which may be taken up by CR associated bacteria. Although soft-bodied, macroscopic radiolarian prey (e.g. various zooplankton larvae) are not torn apart as dramatically, their tissue must also be reduced to easily phagocytosed particles and in this process, dissolved organic compounds are undoubtedly released, thus providing associated bacteria with nutrients.

Another potential source of dissolved organic matter in the CR microcosm is radiolarian waste products. Although it has been suggested that algal endosymbionts absorb waste products released by the host (Yonge, 1940; Muscatine, 1973; Thorington and Margulis, 1981; Anderson, 1983a), this hypothesis has not been tested in radiolaria and both organic and inorganic compounds may diffuse out or be transported by rhizopodial streaming to the associated bacteria and to the surrounding water.

In addition to the potential release of radiolarian metabolites to the surrounding water, endosymbiotic algae may excrete photosynthates extracellularly as has been documented in diatoms (Antia et al., 1963) and other phytoplankton (e.g. Fogg, 1966), thereby providing radiolarian-associated bacteria with another source of dissolved organic matter. However, the enclosing sheath of host cytoplasm surrounding each symbiont may reduce this source.

CR associated bacteria may benefit from the association of hyperiid amphipods with the colonies. The mechanical damage inflicted upon CR by infesting amphipods includes tearing of rhizopodia, disruption of the colony gelatin, consumption of CR endosymbionts and consumption of CR central capsules (Swanberg, 1979; Angel, unpublished). Dissolved organics are probably lost in all of these processes and may be taken up by the CR associated bacteria. Furthermore, amphipod activity (excretion and fecal pellet production) would provide additional nutrients and carbon to the

associated bacterial population. Unfortunately, there are no data to support this hypothesis because I did not measure the abundances of bacteria on amphipod-infested radiolaria.

In order to examine some of the factors that may influence abundances of CR associated bacteria and their growth rates (FDDC), correlation coefficients were calculated for bivariate plots of CR associated bacteria versus several environmental variables. Abundances of both free living and CR associated bacteria showed a positive relationship with concentrations of chlorophyll a and phaeopigment in the surrounding water, and with surface seawater temperature. Whereas free living bacteria respond directly to changes in productivity of the water column (Larsson and Hagstrom, 1979; Morita, 1982), CR associated bacteria are more likely to respond to changes in their immediate microenvironment, i.e. the surfaces of the host colonies. Colonial radiolaria are omnivores that feed on algal as well as animal prey (Swanberg, 1979). Thus, an increase in concentration of chlorophyll a in the surrounding water, and concomittant increase in CR prey, would probably result in greater release of nutrients that might support larger populations of CR associated bacteria.

The relationship between seawater temperature and abundance of free living bacteria ($R = 0.505$, $P < 0.01$) is stronger than that between temperature and CR associated bacteria ($R = 0.470$, $P < 0.01$). This may be related to the different environments that the attached versus the free living populations occupy; although, it is not clear in what manner. FDDC, an indication of CR associated bacterial growth rates (Hagstrom et al., 1979) was significantly (but not strongly) correlated with the concentrations of chlorophyll a and phaeopigment ($R = 0.318$, $P < 0.05$; $R = 0.293$, $P < 0.05$, respectively), but not with seawater temperature. This represents a contrast between bacterial standing stock (abundance) and population growth rate. Because abundance data are a cumulative record of bacterial growth and colonization of CR surfaces, the contrasting FDDC values suggest that bacterial growth rates may vary and are probably controlled by factors that were not taken into consideration in this study.

In order to examine the possibility that "dependent" variables might be more precisely described by more than one independent variable, relationships among the data were explored using multiple regression models. However, these models did not explain more than 45% of the variance among the data, suggesting that the independent

variables measured are probably not optimal for predictive purposes.

Neither the percentage of dividing radiolarian central capsules (which may be an indicator of the nutritional status of CR) nor the abundance of free living bacteria showed a relationship with the abundances or the FDDCs of CR associated bacteria. If the CR were bacterivorous, i.e. capable of feeding on planktonic bacteria, a positive relationship might have been expected (though not necessarily, since other food sources are utilized), however the lack of correlation is supported by numerous TEM examinations; bacteria have never been observed within the food vacuoles of colonial radiolaria (O.R. Anderson, pers. comm.; Angel, unpublished).

There was considerable scatter among abundances (per mm² CR) of the various bacterial morphotypes. Consequently, the correlation coefficients calculated from the plots of bacteria per mm² CR versus the 4 independent variables were insignificant at both 1% and 5% levels.

Estimated daily bacterial carbon demand (BCD) ranged from one to 523 ng carbon/CR with a mean of 132 ng carbon/CR. The wide distribution of BCD values (2.5 orders of magnitude) resulted from the large variance in CR associated bacterial abundances, from 1.75×10^4 to 5.00×10^6 bacteria/CR (a difference of 2.8 orders of magnitude).

If the assumptions employed in the BCD equation are correct, the bacterial carbon consumption rate (expressed on a per volume basis) is from 3 to 5 orders of magnitude greater on CR (0.09 to 19.24 ug carbon/ml CR/day) than in an equivalent volume of surrounding water (0.12 to 12 pg carbon/ml oceanic water/day). This is based on a comparison between the volume corrected BCD rates presented in Table 14 and oceanic bacterial carbon production rates summarized from various cited references in Newell and Christian (1981). Results from another study focussing on populations of heterotrophic bacteria associated with macroscopic aggregates (marine snow) also revealed high production rates. Alldredge et al. (1986) used the tritiated thymidine incorporation method (Fuhrman and Azam, 1980) to measure bacterial production in marine snow and found that the production rates in the aggregates were at least an order of magnitude greater than in an equivalent volume of surrounding water.

The CR-associated bacterial production rates are also high when compared with colonial radiolarian production; an average colony (48 ug carbon) produces about 100 ng carbon/hr (symbiont primary production)(Swanberg, 1983). Because symbiont primary production is only sufficient to compensate for metabolic activity (estimated respiration rate for this colony = 106 ng carbon/hr), most of the radiolarian growth is attributed to tertiary production. The mean bacterial production rate may range between 0.04 and 10 ng carbon/hr in an average colony (48 ug carbon), however, this may be an important sink of carbon in the radiolarian microcosm. The bacteria may also serve as a food source for the protozoa associated with the radiolarian (see Chapter 2). In this way, they would serve not as a sink of carbon, but as a link between the dissolved organic matter pool and the protozoa within the colonial radiolarian microcosm.

Although bacterial production rates on colonial radiolaria are very high in comparison to the surrounding water, the abundance of CR is generally between 0.1 and 1.0 CR/m³ (Swanberg, 1983; see chapter 1). Therefore, the contribution of CR associated bacteria to total pelagic bacterial production, like the contribution of marine snow bacteria (Alldredge et al., 1986), rarely exceeds a few percent.

SUMMARY

Bacteria have been observed on the surfaces of all CR examined. Abundances of these bacteria ranged from 1.75×10^4 to 5.00×10^6 cells/CR and were strongly correlated with CR surface area. Although the morphologies of most CR associated bacteria were similar to those of free living bacteria in surrounding waters, the CR associated bacteria were generally larger, suggesting the CR surfaces are a nutrient-rich microenvironment. The abundances of CR associated bacteria were positively correlated with ambient seawater temperatures and with chlorophyll a concentration, but showed no relationship with abundances of free living bacteria in the surrounding waters. CR associated bacterial production rates ranged from 1 to 523 ng carbon/CR/day, based on bacterial growth rates estimated by the frequency of dividing and recently divided cells (Davis and Sieburth, 1984). This range of production rates is 3 to 5 orders of magnitude greater than heterotrophic bacterial production rates measured for similar volumes of seawater by several different workers. Because the abundance of CR is usually less than 10

colonies/m³, the contribution of CR associated bacterial production to general plankton heterotrophic processes is probably no more than a few percent. Bacterial production may be 3% or more of the radiolarian symbiont primary production and this may be an important sink of carbon in the radiolarian microcosm. Furthermore, the bacteria may serve as prey for other microbial members of the CR microcommunity, thereby forming a link between the dissolved organic matter pool and heterotrophic protozoa.

Table 12. Comparison between the dimensions and cell volumes of CR-associated and free living planktonic bacteria. Dimensions of the DAPI-stained bacteria were determined by epifluorescence microscopy. Mean abundances of the planktonic bacteria were not determined (n.d.)

Bacterial Morphology	Bacterial Cell Dimensions (um)	Bacterial Cell Volumes (um) mean +/- s.e. (sample size) range	Mean Number of Bacteria/CR (x10)
CR-Associated Bacteria			
Cocci	0.4 - 1.0 diameter	0.194 +/- 0.013 (n=133) 0.033-0.523	2.68 +/- 1.13 (n = 12)
Simple Rods	0.4x0.6 - 0.8x2.4	0.301 +/- 0.017 (n=149) 0.059-1.072	2.69 +/- 1.08 (n = 17)
Curved Rods	0.4x1.0 - 0.6x2.0	0.202 +/- 0.009 (n=89) 0.109-0.509	1.29 +/- 0.24 (n = 11)
Filamentous Bacteria	0.2x4.0 - 0.4x15.0	0.873 +/- 0.067 (n=60) 0.123-1.868	1.07 +/- 0.49 (n = 7)
Free-Living Bacteria			
Cocci	0.4 - 0.8 diameter	0.117 +/- 0.008 (n=122) 0.033-0.268	n.d.
Simple Rods	0.4x0.6 - 0.6x1.4	0.157 +/- 0.008 (n=170) 0.059-0.339	n.d.
Curved Rods	0.4x0.8 - 0.6x1.4	0.125 +/- 0.007 (n=83) 0.084-0.339	n.d.

Table 13. The effects of CR taxonomy, CR surface area, concentration of bacteria in the surrounding seawater and ambient seawater temperature on bacterial abundances per mm CR surface area, total abundances of bacteria/CR and frequency of dividing-divided cells (FDDC) of CR-associated bacteria. tabular values are mean +/- standard error. (n = number of CR examined).

Colonial Radiolarian	CR Surface Area (mm)	Concentration of Bacteria in Surrounding Seawater (x10 /ml)	Surface Seawater Temperature (°C)	Number of Bacteria/mm CR Surface Area (x10)	Total Number Bacteria/CR (x10)	FDDC (%)
<i>Slphonosphaera</i> sp.	99.6 +/- 11.2 (n=6)	8.17 +/- 2.09 (n=4)	27.4 +/- 0.3 (n=6)	29.37 +/- 8.44 (n=6)	3.7 +/- 0.92 (n=4)	21.6 +/- 4.5 (n=6)
<i>Collozoum caudatum</i>	567.6 +/- 185.7 (n=3)	4.96 +/- 0.47 (n=3)	28.9 +/- 0.2 (n=3)	22.13 +/- 5.33 (n=3)	12.29 +/- 3.8 (n=3)	14.9 +/- 3.2 (n=3)
<i>Sphaerouzoum</i> sp.	59.1 +/- 8.9 (n=11)	9.79 +/- 1.03 (n=11)	27.6 +/- 0.2 (n=11)	30.56 +/- 7.35 (n=11)	1.67 +/- 0.43 (n=11)	16.8 +/- 7.1 (n=11)
<i>Collosphaera</i> sp.	55.9 +/- 26.6 (n=3)	8.1 +/- 2.6 (n=3)	26.9 +/- 0.1 (n=2)	12.30 +/- 1.13 (n=3)	1.01 +/- 0.67 (n=3)	21.5 +/- 5.1 (n=3)
Unidentified Colony	77.3 +/- 12.4 (n=19)	10.3 +/- 2.1 (n=11)	27.2 +/- 0.2 (n=16)	16.73 +/- 2.48 (n=19)	1.73 +/- 0.42 (n=19)	16.3 +/- 1.7 (n=19)
Mean	171.9	8.26	27.6	22.2	4.08	18.2

Table 14. Summary of the bacterial carbon demands (BCD) of 20 colonial radiolaria collected during OC 177, OC 191, Barbados 1987, and Curacao 1988. The variables of the BCD equation, bacterial abundance, mean bacterial cell volume, and the bacterial growth rate (uFDDC) which is calculated from the frequency of dividing and recently divided bacterial cells (%) are presented below.

Radiolarian Species (Field Excursion)	Protozoan Infestation (type)	Total # Bacteria/CR (x10 ³)	Mean Bacterial Cell volume (μm^3)	FDDC (%)	uFDDC (doublings/day)	BCD ($\mu\text{g carbon/day/CR}$)
(Barbados 1987)						
<i>Sphaerozoum</i> sp.	yes (dysterid ciliate)	2.11	0.396	19.8	0.285	0.181
<i>Sphaerozoum</i> sp.	yes (Gyrodinium sp.)	0.34	0.736	89.6	2.777	0.522
<i>Collosphaera</i> sp.	yes (dysterid ciliate)	1.15	0.285	32.1	0.724	0.180
Unidentified Colony	no	2.79	0.169	21.3	0.339	0.121
Unidentified Colony	yes (Gyrodinium sp.)	0.52	0.234	28.3	0.588	0.054
Unidentified Colony	no	1.21	0.285	18.8	0.249	0.065
Unidentified Colony	yes (Gyrodinium sp. + Cryptobia -like bodonid)	0.27	0.134	21.2	0.335	0.009
Unidentified Colony	no	0.94	0.234	22.5	0.381	0.064
Unidentified Colony	no	0.72	0.077	26.5	0.524	0.022
Unidentified Colony	no	0.31	0.148	23.3	0.41	0.014

Table 14. (cont.)

Curacao 1988									
<i>Siphonosphaera</i> sp.	no	5.00	0.113	33.7	0.781	0.335			
<i>Siphonosphaera</i> sp.	no	3.24	0.169	14.7	0.103	0.043			
<i>Collosphaera</i> sp.	yes (Gyrodinium sp.)	0.02	0.084	31.3	0.696	0.001			
Unidentified Colony	no	0.86	0.523	27.6	0.563	0.193			
Unidentified Colony	yes (Gyrodinium sp.)	1.07	0.159	22.6	0.385	0.050			
Unidentified Colony	yes (Gyrodinium sp.)	0.15	0.268	15.5	0.131	0.004			
OC 177 (1986)									
Unidentified Colony	yes (Cryptobia -like bodonid)	2.76	0.509	16.6	0.171	0.183			
OC 191 (1987)									
<i>Siphonosphaera</i> sp.	no	0.59	0.339	28.2	0.585	0.089			
<i>Collozoum</i> <i>caudatum</i>	yes (Gyrodinium sp. + Cryptobia -like bodonid)	3.92	0.109	25.5	0.488	0.158			
Unidentified Colony	no	1.98	0.791	18.7	0.246	0.293			
mean standard error		1.49 +/- 0.32	0.288 +/- 0.045	26.9 +/- 3.4	0.538 +/- 0.122	0.132 +/- 0.031			

Table 15. Summary of correlation coefficients calculated from bivariate plots of four independent variables including surface seawater temperature, chlorophyll a concentration, phaeopigment concentration and abundance of free-living bacteria in the surrounding seawater and three dependent variables including total abundance of bacteria on CR, abundance of bacteria per mm² CR, and frequency of dividing-divided cells (FDDC). The number of measurements in each bivariate plot is shown between parentheses (), and the significance level of the correlation coefficients (Sokal and Rohlf, 1969) is represented by an asteriks (*) for P<0.05 and a number sign (#) for P<0.01. Tabular values are correlation coefficients (R).

	Number of CR- Associated Bacteria per mm CR	Total Abundance of CR-Associated Bacteria	FDDC	Abundance of Bacteria in Seawater
Surface Seawater Temperature	0.197 (56)	0.470 (50)	0.228 (48)	0.505 (46)
Chlorophyll a Concentration	0.000 (52)	0.386 (52)	0.318 (46) *	0.547 (41) #
Phaeopigment Concentration	0.000 (52)	0.346 (52) *	0.293 (46) *	0.587 (41) #
Abundance of Bacteria in Seawater	0.077 (46)	0.266 (46)	0.138 (46)	

Chapter 5

Trophic Studies of Gyrodinium sp.

INTRODUCTION

There have been numerous reports of dinoflagellate symbioses with planktonic sarcodines. These include the intimate associations of endosymbiotic dinoflagellates with most planktonic foraminifera (Murray, 1897; Rhumbler, 1911; Lee et al., 1965; etc.), and with all colonial radiolaria (CR) (Huxley, 1851; Brandt, 1882; Anderson, 1976; etc.). In addition to these intracellular symbioses, several different dinoflagellates including Dissodinium elegans Pav., Pyrocystis noctiluca Murr. and P. fusiformis Murr. have been observed on the surfaces of several different planktonic foraminiferan hosts (Alldredge and Jones, 1973; Be et al., 1977; Spindler and Hemleben, 1980), but there is no evidence that either associant benefits from the symbiosis. Other unidentified gyrodinoid (or gymnodinoid) dinoflagellates have been observed swimming among the spines of the foraminifera (Spindler and Hemleben, 1980; Gaines and Elbrachter, 1987; Elbrachter, pers. comm.; Spero, pers. comm.; Bijma, pers. comm.), occasionally attaching to the spines and ingesting the host's food.

Extremely dense infestations of a gymnodinoid dinoflagellate, which will be referred to hereafter as Gyrodinium sp. (see Chapter 2) were observed among the external rhizopodia of colonial radiolaria. Although I did not see these dinoflagellates ingesting radiolarian food, their behavior was quite similar to that attributed to dinoflagellates on foraminiferan spines. Gyrodinium sp. swam among the radiolarian rhizopodia and occasionally adhered to a rhizopodium, such that the long axis of the cell was parallel to the rhizopodium, but it is not clear what the dinoflagellate achieved with this behavior.

The objective of this chapter was to learn about the role of Gyrodinium sp. in the radiolarian microcosm. Gyrodinium sp. possesses chloroplasts (see Chapter 2) and therefore has the potential for photosynthesis. The dinoflagellate's ability to assimilate inorganic

carbon in the light and in the dark was examined in a series of light/dark incubations using radioactively labelled seawater. In order to examine the dinoflagellates' ability to feed heterotrophically, while associated with CR,, Gyrodinium sp. were incubated in the dark with radioactively-labelled colonies.

MATERIALS AND METHODS

A. Incorporation of Inorganic Carbon in the Light

Experiments described in this and the next section ("uptake of carbon from radioactively-labelled CR") were done at the Bellairs Research Institute of McGill University in Holetown, Barbados during the spring and summer of 1987. All specimens were collected at a station located roughly two km west of the Bellairs Institute.

The following procedures were performed to test the ability of Gyrodinium sp. to fix inorganic carbon. Radioactively-labelled bicarbonate was added to sterile (autoclaved) seawater. Final concentrations of ^{14}C -Na-bicarbonate (New England Nuclear) ranged from 0.2 to 10.0 $\mu\text{Ci/ml}$ and the specific activities ranged between 0.39 and 2.78 mCi/mmol . A number of different incubation chambers were prepared in order to test the influence of chamber volume and design on the carbon incorporation activity and the investigator's ability to recover cells. The incubation chambers used were : a) 4-chambered Lab-Tek tissue culture slides with an incubation volume of 1 ml, b) 2-chambered Lab-Tek tissue culture slides with an incubation volume of 3 ml and, c) 6-well Nunclon tissue culture plates with an incubation volume of 10 ml. I found that the 2-chambered Lab-Tek slide worked best. It provided a sufficient volume of seawater to minimize density-related stress and possessed the optical characteristics needed to permit clear visualization of individual cells to be collected at the end of the experiment. Loss of $^{14}\text{CO}_2$ was minimized by covering the incubation chambers with clear plastic covers. Control samples which contained radioactively-labelled incubation medium (but did not contain dinoflagellates) were sampled once at the onset of the incubations and again after experiments were terminated to determine if there was loss of $^{14}\text{CO}_2$ to the atmosphere. The results indicated there was not a noticeable change in activity in these control samples.

Dinoflagellates were micropipetted off the surfaces of infested colonial radiolaria (mostly Sphaerozoum spp. and unidentified colonies), deposited in a sterile seawater rinse and then transferred into the incubation chambers. Micropipetting was done with the aid of a fiber-optics ring-shaped light source and a Wild M-5 dissecting microscope. This optical combination provided the dark-field illumination necessary to see the small dinoflagellates at relatively low magnifications while minimizing the exposure of cells to light; this was especially important when manipulating cells used in the dark controls. The light level measured at the microscope stage was 3.5 $\mu\text{E}/\text{m}^2/\text{sec}$. The number of dinoflagellates in each chamber did not exceed 50 cells. Dinoflagellates used in these experiments were taken from colonies collected on the same day or one day previously. All newly-collected CR, including those infested with Gyrodinium sp., were maintained in the laboratory at 25°C near a fluorescent (Cool-White) light bank (60 $\mu\text{E}/\text{m}^2/\text{sec}$) with a 12:12 light:dark cycle.

Incubation chambers, for both light measurements and dark controls (incubated in chambers wrapped with aluminum foil), were placed 12.5 cm from a fluorescent white-light bank where the measured light intensity was 60 $\mu\text{E}/\text{m}^2/\text{sec}$ and the water temperature was maintained at 25°C ($\pm 1^\circ\text{C}$) by circulating the air around the jars with a small air fan. Durations of these experiments ranged from 2.5 to 6.5 hrs; and the incubations were carried out during the daylight hours to avoid artifacts resulting from disruption of endogenous light-dark cycles. A control group containing glutaraldehyde-fixed cells was set up on 4/1/87 by arranging the same experimental system as used in the light and dark chambers; but in addition, glutaraldehyde (3%, final concentration) was added.

In order to measure the actual concentration of radioactive bicarbonate being used in each experiment, replicate 100- μl aliquots of the incubation medium were removed from each incubation chamber prior to addition of the dinoflagellates. These subsamples were added to mini-scintillation vials containing 0.5 ml phenethylamine to prevent acidification of the radioactive bicarbonate and loss of $^{14}\text{CO}_2$, and 4 ml Ecolite (WestChem, CA) scintillation fluor.

Experiments were terminated by micropipetting individual dinoflagellates out of the chambers, through a non-radioactive seawater rinse and onto 25 mm dia, 0.45 μm Millipore filters. The number of Gyrodinium sp. on each filter ranged from two to 30

dinoflagellates. These filters were placed over concentrated HCl for 10 min. to eliminate traces of H^{14}CO_3 , oven dried for 10 min. at 60°C and placed in mini-scintillation vials with 4 ml Ecolite fluor for liquid scintillation counting later at LDGO.

In order to test whether Gyrodinium sp. passively adsorbs inorganic carbon, dinoflagellates were killed with 2% glutaraldehyde, incubated in seawater with ^{14}C -bicarbonate for 4.5 hrs. and then treated as above.

The DPM measured from each filter were converted to pg carbon fixed/dinoflagellate/hr based on the total specific activity of radioactive bicarbonate estimated in each culture vessel. Carbonate alkalinity of the seawater was not determined in these experiments, but subsequent measurements of this variable in several batches of similarly prepared autoclaved seawater, allowed to equilibrate with the atmosphere for the same duration of time as the ^{14}C - experimental medium, indicated the mean concentration of dissolved $\text{CO}_2 = 2.4 \text{ mM}$ (st. err. = 0.2); therefore, I used this concentration to convert results from DPM to "picomoles of carbon fixed".

B. Uptake of Carbon From Radioactively-labelled CR

In conjunction with the measurements of light and dark uptake of carbon, I tested the ability of dinoflagellates to take up carbon from radioactively-labelled colonial radiolaria.

Radioactive seawater media with concentrations ranging from 0.2 to 5 $\mu\text{Ci/ml}$ were prepared by diluting stock solutions of $\text{NaH}^{14}\text{CO}_3$ (New England Nuclear) in sterile seawater. Ten ml aliquots of the media were dispensed into 6-well Nunclon tissue culture dishes. Healthy colonial radiolaria (free from protozoan infestations as determined by microscope examinations) were immersed in two subsequent sterile seawater rinses and placed (one per well) in the filled wells of the tissue culture dishes 12.5 cm from a fluorescent light bank emitting $60 \text{ uE/m}^2/\text{sec}$. Colonies were illuminated in this manner for periods of 8-10 hrs.; sufficient time for the radiolarian endosymbionts to fix and translocate considerable amounts of radioactive carbon to the host cells (Anderson et al., 1983).

At the end of the incubation periods, radioactively-labelled colonies were immersed three times (5 minutes for each rinse) in

beakers containing 100 ml sterile seawater to remove non-assimilated ^{14}C , and then transferred to fresh sterile seawater in clean 6-well Nunclon tissue culture dishes. Dinoflagellates were micropipetted from freshly-collected, dinoflagellate-infested CR, washed once in sterile seawater and then transferred to the radioactively-labelled colonies in the wells of the Nunclon dishes. Nunclon plates were wrapped with aluminum foil and incubated at room temperature (26°C) for durations lasting between 2.5 and 14 hours. Incubations were terminated by micropipetting dinoflagellates out of the Nunclon wells and treating them as described in the previous section.

C. Leakage of Carbon From Radioactively-labelled CR

The following experiment was done in order to examine the possibility that radioactively-labelled radiolaria leak inorganic carbon (in addition to organic carbon) to the surrounding water. Five radiolarian colonies, roughly equal in size (10 mm long) were radioactively labelled by incubating them in seawater with 0.3 $\mu\text{Ci/ml}$ $\text{NaH}^{14}\text{CO}_3$ in front of a light bank for 4.5 hours. The "labelled" CR were then immersed in three successive filtered seawater baths (as described above) to eliminate non-assimilated ^{14}C . Following the rinsing, each of the radiolarian colonies was incubated in the dark for 4.5 hrs in a 20 ml scintillation vial filled with filtered seawater. At the end of the dark incubations, the vials were gently swirled to mix the contents and two 200 μl aliquots were removed from each and placed in separate scintillation vials. In one scintillation vial, 100 μl of phenethylamine were added in order to buffer the contents and retain bicarbonate in solution. Into the other vial, 3 drops of 1 N HCl were added to convert bicarbonate to carbon dioxide, thereby eliminating all dissolved inorganic carbon. Five ml of Eco-lite scintillation fluor were added to each of the scintillation vials and each vial was counted for 100 minutes.

RESULTS

A. Incorporation of Inorganic Carbon in the Light

The rates of light and dark uptake of inorganic carbon are presented in Table 16 as mean DPM/dinoflagellate/hr. The DPMs of most experimental vials with dinoflagellates were significantly greater than the background blanks (see Appendix D). However,

several of the dark uptake rates were equal to or greater than the rates recorded for illuminated treatments. In an adsorption control, performed in the light, glutaraldehyde-killed dinoflagellates ("dead" treatment, Table 16) did not take up radioactive carbon.

Mean carbon uptake rates for both light and dark treatments were converted from DPM to picogram carbon/dinoflagellate/hour and presented in Table 17. Carbon uptake rates ranged across an order of magnitude, from 2.5 to 22.4 pg carbon/cell/hr in the illuminated treatments and from 0 to 18.7 pg carbon/cell/hr for the dark incubations. The mean light and dark uptake rates (the two middle columns in Table 17) were positively correlated ($r^2=0.94$).

B. Uptake of Carbon From Radioactively-labelled CR

Heterotrophic carbon uptake experiments are summarized in Table 18. Unlike the uptake experiments described in the preceding section, I could not calculate picograms of carbon from the DPM values because the specific activities of the radioactive carbon within the CR were unknown. The radioactive carbon in the host CR is presented in Table 18 as DPM and ug Carbon/CR to demonstrate that the colonies contained significant amounts of radioactive label, so that even slight carbon uptake by single dinoflagellate cells would be detectable. The experiment carried out on 4/2/87 yielded zero DPM for a total of 43 dinoflagellates. It is important to note that most of the dinoflagellates (I did not record the precise numbers) that were retrieved at the end of that experiment were found adhering quite resolutely to the bottom of the dish, far from the labelled CR and it is possible that they did not come in contact with the CR throughout the experiment. Thirty out of the 53 dinoflagellates that were retrieved at the end of the 8/29/87 experiment were also not taken directly from the CR and this may have contributed to the low uptake rate that was measured. In the other two experiments listed, most of the dinoflagellates were removed either from the surface of the labelled CR or from the water where they swam freely.

The mean carbon uptake rate in these experiments was 2.0 DPM/dinoflagellate/hr (excluding the results from 4/2/87). Although the uptake rate per dinoflagellate appears very low, there were 9 dinoflagellates per scintillation vial (overall mean) and the DPM per vial was significantly greater than background DPM (generally ~ 20 DPM). Although it is impossible to convert the DPM values to carbon uptake rates, the values are very similar to the DPMs of the

dinoflagellates studied in the inorganic carbon uptake experiments (see Appendix D).

C. Leakage of Carbon From Radioactively-labelled CR

Both organic and inorganic carbon were released by radioactively-labelled colonial radiolaria (see Table 19). In all of the experiments, the DPM of inorganic carbon (mean = 20.62 DPM) was higher than the DPM of organic carbon (mean = 9.54 DPM). Because the specific activity of the labelled carbon inside the CR cannot be determined, the concentrations of the various compounds represented by the DPMs are not known.

DISCUSSION

A. Uptake of Inorganic Carbon

Gyrodinium sp. appeared colorless when viewed by light microscope. However, examination of this dinoflagellate with an epifluorescent microscope revealed red autofluorescence in the cell, indicating that it contains chlorophyll. Furthermore, a fine structure study of Gyrodinium sp. (Chapter 2, Figures 17, 18, 20) showed that the cell contains numerous chloroplast lobes, and there are starch deposits around the pyrenoids. These ultrastructural data suggest that Gyrodinium sp. is capable of photosynthesis.

Inorganic carbon uptake measurements were carried out using the ^{14}C light/dark bottle approach (Parsons et al., 1984). In order to minimize artifacts due to heterotrophic (bacterial) carbon uptake and high "dark-bottle" blanks (Parsons et al., 1984; Carpenter and Lively, 1980; Taguchi and Platt, 1977; Sorokin, 1971), incubation media were prepared with sterile seawater. Nevertheless, in two of the seven experiments (see Table 17), dark uptake rates were equal to or greater than the parallel "light" results and in general, the differences between light and dark uptakes were small. In order to examine some of the experimental factors that may have contributed to the high dark uptake rates, I varied the durations of the incubations and used different concentrations of radioactive bicarbonate and chambers of various sizes, yet changing these variables did not have a noticeable effect on the results. In order to determine if adsorption contributes to the carbon uptake process, glutaraldehyde-killed cells ("dead" treatment) were incubated in

radioactively-labelled seawater. Negligible carbon uptake in this control suggests that the uptake of radioactive bicarbonate is an active process that occurs in both light and dark incubations.

The mean rate of inorganic carbon uptake in the light (without subtracting the dark uptake) was 8.9 pg carbon/dinoflagellate/hr (st. err. = 2.9), and ranged from 3.6 to 22.8 pg carbon/dinoflagellate/hr. It is not clear how the dark inorganic carbon fixation takes place and why dark fixation rates were so high. Until this phenomenon is understood, the difference between the light and dark inorganic carbon fixation rates will be used as the representative light-driven carbon fixation rate. The mean Gyrodinium sp. inorganic carbon uptake rate, based on the difference between light and dark measurements (excluding the two negative values in Table 17), was 2.88 pg carbon/cell/hr (st. err. = 0.47).

There are other examples of high dark uptake rates in tropical algae. Steven (1971), reported high dark CO₂ uptake during a study of primary productivity at a station located approximately 8 km northwest of the station at which the Gyrodinium sp. used in these measurements were collected. By changing his procedure and starting incubations at sunrise instead of late-morning, dark-bottle counts were drastically reduced, thereby suggesting that dark uptake of inorganic carbon by algae may vary at different times during the diurnal cycle. It is possible that oceanic phytoplankton (including Gyrodinium sp.) may accumulate and store the chemical reduction potential necessary for the dark reactions of photosynthesis and utilize these in the absence of light, much as C₄ plants do (Morris, 1980; Legendre et al., 1983).

The small differences between light and dark uptake rates may have been related to the low light intensities used in the illuminated carbon uptake measurements. The light intensities measured in situ, at the depths that radiolaria with Gyrodinium sp. infestations were collected (2 to 4 m below the surface), fluctuated between 350 and 500 uE/m²/s) (in the photosynthetically active range (PAR) of the visible spectrum) on an average day. In comparison, the light source used in the "light" carbon uptake experiments in the laboratory emitted 60 uE/m²/s) (PAR); i.e. 6 to 8 fold lower than the normal in-situ light regime and this low-intensity light regime may have caused photostress (Prezelin, 1987) and thus, repressed carbon uptake rates. Prezelin and Sweeney (1978) found that light intensities less than 50 to 100 uE/m²/s) had detrimental effects on

various cell functions, including reductions in photosynthetic capacity and rates of dark respiration in Gonyaulax polyedra.

The volume specific uptake rate of Gyrodinium sp. (average cell volume = $954 \text{ } \mu\text{m}^3$) was $3.02 \text{ pg C/hr/1000}\mu\text{m}^3$. This value is very close to the volume specific carbon uptake rate of another dinoflagellate, Gonyaulax tamarensis, grown in nutrient replete conditions at $58 \text{ } \mu\text{E/m}^2/\text{s}$ (PAR); $3.08 \text{ pg C/hr/1000}\mu\text{m}^3$ (Langdon, pers. comm.). Rivkin and Seliger (1981) measured the carbon uptake rates of several temperate estuarine dinoflagellates and from their results, I calculated a mean uptake rate of $4.33 \text{ pg C/hr/1000 } \mu\text{m}^3$ for two species of Gymnodinium and two species of Gonyaulax. The light intensities used in their (Rivkin and Seliger, 1981) incubations, 80 and $210 \text{ } \mu\text{E/m}^2/\text{s}$ (PAR), were higher than the intensity used by Langdon (pers. comm.) and in my measurements and this difference in irradiance energy may explain their slightly higher results.

Although they seem to fix carbon at rates comparable to other phototrophic dinoflagellates, thin sections of Gyrodinium sp. (Chapter 2) reveal very little osmiophilic storage material within the cell. Aside from the starch caps deposited around the pyrenoid, there is very little evidence of cytoplasmic starch granules or lipid droplets which normally indicate that growth conditions are favorable for photosynthesis (Dodge, 1973). In light of the apparent contradiction between substantial carbon uptake rates and meager reserve materials, it is possible that small organic molecules stored in vacuoles or elsewhere were not detected owing to their lack of stain.

B. Uptake of Carbon From Radioactively-labelled CR

It is becoming increasingly obvious that many of the aquatic protozoa that were previously considered autotrophic or heterotrophic are actually mixotrophs (Pfeffer, 1881), capable of both modes of nutrition and there are many examples of mixotrophy among the dinoflagellates (see Gaines and Elbrachter, 1987). In order to examine the possibility that Gyrodinium sp. may feed on organic carbon sources in the radiolarian microcosm, I incubated this dinoflagellate in the dark with radioactively-labelled colonies. The results of these "heterotrophy" experiments, presented as DPM/dinoflagellate/hour, showed that there is carbon uptake in the dark. However, I could not convert the DPM to carbon uptake rates because it is not clear what the dinoflagellates feed on nor how the

isotope becomes distributed within the labelled CR (Conover and Francis, 1973).

The "heterotrophic" uptake experiments were done to examine the ability of Gyrodinium sp. to take up organic substrates from the radiolarian microcosm. Although radioactively-labelled CR were washed 3 times in "cold" seawater following labelling and prior to incubations with Gyrodinium sp., I did not determine whether the incubation medium contained H^{14}CO_3 at the end of each experiment, as a result of CR respiration. H^{14}CO_3 may also have become entrained within the CR gelatin during the initial labelling and gradually leaked out during dark incubation of the dinoflagellates with CR.

The results of a recent experiment using 5 radioactively-labelled CR indicate that both organic and inorganic carbon compounds are released from the radiolaria to the surrounding water. In light of results from the previous set of experiments (light and dark fixation of inorganic carbon by Gyrodinium sp.), it is likely that part of the carbon fixed by the dinoflagellates in the "heterotrophic" uptake experiments was inorganic carbon. However, this does not necessarily preclude the osmotrophic uptake of organic carbon.

Ultrastructural evidence supporting osmotrophy is presented in Chapter 2. Close inspection of the girdle region of Gyrodinium sp., near the point of flagellar insertion to the body, shows invagination (Chapter 2, Figures 21 and 23) which may be evidence of pinocytotic activity. In order to verify that these invaginations are related to osmotrophy, it is necessary to use electron dense marker particles, such as colloidal gold or ferritin (Anderson, pers. comm.).

Most dinoflagellates, especially the phototrophs, do not feed osmotrophically, mainly because they cannot compete for DOM with planktonic bacteria (Gaines and Elbrachter, 1987; Richardson and Fogg, 1982), however, environments which contain high levels of DOM might support osmotrophic growth (e.g. Cryptocodinium cohnii which is cultured on rotting seaweed (Kinne, 1977); or in organically enriched culture media (Gold and Baren, 1966)). Although I have not measured this, it is possible that CR release large quantities of DOM which would attract osmotrophic protozoa and bacteria. The abundant populations of very large bacteria found on the surfaces of CR rhizopodia (Chapters 2 and 4) suggest the microenvironment around the colony is very nutrient rich.

Another mechanism that may help explain the uptake of radioactive carbon by Gyrodinium sp. in the "heterotrophy" experiments is food-scavenging from the host CR (Gaines and Elbrachter, 1987). The association of Gyrodinium sp. with radiolarian rhizopodia is very similar in appearance to that of Amphidinium cf. phaeocysticola Lebour with the spines of the planktonic foraminiferan Globigerinoides sacculifer (Gaines and Elbrachter, 1987). Both Elbrachter (pers. comm.) and Spero (pers. comm.) noted that the associated dinoflagellates scavenged food from the foraminiferan spines. TEM examination of Gyrodinium sp. on surfaces of colonies collected near Curacao suggests they do not feed phagocytotically, but this may not be true for all Gyrodinium sp. populations. Unfortunately I do not have TEM data from the dinoflagellates collected near Barbados (where the heterotrophic uptake studies were carried out) to support or refute the Curacao data.

In order to estimate the potential contribution of Gyrodinium sp. to autotrophic carbon fixation in the CR microcosm, I have assumed that a hypothetical CR has 300 central capsules (Swanberg, 1979) and each central capsule has 30 endosymbionts (Anderson, 1983). If the average endosymbiont fixes 20 pg carbon/hr (Anderson, 1980) at a constant rate, during 10 daylight hours, the total CR carbon assimilation = 1.8 ug carbon/day, while the average Gyrodinium sp. fixes 89 pg carbon/10 daylight hours. The abundances of Gyrodinium sp. vary among different colonies and I have observed between a handful to an estimated 40,000 cells per CR. Therefore, 5000 Gyrodinium sp. would fix a minimum of 0.44 ug carbon/day (using the inorganic carbon uptake rates presented above), whereas 20,000 Gyrodinium sp. may fix 1.76 ug carbon/day; roughly the same daily production rate as the radiolarian endosymbionts in this model. Although additional work is needed to clarify the feeding behavior of Gyrodinium sp., the results presented here suggest that this dinoflagellate may play an important role in the flow of carbon through the radiolarian microcosm, especially when abundances of Gyrodinium sp. on CR are high.

SUMMARY

Gyrodinium sp. incorporated inorganic carbon in both illuminated and dark conditions in a series of light/dark incubations using sterile seawater with radioactive bicarbonate. The dark uptake

is not a result of bicarbonate adsorption to the cell and the underlying dark uptake mechanism is not known. The differences between light and dark uptake rates were small but generally greater than zero, suggesting that the dinoflagellate fixes carbon by photosynthesis. The mean volume-specific carbon uptake rate (light - dark uptake) of Gyrodinium sp. was 3.02 pg carbon/hr/1000 μm^3 ; almost identical to the uptake rate of Gonyaulax tamarensis, 3.08 pg carbon/hr/1000 μm^3 that was cultured at a similarly low light intensity (60 $\mu\text{E}/\text{m}^2/\text{s}$ (PAR); Langdon, pers. comm.). The low carbon uptake rate of Gyrodinium sp. was probably due to the low light levels that were used during these incubations since in situ light levels are normally 6 to 8 times greater. Gyrodinium sp. were also incubated in the dark with radioactively-labelled CR to determine if the dinoflagellates can take up radioactive label from the radiolarian. Low levels of the radioactive tracer were found in the dinoflagellates recovered during these experiments, however, it is not clear whether Gyrodinium sp. took up radioactively-labelled organic carbon released by the radiolarian or whether the dinoflagellates fixed $^{14}\text{CO}_2$ that was released by the colony.

Although Gyrodinium sp. is one of the smaller members (average cell volume = 954 μm^3) in the CR microcommunity, abundances of this dinoflagellate often exceed 10,000 cells/CR. Estimates of the carbon fixed by such dense populations of algae suggest it may play an important role in the production and flow of carbon and energy through the CR microcosm.

Table 16. Uptake of inorganic carbon by Gyrodinium sp. (dino) in illuminated (60 uE/m2/sec) and dark conditions, using radioactive bicarbonate. Mean uptake rates (DPM/dino/hr) were calculated by subtracting the mean filter blank DPM (See Appendix A) from the total DPM per scintillation vial (scint. vial) and dividing by the number of dinoflagellates/vial.

Date	Volume of Incubation Medium (ml)	Duration of Experiment (hr)	Concentration of ¹⁴ C-bicarbonate (uCi/ml)	Treatment	Inorganic Carbon Uptake Rate		Mean # of dinos per scint. vial (# of scint. vials counted)
					mean	DPM/dino/hr +/- s.e.	
3/28	1	3.5	10	light	5.58	1.22	5.8 10.0
				dark	3.90	0.43	5.0 2.0
3/29	10	5	2	light	3.22	0.91	5.3 3.0
				dark	2.62	0.71	3.3 4.0
4/1	3	4.5	5	light	0.91	0.22	6.2 6.0
				dead	0.05		2.5 2.0
				dark	0.05		7.0 2.0
4/6	3	6.5	5	light	1.33	0.12	21.4 7.0
				dark	1.67	0.20	6.3 3.0
4/9	3	4	2	light	0.55	0.17	10.0 5.0
				dark	0.56	0.15	6.2 5.0
4/17	3	3.5	2	light	4.75	0.70	7.5 4.0
				dark	2.17	0.18	5.7 3.0
8/14	3	2.5	1	light	0.34	0.06	8.4 5.0
				dark	0.03	0.02	8.3 4.0

Table 17. Summary of light and dark inorganic carbon uptake rates by Gyrodinium sp. All rates are presented as picograms of carbon per dinoflagellate per hour.

Date of Experiment	Carbon Uptake Rate In the Light	Carbon Uptake Rate In the Dark	Difference Between Light and Dark Uptake Rates
3 / 2 8	10.8	7.6	3.2
3 / 2 9	22.8	18.7	4.1
4 / 1	2.5	0.1	2.4
4 / 6	3.6	4.7	-1.1
4 / 9	3.6	3.7	-0.1
4 / 1 7	15.6	14.5	1.1
8 / 1 4	3.6	0	3.6
mean +/- st.err.	8.9 2.9	7 2.7	1.9 0.7

Table 18. Rates of carbon uptake by Gyrodinium sp. associated with radioactively-labelled colonial radiolaria. Mean dinoflagellate carbon uptake rates were calculated by subtracting mean filter blanks (see Appendix A) from total DPM/scintillation vial (scint. vial) and dividing by the number of dinoflagellates per vial. DPMs measured in host CR were converted to ug C/CR Because They represent photo-synthetic carbon uptake by the radiolarian colony. The uptake of radioactive carbon by Gyrodinium sp. cannot be converted from DPM to a carbon uptake rate Because the specific activity of the tracer within the CR was not determined (n.d.).

Date	Duration of Experiment (hr)	Photo-synthetically Fixed Carbon in Host CR DPM (ug C/CR)	Mean Rate of Carbon Uptake by Gyrodinium sp. DPM/dino/hr +/- s.e.	Mean # of dinos per scint. vial (# scint. vials counted)
3/30	2.5	66183 0.36	2.6 1.0	9.5 2.0
4/2	5	138398 0.1	0.0 0.0	10.8 4.0
4/17	3.5	n.d.	2.7 0.9	5.2 6.0
8/29	15	27587 0.38	0.6 0.1	8.8 6.0

Table 19. Leakage of carbon from radioactively-labelled colonial radiolaria. After three 10-minute rinses in "cold" seawater, each of the labelled colonies was incubated in "cold" seawater in the dark for 4.5 hrs. At the end of the incubation, 200 ul aliquots of the surrounding seawater were tested for presence of organic and inorganic radioactive carbon by comparing between the DPM of acidified and non-acidified samples. Background DPM = 27.89. Counting time was set at 100 min per sample.

CR	DPM colonial radiolarian	DPM seawater before acidification	DPM seawater after acidification	DPM seawater inorganic carbon	DPM seawater organic carbon
<i>Sphaerozoum punctatum</i>	4955.88	58.74	37.55	21.19	9.66
<i>Sphaerozoum punctatum</i>	2382.89	38.64	28.39	10.25	0.5
<i>Collosphaera huxleyi</i>	3149.13	57.42	33.98	23.44	6.09
<i>Collosphaera huxleyi</i>	6221.84	79.11	50.82	28.29	22.93
<i>Collosphaera huxleyi</i>	10532.11	55.34	36.4	18.94	8.51
mean				20.62	9.54
st. err.				2.78	3.31

Chapter 6

THE UPTAKE OF CARBON BY HYPERIID AMPHIPODS ASSOCIATED WITH COLONIAL RADIOLARIA

INTRODUCTION

Hyperiid amphipods have been observed among most of the oceanic gelatinous zooplankton (Laval, 1974; Harbison et al., 1977; Madin and Harbison, 1977; Harbison et al., 1978). Although many of the zooplankton hosts (e.g. siphonophores, medusae) are predators that normally feed on crustacean prey, the hyperiids are apparently immune to the hunting apparatus of the host (Laval, 1980). After examining the morphologies of gammarid (benthic) amphipods, and comparing these to the hyperiids, Pirlot (1932) proposed that the hyperiid amphipods evolved from a benthic ancestor and adopted a similar way of life in the planktonic environment by parasitizing gelatinous zooplankters. This hypothesis is supported by the observation that almost all of the known hyperiid amphipods are associated with gelatinous zooplankton at some stage of life (Laval, 1980). Laval does not consider the hyperiids true parasites, but chooses instead to call them "parasitoids" (a term borrowed from entomology; Askew, 1971) because their relationship with the host changes when they reach the adult stage. During the juvenile and post-juvenile stages, the amphipods behave as parasites, but once they reach the adult stage, many of the hyperiids prey upon their former hosts (Laval, 1980).

Several species of hyperiid amphipods, including Oxycephalus sp., Lestrigonus sp., Brachyscelus sp. and several different species of Hyperietta, have been observed among the colonial radiolaria (Brandt, 1885; Harbison et al., 1977; Swanberg, 1979; Chapter 2, this thesis). In general, there was not a noticeable selectivity of amphipods for specific host species, however it was noted that most of the the Hyperietta spp. were exclusively associated with CR (Harbison et al., 1979; Swanberg and Harbison, 1980). Although juvenile amphipods are not very active inside the colonies, larger, more developed individuals have been observed feeding on radiolarian central capsules (Brandt, 1885; Swanberg, 1979). Because

these observations have been the only clear examples of predation on colonial radiolaria, I chose to examine the predation process quantitatively and to determine if the juvenile amphipods also feed on radiolarian carbon.

The following studies were done to assess the flow of carbon through the CR hosts and to estimate the proportion of this carbon that was assimilated by the associated hyperiid amphipods. Carbon uptake by the amphipods was quantitatively estimated from measurements of 1) amphipod respiration, 2) amphipod uptake of ^{14}C from radiolaria with ^{14}C -labelled endosymbionts and, 3) reduction in numbers of living radiolarian central capsules in a colony over time due to amphipod ingestion.

MATERIALS and METHODS

Colonial radiolaria and associated amphipods were hand-collected by SCUBA divers (see chapter 1) during 7 field trips (Table 20; see also Figure 1). CR were usually examined within two to three hrs. of collection and the number of amphipods in each parasitized colony recorded. Colonies and/or their amphipod parasitoids were then used for the observations and experiments described below.

A. Amphipod Respiration

Amphipod respiration rates were determined by measuring the combined (gross) respiration rates of amphipods and their CR host, and subsequently subtracting empirically produced estimates of CR respiration rates that were derived from Figure 35 (see below). Amphipods were allowed to remain within intact colonies to simulate their normal microenvironment. Furthermore, if amphipods were removed from the colony, the hydrophobic nature of their exoskeleton caused them to become trapped in the air-water interface; in their struggle to descend below the surface, their activity rose many fold above the level observed inside the colony. Laval (1980) noted that metabolic rates of hyperiid amphipods may be higher than normal in animals that had been stressed by removal from their hosts.

Oxygen consumption by infested colonies was measured by placing the colonial radiolaria in special air-tight tubes (1 colony per tube) filled with sterile seawater (Swanberg et al., 1986). The

amphipod-infested colonies selected for these respiration measurements contained neither viable prey nor noticeable protozoan infestations which would affect the respiration measurements. However, it is possible that bacteria on the surfaces of these otherwise "clean" colonies may have influenced the measured rates. These tubes and three control tubes, which contained only sterile seawater, were wrapped with aluminum foil to eliminate light and incubated in a Haake FK2 constant-temperature circulating bath set at ambient seawater temperatures (25°C to 28°C) for periods of three to 5 hrs. All respiration rate experiments were carried out in the late evening and night hours, generally between 8 p.m. and 2 a.m. to minimize disruption of endogenous rhythms of endosymbiont primary productivity and respiration of radiolarian cells and amphipods. At the end of the incubations, the concentration of residual dissolved oxygen in each tube was measured by the Winkler method (Strickland and Parsons, 1972) which was modified for micromolar oxygen levels (Swanberg et al., 1986). Residual dissolved oxygen values were subtracted from the mean oxygen concentration that was calculated from the sterile seawater controls. These differences were divided by the incubation times to yield gross radiolarian respiration rates (ul oxygen/hr).

To calculate the net amphipod respiration rate, the net radiolarian respiration rate (NRR) was subtracted from the gross value. The NRR was calculated by multiplying the number of radiolarian cells per colony by the mean oxygen consumption rate (OCR) per cell. The mean OCR per cell was determined by plotting the respiration rates of 29 amphipod-free colonies against the number of cells per colony and calculating the regression equation for this curve (Figure 35). Although there was considerable variability in the number of cells per colony, most colonies were similar in size, ranging from 8 to 18 mm in length. The 29 colonies investigated consisted of radiolaria from both the Collosphaerid and the Sphaeroid families; physiological differences among different CR taxa probably accounted for some of the variance in the respiration data ($R^2 = 0.41$). Another factor which may have contributed to the variability in respiration rates within and among species was the number of endosymbionts within each colony. I did not record the concentration of endosymbionts in the colonies and it is very likely that the variance among the respiration rates would have decreased if the symbiont respiration had been taken into account. Although the correlation coefficient ($R = 0.64$) is relatively low, there is a

significantly positive relationship ($P < 0.1$) between the number of cells and CR respiration rate (Campbell, 1974).

Amphipod respiration rates were converted from moles oxygen/hr to grams carbon/hr to facilitate a comparison between respiratory carbon uptake and the rates measured by the two methods described below. The following conversion equation was used :

$$\text{moles O}_2 \text{ respired} \times 12 \text{ g carbon/mole} \times \text{RQ} = \text{g carbon consumed}$$

RQ, the respiratory quotient (CO_2 released/ O_2 consumed) is determined by the quality of the food that is consumed and respired by the animal (Parsons et al., 1979). Although it was not confirmed in these experiments, I have assumed that the amphipods inside the colonies feed on radiolarian carbon. Anderson et al. (1983) found that a major part of the biomass of a Collosphaera huxleyi colony consisted of protein; therefore, an $\text{RQ} = 0.8$ (appropriate for proteins) was used (Prosser and Brown, 1961). I did not work exclusively with C. huxleyi, but many of the unidentified colonies (see Table 21) had the appearance of Collosphaeridae (colonies with siliceous skeletons surrounding the cells). Both Acrosphaera spp. and Collosphaera spp. belong to the Collosphaeridae which have a high content of cellular protein (Anderson, 1983). Unidentified colonial radiolaria were assumed to have a chemical composition similar to C. huxleyi.

B. Radio-isotopically Measured Carbon Uptake (RMCU)

Amphipod-infested colonies were rinsed three times with sterile seawater to eliminate foreign microplankters before incubation in clear plastic flasks containing radioactively-labelled bicarbonate in sterile SW. The volumes of the incubation media ranged from 14 ml to 100 ml with the ratio of colony volume to surrounding medium always set at 1:100 or more to minimize containment artifacts. The final concentrations of the ^{14}C -Na-bicarbonate used in these experiments ranged from 0.6 to 2.0 $\mu\text{Ci/ml}$ and the calculated specific activities ranged between 0.2 and 0.5 mCi/mmole . The specific activity of the radioactive bicarbonate was determined by setting up a third flask with non-radioactive, sterile seawater in which total CO_2 concentration was measured by the method of Strickland and Parsons (1972). The flasks were maintained at room temperature (25°C) and illuminated by a "Cool White" fluorescent light bank which delivered $60 \text{ uE/m}^2/\text{sec}$ with a

light/dark cycle of 12/12. Control samples consisted of free amphipods (removed from the host colonies just prior to incubation) incubated under the same conditions as described above. These controls tested the ability of the animals to take up inorganic carbon from the water.

All flasks (controls and amphipod-infested colonies) were incubated for 24 to 26 hrs, whereupon the amphipods were removed from the colonies and controls, placed on 0.45 μ m Millipore HA filters and washed several times with filtered seawater. Next, the amphipods were acid fumed for 30 min over concentrated HCl, briefly oven-dried (60°C for 20 min) and transferred with the filters to mini-scintillation vials which were filled with 4 ml of Eco-Lite (WestChem Inc, CA) scintillation fluor. The ^{14}C -labelled radiolarian hosts were treated as above and all samples were counted in a liquid scintillation counter. Conversion of CPM to DPM was done with an external standard and DPMs were converted to carbon by dividing by the specific activities of the incubation media. Net carbon consumption rates were calculated by subtracting the mean carbon uptake of the control amphipods from the carbon uptakes of the amphipods that were removed from the colonies and dividing this by the incubation time.

The duration of these experiments was longer (24 to 26 hrs) than for the respiration measurements (3 to 5 hrs) in order to allow sufficient time for the transfer of radioactive carbon from seawater, through several different carbon pools within the colony (Anderson et al., 1985) and finally to the hyperiid amphipods.

C. Consumption of CR Cells by Amphipods

The rate at which amphipods consume CR cells was determined by observing the decrease in total number of intact central capsules over a period of 2 days. The amphipod-infested CR were observed 5 or 6 times during the 2 day period and after each examination, the colonies were returned to the seawater-filled glass jars in which they were originally collected. Between examinations, the jars were kept at room temperature (25°C) and placed in front of a fluorescent white-light bank which provided 60 $\mu\text{E}/\text{m}^2/\text{sec}$ on a 12/12 light/dark cycle. Several amphipod-free colonies were observed for two to 4 days and the number of central capsules did not change, therefore, I concluded that the reduction in number of intact central capsules was the result of amphipod feeding.

The measured feeding rates were converted to carbon consumption rates by multiplying the carbon content of a central capsule by the number of cells consumed over a given period of time. The carbon content of a central capsule was measured in the following manner. Central capsules were separated from uninfested colonies by repeatedly passing the colonies through a clean pasteur pipet. Attached rhizopodia and extra-cellular "debris" were further removed from the cells by passing the isolated cells through successively smaller drawn-out pipets and finally, depositing the cells in filtered (0.45 μ m Millipore) seawater. These cells were then collected on precombusted quartz-fiber-filters, dried for 12 hrs at 60°C and frozen desiccated until analyzed. Cells were analyzed for elemental carbon content using a Carlo Erba NA 1500 C and N elemental analyzer.

At the end of each experiment, amphipods were removed from the colonies, preserved in 4% buffered formalin and subsequently identified to species using the descriptions of Bowman (1973).

Measurement of Amphipod Length

Lengths of hyperiid amphipods inside CR were measured with the aid of an ocular micrometer. When the amphipods were seen in a "stretched out" position, it was easy to measure the body length directly, from the uropods to the tip of the head. Often, however, the amphipods were arched which made direct measurement difficult and inaccurate. In these situations, I measured the distance between the two ends of the body and sketched the general shape of the amphipod on paper. From this, I was able to calculate the length of the arc that runs from the tip of the head to the ends of the uropods.

RESULTS

The number of colonial radiolarians infested with amphipods generally did not exceed 15% of the colonies in a given population (Table 20). The overall average infestation rate calculated from radiolarian colonies at 159 stations was 7.15% (st. err. = 1.87), but on occasion, populations with more than 40% infestation were encountered. Amphipod infestation rates were generally higher among Caribbean populations than among "oceanic" radiolaria collected during cruises (Chapter 2), but there was no obvious relationship between high infestation rates and season.

A. Amphipod Respiration

Amphipod respiration rates are presented in Table 21. The mean amphipod carbon demand based on respiration rate was 19 ng carbon/day/amphipod (st. err.=3). Most of the respiration data are mean values that were calculated from colonies which had more than 1 amphipod within them. The daily carbon demand, as estimated solely from respiratory requirements, was quite similar among the animals measured. The amphipods taken for the respiration experiments ranged between 0.75 and 1.20 mm in length, thereby probably including both juvenile and post-juvenile individuals (Swanberg, pers. comm.), however no significant relationship ($R^2 = 0.28$) was found between animal length and respiration rate. It was also unclear whether the taxonomic identity of the host colony had any bearing on the amphipod respiration rates. Many of the amphipod-infested colonies taken for respiration measurements (see Table 21) could not be identified to species (see comments on "unidentified species" in Chapter 1).

B. Radio-isotopically Measured Carbon Uptake (RMCU)

Amphipods used in the ^{14}C uptake experiments (RMCU) were similar in size to one another (mean length = 0.74 mm, st. err. = 0.02). The Fisher-Behrens test for comparison between the means of samples with different variances (Campbell, 1974) was applied to the data to compare the gross carbon uptake rates of amphipods in radiolaria with those of carbon uptake rates by control amphipods. The differences between the experimental and control uptake rates were significant ($P < 0.01$). Net carbon uptake rates were calculated by subtracting the average carbon uptake measured for living "control" amphipods from the gross uptake rates. Although the amphipods used in these experiments were of similar body lengths, there was considerable variability in net carbon uptake rates (see Table 22), from 35 to 310 ng carbon/day/amphipod. The mean net carbon uptake rate was 147 ng carbon/day/amphipod (st. err. = 54).

C. Central Capsule Consumption

Most of the colonies in which central capsule (cc) consumption was observed belonged to the family Collosphaeridae Muller, 1858. The ccs of the Collosphaeridae are surrounded by siliceous shells; which appear slightly opaque when intact, yet clearly translucent when empty of protoplasm (i.e. consumed, see Figure 36). This

morphological feature facilitated counting "consumed" ccs in the parasitized colonies. Although cytoplasmic depletion may be due to natural cell death inside the colonies (Anderson, pers. comm.), empty shells were usually observed within colonies that showed evidence of amphipod activity.

Consumption rates were calculated for three amphipod-infested colonies by recording the decrease in number of intact radiolarian central capsules at 5 intervals spaced over a period of two days. Average cc consumption rates presented in Table 23 were based on regression equations calculated from the plots of "number of consumed central capsules" versus time. The correlation coefficients of the regression equations were 0.83 for the amphipods in the A. spinosa colony and 0.96 and 0.97 for the amphipods in each of the Collosphaera sp. colonies. The average carbon uptake rate based on cc ingestion was 964 ng carbon/day/amphipod (st. err. = 174).

In addition to ingestion of the cytoplasmic contents of the central capsules, amphipods often consumed algal endosymbionts that were associated with the ccs. It is not clear to what extent these endosymbiotic algae were digested because several amphipod fecal pellets emitted a pale red autofluorescence (indicative of either chlorophyll or one of its breakdown products, e.g. phaeophytin) when they were examined by epifluorescence microscopy.

The majority of amphipods that were observed on the surface and inside colonies did not consume central capsules during a given observational interval. In several cases, however, I found empty radiolarian shells and/or amphipod fecal pellets inside CR and severe rhizopodial damage that was probably caused by invading amphipods (see Table 24). These observations suggested that there were more central capsule consuming amphipods among the radiolaria than I had directly observed, but the amphipods had evidently left the CR at some point prior to my inspection.

DISCUSSION

It is somewhat surprising to find that colonial radiolaria seem not to be consumed by any of the potential predators in the surface waters of the open ocean. The scarcity of known predators may, however, be due to ignorance on our part because the workers who

have analyzed the gut contents of oceanic fishes probably did not attempt to identify the remains of radiolarian shells (if present) in their specimens.

Colonial radiolaria appear relatively defenseless since they are readily seen yet cannot swim nor sink rapidly to escape from large predators. However, there may be something unsavory in their chemical composition (for instance terpenoids, such as those released by zooxanthellae of certain gorgonians, Ciereszko, 1962), since a number of different fishes and an isopod rejected CR after mouthing them (Swanberg, 1979). Furthermore, Strelkov and Reshetnyak (1971) report that fish are "scared away" by the gelatin of the CR and actually avoid the colonies.

Although this passive form of defense seems to deter most predators, several different hyperiid amphipods, including Hyperietta sp. (observed by Harbison et al., 1977, and Swanberg, 1979), Streetsia porcella (studied by Harbison et al., 1977), Oxycephalus clausi (reported by Harbison et al., 1978), Lestrigonus sp. and Brachyscelus sp. (both observed by Swanberg, 1979) are apparently resistant or immune to the chemical deterrents and are thus able to feed on the colonial radiolaria. Furthermore, the hyperiids possess a waxy cuticle (Laval, 1980) which probably provides them with protection against radiolarian feeding rhizopodia that successfully capture and digest most other small crustaceans. Swanberg (1979) recorded the association of several other small invertebrates with CR, however, none of these observed were actually feeding on the radiolaria. As the only predators of colonial radiolaria, hyperiid amphipods probably benefit from a lack of competition for food. They would also increase their fitness by depositing juveniles in the presumably unpalatable colonies, thus providing the non-swimming young with protection from potential planktonic predators.

A. Amphipod Respiration

The weight specific respiration rates of several planktonic crustaceans are shown in Table 6 and highlight the great difference between Hyperietta spp. and other similar invertebrates with respect to metabolic rates. All of the cited respiration rates were determined by measuring oxygen consumption. The weight specific respiration rates quoted from other sources were adjusted to theoretical values at 25°C by assuming $Q_{10} = 2.0$ (Parsons et al., 1979). Q_{10} values are

rarely constant over the temperature range 5° to 25°C (Mantel, pers. comm.), therefore, I have used this value only as a means to demonstrate that the measured respiration rates of hyperiid amphipods associated with CR were very low in comparison to other planktonic crustacea.

Daily carbon consumption rates based on amphipod respiration measurements were lower than the consumption rates measured by RMCU, and by amphipods feeding on central capsules, by an order of magnitude or more. Furthermore, the correlation coefficient of the regression equation that was used to predict radiolarian respiration from the number of central capsules per CR (Figure 35) was not high ($R = 0.64$), and it is possible that the use of this equation underestimated the amphipod respiration rate. Because of the above and the observation that weight specific respiration rates of Hyperietta spp. were more than an order of magnitude lower than the respiration rates of various planktonic crustacea (Table 25), I consider these rates underestimates of the hyperiid carbon demand.

The experimental design of the respiration measurements may also have caused an artificial decrease in amphipod metabolism. Amphipod-infested colonies were incubated in the dark to prevent photosynthetic evolution of oxygen by the algal endosymbionts. This dark incubation may have induced a behavioral or a physiological response in the amphipods. Marshall and Orr (1972) and Fernandez (1977) found that the respiration rates of Calanus spp. and other planktonic copepods declined dramatically when the animals were transferred from lighted conditions to the dark. It is possible that the hyperiid amphipods respond in a similar manner, by respiring more slowly in the dark. A dark-induced reduction in amphipod respiration rate may also be related to available oxygen within the colonies. Animals that normally inhabit oxygen-saturated environments may alter their respiration rates in proportion to the available oxygen level (Prosser, 1973). This has been observed with Calanus finmarchicus (Marshall et al., 1935) and with two mysids (Jawed, 1973); all are free-living plankters. Although the intra-colony oxygen concentration was not measured, hyperiid amphipods embedded within CR probably experience oxygen-rich conditions during the daytime due to symbiont photosynthetic activity, and oxygen stress at night, when photosynthesis does not compensate for the combined respiration of radiolarian and associated amphipods.

B. Carbon Uptake Measured By RMCU

Although most amphipods did not feed directly on radiolarian central capsules, the results of several tracer experiments (radioisotopically measured carbon uptake, RMCU) indicate that they were consuming photosynthetically-fixed carbon. Colonial radiolaria were labelled by inducing the photosynthetic uptake of ^{14}C by the algal endosymbionts. Therefore, the uptake of this isotope by the amphipods reflects their consumption of endosymbiont primary production. The ratio of mean amphipod carbon uptake rate (147 ng/day) divided by the mean CR carbon uptake rate (1.23 ug/day) is 12%, suggesting the amphipods are significant consumers of the primary productivity in the CR microcosm. However, because we do not know precisely what the amphipods consume in the CR, it is not possible to calculate the amount of radiolarian carbon this uptake represents. We can only analyze the amount of photosynthetically fixed carbon that is consumed.

The amphipods used in the RMCU measurements were very similar in size (and thus probably in developmental stage as well), however there was considerable variability among their carbon uptake rates (Table 22). The large variance was present both among the amphipods measured on a given date and between the 4 different measurements. This variance may be due to individual differences in amphipod metabolic rates, it may be due to behavioral differences among individuals (within one infested colony, the various amphipods rarely exhibited the same behavior, i.e. some were resting whereas others were active) and it may also reflect differences in physiological state of amphipods taken from different populations. The average carbon uptake rates measured in Curacao were lower than those in Barbados. If amphipods are prudent predators (or well-adapted parasites), their carbon consumption rates may reflect the physiological status of the host colonies; thus consumption rates may be less when the colonies are not "well-fed".

Fecal pellets were observed around many of the amphipods but I did not examine any of these to determine if they contained identifiable remains. The Hyperietta spp. probably ingest rhizopodia or even radiolarian food that is being transported within the colony, but aside from observations of endosymbiont consumption on the part of central capsule-consuming amphipods, I do not have further knowledge of their diet. Harbison et al. (1977) reported that hyperiid amphipods found on gelatinous zooplankters may consume the food

of their hosts and in many cases actually feed on the host tissue. If the amphipods do consume partially digested food of the radiolaria, this carbon uptake would not have been detected in the RMCU measurements because it was not radioactively labelled, thus resulting in an underestimate of carbon uptake. There are two additional factors which may contribute toward underestimation of carbon uptake rates. A) The RMCU is an estimate of the carbon that the amphipod incorporates into its own tissues, but excreted carbon is not accounted for, so the true uptake rate may be higher than presented here. B) The carbon uptake rates were calculated for the full period of time that the infested colonies were incubated in the labelled seawater. Since several hours are probably required to translocate ^{14}C from seawater to amphipods (Anderson, 1983), the measured carbon uptake averaged over the entire incubation period would be an underestimate of the true carbon consumption rate.

C. Central Capsule Consumption

Rates of central capsule consumption by amphipods were measured in only 3 of the 218 infested CR. It might appear, from these data, that amphipod consumption of radiolarian cells is a rare and insignificant event in the amphipod-radiolarian association, however this behavior has also been recorded by Swanberg (pers. comm.). Furthermore, I have found 25 colonies (Table 24), which amphipods had occupied, and then abandoned prior to, or soon after collection. These colonies usually contained amphipod molts and/or amphipod fecal pellets, in addition to remains of central capsules which were presumably eaten by amphipods. It is not clear why some amphipods feed on central capsules while others collected within the same CR population do not appear to do so. One factor that may influence the feeding behavior of hyperiids is the nutritional status of the host (Harbison et al., 1977). If host CR capture sufficient prey, the amphipods could feed solely on the radiolarian food and would not need to consume radiolarian cells, as observed with Lestrigonus schizogeneois on Phialidium sp. (Laval, 1972).

Laval (1980) referred to hyperiid amphipods as parasitoids of gelatinous zooplankters because the juveniles act as parasites, feeding conservatively on the host tissue. Upon reaching adulthood, feeding increases and the amphipod becomes a predator, often destroying its prey even though it is smaller than the gelatinous host. My observations suggest this pattern is probably also true for the CR-hyperiid amphipod association. Juveniles and young post-

juveniles cannot swim and it would not be an advantageous strategy for them to destroy their source of food and shelter. Although they seem morphologically adapted to surfaces, adult amphipods are capable swimmers and will probably not jeopardize their survival by destroying their hosts. In a similar host-parasitoid association between Sapphirina angusta and Thalia democratica, Heron (1973) found that the fertilized female copepod acts as a predator, often inflicting fatal damage upon the tunicate host whereas juvenile copepods usually feed conservatively until their maturity.

It is possible to estimate the impact of amphipods on CR by comparing the rate of carbon consumption to the amount of carbon contained within a colony and from this to estimate the minimum time required to digest an entire colony. Colonies may contain less than 1 microgram to tens of milligrams of carbon or more, depending on the species and size (Swanberg, 1979; Angel, unpublished). Unless the radiolarian cell division rate (cc division rates have not been determined for colonial radiolaria) surpassed the amphipod cc consumption rate (see Table 23), an amphipod-parasitized colony with few central capsules would be destroyed within a few days. On the other hand, large colonies with hundreds or thousands of central capsules would be less threatened by this cell consumption activity.

On two separate occasions, I collected amphipod-infested CR which appeared healthy. The colonies were initially examined, and then left in the same jars in which they had been originally collected. Upon re-examination, several days later, the amphipods had consumed all of the radiolarian cells. The remains of the colonies were very similar in appearance to the amorphous aggregates known as "marine snow". I propose that this phenomenon of colony destruction occurs in the sea as well and may contribute to the conversion of living colonial radiolaria to marine snow. Microscopic examination of several marine snow samples that were collected in the Gulf Stream and near Barbados has revealed the presence of empty shells of collosphaerid radiolaria, suggesting that colony destruction occurs in situ as well. Furthermore, Harbison et al. (1977) found Hyperietta stebbingi on samples of marine snow. They hypothesized that the marine snow particles were the remains of radiolarian colonies because they had observed H. stebbingi almost exclusively on colonial radiolaria.

There is an interesting limnological parallel to the parasitism of amphipods on CR. A population of Volvox tertius (colonial alga) in

an Australian reservoir was parasitized by Ascomorphella volvocicola (a parasitic rotifer). During the three months that the reservoir was monitored (Ganf et al., 1983), there was a volvox bloom which reached a maximum density of 2.74×10^5 colonies/m², followed soon thereafter by some fluctuation in population density and eventually a collapse. The authors proposed that the population crash was caused by the damage incurred to the algal colonies by the rotifers. There are no records of hyperiid amphipods destroying entire populations of CR, however, high infestation rates have been observed in various parts of the North Atlantic Ocean (Harbison, pers. comm.; Swanberg, pers. comm.) suggesting that the possibility does exist.

SUMMARY

The frequency of amphipod infestation was generally low (overall average = 7%), but in some populations exceeded 40% of the collected CR. The occurrence of amphipod infestations among colonial radiolaria is however, unpredictable, mostly because very little is known about the biology and ecology of the Hyperietta spp. The majority of the associated amphipods were juveniles, and the associated adult amphipods were almost exclusively females. This suggests that the CR are an important element in the life cycle of these crustaceans (Harbison et al., 1977; Swanberg, 1979; Swanberg and Harbison, 1980; Laval, 1980). Respiration rates of Hyperietta spp. were lower, often by an order of magnitude or more, than the carbon uptake rates determined by a) a radioactive tracer experiment (RMCU) and b) the consumption rate of radiolarian central capsules. Weight-specific respiration rates were also an order of magnitude lower than the respiration rates of several other pelagic crustaceans (literature values), therefore, the reported respiration rates were considered underestimates of the true respiration rates. Amphipod uptake of non-central capsule carbon (RMCU) suggests that these crustaceans can feed on more than one type of cytoplasmic structure within the CR, but it is not clear what, aside from central capsules the amphipods eat. Although there are only three estimates of amphipod cell consumption rate, many qualitative observations indicate that this phenomenon is rather common. It is not clear, however, what triggers the adult amphipods to consume radiolarian central capsules. Because only gravid females were observed feeding on the radiolarian cells, this behavior may be related to reproductive activities. As a rule, juvenile amphipods

behave as parasites, consuming carbon at the low rates measured by RMCU. Adult females are either parasites or predators, capable of destroying the colony. The potential impact of central capsule consumption on the radiolarian colony depends on the numerical ratio of amphipods to radiolarian cells; colonies with few cells are at much greater risk than large colonies with hundreds or thousands of cells. Although more data and measurements are needed to make conclusive statements, this study suggests that the small hyperiid amphipods associated with CR may represent an important sink of radiolarian production.

Table 20. Summary of amphipod infestation rates in CR collected during 7 field trips.

Field Station or Cruise	Mean Number of CR Collected per Dive (+/- st. err.)	Mean % of CR with Amphipods (+/- st. err.)	Range of Amphipod Infestation Rates (%)
R.V. Cape Florida 85-14 Oct/Nov 1985	22.77 (3.49)	0.23 (0.16)	0-2
Barbados Mar/Apr 1986	27.55 (2.87)	15.67 (2.92)	0-43
R.V. Oceanus 176 May/June 1986	22.52 (2.73)	8.64 (2.53)	0-37
R.V. Oceanus 177 Aug 1986	12.18 (1.15)	4.1 (1.27)	0-43
Barbados Mar/Apr 1987	35.13 (3.43)	3.64 (1.14)	0-16
R.V. Oceanus 191 Jul 1987	15.42 (1.69)	5.63 (2.19)	0-33
Curacao 1988 Mar 1988	34.28 (3.73)	12.11 (4.36)	0-33

Table 21. Amphipod respiration rates and respiratory carbon demand. Carbon demand was calculated by converting the oxygen consumption rate to nmole O₂ and multiplying by a respiratory quotient (RQ=0.8) and the molecular weight of carbon. (st. err. = standard error)

Colonial Radiolarian	Number of Amphipods per Colony	Average Amphipod Length (mm)	Amphipod Respiration Rate (nl O ₂ /hr/amphipod)	Amphipod Carbon Demand Estimated from Respiration Rate (ng carbon/day/amphipod)
<i>Acrosphaera</i> sp #1	8	1	0.95	10.37
<i>Acrosphaera</i> sp # 2	9	0.9	3.45	37.7
<i>Sphaerozoum</i> sp # 1	3	1.2	0.93	10.15
<i>Sphaerozoum</i> sp # 2	5	1.1	1.16	12.67
unidentified colony # 1	1	1.1	1.4	15.29
unidentified colony # 2	1	0.75	1.3	14.21
unidentified colony # 3	8	0.95	2.36	25.8
unidentified colony # 4	6	1.2	1.28	13.99
unidentified colony # 5	10	1	3.48	38.04
unidentified colony # 6	9	0.85	1.33	14.52
unidentified colony # 7	5	1.2	1.3	14.21
unidentified colony # 8	1	1.1	1.57	17.16
unidentified colony # 9	3	0.9	2.47	27
Mean		1.01	1.77	19.32
st. err.		0.04	0.23	2.57

Table 22. Radioactive carbon uptake by amphipods embedded inside colonial radiolaria (RMCU). Radiolaria with amphipod infestations were incubated in illuminated (60 uE/m2/sec) radioactively-labelled seawater for 24 - 26 hrs (light/dark cycle = 12/12) to determine the rate of carbon uptake by the amphipods. (st. err. = standard error)

Field Station Date	Number of Amphipods Tested	Average Amphipod Length (mm) (+/- st. err.)	ug Carbon Fixed by CR symbionts	Amphipod Carbon Uptake (ng/day/amphipod) (+/- st. err.)
Barbados 4/16/87	3	(0.78) (+/- 0.03)	1.72	310 (+/- 61)
Barbados 8/28/87	4	(0.70) (0.00)	0.56	178 (+/- 16)
Curacao 4/1/87	5	(0.79) (+/- 0.03)	1.28	35 (+/- 14)
Curacao 4/9/88	10	(0.69) (0.02)	1.36	64 (+/- 8)

Mean Amphipod Carbon Uptake = 147 ng/day/amphipod (st. err. = 54)

Mean Amphipod Length = 0.74 mm (st. err. = 0.02)

Mean Amount of Carbon Fixed by CR symbionts = 1.23 ug Carbon/CR (st. err. = 0.24)

Mean Carbon Uptake by Control-Amphipods = 37 ng/day/amphipod (st. err. = 12)

Table 23. Amphipod consumption of radiolarian central capsules (cc). The rate of central capsule consumption was determined by observing the reduction in number of intact ccs over a period of two days. carbon consumption rates were calculated by multiplying central capsule Ccarbon content (ng) by the cc consumption rate. Carbon content of *Acrosphaera spinosa* = 91 ng/cc; carbon content of *Collosphaera* sp. = 30 ng/cc.

Field Excursion	Colonial Radiolarian	Number of Amphipods per CR	Amphipod Species	Average Amphipod Length (mm)	Number of Central Capsules Consumed per Amphipod/hr.	Carbon Uptake Rate (ng carbon/day/amphipod)
R.V. Cape Florida 85-14 (Nov 1985)	<i>Acrosphaera spinosa</i>	3	<i>Hyperietta</i> sp.	1.4	0.6	1310
Curacao 1988 (Apr 1988)	<i>Collosphaera</i> sp.	1	<i>Hyperietta stephenseni</i>	1.8	1.4	1008
Curacao 1988 (Apr 1988)	<i>Collosphaera</i> sp.	1	<i>Hyperietta stephenseni</i>	1.6	0.8	576
Mean				1.6	0.9	965

Table 24. Correlations between amphipods in colonial radiolaria and empty radiolarian central capsules (cc).

Field Excursion	Colonial Radiolarian	Ratio of Consumed-ccs/Total ccs	Evidence of Amphipod Activity
Barbados 1986	<i>Siphonosphaera</i> sp.	13/95	5 amphipod fecal pellets
"	<i>Collosphaera</i> sp.	3/51	large entry hole in CR
"	<i>Siphonosphaera</i> sp.	several empty shells	large entry hole in CR
"	<i>Collozoum</i> sp.	14/137	Several fecal pellets
"	<i>Siphonosphaera</i> sp.	23/202	large entry hole in CR
"	<i>Siphonosphaera</i> sp.	80/300	large entry hole in CR
"	<i>Collozoum inerme</i>	5/83	3 amphipod molts
"	<i>Collosphaera</i> sp.	32/200	amphipod present
"	<i>Siphonosphaera</i> sp.	9/250	amphipod fecal pellets
R.V. Oceanus 176	<i>Acrosphaera spinosa</i>	129/514	1 amphipod present
"	<i>Collozoum pelagicum</i>	30/65	4 amphipods present
"	<i>Collosphaera</i> sp.	5/124	none
"	<i>C. pelagicum</i>	28/153	1 amphipod present
R.V. Oceanus 177	<i>A. spinosa</i>	6/45	2 amphipods present
"	<i>C. inerme</i>	5/181	1 amphipod molt
"	<i>Siphonosphaera</i> sp.	3/132	several fecal pellets
Barbados 1987	unidentified colony	10/201	1 molt + fecal pellets
"	<i>Sphaerouzoum</i> sp.	5/965	2 amphipod molts
"	<i>A. spinosa</i>	41/363	2 amphipods present
"	<i>Collosphaera</i> sp.	12/182	2 amphipod molts
"	<i>A. spinosa</i>	22/110	none
"	unidentified colony	50/297	3 molts + 1 fecal pellet
R.V. Oceanus 191	<i>A. spinosa</i>	12/51	1 amphipod present
"	unidentified colony	4/312	3 molts + 1 fecal pellet
"	<i>A. spinosa</i>	several empty shells	1 amphipod present

Table 25. Weight-specific respiration rates of selected pelagic crustacea. Theoretical weight-specific respiration rates at 25°C were calculated by assuming $Q_{10} = 2$ for the temperature range 5 - 25°C.

Crustacean (Source)	Weight-Specific Respiration Rate ($\mu\text{l O}_2$ /day/mg dry weight)	Temperature at which Respiration Was Measured (°C)	Theoretical Weight- Specific Respiration Rate at 25°C ($\mu\text{l O}_2$ /day/mg dry weight)
<i>Calanus finmarchicus</i> (Conover, 1960)	47	18.5	61
<i>Acartia clausi</i> (Conover, 1960)	78	5	312
<i>Phronima sp</i> (Conover, 1960)	10	8	34
<i>Hyperia galba</i> (Conover, 1960)	14	5.6	54
<i>Phronima sedentaria</i> (Mayzaud, 1973)	17	13	41
<i>Acartia clausi</i> (Mayzaud, 1973)	67	15	134
<i>Euterpina acutifrons</i> (Coull & Vernberg, 1970)	108	25	108
<i>Hyperietta spp</i> (present study)	7	25	7
<i>Gnathophausia gracilaris</i> and <i>Gigantocypris agassizi</i> (Childress, 1971)	1.2	5.5	5

Figure 35. Colonial radiolarian respiration rate vs number of central capsules per colony

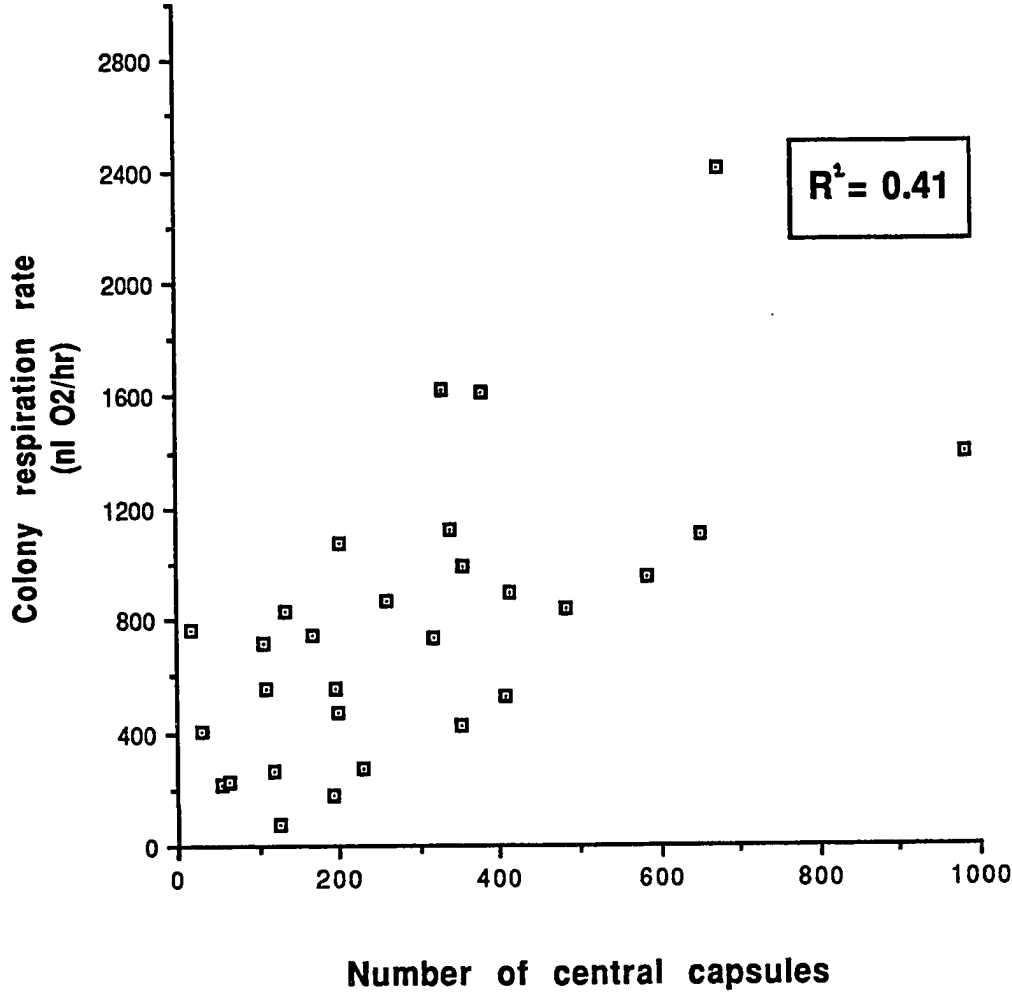
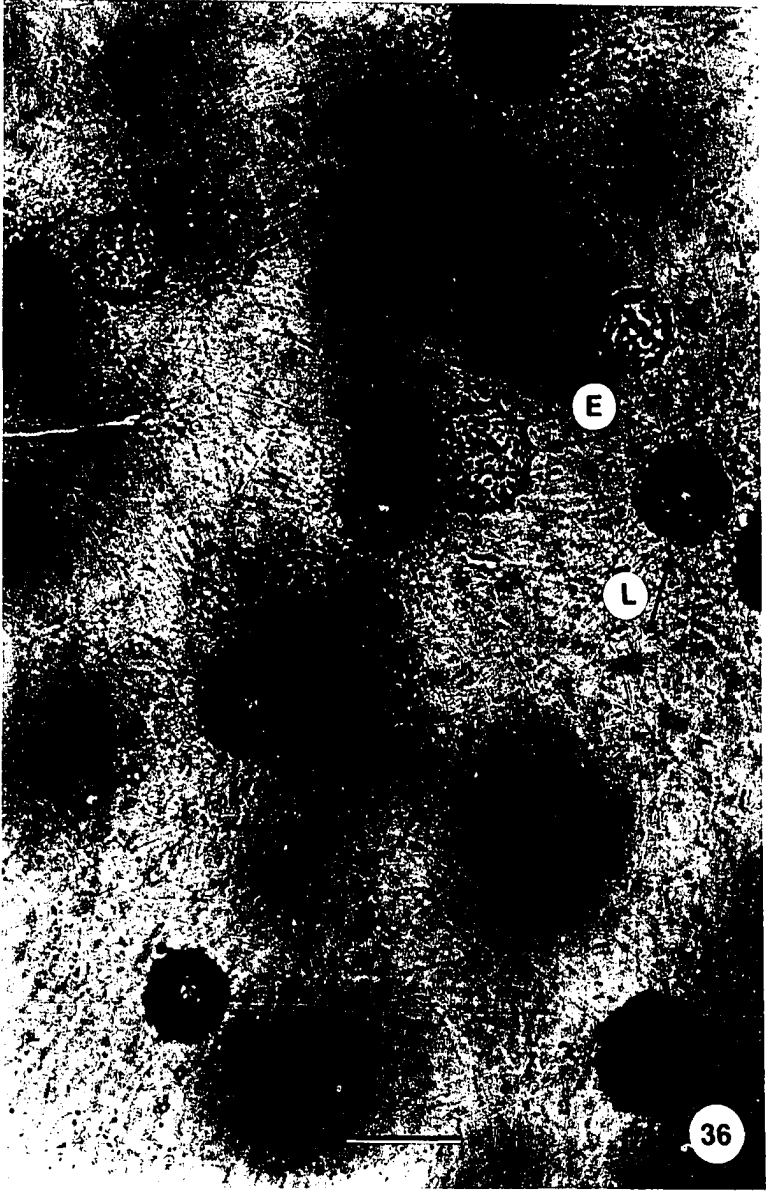


Figure 36. A section of an Acrosphaera spinosa colony showing both living (L) and empty (E) central capsules. Amphipod feeding activity has emptied the radiolarian central capsules of their cytoplasmic contents and the associated endosymbiotic algae; all that remains is the siliceous shell. Scale = 100 um.



Final Discussion

Until recently, it was widely accepted that the trophic structure of most marine communities is fairly simple and includes a chain of increasingly larger consumers (e.g. Ryther, 1969; Steele, 1974). It was assumed that the zooplankton herbivores are extremely efficient grazers that consume nearly all of the phytoplankton production. However, it has become increasingly clear that the planktonic food web is more complex and as much as 50% or more of primary production may be assimilated by prokaryotes (Pomeroy, 1974; Williams, 1981). This microbial production is then consumed by heterotrophic protozoa which serve a double function in the food web, a) as remineralizers of essential nutrients needed by bacteria and phytoplankton and b) as prey for larger zooplankters.

Numerous workers have shown that the free-living microheterotrophs (heterotrophic protozoa and bacteria) are often the dominant organisms in pelagic communities (e.g. Sieburth et al., 1978; Fenchel, 1982; Azam et al., 1983; Li et al., 1983). In addition to the free-living microheterotrophs, highly dense microbial communities have been observed in detrital matter in pelagic waters (Silver et al., 1978; Trent et al., 1978; Shanks and Trent, 1979; Caron et al., 1982; Silver et al., 1984). It has been shown that the production rates of particle-bound microbes are considerably higher than those in the surrounding water (Knauer et al., 1982; Prezelin and Alldredge, 1983; Alldredge et al., 1986). However, the quantitative contribution of particle bound microbes to the pelagic food web remains an unresolved issue.

In this study, I have examined the microbial community associated with colonial radiolaria and estimated its contribution to the flow of carbon through the radiolarian microcosm. Unlike the microbial communities which are associated with a non-living matrix in marine snow particles, the framework of the CR microcosm is a living protozoan. There are certain merits and limitations to the study of the CR microcosm. The merits include the stability of the CR microcosm and the limited number of organisms that are involved.

Colonial radiolaria feed on small plankters, including tintinnids, copepods, mollusc larvae, ostracods, larvaceans and various algae

(Swanberg, 1979). The predatory nature of CR limits the members of the microcosm to the few groups that are immune to the sticky radiolarian rhizopodia. This is unlike the situation found among marine snow microcommunities, where the composition of the community is determined by the ability of one microbe to outcompete or coexist with another microbe (Davoll, 1984). Another meritorious characteristic of the CR microcosm is its stability. The radiolarian cells have a homeostatic influence on the colony microenvironment through a continuous process of renewal and repair. By maintaining relatively constant conditions, invasion of the microcosm by new colonizing species is minimized and this serves to stabilize the microcosm even further. In comparison, detrital communities are in a constant state of flux. After the initial colonizers have become established, a continuous process of succession occurs (Davoll, 1984) which degrades the organic matrix (Alldredge, 1979) and alters the composition of the attached microbial community.

One of the limitations of work with the radiolarian microcosm is its internal complexity. The radiolarian colony consists of radiolarian cells and endosymbiotic algae embedded within a dense network of rhizopodia. Associated organisms are found within the colony and/or on the outer surfaces. In order to measure the contributions of the various organisms to the flow of carbon through the microcosm, it is often necessary to separate them from the colony, thereby losing information on the undisturbed in situ processes.

The goals of this thesis were to describe the microbial community associated with CR and to measure its contribution to the flow of carbon through the radiolarian microecosystem. I have devoted the first three chapters to the description of the host colonies and associated organisms because most of the members of the radiolarian microcosm were previously unknown. Although hyperiid amphipods were described by Brandt (1885) and more recently, by Harbison et al. (1977) and Swanberg (1979), the other associated organisms, including bacteria, a bodonid flagellate, a gyrodinoid dinoflagellate and a dysterid ciliate have not been described and may even be new species. The associated microbes were examined by inverted microscope and recognized by their morphological features and characteristic swimming patterns. It is likely that the infesting organisms were consistently the same species or genus, however, due to their small size and the crude

means used to recognize them, it is possible that there are even more organisms associated with CR than I have described in this study.

In order to relate this microecosystem study to the oceanic populations of the host colonies, I began the thesis with a chapter describing the biogeography of the colonial radiolaria. The abundances and the geographical distribution of radiolarian colonies that I collected were very similar to those described by Swanberg (1979). Radiolarian abundances were generally lower in the Gulf Stream (OC 177 and OC 191) and in the productive waters of the Caribbean than in the oligotrophic waters on the eastern side of the North Atlantic, near Africa (OC 176). This distribution pattern provides further support for the hypothesis proposed by Swanberg (1983) whereby colonial radiolaria fare better in waters with low particulate matter loads, as compared to the turbid waters in coastal regions. He explained that the abundance of particulate matter in productive waters may clog the radiolarian's passive feeding apparatus, thus immobilizing the sarcodine.

The most widely distributed genera encountered were Sphaerozoum, Acrosphaera, Collosphaera, and Rhaphidozoum. The species Collozoum caudatum and C. inerme were widely distributed on the western side of the Atlantic, but were almost totally absent in the oceanic waters off the northwest coast of Africa. Among the rare species in my collections; C. serpentinum and C. stellatum were not widely distributed and overall, fewer than 50 specimens of each were collected.

Swanberg (1979) suggested that these two species of Collozoum (C. serpentinum and C. stellatum) may actually be different developmental stages of Collozoum pelagicum. It would be fairly straightforward to verify this hypothesis using modern molecular techniques, however, until this is done, I will consider these as two different species.

The temporal variation in CR community composition and species richness was not notable during two 8-week field trips to Barbados during March and April in two successive years. Drastic reductions in CR abundance and in species richness corresponded to decreases in the seawater salinity. When salinities returned to oceanic levels (@ 36 ‰), normal CR communities were observed once again.

Cluster and ordination analysis of the CR samples collected in the Caribbean shows that there are distinct radiolarian assemblages, but, aside from the effect of salinity and temperature, I did not correlate these with other environmental variables. Therefore, it is not clear whether the clusters are random radiolarian assemblages or are related to extrinsic factors. The oceanic cruise samples were also analyzed by cluster and ordination analysis and these revealed a clear difference between samples collected on the eastern and the western sides of the North Atlantic Ocean during the summer of 1986. The mean surface water temperature was 8° to 11° C colder on the eastern side of the ocean and it is possible that some CR taxa are more sensitive to temperature than others (Anderson, 1983), though there may have been differences in other variables (e.g. salinity) as well. With further information on the correlation between environmental variables and CR assemblages, it may be possible to identify water masses on the basis of CR found therein.

Whereas radiolarian distribution is probably influenced to a large extent by environmental variables, it is not clear what determines the association of microbial organisms with CR. The rates of infestation (or association) of some microorganisms, e.g. Cryptobia-like bodonid flagellates, with the CR was higher in the more productive regions (i.e. in the Caribbean) than elsewhere. Increased infestation rates may indicate that a large proportion of the colonies in the more eutrophic waters were unhealthy. Swanberg (1979) found that radiolaria with heavy ciliate infestations died soon after being collected. However, I did not find a significant difference between the longevity of infested versus uninfested colonies when these were maintained in the laboratory. An alternative explanation for the increased infestation rates among CR in productive regions is that associated microorganisms may be attracted to and feed on the dissolved organic matter (DOM) released during radiolarian sloppy feeding. In productive waters, there are greater abundances of prey organisms, in comparison to oligotrophic regions, and therefore, an increase in radiolarian predation rate (greater numbers of prey caught) with subsequent release of increased amounts of DOM. This would attract greater numbers of microorganisms, if indeed the DOM were the attractant.

There were some spatial differences in the distribution of organisms associated with CR, but the most notable was that of Gyrodinium sp. This dinoflagellate was observed on radiolaria in all of the regions that were sampled on the western side of the North

Atlantic, but was not observed on any of the colonies collected during OC 176, near the northwestern coast of Africa. It is possible that the plankton communities on opposite sides of the Atlantic Ocean are sufficiently isolated, either physically or environmentally, so that there is no exchange of planktonic organisms (e.g. Gyrodinium sp.). Infesting organisms exhibited considerable host selection, e.g. high infestation rates and abundances of both Cryptobia-like bodonid flagellates and Gyrodinium sp. among Collozoum caudatum. It is not clear what attracts the infesting organisms to these colonies preferentially over other CR species.

All of the radiolaria examined, from both oceanic (oligotrophic) and Caribbean (productive) populations had large communities of bacteria associated with their surfaces. Bacterial production rates on CR (calculated from growth measurements) were very high in comparison to the mean production rates attributed to the planktonic bacteria in an equivalent volume of surrounding seawater. However, the abundance of colonial radiolaria is low in most waters, therefore the contribution of the CR-bound bacterial production to total bacterial production in the pelagic environment is quite small. The bacteria are a sink for the dissolved organic carbon released by the radiolarian microcosm. This may include photosynthetic exudates released by the algal endosymbionts, radiolarian excretions and organic compounds released by radiolarian sloppy feeding. If the protozoa associated with the radiolaria are bacterivores, CR-associated bacteria would also serve as a link between the dissolved organic matter pool and higher trophic levels within this microecosystem.

One of the protista associated with the CR that may be a bacterivore is Gyrodinium sp. This naked dinoflagellate contains chloroplasts and is able to incorporate inorganic carbon in both light and dark conditions (Chapter 5), but it has been shown that many other photosynthetic protists are also bacterivores (e.g. Ceratium hirundinella (Dodge and Crawford, 1970), Ochromonas malhamensis and O. danica (Pringsheim, 1952; Aaronson and Baker, 1959). In addition to potential phagotrophy, Gyrodinium sp. may also feed osmotrophically. The results of tracer experiments, and a fine structure study suggest that the dinoflagellate may take up dissolved organic matter by pinocytosis. If this is true, the dissolved organic carbon pool would be partitioned among bacteria and dinoflagellates. Among these possible trophic schemes, the only rate that was

determined for the dinoflagellates in this study was their inorganic carbon uptake rate (chapter 5).

Incubations using light levels that were 6 to 8 times lower than the light intensities normally experienced in situ showed that the average Gyrodinium sp. fixes 2.9 pg carbon/hr. Although the light driven carbon uptake rate of a single dinoflagellate is relatively low, the total amount fixed (photosynthetically) by a large population of Gyrodinium sp. ($>10^3$ cells/CR) may be 10% or more of the carbon fixed by the symbionts of an average radiolarian (300 central capsules). The photosynthetic activity of Gyrodinium sp. probably does not affect the functioning of the radiolarian colony. However, the activities of another member of the CR microcosm, the parasitic hyperiid amphipod are much less benign and may cause considerable damage to the radiolarian.

Juvenile hyperiids are relatively inactive and do not appear to cause much visible damage to the radiolarian colony. The mean uptake of photosynthetically-fixed carbon from the radiolaria was 147 ng carbon/day/juvenile amphipod. In an average radiolarian colony of 48 ug carbon, this uptake would amount to the loss of less than 0.15% of the radiolarian carbon/day; a relatively insignificant loss in light of the radiolarian's ability to regenerate biomass. However, adult amphipods are much more active and may consume the entire contents of the radiolarian central capsules. Adult uptake rates based on central capsule consumption ranged from 580 to 1310 ng carbon/day/amphipod; almost an order of magnitude more than the juvenile uptake rate. The growth rate of colonial radiolaria has never been measured, therefore it is not possible to predict whether radiolarian production can offset amphipod consumption. In two heavily infested colonies (10 or more amphipods), the amphipods consumed all of the host's central capsules within only two or three days and transformed a healthy colony into an amorphous gelatinous aggregate, similar to marine snow. These examples indicate that the amphipods may be both parasites and predators of the CR, and that it is probably more accurate to describe their relationship with the host colonies as "parasitoids" (Laval, 1980).

I have constructed a model (Figure 37, below) compiled from previously published data and results from this thesis, in order to summarize the contributions of associated organisms to the flow of carbon through the radiolarian microcosm, and to place these in the context of what we currently know about colonial radiolarian

production. Because the model includes production rates that were measured in several different species of radiolaria, it cannot be used as a formal carbon budget (since there are probably numerous differences in the physiology of different species) but instead, should be regarded as an approximation of processes within the CR microcosm. In this model, photosynthetic carbon uptake, tertiary production and respiration rates were adapted from Swanberg (1983). Swanberg (1979) found that an average Acrosphaera spinosa colony with 480 central capsules (mean central capsule carbon = 100 ng) photosynthetically incorporates from 18 to 106 ng carbon/hr at light intensities ranging from 700 to 2200 $\mu\text{E}/\text{m}^2/\text{sec}$.

However, only a fraction of the photosynthetically-fixed carbon that enters the radiolarian microcosm (through translocation from algal endosymbionts) reaches the radiolarian cells. Anderson et al. (1983) measured the rate of carbon translocation from the endosymbionts of Collosphaera huxleyi to the host cells and this translocation rate (0.22 ng carbon/hr) is presented here because translocation from endosymbionts to radiolarian cells has not been measured in A. spinosa. In addition to the carbon gained in the translocated photosynthates, Anderson (1976a) found that Collozoum inerme cells may ingest (and digest) 4% of the algal endosymbionts each day. By farming a small part of the algal symbiont population, the radiolarian maintains the algae at a steady (manageable) state and also benefits nutritionally; a definite advantage in oligotrophic waters. The carbon content of an average algal endosymbiont was estimated as 48.6 pg carbon/endosymbiont, assuming its volume specific carbon content is the same as that of Gonyaulax tamarensis (Langdon, 1987). If there are 480 central capsules (ccs) per colony, and each central capsule has 20 endosymbionts (Anderson, 1976a), digestion of 4% of this algal population would add 0.49 to 0.73 ng carbon/hr to the radiolarian cells.

Because there are not respiration data for A. spinosa, I have adopted the approach used by Swanberg (1983). Swanberg assumed the weight specific respiration rate of A. spinosa is similar to that of Collozoum pelagicum and Sphaerouzoum punctatum, therefore a colony with 480 ccs would respire 110 ng carbon/hr.

There are no direct measurements of colonial radiolarian tertiary production. However, Swanberg (1983) estimated that the radiolarian photosynthetic carbon incorporation rate (measured at high light intensities) was roughly equivalent to the respiration rate,

and suggested that the majority of radiolarian production must come from predation. The tertiary production rate he proposed, 4.2 mg C/m²/yr, is based on the mean annual collosphaerid radiolarian production calculated from the flux data at Parflux station E (Takahashi and Honjo, 1981). This production rate is equivalent to 32 ng C/hr/CR assuming there is a steady state population of 15 CR/m².

In Figure 37, the five groups of organisms associated with the colonies and their carbon uptake rates have been underlined to indicate that these were the focus of this study. Question marks indicate that the designated path of carbon flow is possible, but has not been shown. The production rates of dysterid ciliates and Cryptobia-like bodonids were not measured in this study, however, these protozoa may be bacterivores in the CR microcosm. Whereas it is premature to state that they digest their intra-cellular bacteria, there is ample evidence that the dysterids consume cells that contain chloroplasts. The partially digested chloroplasts have the ultrastructural features of dinoflagellate plastids, and it is possible that the dysterids graze the Gyrodinium sp. when these two types of associated organisms co-occur (see Tables 9 and 10, chapter3).

The flow of carbon to associated bacteria was calculated by estimating bacterial growth rates using the FDDC method (Davis and Sieburth, 1984) and a set of assumptions related to bacterial growth (see chapter 4). The wide range of bacterial production rates (0.04 - 10 ng C/hr) is mainly the result of large variance in radiolarian surface area since neither abundance of bacteria per mm² radiolarian surface area, nor bacterial growth rates showed large variance. Bacterial production is a function of available dissolved organic matter (DOM), and these production rates may be an indirect indication of the rate of DOM release from the colonies. Because bacteria are an integral part of the radiolarian microcosm (bacteria have been observed on all of the colonies examined), there will be a flow of carbon from the CR to bacteria whenever DOM is released at the radiolarian surface. As stated above, the bacteria may serve as a DOM sink or a regenerative link if they are grazed by the resident protozoa, however, bacterivores have not been identified in the microcosm.

The mean light-driven inorganic carbon uptake rate (calculated by subtracting dark uptake controls from light uptake) of Gyrodinium sp. was 2.88 pg carbon/cell/hr. Although the average abundance of Gyrodinium sp. in infested A. spinosa colonies, was 622

cells/CR, dinoflagellate infestations among other CR in the same size range as the CR in the model (48 ug carbon), sometimes exceeded 10,000 cells/CR (see chapter 3). Therefore, the range of Gyrodinium sp. uptake rates in the model includes the uptake of a single cell and the total uptake rate calculated for 10,000 cells. At the upper end of the estimated range, dense populations of Gyrodinium sp. may fix carbon at rates that are equal to the radiolarian endosymbiont production, however the consequences of this production to the CR microcosm are not clear.

I did not trace the source of the inorganic carbon taken up by Gyrodinium sp., but this may include CO₂ excreted by radiolarian respiration (which would demonstrate carbon recycling within the CR microcosm). Gyrodinium sp. incorporated considerable amounts of inorganic carbon in the absence of light energy (dark uptake). Dark uptake rates ranged between 0 and 18.7 pg carbon/cell/hr, as compared to total (light + dark) uptake rates which ranged from 2.5 to 22.8 pg carbon/cell/hr (chapter 5). The mechanism driving the dark uptake of inorganic carbon is not known, however, I have excluded dark uptake rates from the model pending further experimentation and the rates shown represent the "light minus dark" inorganic carbon uptake.

Hyperiid amphipod production was assigned to two categories representing differences in trophic behavior on the part of juvenile and adult amphipods. Although the production rates of adult amphipods that do not consume central capsules were not measured (see chapter 6), I assigned them the same production rates as juveniles until further data are available. Parasitized radiolaria contained either adult or juvenile amphipods; the two life stages were mutually exclusive (Swanberg, 1979; Angel, unpublished), therefore, the separate arrows in the model represent mutually exclusive production rates. Parasitized A. spinosa colonies contained from one to 5 amphipods per colony (other CR species sometimes had 20 or more amphipods per colony), thus the ranges of values in the model included the lowest uptake rate calculated for one amphipod and the highest uptake rate multiplied by 5 amphipods. In comparison to the radiolarian production (41 to 85 ng carbon/hr, from the sum of symbiont photosynthesis and tertiary production), amphipod production rates (one to 64 ng carbon/hr for juveniles and 24 to 272 ng carbon/hr for central capsule-consuming adults) are very high and amphipods are probably the largest consumers of radiolarian carbon in the microcommunity.

Although their potential impact on radiolarian biomass is considerable, amphipod infestations were usually rare events (often less than 5% infestation among all colonies collected during a field excursion; see chapter 3), and hyperiid amphipod feeding is probably not a major influence in most radiolarian populations. The flow of carbon to the microbial members of the radiolarian microcosm has only been partially measured and it appears that both bacteria and Gyrodinium sp. may be important in the cycling of organic and inorganic carbon through the system. Whereas the paths and rates of carbon flow within the CR microcosm are only partially understood, it is probably safe to conclude that the protozoa and the bacteria associated with the radiolaria do not contribute significantly toward the demise of the colonies.

The model of carbon flow through the radiolarian microcosm demonstrates the complexity of even the smallest communities in the pelagic environment. One of the unique characteristics of the radiolarian microcommunity is the fact that it is a self supporting system. Carbon is incorporated by the radiolarian, either by predation or through endosymbiont activity, and some of this carbon is then utilized by associated organisms. Goldman (1984) proposed that small flagellates may survive in oligotrophic waters by migrating between organic microaggregates (which contain "up to three orders of magnitude greater concentrations of microbial populations and nutrient concentrations") to fulfill their nutritional needs. The presence of the protozoa in the CR microcosm may be an example of this proposed survival mechanism since it is unlikely that the individual species would succeed in the surrounding waters in the absence of patches of elevated concentrations of nutrients or microbial prey. Goldman (1984a) also emphasized the significance of the dynamic microaggregate communities to recycling and regeneration of nutrients in pelagic environments. The activities of organisms associated with the CR may therefore play an active role in exporting nutrients to the surrounding waters.

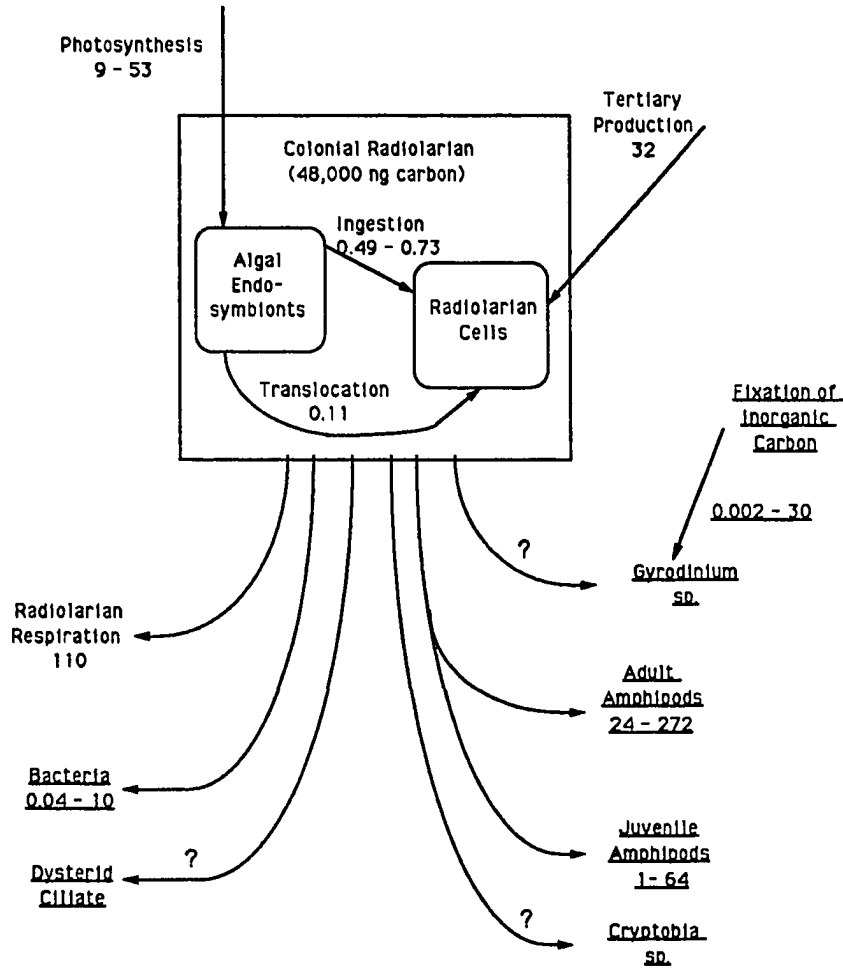
Among the new questions this research has evolved are some of the same questions that Dr. Swanberg raised a decade ago in his dissertation on the "macro"- ecology of colonial radiolaria (Swanberg, 1979). We still do not have measurements of the growth rates of colonial radiolaria. Although the colonials generally do not thrive in laboratory conditions, it is likely that they may be maintained and even induced to grow in vitro, using the same techniques that are applied to the culture of solitary radiolaria and planktonic

foraminifera. More and better data are needed on the trophic activity of radiolarian colonies. Although there have been occasional observations of algal remains within colonies, it is not known whether colonial radiolaria are true carnivores or whether some are also omnivores. The unsatisfactory state of colonial radiolarian taxonomy was one of the problems that I encountered repeatedly in this study. Because the current keys that are based on morphological features are insufficient to identify developmental stages, it may be necessary to apply new technology, such as the use of immunological or nucleic acid probes to identify the "unidentified colonies". The presence of bacterial populations on all CR that were examined in this study raises a broader question regarding past measurements of planktonic sarcodine metabolic activities. If bacteria and other microorganisms are associated with all planktonic sarcodines, are the currently accepted metabolic rates gross overestimates of the true "axenic" values or are they only slightly inflated?

There are a number of more specific questions, directly related to this study that require further clarification. First of all, there is a need to describe the associated protozoa in detail and assign these to known species or new species. There are still many question marks in the model, therefore, further work is needed to understand a) how Gyrodinium sp. takes up inorganic carbon in the dark b) whether Gyrodinium sp. takes up dissolved organic matter c) what are the chemical cues that attract the various protozoa to the colonies d) whether any of the protozoa feed on the bacteria that are associated with the CR. The feeding behavior of hyperiid amphipods associated with the colonies requires further study. With respect to the radiolaria, hyperiid amphipods were only rarely observed consuming central capsules. It would be useful to learn what induces this destructive behavior and whether it is more common than has been presently observed.

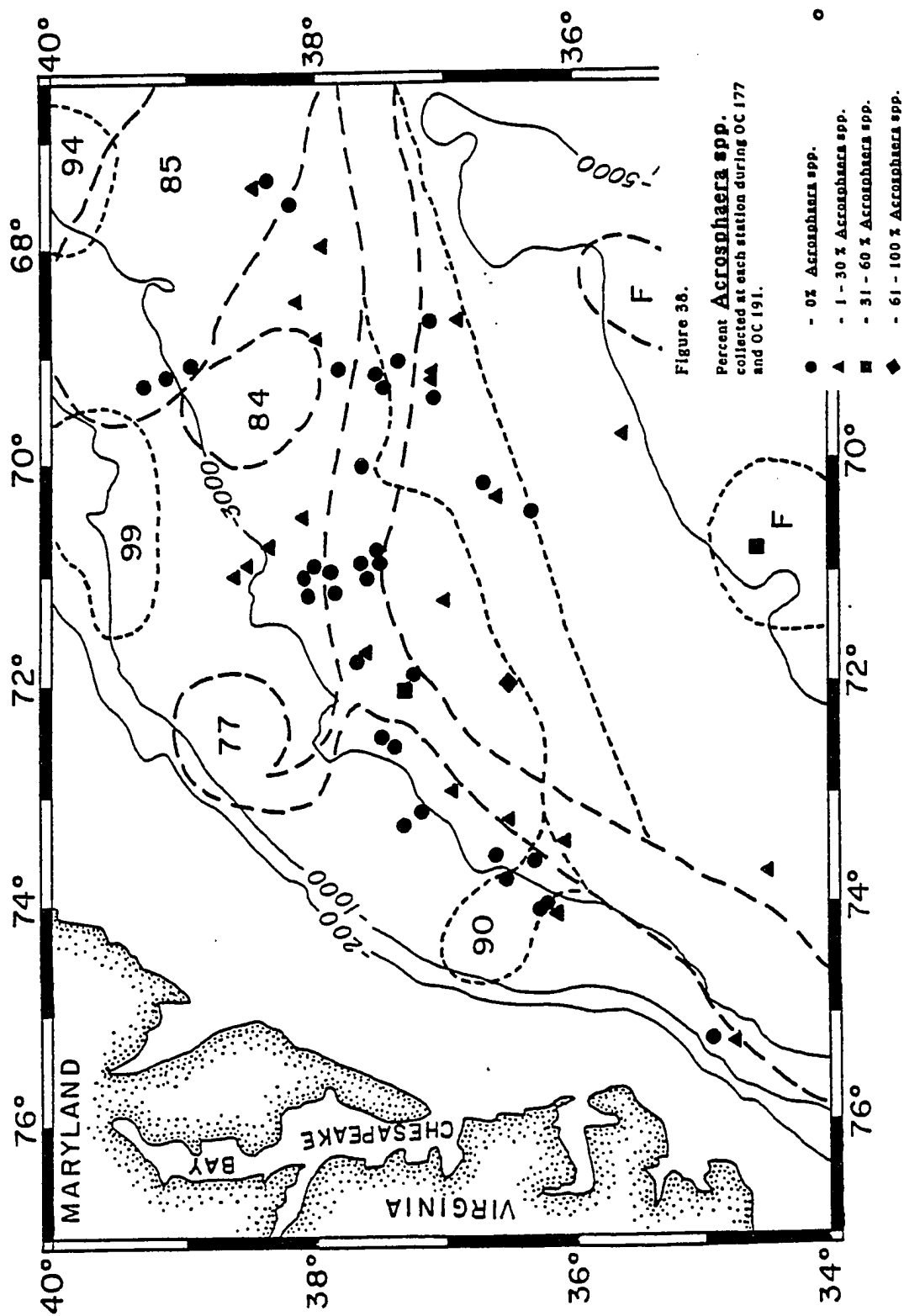
Michaels et al. (1988) have found that planktonic sarcodines, including acantharia, foraminifera and radiolaria sometimes constitute the bulk of the particulate carbon in oceanic sediment trap samples. In light of this observation, and the growing interest in global oceanic fluxes, it is important to gain a better understanding of the microbial community associated with colonial radiolaria and its role in the flow of carbon through the living colonies, even before their ultimate sinking out of oceanic surface waters.

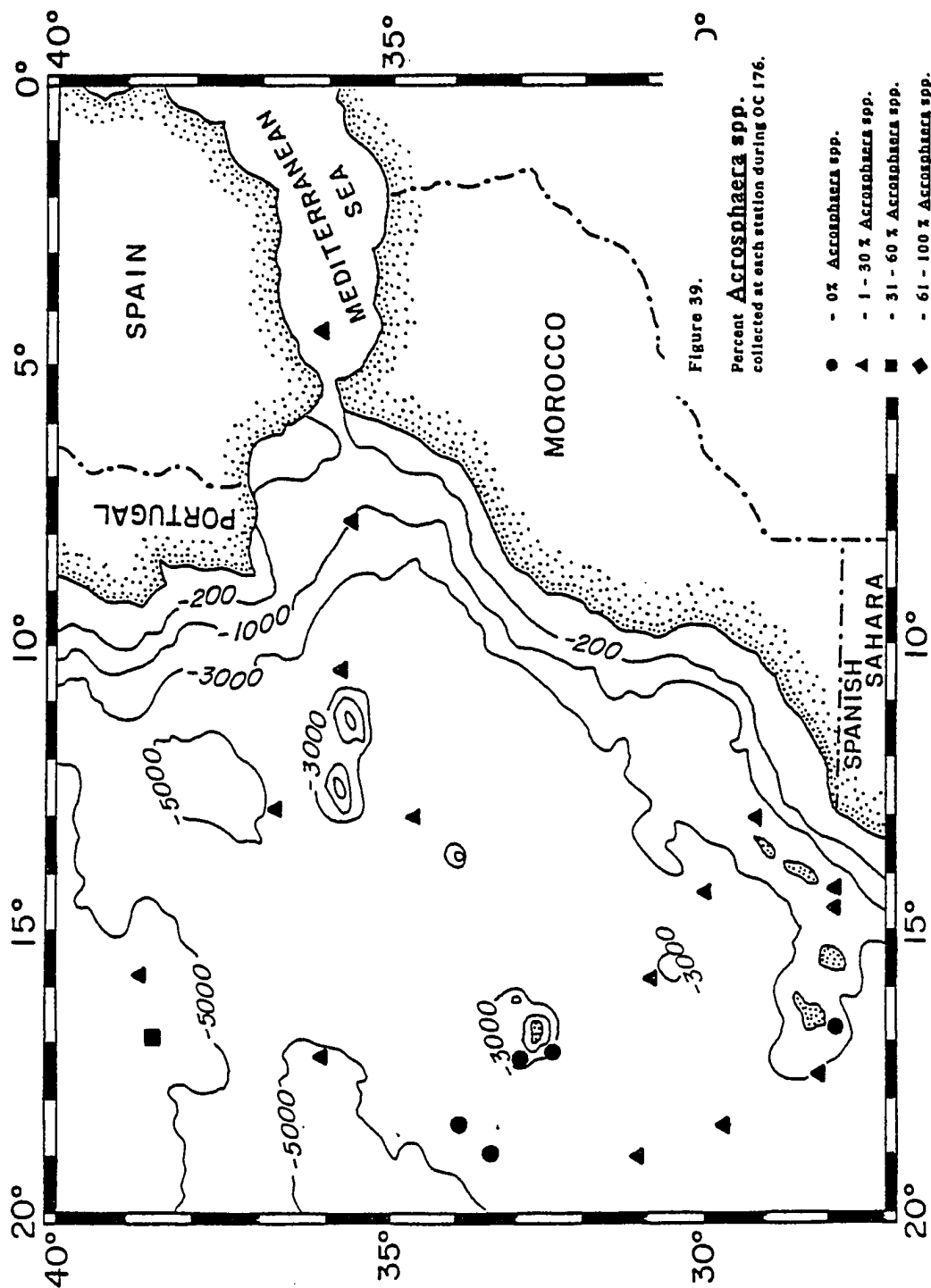
Figure 37. Carbon flow within the colonial radiolarian microcosm. Underlined organisms and flow rates indicate data that were taken from this study; the algal-endosymbiont photosynthetic carbon uptake (measured in *Acrosphaera spinosa*) was taken from Swanberg (1979), radiolarian tertiary production was estimated by Swanberg (1983), ingestion of endosymbiotic algae was calculated from the rate of endosymbiont disappearance in *Collozoum inerme* (Anderson, 1976a) and the translocation of carbon from endosymbionts to host cells was based on the rate measured in *Collosphaera huxleyi* (Anderson et al., 1983). The carbon content of an average *A. spinosa* colony with 480 central capsules = 48,000 ng carbon (Swanberg, 1983). All numerical values indicate carbon flow in ng carbon/hr normalized to 24 hours.

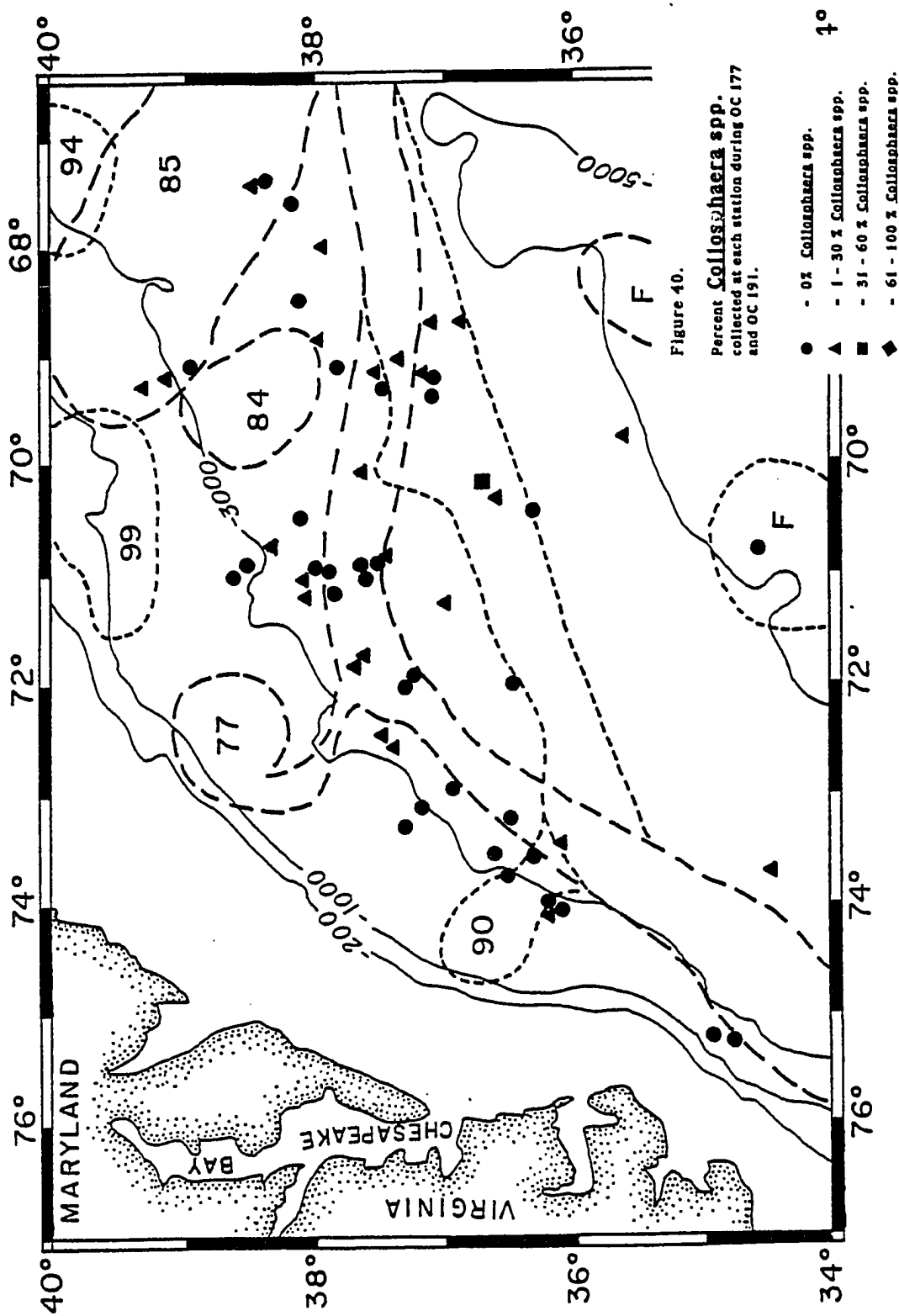


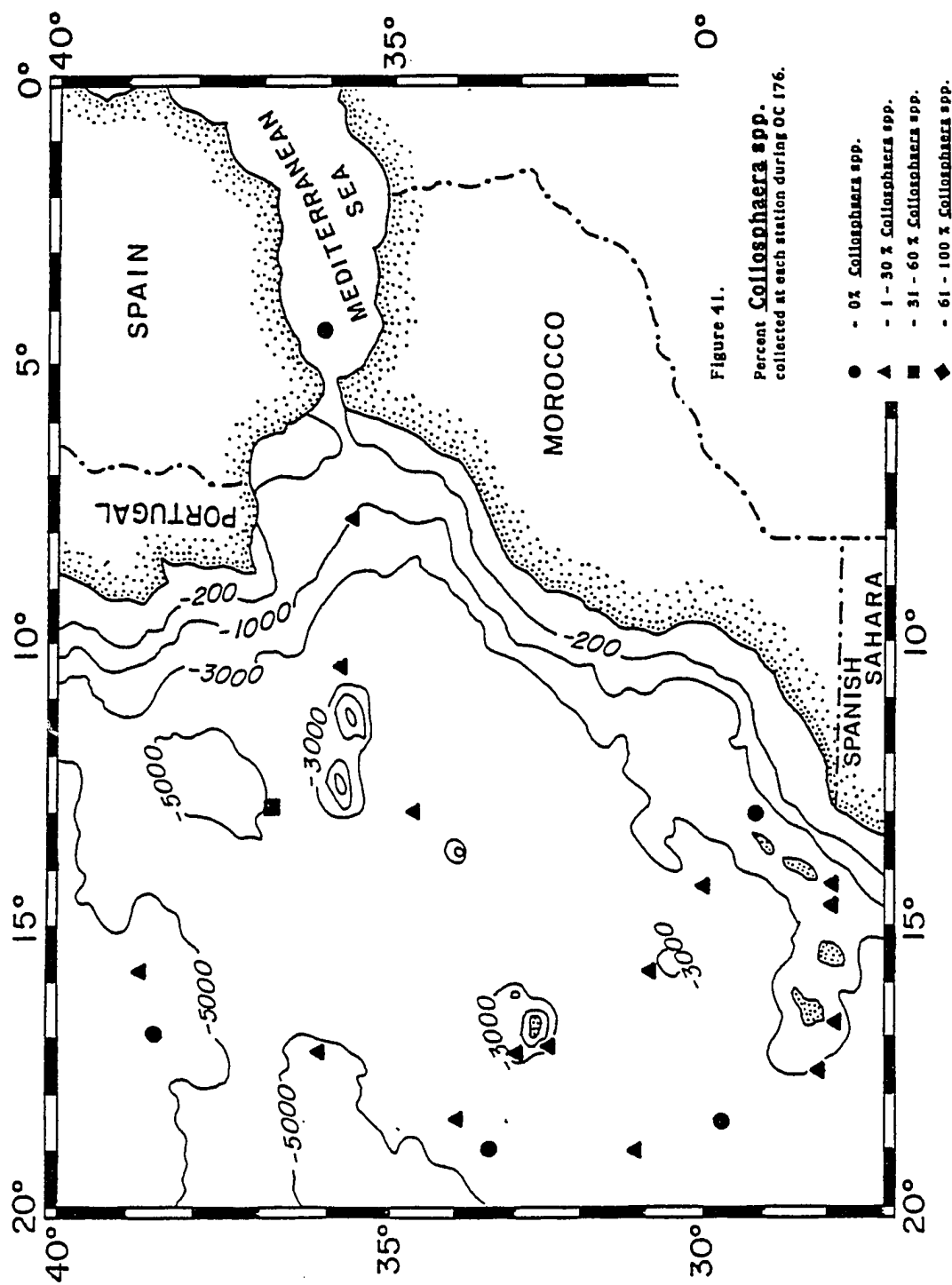
Appendix A

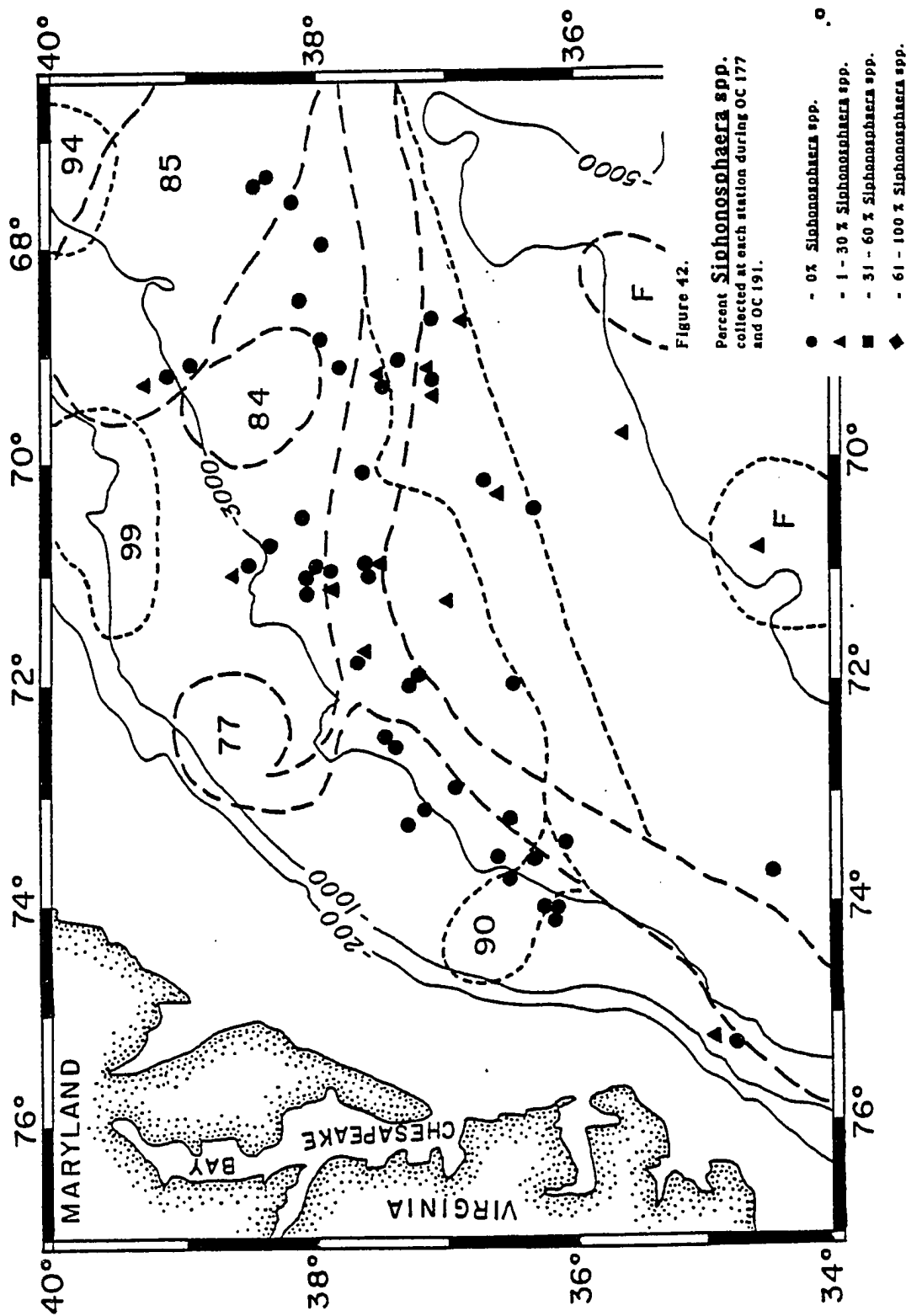
The following figures (fig. 38 to 57) illustrate the distributions of 10 CR taxa in 2 regions of the northern Atlantic Ocean, during cruises OC 176, OC 177 and OC 191. Collozoum stellatum was not observed at any of the stations during OC 176, therefore a map of its distribution is not presented for that region. In addition to the geographic distribution, each figure shows the relative proportion (percent) of the taxon among the total number of colonial radiolaria collected at each dive station. For simplicity, relative proportions were divided into 4 categories : 0; 1 - 30%; 31 - 60%; 61 - 100%; these categories were represented by 4 different symbols. Solid lines represent isobaths (in meters below sea level), and the dashed lines illustrate the path of the Gulf Stream as recorded by satellite between 7/27 and 8/3 during both 1986 (the loosely spaced dashed lines) and 1987 (the tightly spaced dashed lines) (Clark, 1986; Clark, 1987). Eddies that emerged from the Gulf Stream are presented as semi- or fully enclosed rings and were designated alphanumeric codes (e.g. 77, 84, F, etc.).

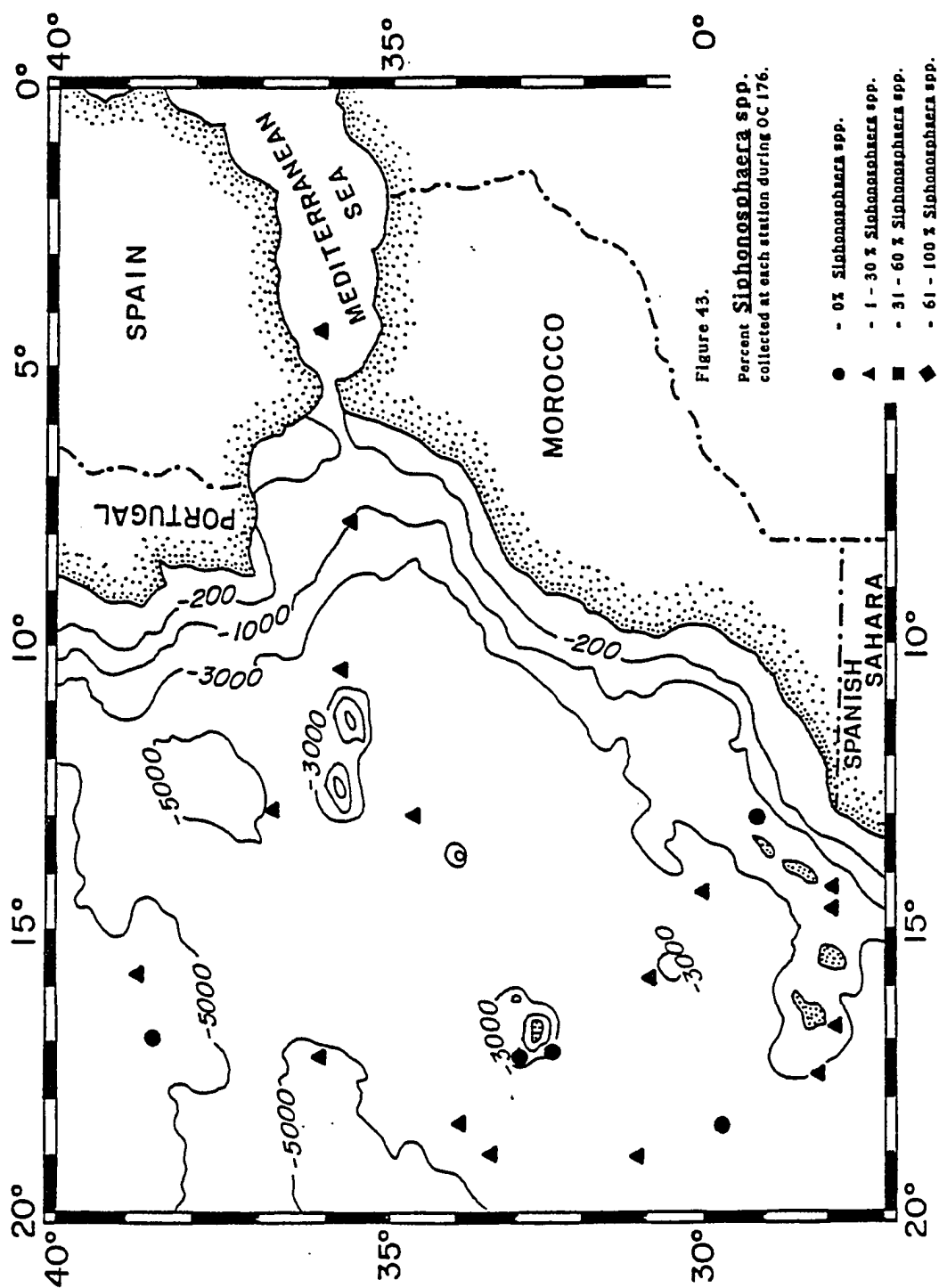


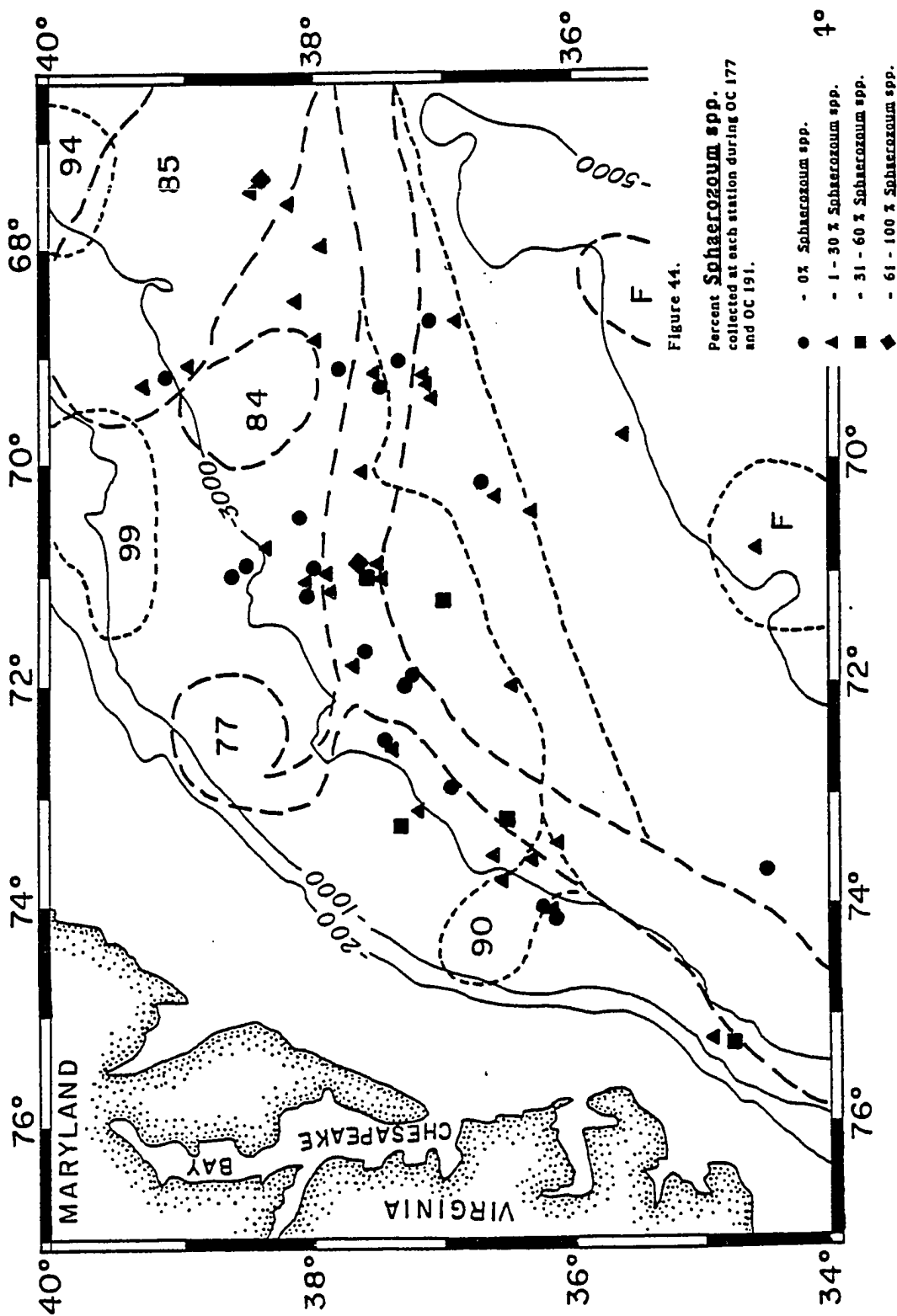


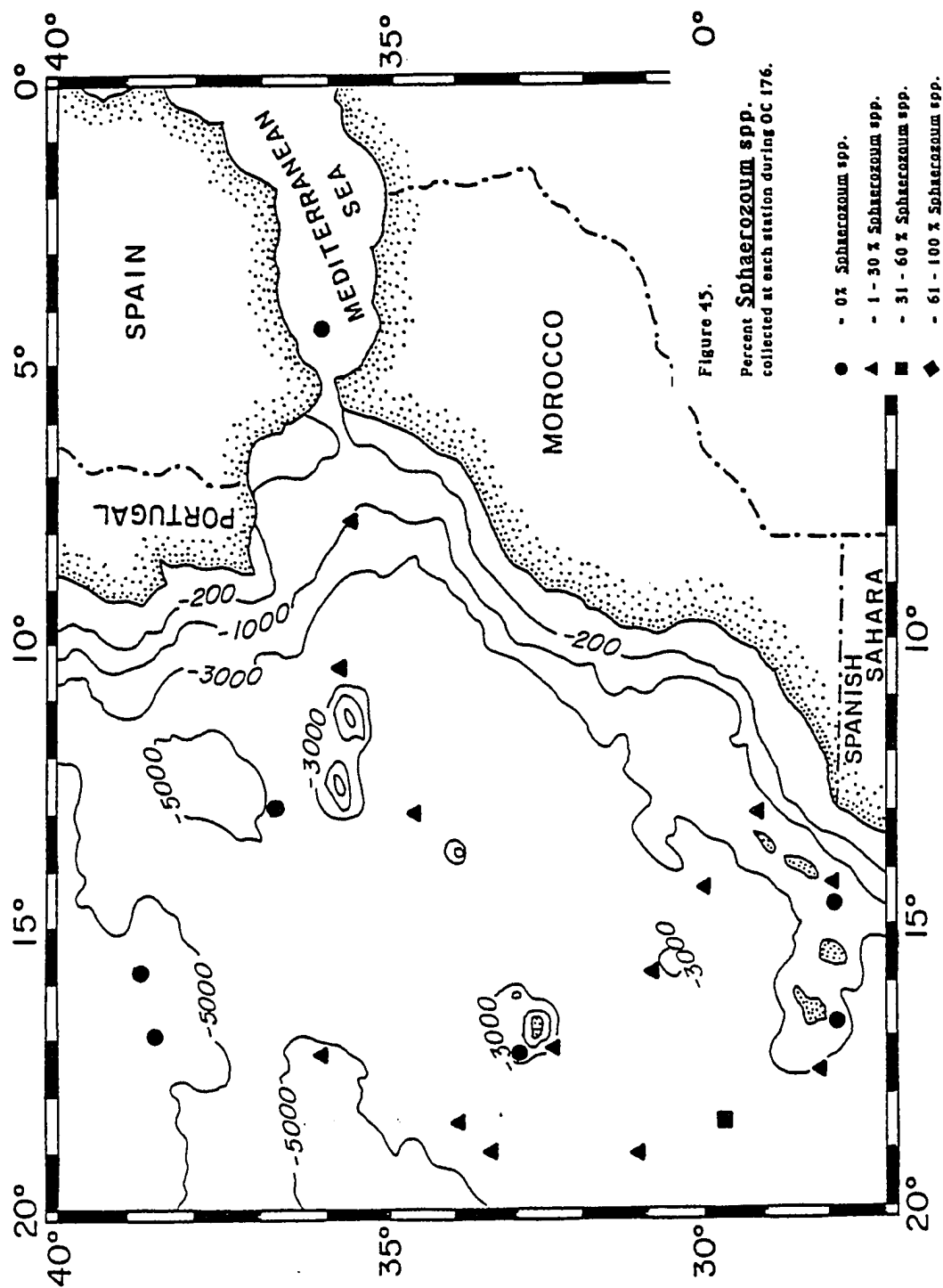


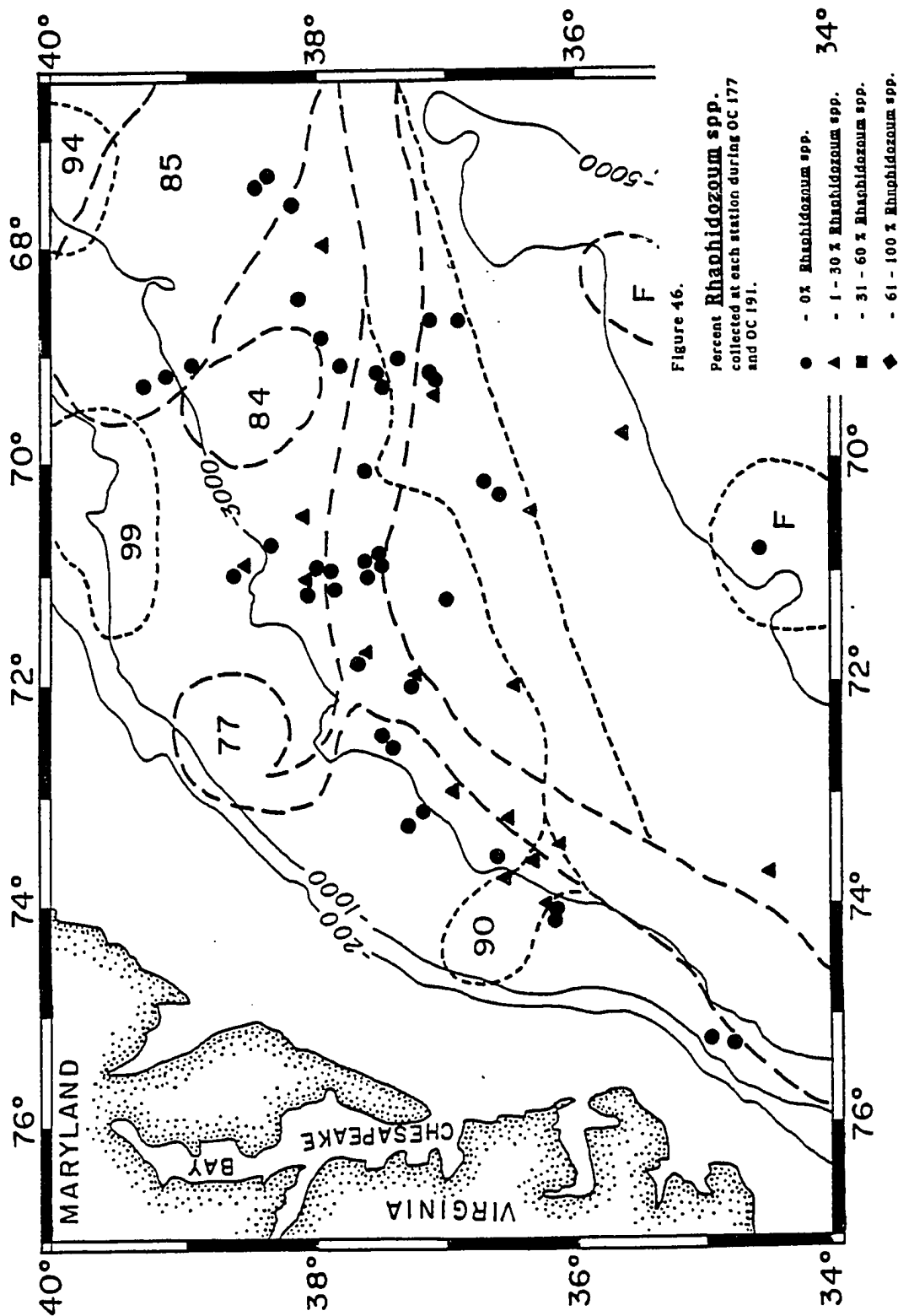


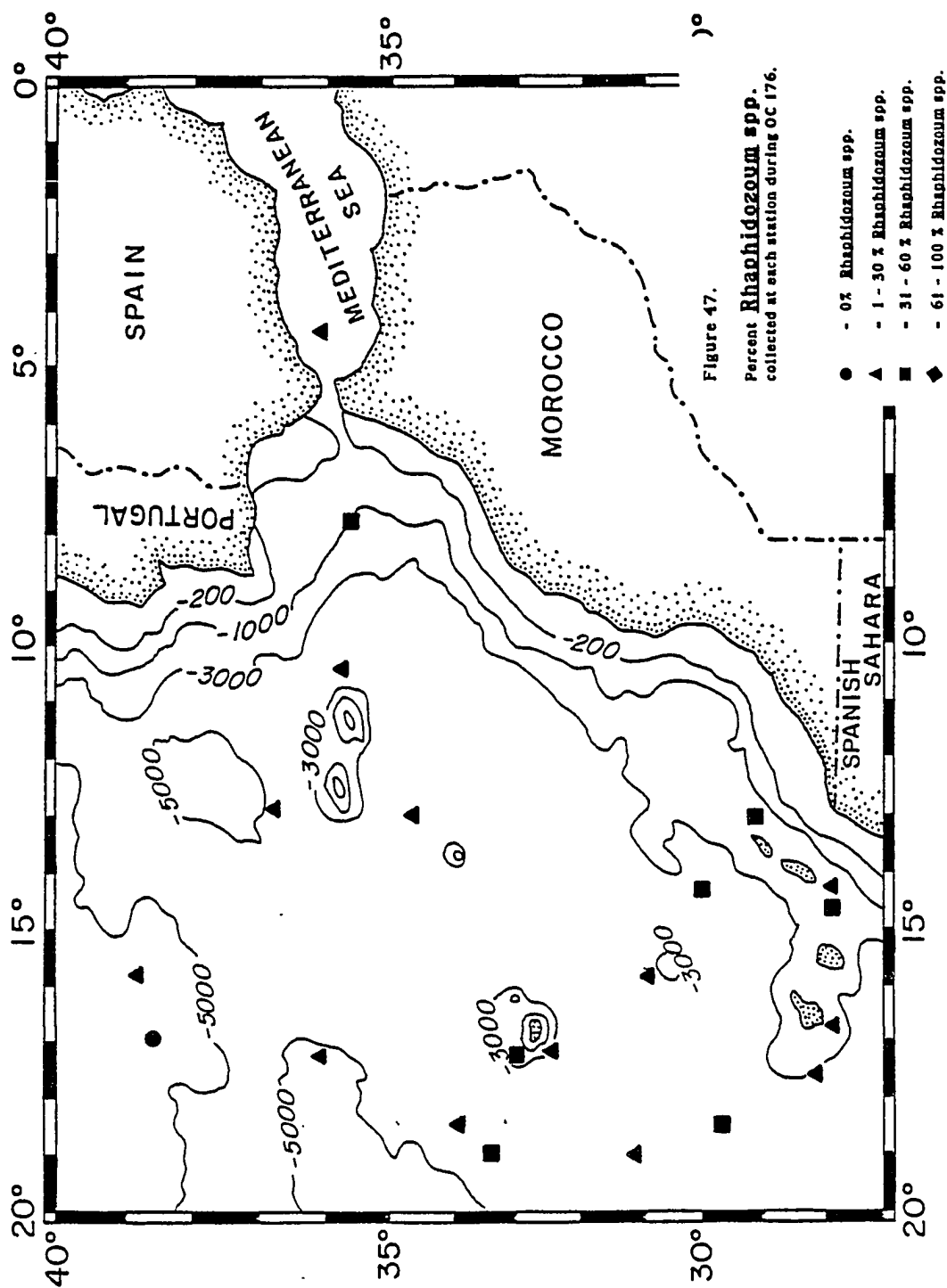


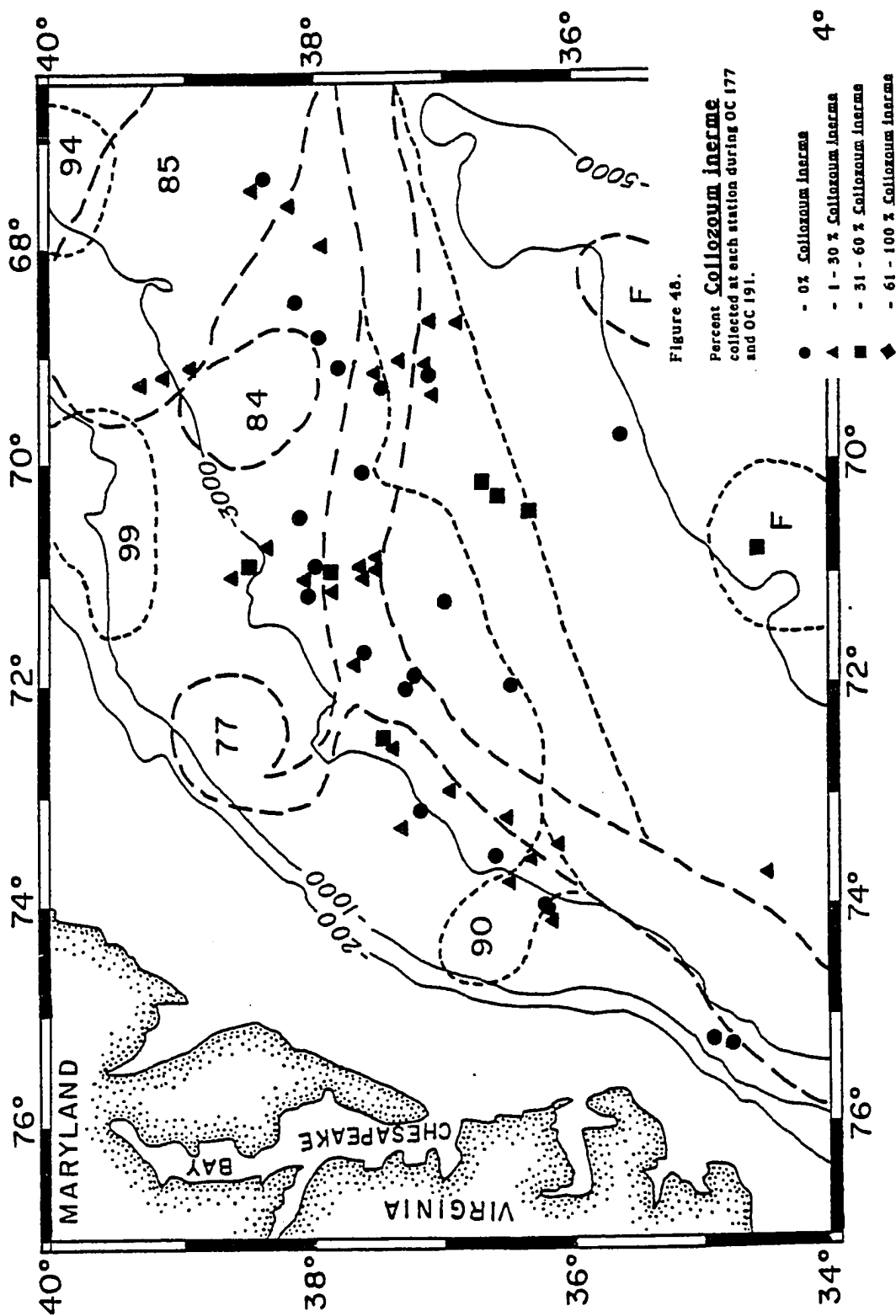


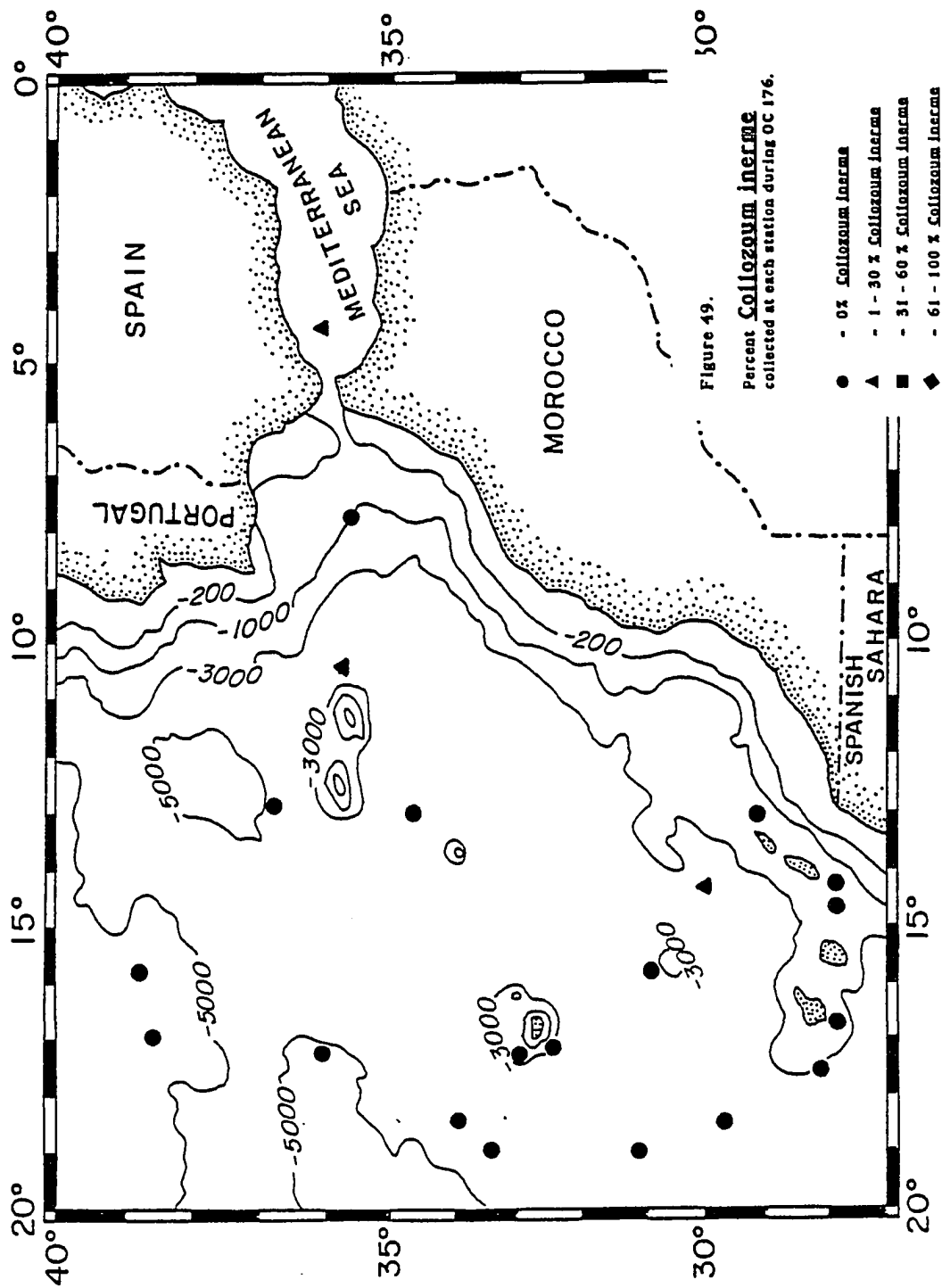


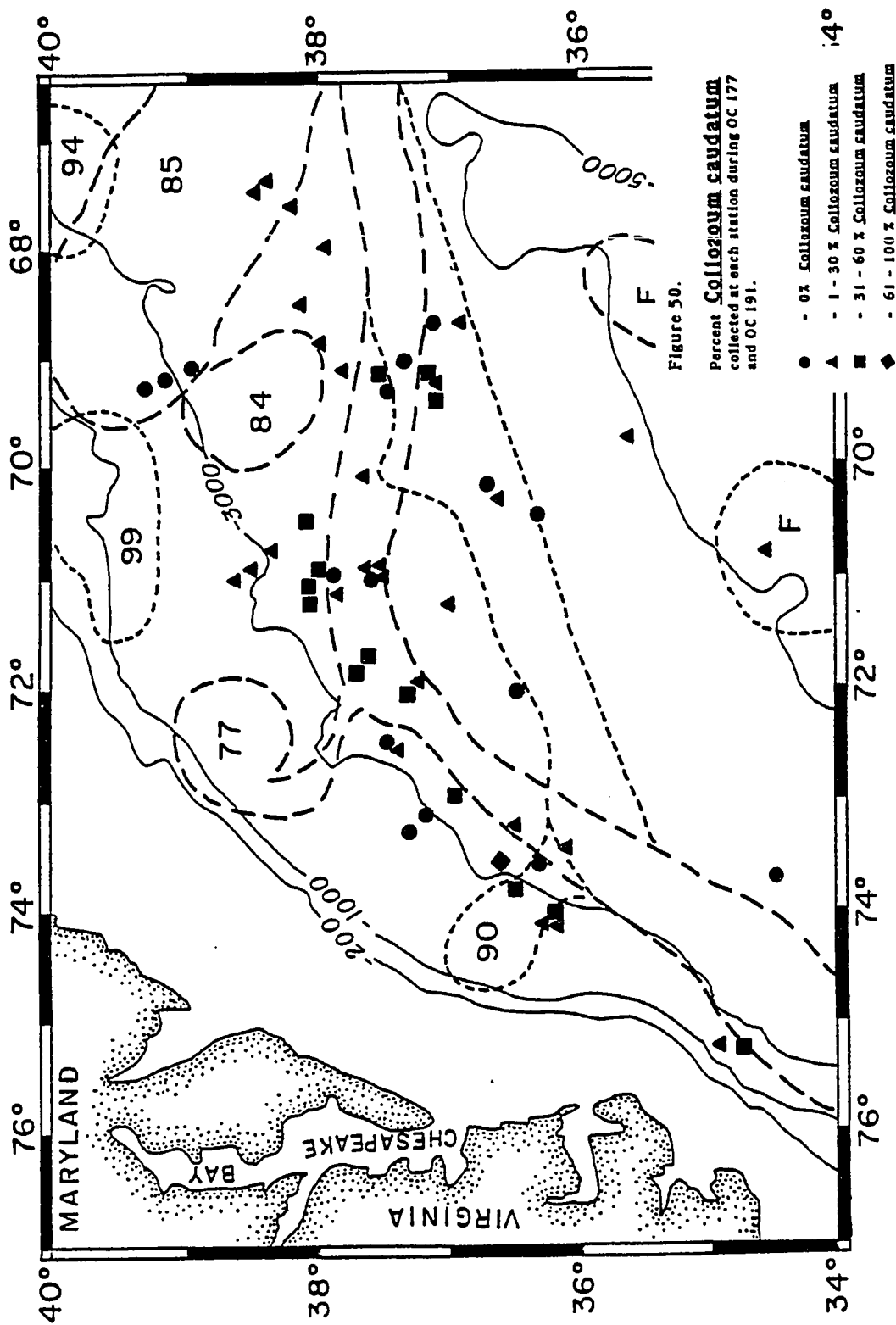


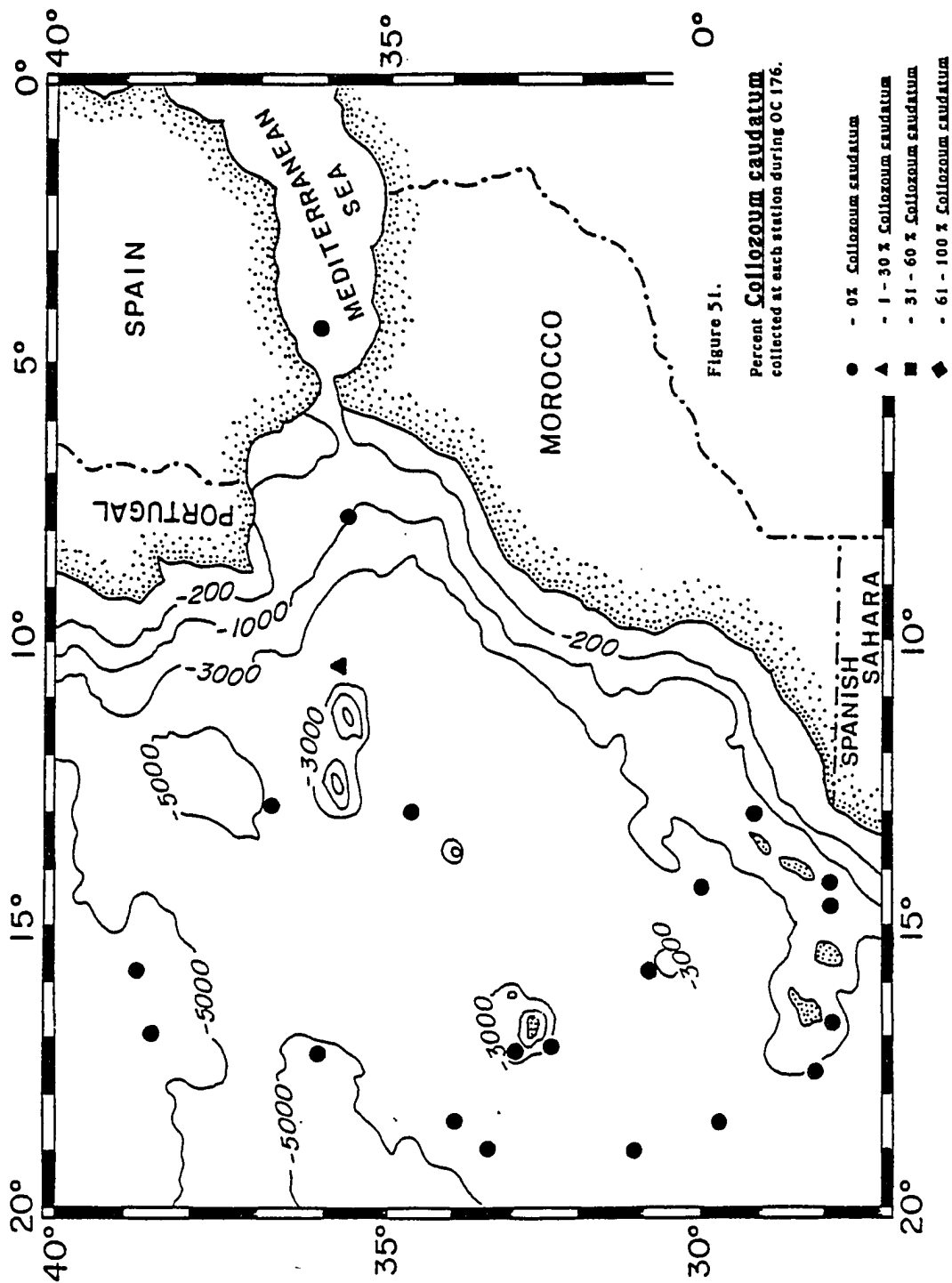


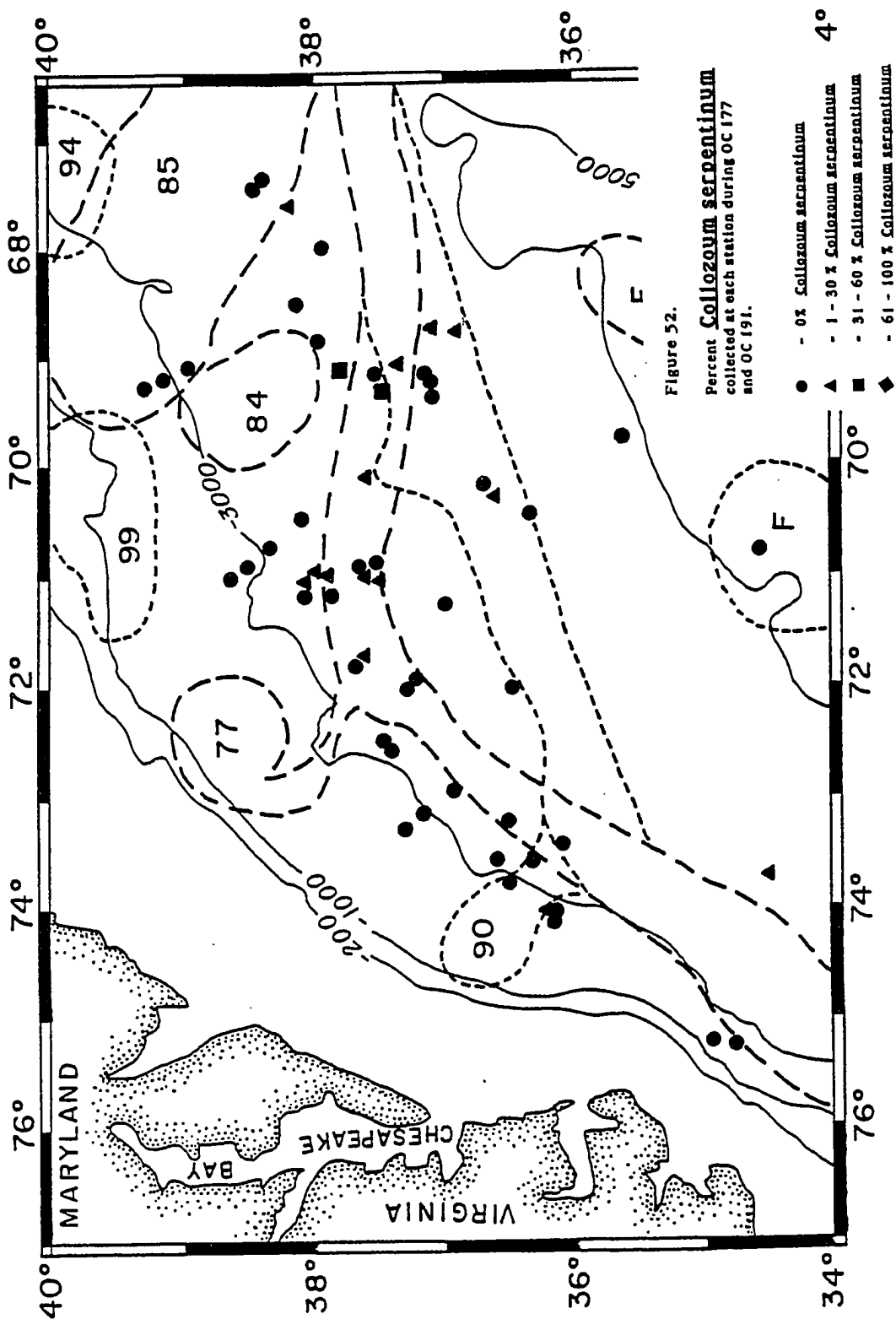


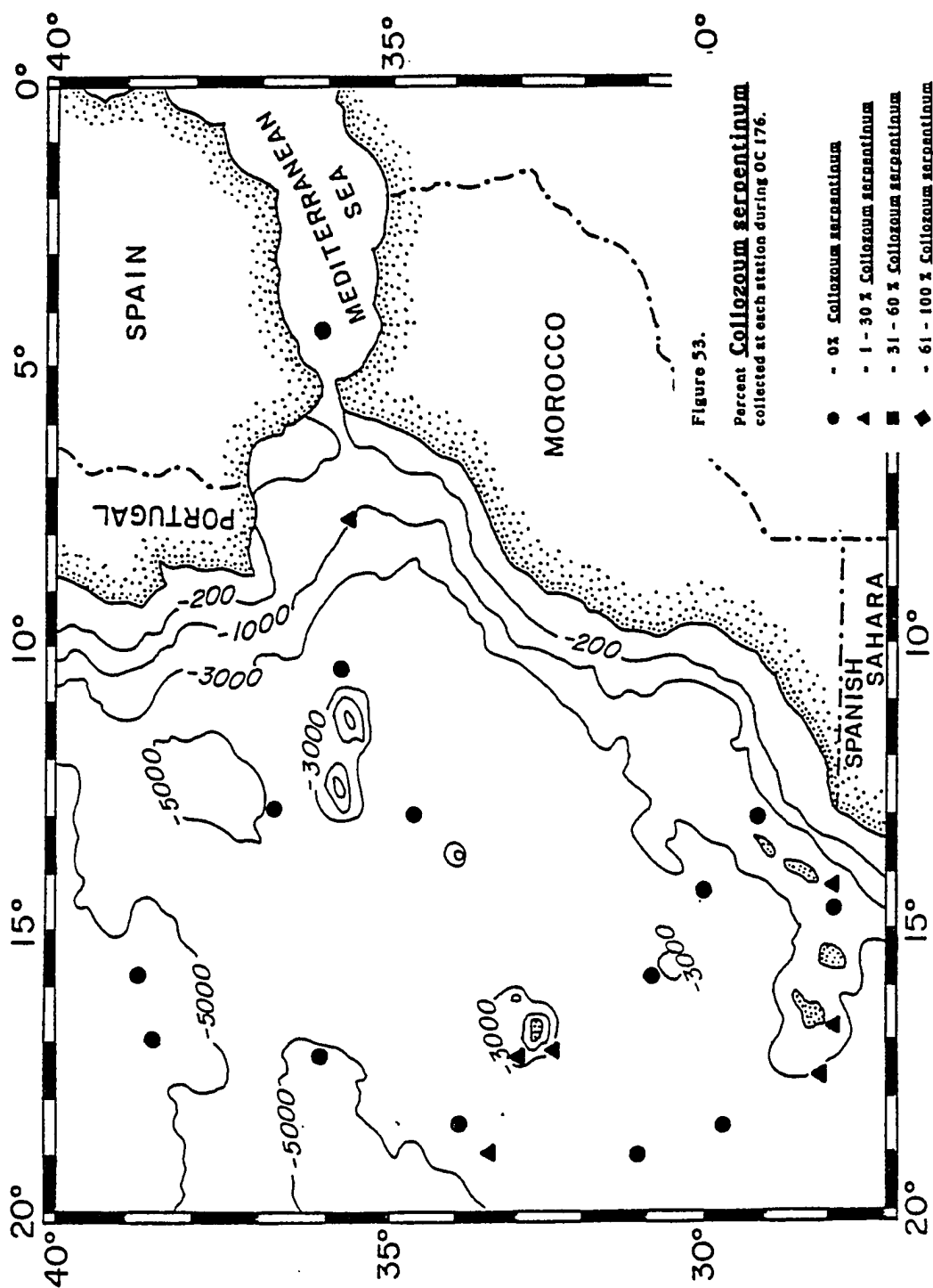


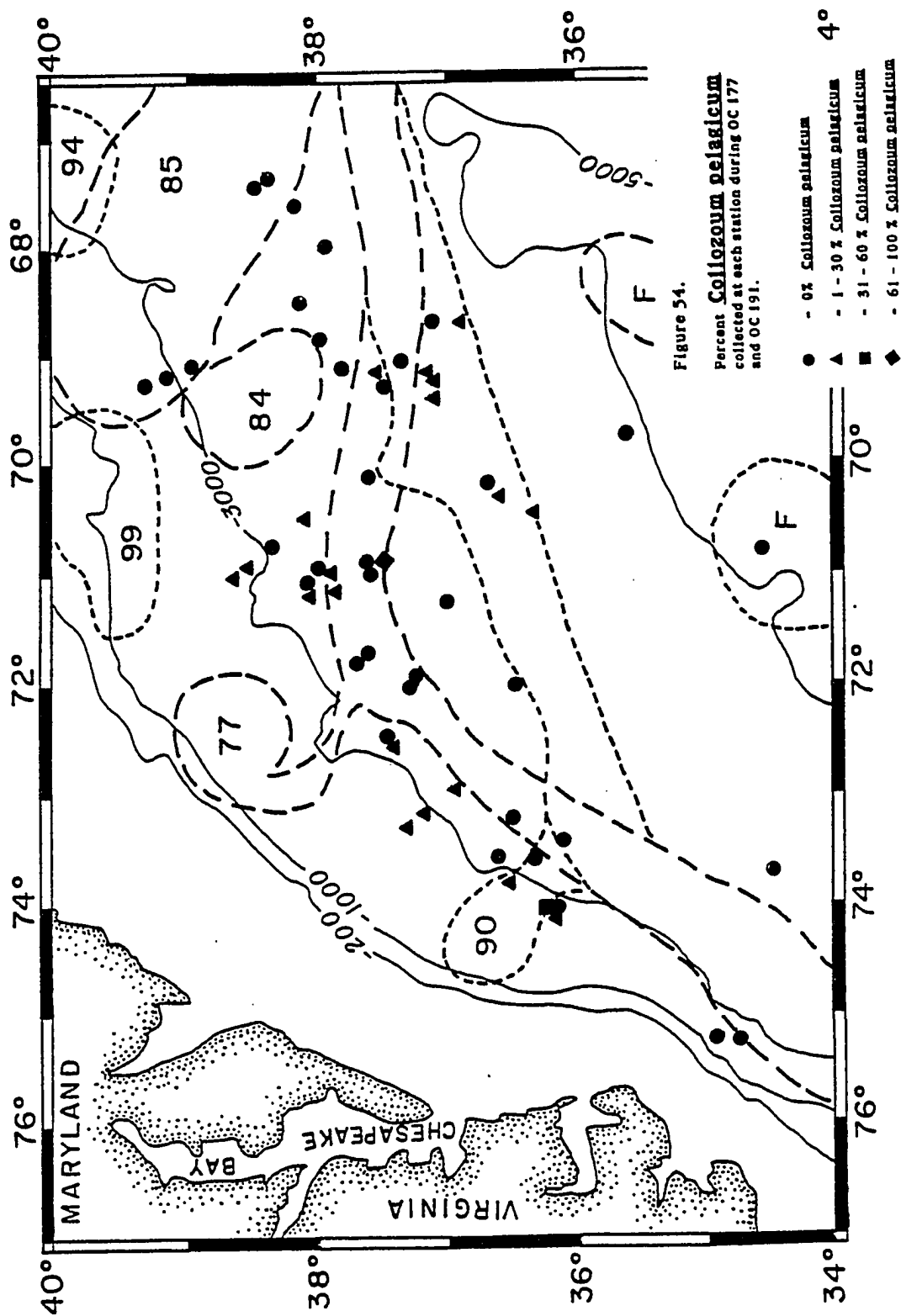


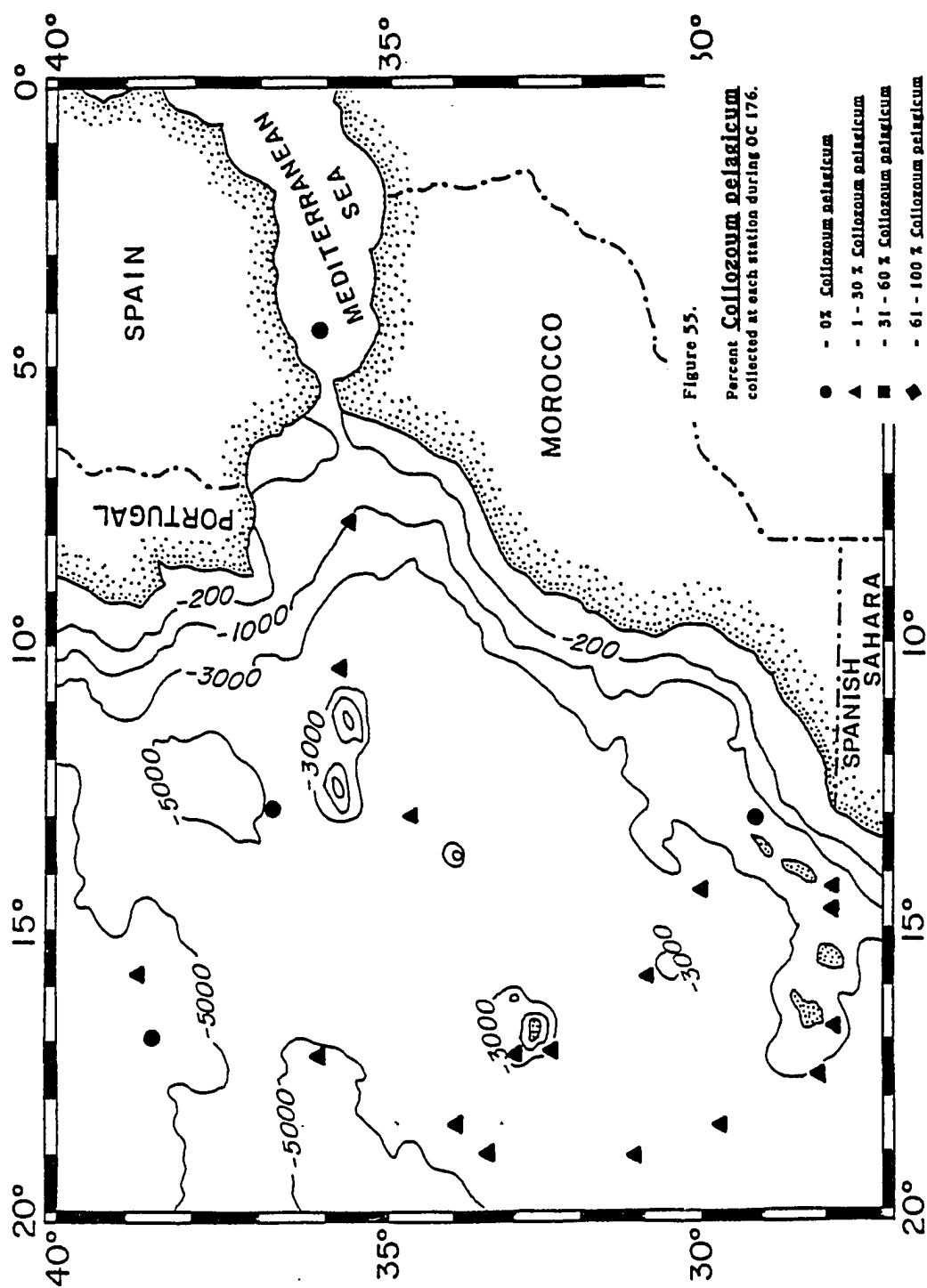


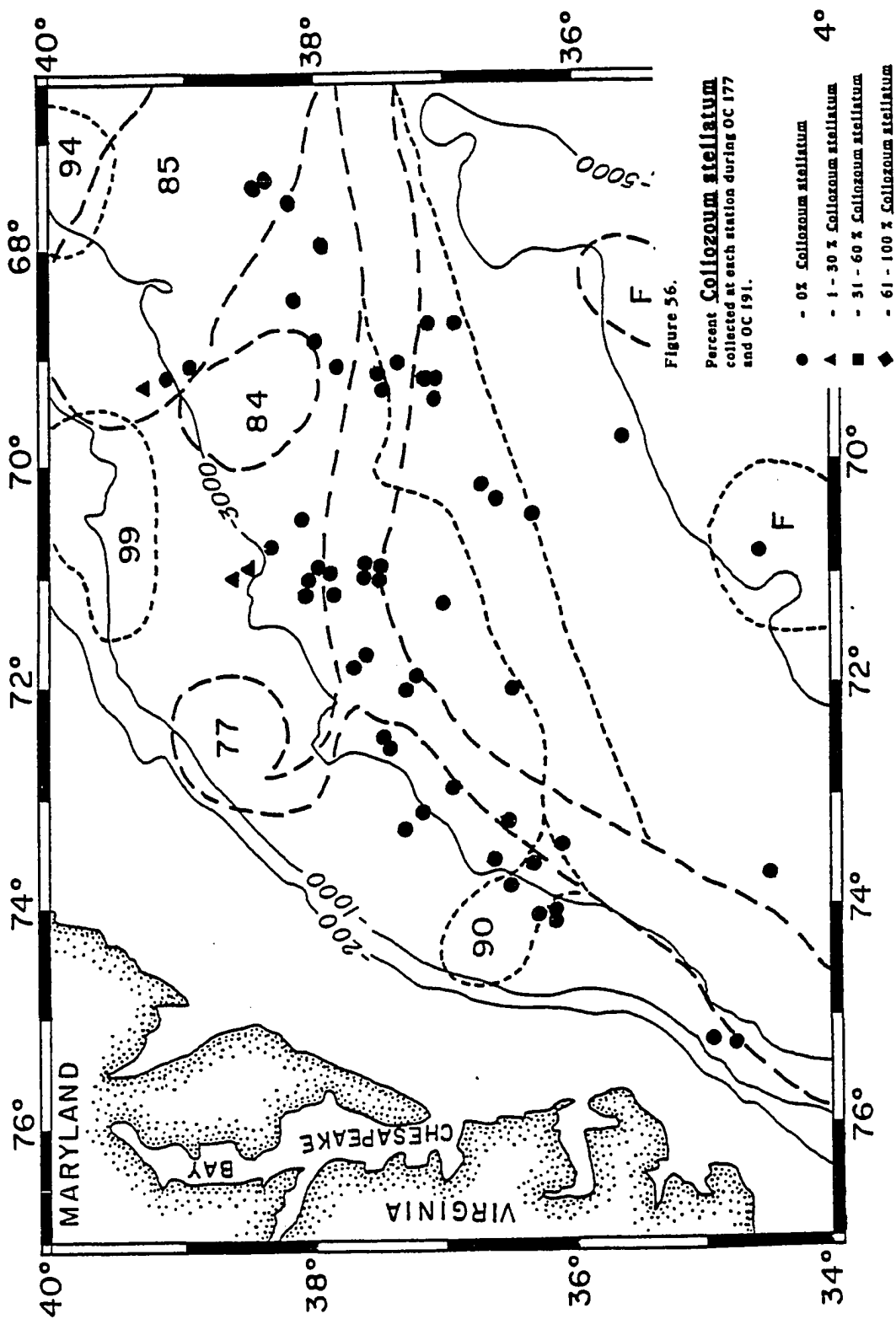








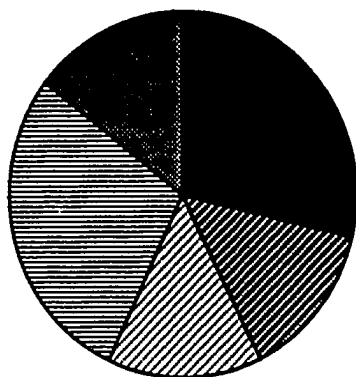




Appendix B

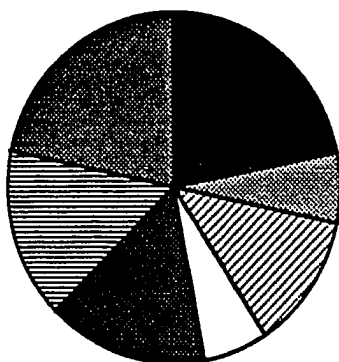
The following pie graphs describe the taxonomic composition of colonial radiolarian assemblages collected during the three Caribbean field excursions, Barbados 1986, Barbados 1987 and Curacao 1988. The data are presented in chronological order; each sample was collected on a different date as shown at the top of each graph. The arrangement of CR taxa in each pie graph corresponds to the order of the taxa listed in the adjacent legend; the pie segment to the right of 12:00 corresponds to the first taxon listed in the legend and so on around the pie in a clockwise direction.

3/10/86
(7 CR examined)



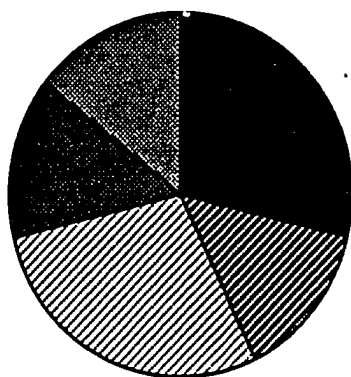
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Sphaerozoum spp.
- ▧ Collozoum caudatum
- unidentified colonies

3/12/86
(32 CR examined)



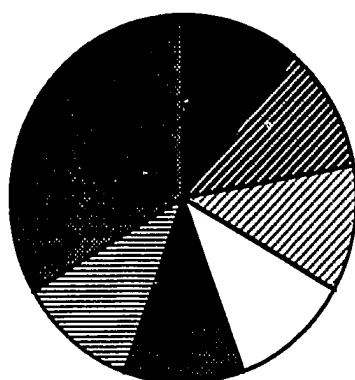
- Acrosphaera spp.
- ▨ Siphonosphaera spp.
- ▩ Sphaerozoum spp.
- ▧ Rhaphidozoum spp.
- ▧ Collozoum inerme
- ▧ Collozoum caudatum
- unidentified colonies

3/17/86
(7 CR examined)



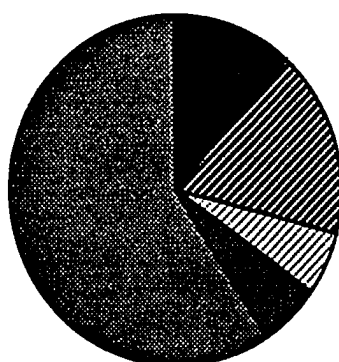
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Sphaerozoum spp.
- ▧ Collozoum inerme
- unidentified colonies

3/19/86
(9 CR examined)



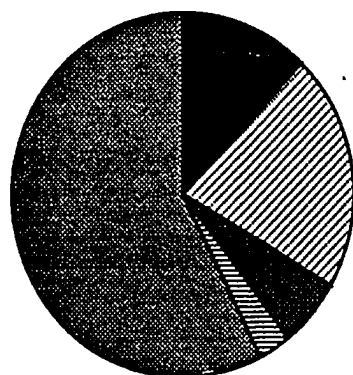
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum caudatum
- ▩ unidentified colonies

3/20/86
(17 CR examined)



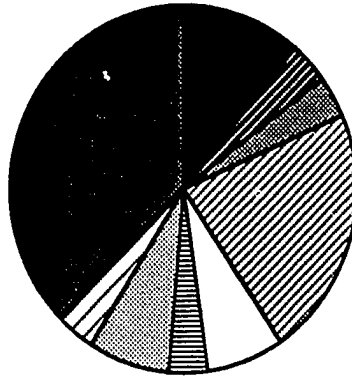
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum caudatum
- ▩ unidentified colonies

3/24/86
(32 CR examined)



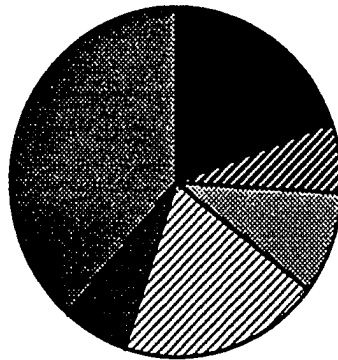
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum caudatum
- ▩ unidentified colonies

3/26/86
(26 CR examined)



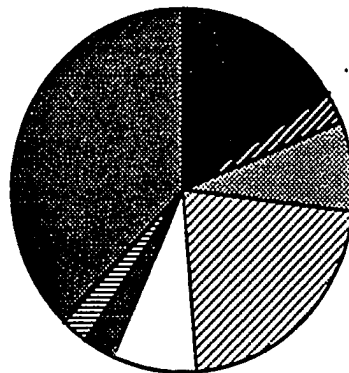
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▨ Collozoum caudatum
- ▩ Collozoum serpenterum
- ▧ Collozoum pelagicum
- unidentified colonies

4/1/86
(30 CR examined)



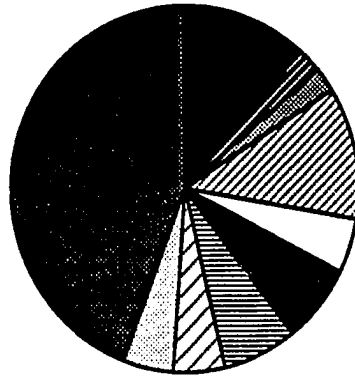
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Collozoum inermis
- unidentified colonies

4/3/86
(35 CR examined)



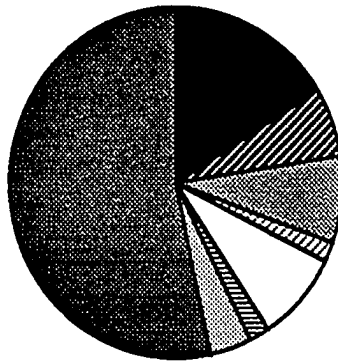
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▨ Collozoum inermis
- ▩ Collozoum caudatum
- unidentified colonies

4/8/86
(43 CR examined)



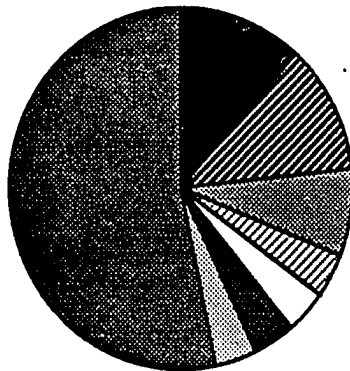
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inermis
- ▨ Collozoum caudatum
- ▩ Collozoum pelagicum
- ▧ Collozoum rhizoides
- unidentified colonies

4/10/86
(48 CR examined)



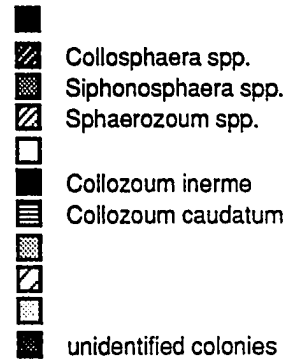
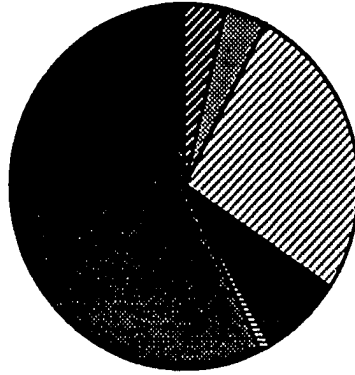
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum caudatum
- ▨ Collozoum serpentenum
- ▩ Collozoum pelagicum
- ▧ Collozoum rhizoides
- unidentified colonies

4/14/86
(25 CR examined)

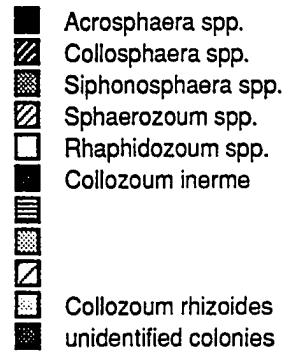
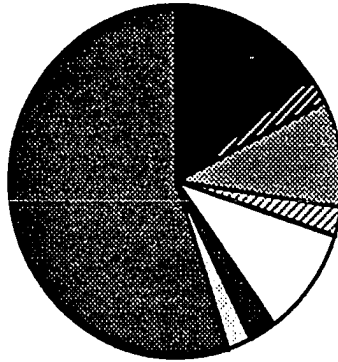


- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inermis
- ▨ Collozoum serpentenum
- ▩ Collozoum pelagicum
- ▧ Collozoum rhizoides
- unidentified colonies

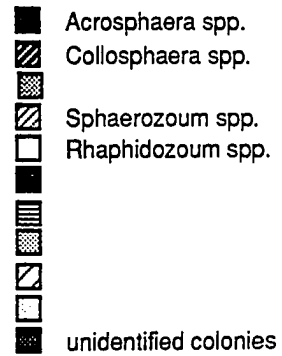
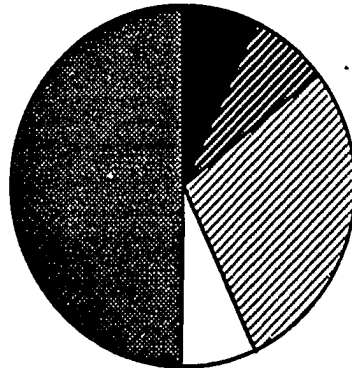
4/16/86
(26 CR examined)



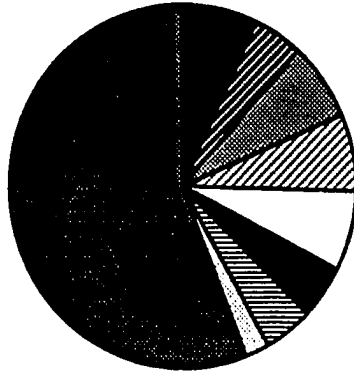
4/21/86
(39 CR examined)



4/23/86
(13 CR examined)

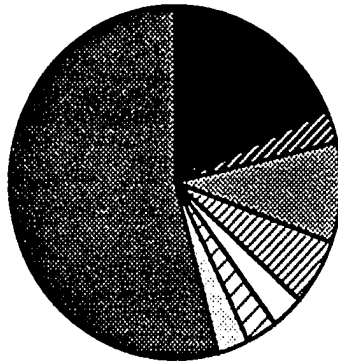


4/26/86
(42 CR examined)



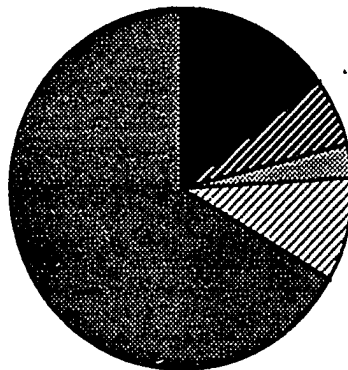
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum caudatum
- ▩ Collozoum rhizoides
- unidentified colonies

4/28/86
(33 CR examined)



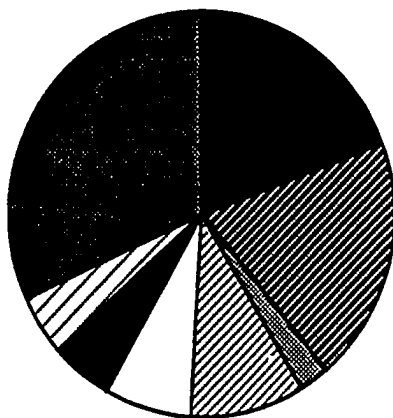
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum pelagicum
- ▨ Collozoum rhizoides
- unidentified colonies

4/30/86
(32 CR examined)



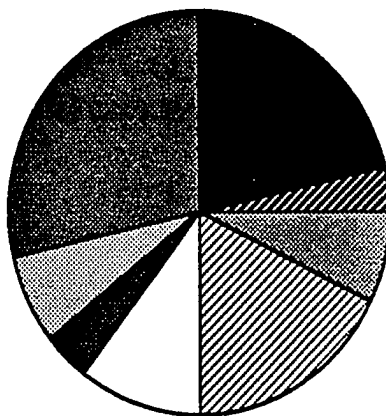
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- unidentified colonies

2 / 24 / 87
(42 CR examined)



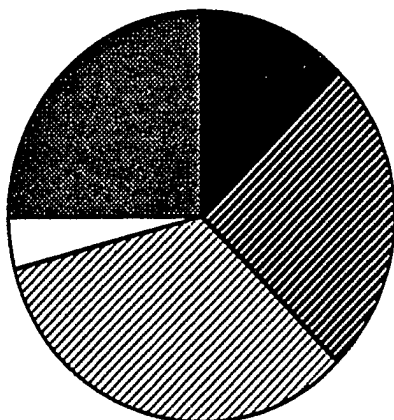
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum pelagicum
- ▩ Collozoum pelagicum
- ▧ Collozoum pelagicum
- unidentified colonies

3 / 1 / 87
(28 CR examined)



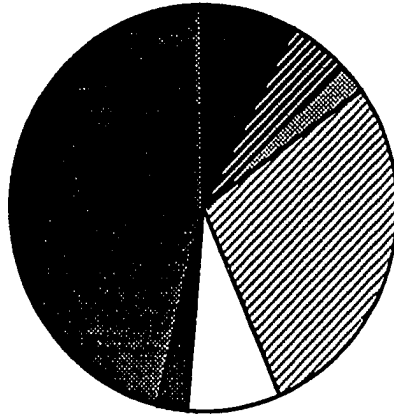
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum serpentenum
- ▩ Collozoum serpentenum
- ▧ Collozoum serpentenum
- unidentified colonies

3 / 3 / 87
(25 CR examined)



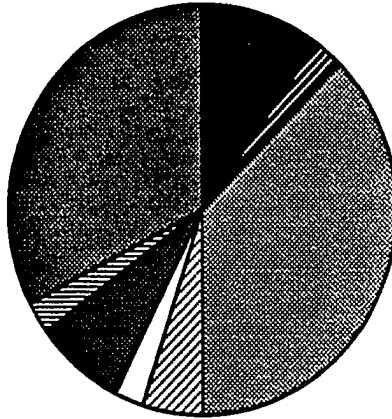
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum serpentenum
- ▩ Collozoum serpentenum
- ▧ Collozoum serpentenum
- unidentified colonies

3/6/87
(41 CR examined)



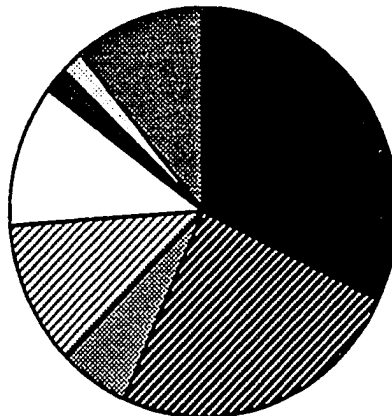
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨
- ▩
- ▧
-
- unidentified colonies

3/9/87
(10 CR examined)



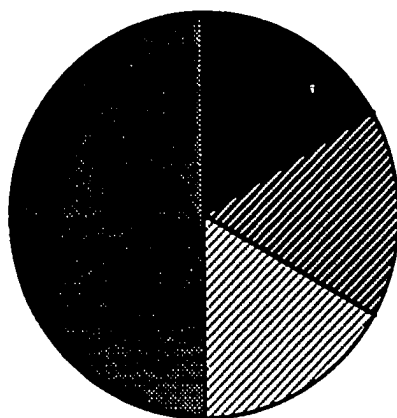
- Acrosphaera spp.
- ▨ Sphaerozoum spp.
- ▩ Collosphaera spp.
- ▧ Rhaphidozoum spp.
- Siphonosphaera spp.
- Collozoum inerme
- ▨ Collozoum serpentinu
- ▩
- ▧
- Collozoum pelagicum
- unidentified colonies

3/13/87
(53 CR examined)



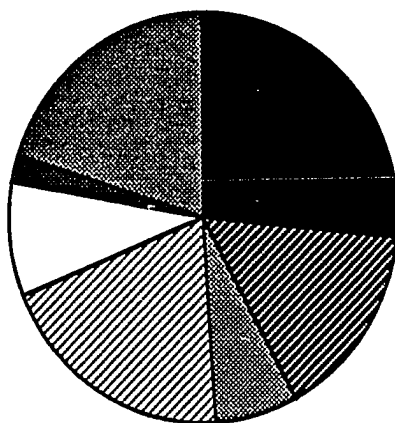
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨
- ▩
- ▧
- Collozoum rhizoides
- unidentified colonies

3/16/87
(6 CR examined)



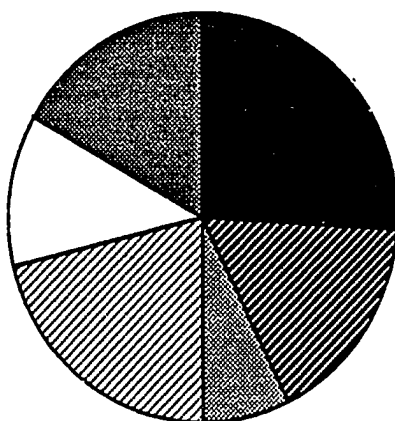
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ unidentified colonies

3/19/87
(44 CR examined)



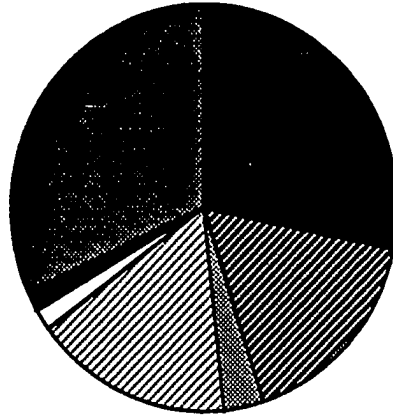
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ unidentified colonies

3/21/87
(44 CR examined)



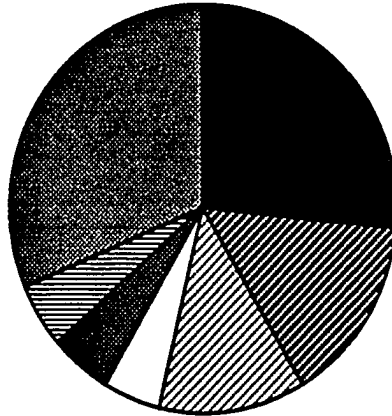
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ unidentified colonies

3/25/87
(61 CR examined)



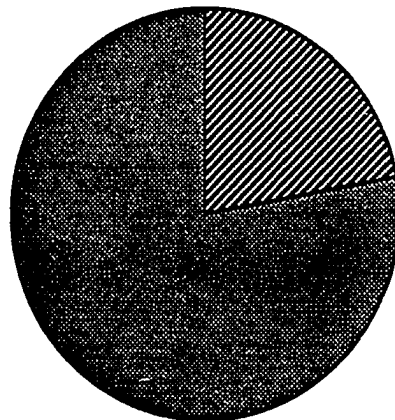
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨
- ▩
- ▧
-
- unidentified colonies

3/31/87
(41 CR examined)



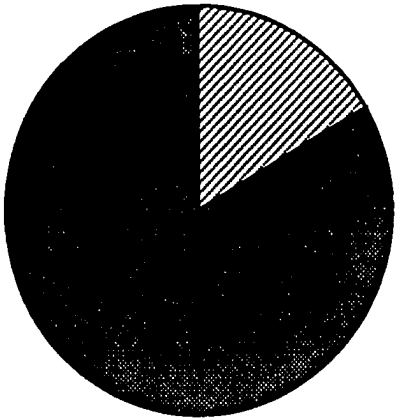
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum inerme
- ▨ Collozoum caudatum
- ▩
- ▧
-
- unidentified colonies

4/4/87
(10 CR examined)

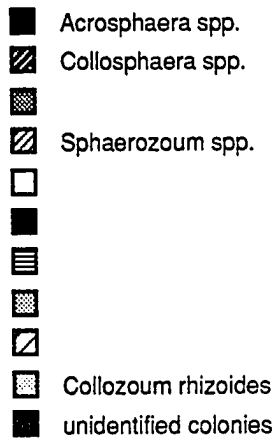
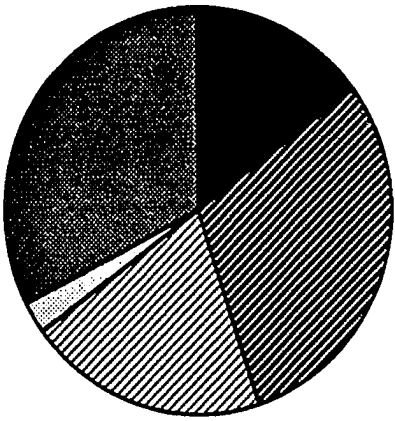


-
- ▨ Collosphaera spp.
- ▩
- ▧
-
-
- ▨
- ▩
- ▧
-
- unidentified colonies

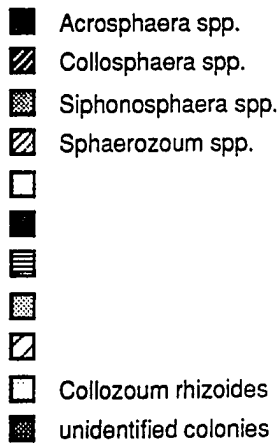
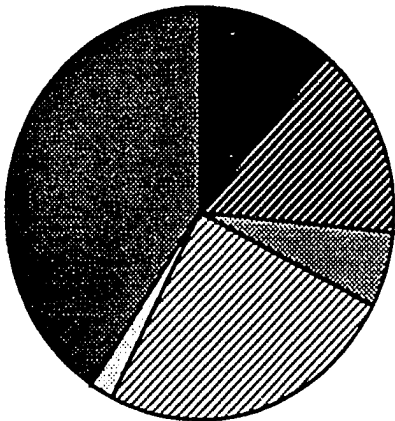
4/6/87
(6 CR examined)



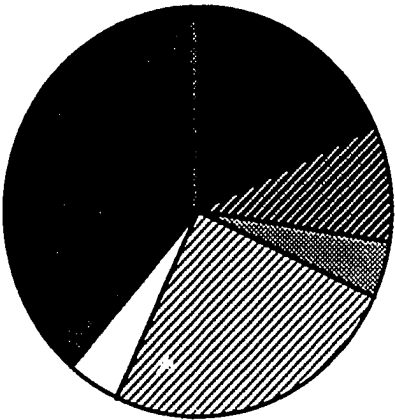
4/8/87
(41 CR examined)



4/11/87
(52 CR examined)

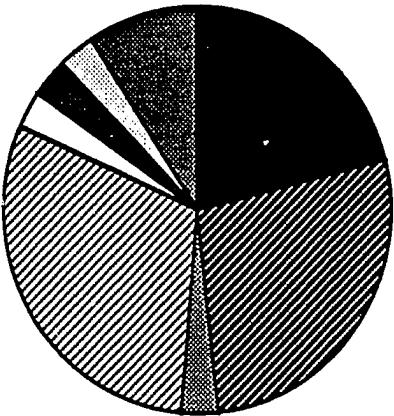


4/13/87
(45 CR examined)



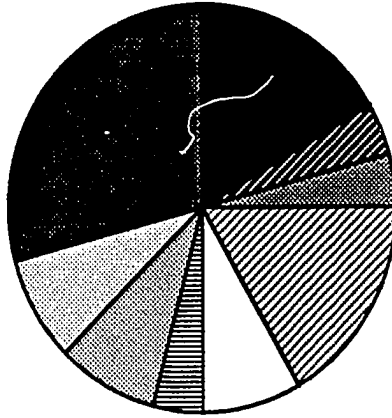
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▤ Siphonosphaera spp.
- ▩ Sphaerozoum spp.
- Rhaphidozoum spp.
- unidentified colonies

4/16/87
(33 CR examined)



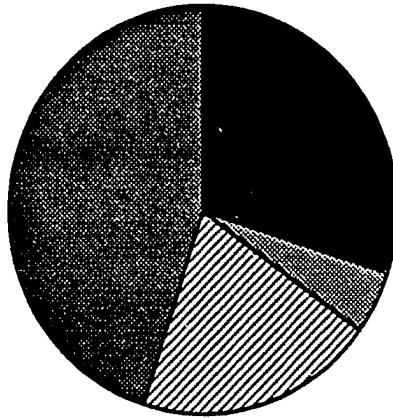
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▤ Siphonosphaera spp.
- ▩ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▧ Collozoum inerme
- unidentified colonies

3/28/88
(25 CR examined)



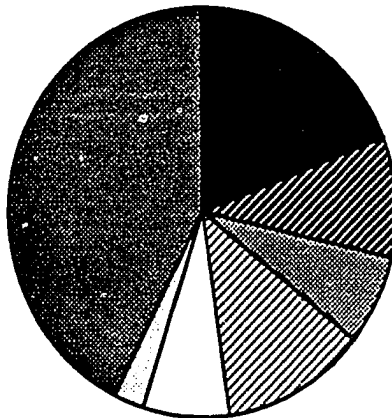
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum caudatum
- ▩ Collozoum serpentenum
- ▧ Collozoum rhizoides
- unidentified colonies

3/30/88
(20 CR examined)



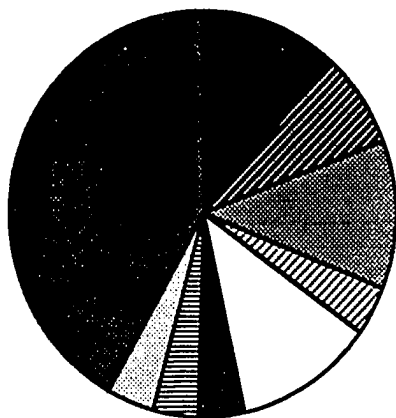
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum caudatum
- ▩ Collozoum serpentenum
- ▧ Collozoum rhizoides
- unidentified colonies

4/1/88
(43 CR examined)



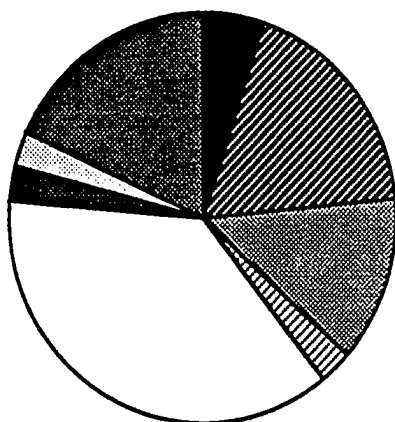
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum caudatum
- ▩ Collozoum serpentenum
- ▧ Collozoum rhizoides
- unidentified colonies

4 / 4 / 88
(26 CR examined)



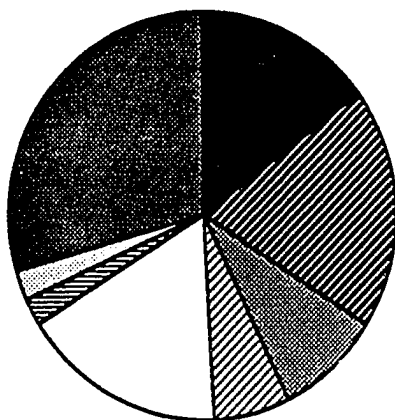
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▤ Collozoum inermis
- ▥ Collozoum caudatum
- ▦ Collozoum rhizoides
- unidentified colonies

4 / 6 / 88
(39 CR examined)



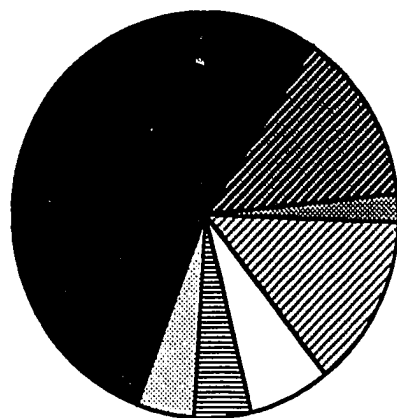
- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▤ Collozoum inermis
- ▥ Collozoum caudatum
- ▦ Collozoum rhizoides
- unidentified colonies

4 / 8 / 88
(47 CR examined)



- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- ▤ Collozoum inermis
- ▥ Collozoum caudatum
- ▦ Collozoum rhizoides
- unidentified colonies

4/11/88
(43 CR examined)



- Acrosphaera spp.
- ▨ Collosphaera spp.
- ▩ Siphonosphaera spp.
- ▧ Sphaerozoum spp.
- Rhaphidozoum spp.
- Collozoum caudatum
- ▩ Collozoum rhizoides
- ▧ unidentified colonies

Appendix C. Surface seawater temperatures and positions of dive stations during OC 176, OC 177, OC 191, and Barbados 1986, 1987 and Curacao 1988.

Date	Station	Position	Surface Seawater Temperature (°C)
R.V. Oceanus 176			
5/23/86	1533	34°38.5'N12°57.9'W	17.5
5/25/86	1536	30°52.0'N15°48.8'W	18.5
5/26/86	1538	30°01.3'N14°17.0'W	18.8
5/27/86	1542	29°10.0'N12°59.3'W	19.2
5/28/86	1545	27°55.0'N14°14.0'W	19.2
5/29/86	1547	27°54.0'N14°34.0'W	19.0
5/31/86	1553	27°54.8'N16°40.9'W	19.2
6/1/86	1557	28°08.0'N17°33.0'W	19.8
6/2/86	1560	29°43.3'N18°27.9'W	19.8
6/3/86	1562	31°08.9'N18°59.3'W	19.2
6/4/86	1566	33°26.0'N18°56.0'W	18.5
6/5/86	1568	33°57.0'N18°28.0'W	18.5
6/6/86	1572	32°30.2'N17°11.4'W	18.7
6/9/86	1574	33°02.2'N17°18.9'W	18.5
6/10/86	1577	36°05.8'N17°11.2'W	18.1
6/11/86	1579	38°38.8'N16°54.5'W	17.0
6/12/86	1582	38°50.5'N15°46.5'W	17.0
6/13/86	1586	36°50.5'N12°49.6'W	17.3
6/14/86	1588	35°47.0'N10°24.3'W	19.5
6/15/86	1590	35°38.0'N7°46.2'W	20.4
6/16/86	1593	36°05.6'N4°23.0'W	20.4
R.V. Oceanus 177			
7/29/86	1600	38°05.1'N71°11.0'W	28.0
7/30/86	1602	38°06.4'N71°04.0'W	28.2
"	1604	38°08.3'N70°28.2'W	28.2
7/31/86	1605	37°43.8'N69°56.9'W	28.5
"	1607	37°08.7'N69°14.0'W	28.5
"	1608	37°08.6'N69°14.1'W	28.5
8/1/86	1610	37°50.0'N69°08.1'W	28.6
"	1612	37°32.8'N69°15.2'W	28.6
8/2/86	1614	37°30.1'N69°16.0'W	28.3
"	1615	37°06.5'N69°23.0'W	28.3
8/4/86	1617	38°00.4'N70°58.0'W	24.0
"	1618	37°53.0'N71°09.1'W	24.0
8/5/86	1620	37°38.8'N71°43.6'W	28.0
"	1621	37°42.2'N71°48.2'W	28.0
8/6/86	1623	36°56.2'N72°55.6'W	28.0
8/7/86	1627	36°38.9'N73°35.0'W	28.4
8/8/86	1629	37°19.8'N73°17.7'W	26.8
"	1630	37°11.8'N73°07.6'W	28.8
8/9/86	1632	36°08.4'N74°04.1'W	28.8
"	1633	36°15.1'N74°01.5'W	28.7
8/10/86	1635	36°13.3'N74°03.9'W	28.7
8/13/86	1638	36°21.7'N73°35.2'W	28.7
"	1639	36°33.2'N73°16.3'W	28.7

Appendix C. (cont.)

Date	Station	Position	Surface Seawater Temperature (°C)
8/14/86	1641	37°26.4'N72°33.9'W	29.2
"	1642	37°28.2'N72°29.9'W	29.2
8/15/86	1643	37°54.2'N71°01.9'W	29.2
"	1644	37°38.2'N70°59.7'W	29.2
"	1645	37°55.9'N71°01.8'W	29.2
8/16/86	1646	38°39.1'N71°01.3'W	28.0
"	1647	38°33.6'N70°56.5'W	28.0
"	1648	38°23.2'N70°44.8'W	28.0
8/17/86	1650	37°37.9'N70°59.8'W	29.5
"	1651	37°38.2'N70°55.2'W	29.5
8/19/86	1652	36°21.8'N70°26.5'W	27.2
"	1653	36°37.6'N70°18.5'W	27.2
"	1654	36°43.7'N70°11.4'W	27.2
8/20/86	1656	37°22.5'N69°03.8'W	26.8
8/21/86	1659	37°08.2'N68°42.9'W	27.3
"	1660	36°54.4'N68°42.7'W	27.3
8/23/86	1661	38°58.1'N69°06.9'W	28.0
"	1662	39°09.3'N69°12.1'W	28.0
"	1663	39°19.5'N69°16.2'W	28.0
R.V. Oceanus191			
7/15/87	1713	?	
7/16/87	1715	35°38.9'N69°45.4'W	27.0
7/16/87	1717	?	
7/17/87	1719	34°34.2'N70°47.7'W	27.0
7/18/87	1722	34°29.9'N73°44.2'W	27.5
7/19/87	1725	34°45.5'N75°15.5'W	29.5
7/19/87	1726	34°56.9'N75°14.1'W	29.5
7/20/87	1728	36°09.1'N73°27.2'W	30.2
7/21/87	1731	36°30.3'N72°00.7'W	28.6
7/22/87	1733	37°16.5'N71°58.4'W	25.6
"	1734	37°16.6'N71°59.8'W	25.6
7/23/87	1736	37°02.1'N71°15.9'W	28.1
"	1737	37°32.5'N70°55.2'W	28.8
7/24/87	1740	38°00.6'N68°52.7'W	29.1
"	1741	38°09.7'N68°30.5'W	29.1
7/25/87	1743	37°58.2'N67°58.6'W	28.8
7/26/87	1746	38°27.2'N67°24.4'W	28.8
7/27/87	1750	38°12.4'N67°36.2'W	29.0
7/28/87	1753	38°25.4'N67°23.1'W	27.5
Barbados	Bellairs	13°09.6'N59°39.6'W	
1986			mean = 26.7 +/- 0.1
1987			mean = 27.0 +/- 0.1
			(mean +/- st. err.)
Curacao	CARMABI	12°03.6'N68°72.0'W	
1988			mean = 26.7 +/- 0.1

Appendix D. Raw data from measurements of light and dark uptake of inorganic carbon by *Gyrodinium* sp. (dino). All uptake incubations were done in clean, plastic tissue culture dishes. The light intensity During light incubations was 60 uE/m2/sec. DPM per dino/hr was calculated by subtracting mean DPM of filter blanks from gross DPM.

Date	Vial #	Incubation Time (hr)	Concentration of Radioactive Isotope (uCi/ml)	Volume of Incubation Medium (ml)	Number of Dinos per Vial	Treatment	DPM per Vial	DPM per Dino per hour	Mean DPM per Dino per hour +/- s.e.
3/28/87	1	3.5	10	1	8	light	44.00	1.17	5.58
	2	..	..	..	5	..	105.25	4.90	+/- 1.22
	3	..	..	..	13	..	161.25	3.12	
	4	..	..	..	5	..	185.75	9.50	
	5	..	..	..	2	..	51.00	4.50	
	6	..	..	..	2	..	47.50	4.00	
	7	..	..	..	2	..	58.00	5.50	
	8	..	..	..	5	..	80.75	3.50	
	9	..	..	..	11	..	588.25	14.77	
	10	..	..	..	7	..	140.25	4.93	
	11	..	..	..	5	dark	80.23	3.47	3.90
	12	..	..	..	5	..	95.28	4.33	+/- 0.43
	13					blank 1	20.00		
	14					blank 2	19.00		
						Mean Blank	19.50		
3/29/87	1	5	2	10	6	light	58.85	1.22	3.22
	2	..	..	..	6	..	121.65	3.38	+/- 0.91
	3	..	..	..	4	..	121.25	5.05	
	4	..	..	..	4	dark	48.25	1.40	2.62
	5	..	..	..	3	..	66.45	3.08	+/- 0.71
	6	..	..	..	4	..	77.25	2.85	
	7	..	..	..	2	..	51.75	3.15	
	8					blank 1	21.00		
	9					blank 2	19.50		
						Mean Blank	20.25		
4/1/87	1	4.5	5	3	10	light	76.00	1.20	0.91
	2	..	..	..	5	..	62.95	1.82	+/- 0.22
	3	..	..	..	6	..	36.85	0.55	
	4	..	..	..	5	..	31.00	0.40	
	5	..	..	..	5	..	44.50	1.00	
	6	..	..	..	6	..	34.69	0.47	
	7	..	..	..	4	dark	23.80	0.08	0.05
	8	..	..	..	3	..	22.00	0.00	
	9	..	..	..	5	dead	22.00	0.00	0.05
	10	..	..	..	5	..	24.30	0.09	
	11					blank 1	23.30		
	12					blank 2	21.20		
						Mean Blank	22.25		
4/6/87	1	6.5	5	3	20	light	265.10	1.88	1.33
	2	..	..	..	30	..	303.45	1.45	+/- 0.12
	3	..	..	..	20	..	219.60	1.53	
	4	..	..	..	25	..	183.20	1.00	
	5	..	..	..	20	..	142.90	0.94	
	6	..	..	..	25	..	228.70	1.28	
	7	..	..	..	10	..	100.65	1.23	
	8	..	..	..	7	dark	113.52	2.04	1.67
	9	..	..	..	4	..	56.58	1.38	+/- 0.20
	10	..	..	..	8	..	101.30	1.55	
	11					blank 1	22.90		
	12					blank 2	20.66		
						Mean Blank	20.70		

Appendix D. (cont.)

Date	Vial #	Incubation Time (hr)	Concentration of Radioactive Isotope (uCi/ml)	Volume of Incubation Medium (ml)	Number of Dinos per Vial	Treatment	DPM per Vial	DPM per Dino per hour	Mean DPM per Dino per hour +/- s.e.
4/9/87	1	4	2	3	10	light	41.00	0.44	0.55 +/- 0.17
	2	..	..	..	10	..	35.80	0.31	
	3	..	..	..	10	..	70.60	1.18	
	4	..	..	..	10	..	46.20	0.57	
	5	..	..	..	10	..	32.60	0.23	
	6	..	..	..	10	dark	41.40	0.45	0.56 +/- 0.15
	7	..	..	..	8	..	45.16	0.68	
	8	..	..	..	3	..	36.24	1.07	
	9	..	..	..	4	..	26.92	0.22	
	10	..	..	..	6	..	32.04	0.36	
	11					blank 1	23.70		
	12					blank 2	23.25		
						Mean Blank	23.40		
4/17/87	1	3.5	2	3	6	light	104.98	3.98	4.75 +/- 0.70
	2	..	..	..	8	..	195.00	6.20	
	3	..	..	..	12	..	200.74	4.27	
	4	..	..	..	6	..	116.95	4.55	
	5	..	..	..	5	dark	54.13	1.87	2.17 +/- 0.18
	6	..	..	..	6	..	66.34	2.14	
	7	..	..	..	6	..	73.69	2.49	
	8					blank 1	21.24		
	9					blank 2	21.66		
						Mean Blank	21.45		
8/14/87	1	2.5	1	3	14	light	34.32	0.43	0.34 +/- 0.06
	2	..	..	..	8	..	29.67	0.52	
	3	..	..	..	9	..	26.92	0.34	
	4	..	..	..	6	..	21.97	0.18	
	5	..	..	..	5	..	22.40	0.25	
	6	..	..	..	8	dark	20.07	0.04	0.03 +/- 0.02
	7	..	..	..	11	..	18.00	0.00	
	8	..	..	..	10	..	21.02	0.07	
	9	..	..	..	4	..	19.19	0.00	
	10					blank 1	18.74		
	11					blank 2	19.80		
						Mean Blank	19.27		

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