THE ECOLOGY OF COLONIAL RADIOLARIANS: THEIR COLONY MORPHOLOGY, TROPHIC INTERACTIONS AND ASSOCIATIONS, BEHAVIOR, DISTRIBUTION, AND THE PHOTOSYNTHESIS OF THEIR SYMBIONTS

by

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This dissertation is dedicated to my mother, Marian Swanberg

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ABSTRACT

Colonial radiolarians (Spumellaria) are among the most common and abundant large zooplankton, but they have been little studied by modern biologists. Colonies were found on 98% of epipelagic diving stations in the period from 1977 to 1979. Measured abundances ranged from .04 to 540 colonies per m^3. Colony morphology of common genera and species is described and three new shell-less species which reach a length in excess of 1 m are discussed in detail. Some simple behavioral responses are documented, including control of colony buoyancy and position of algae in the colonies. Radiolarians feed on a wide variety of planktonic organisms including tintinnids, copepods, appendicularians, mollusc larvae and hydromedusae. They are hosts to parasitic hyperiid amphipods, particularly those of the genus *Hyperietta*. Radiolarians are prey of the amphipod *Oxycephalus clausi*, an unidentified turbellarian and possibly the Harpacticoid copepods *Miracia efferata* and *Sapphirina* sp. Colonial radiolarians are also hosts to symbiotic dinoflagellates.

Experiments were done at sea on the net incorporation of CO_2 by these algae using ^{14}C labelled $NaHCO_3$. Data from these experiments were related to content of carbon and chlorophyll as a function of colony size (cell number). Carbon content of colonies related well with colony size. Mean values were 50, 85, 100 and 200 ng C per radiolarian cell for *Collozoum inerme*, *C. longiforme*, *Acrosphaera spinosa* and *Collozoum radiosum* respectively. Chlorophyll content varied widely between colonies and chlorophyll per radiolarian cell decreased with increasing colony size in *Acrosphaera spinosa*. Net carbon incorporation increased with colony size at given light intensities as did photosynthetic assimilation (mmoles $CO_2 \cdot$mg Chl $a^{-1} \cdot hr^{-1}$) in *A. spinosa*. In experiments on the effect of light intensity on photosynthesis, there was no evidence for photoinhibition at high intensities in *Acrosphaera spinosa*. Replicate pieces of the large colonies of *C. longiforme* were incubated together, each colony at a different light intensity. Representative pieces were measured and used for chlorophyll carbon and nitrogen analysis and counted for abundance of radiolarian and algal cells and tintinnid prey. Incorporation per unit length varied little within colonies. Photosynthetic assimilation followed no predictable pattern as a function of light intensity. However, it related directly to abundance of tintinnid prey remains. This effect apparently overrides that of light intensity. Total photosynthesis incorporation was only 0.1 to 0.8% of the total colony carbon per hour. The contribution of colonial radiolarians to total productivity of the regions studied was insignificant. However, the radiolarians' productivity is available to a unique portion of the planktonic food web. Because of their size and abundance radiolarians are important as substrates in their environment.

Name and Title of Thesis Supervisor: G. Richard Harbison, Associate Scientist

PREFACE AND ACKNOWLEDGEMENTS

For eight years a number of researchers have been observing and collecting oceanic plankton *in situ* through the use of SCUBA. In addition to the task of convincing their colleagues that the method was worthwhile these diving scientists have often been faced with the problem of simply recognizing the new or unknown organisms as such in their own environment. Often the *in vivo* morphology of planktonic animals is different from that of preserved specimens. This problem has often been made more difficult by the sheer abundance of "elusive" or "rare" species. One hardly expects to find the most abundant organism to be unknown.

The inadequacy of conventional sampling techniques is underscored when one realizes that many of the "new" organisms are not new at all, but merely forgotten. All too often have we found our exciting discoveries elegantly drawn in some dusty 19th century monograph. The radiolarians are an excellent example of this. Quite a number of experienced investigators have mistaken the colonial radiolarians for mollusc egg masses to which they bear a superficial resemblance. I, too, thought they were egg masses until February of 1975 in the Sargasso Sea when I suddenly realized that "egg masses" were the most common thing in the ocean, yet nothing ever seemed to lay them. Oblivious to the näiveté of that idea (and the fact that it took me about 150 open-ocean dives to realize it), I decided that anything that was that common was worth closer examination. As luck would have it, the first specimen I chose to examine was a new species and very different in morphology from what is expected from a

radiolarian (this species is described in this work as *Collozoum* sp. A). Great credit goes to my good friend, Ronald Gilmer, who suggested on that cruise that the organisms might have been radiolarians. I also thank Georges Merinfeld of Dalhousie University, who confirmed this and introduced me to some of the key literature for the group. Dr. G. Richard Harbison, my thesis advisor, has had a great deal to do with recognizing the most important directions of this research and is to be commended for somehow keeping me from becoming too side-tracked. His generous financial and intellectual support has been completely indispensible in this undertaking.

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I especially thank Anita M. Brosius, whose labor of love allowed this work to appear in its present form. Her invaluable assistance on two cruises with diving, routine laboratory procedures and photography enabled me to accomplish a great deal more than otherwise would have been possible. She did all of the graphics and often lent a patient ear and an encouraging voice. I also thank Jane Peterson for her patient and expert typing and my good friend, Dr. Laurence P. Madin for his patient and critical listening during the writing process. All of those who dove with me, assisted in collecting and especially the members of the crews of the R/V ATLANTIS II and R/V OCEANUS have helped a great deal throughout the years. Finally, I would be remiss if I did not express my gratitude to Dr. W. M. Hamner, whose insight pioneered the *in situ* work on zooplankton. His generosity enabled me to participate in plankton research as an undergraduate at the University of California and his enthusiasm kindled my interest in the plankton.

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GENERAL INTRODUCTION

Over most of the past 100 years our knowledge of planktonic life in the epipelagic environment has been limited to our interpretation of preserved collections, and to the natural history and behavioral observations made by scientists in the latter quarter of the nineteenth century. For a host of reasons, the primary emphasis in the research of the past 60 years has been placed on quantitative investigations of the plankton. One artifact of this approach has been the disappearance of a few groups from the modern plankton literature. It is well known (Harbison et al., 1978) that ctenophores, siphonophores and some other soft-bodied (gelatinous) metazoan organisms break up or become unrecognizable in formalin preparations. It is perhaps less well known that colonial radiolarians dissolve in formalin or even that radiolarians form colonies. All these groups were heavily studied in the last century.

Recently, *in situ* observations and the collection of intact healthy organisms for experimentation have inspired a different perspective on the oceanic planktonic community.

This research began with the realization in the spring of 1975 that the organisms most frequently encountered by divers in the surface waters of the Atlantic Ocean were colonial radiolarians. The overwhelming feature of this fact is that these protozoans are practically unknown as components of the oceanic food chain and go unreported in most plankton samples. This research will attempt to place the colonial radiolarians in proper perspective with the rest of the epipelagic planktonic community by describing their size, abundance, functional morphology, trophic relationships and primary productivity.

Biologists who are unfamiliar with the radiolaria will find the following brief description of their taxonomy, morphology and life history useful.

The super-class Actinopoda is divided into four major classes (Cachon and Cachon, in prep.).[1] These are Acantharia, Phaeodaria, Polycystina and Heliozoa. The "radiolaria" are the Phaeodaria and Polycystina. The Polycystina are characterized by a skeleton of spines and shells made of silicon dioxide. They have an axopodial system which issues from axoplasts, usually through pores called fusules in a capsular membrane made of a glycoprotein substance (Hollande et al., 1970). This separates the inner part of the cell, or central capsule, from the remainder. Frequently there are symbiotic dinoflagellates in the extra-capsular region.

There are two orders of Polycystina: Spumellaria and Sphaerellaria. The order Spumellaria (Peripylea) is characterized by spherical central capsules and uniformly distributed fusules. The sub-order Collodaria (Sphaerocollida) includes a number of species of colonial radiolarians. The shells or spines are relatively simple. There are a number of families including the Sphaerozoidae (forming spicules or no skeleton) and Collosphaeridae (forming spherical shells) which group together all the colonial forms. Detailed cytological studies support this classification scheme for the radiolarians (Cachon and Cachon, 1971, 1972a, b, 1976). There is some evidence that other radiolarians, specifically certain deep

[1]The levels of these taxa are in dispute. Cachon and Cachon (personal communication) have provided the best and most recent classification scheme for the radiolaria. Older parallel forms are provided in parentheses where appropriate.

living Tuscaroridae (Phaeodaria) form colonies also (Haecker, 1908, personal observation). Colonial radiolarians in this report will be considered to be those collodarian radiolarians in the families Sphaerozoidae and Collosphaeridae (Hollande and Enjumet, 1953) forming multicellular gelatinous masses.

Within the central capsules of colonial Collodaria are found the nuclei, vacuoles, mitochondria, endoplasmic reticulum, Golgi apparatus, and often one or several oil droplets (Figure 1). Many form crystals of strontium sulfate (Hollande and Martoja, 1974) in the later phases of their reproductive cycle. Some species (particularly in the family Collosphaeridae) form blue or violet pigment granules in the reproductive stage (Brandt, 1885). The reader is referred to Anderson (1976a,b,c; 1978), Hollande and Enjumet (1953), Hollande et al. (1970) and Cachon and Cachon (1976) for more detailed morphological information on the Collodaria.

Outside of the central capsule is the extra-capsular region enclosing the cytoplasm. In the Sphaerozoidae and Collosphaeridae this region always encloses zooxanthellae (dinoflagellates), which belong either to the genus *Amphidinium* or *Endodinium* (Hollande and Carré, 1974; Taylor, 1974). These encysted dinoflagellates are non-motile and have no external flagellar structure. Extracapsular bodies are also found in the ectocytoplasm of many radiolarian species (Brandt, 1885, 1902). These are thought to be storage bodies.

Skeletal structures of simple or complex spines are found in the extracapsular region, usually immediately surrounding the central capsule, but occasionally, as in the case of some species of *Sphaerozoum* and

Figure 1. A central capsule of *Collozum* (= *Myxosphaera*) *coeruleum* in the reproductive stage of its life cycle. Visible are the crystals of $SrSO_4$ (C), blue pigment granules (P), the large oil droplet (ϕ), the central capsule membrane (CM) and the symbiotic zooxanthellae (Z). Scale = 10 μm.

Figure 2. A single cell of *Sphaerozoum* sp. showing the siliceous spicules gathered around the central capsule. S = spicule, Z = zooxanthella. Scale = 50 μm.

Figure 3. *Collosphaera huxleyi*, showing the spherical shell (Sh) perforated by pores. Shell is 105 μm diameter.

Figure 4. A reproductive colony of *Siphonosphaera tenera* showing the central capsules scattered over the surface of a single large alveolus. Colony is 4.5 mm diameter.