

# Video plankton recorder reveals high abundances of colonial Radiolaria in surface waters of the central North Pacific

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*Colonial spumellarian Radiolaria are heterotrophic protists that form large (up to several meters in length), gelatinous structures in the surface waters of all tropical and subtropical oceanic ecosystems. These species are morphologically and trophically complex and some, but not all, produce silica skeletal structures of considerable paleontological significance. Skeletonless species of Radiolaria are poorly sampled by plankton nets, which can severely damage these delicate organisms. Therefore, abundances of colonial Radiolaria typically have been underestimated in quantitative studies of zooplankton abundance and biomass. Here we document the abundances of colonial Radiolaria in the central North Pacific based on analysis of video images from a miniaturized video plankton recorder. We observed abundances of radiolarian cells in colonies that exceeded previous reports of total Radiolaria by more than ten-fold, and counts of skeleton-bearing Radiolaria by more than two to three orders of magnitude. Biomass (carbon) within these colonies was similar to or greater than the total radiolarian biomass (i.e. including all solitary species) previously reported for the Pacific. Symbiont productivity within colonial Radiolaria was estimated to constitute a modest but significant fraction of total primary productivity (up to ≈9%) in the upper 150 m. These findings indicate an important contribution of skeletonless spumellaria to food webs and biogeochemical cycles of these communities.*

## INTRODUCTION

Polycystine Radiolaria are one of the most conspicuous zooplankton taxa inhabiting the oceanic waters of the tropics and subtropics. Radiolaria are single-celled, eukaryotic organisms that are exclusively marine and, almost exclusively oceanic in their distributions. The unique morphologies and complex life histories of these organisms have captured the attention and imagination of biologists and micropaleontologists for more than 150 years (Ehrenberg, 1847; Haeckel, 1887). Radiolaria exist as single cells ranging in size from less than 30 µm to more than 1 mm. Each cell possesses a segregated central capsule that contains the nucleus, mitochondria and other cellular organelles, and a large pseudopodial network (Anderson, 1983). In addition some, but not all, Radiolaria produce silica skeletal structures of

considerable paleontological significance (Casey, 1971; Kling, 1978).

Radiolaria are morphologically and trophically complex (Anderson, 1983; Swanberg, 1983; Caron and Swanberg, 1990; Angel, 1991; Swanberg and Caron, 1991). The pseudopodial net produced by these species can be extensive, and is used to ensnare and phagocytose a wide variety of prey ranging from bacteria to relatively large zooplankton. In addition, many surface-dwelling species of Radiolaria possess symbiotic algae, predominantly dinoflagellates, within the outer pseudopodial network that are photosynthetically active and which contribute significantly to the nutrition of the host (Caron *et al.*, 1995).

Although Radiolaria are capable of existence as single cells, numerous species (largely within the Order Spumellaria) form colonies of individuals by extending their

cytoplasm to form an anastomosing web of pseudopodia enclosed within a common gelatinous matrix. These colonies often contain thousands of individual central capsules, and form macroscopic structures in a variety of shapes (spheres, cylinders, discs, even branching cylinders) (Swanberg, 1979). These colonies can range in size up to a few centimeters in diameter and several meters in length.

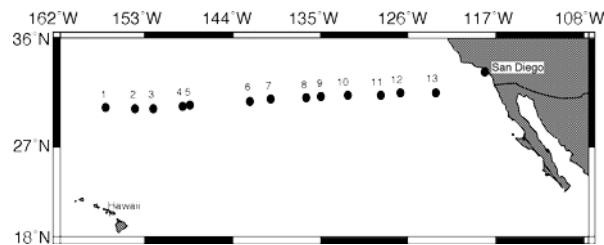
Despite their complex trophic activities in marine ecosystems, the abundances of many colonial Radiolaria in oceanic ecosystems are still poorly known. These species are not abundant enough to be sampled effectively using standard bottle casts, and plankton nets do not adequately estimate their abundances because many colonial Radiolaria lack siliceous skeletons. These skeletonless forms are easily destroyed in nets or extruded through the mesh. In addition, sample processing for Radiolaria from net or water bottle samples usually involves the digestion of organic material to allow visualization of the skeleton for identification (Cifelli and Sachs, 1966; Renz, 1976; Kling, 1979; Dworetzky and Morley, 1987; Kling and Boltovskoy, 1995). Colonies lacking skeletons are destroyed during processing and thus these species are excluded from estimates of radiolarian abundance. Sample processing also disaggregates individual skeleton-bearing Radiolaria in colonies, and thus makes it impossible to determine the number or size of colonies from which cleaned skeletons arose.

We employed a submersible video plankton recorder to determine the abundance and distribution of colonial Radiolaria in surface waters (0–150 m) along a west–east transect in the eastern North Pacific ocean. We found that abundances based on the video record were much higher (up to three orders of magnitude) than abundances based on plankton net tows. We conclude that skeletonless forms of colonial Radiolaria have been severely underestimated by traditional collection and counting methods.

## METHOD

This study was conducted aboard the R/V 'New Horizon' during July and August of 1996 along a transit line in the central North Pacific Ocean (Figure 1). A miniaturized video plankton recorder (mini-VPR) was used for obtaining abundance estimates of colonial Radiolaria. The mini-VPR is a miniaturized version of an instrument developed and applied to study small-to-large scale distributions of zooplankton (Davis *et al.*, 1992a, 1992b, 1996; Ashjian *et al.*, 2001).

The components of the mini-VPR were a Hitachi Denshi KP-M1 CCD camera synchronized with a Hamamatsu 9 Watt strobe which were mounted to face each other at an oblique angle. The camera was focused on a



**Fig. 1.** Station locations along the transect aboard the R/V 'New Horizon' during July and August 1996.

77 cm<sup>3</sup> volume between the two units within the beam of the strobe. Images were recorded on a Sony Hi-8 video cassette recorder which allowed tows of 2 h duration. The entire package was powered by a 24 V NiCad battery. These components were mounted in underwater housings rated to 250 m. The mini-VPR was mounted on an aluminum frame together with a Seabird SBE25 Sealogger which recorded depth. The instrument package was continuously lowered and raised four times at most stations between the surface and 150 m at a rate of 12 m min<sup>-1</sup> while the ship was moving ahead at 1 knot. Discrete depths were examined at three stations. Images were recorded at two depths at stations 4, 5 and 12 that corresponded to specific hydrographic or biological features (deep chlorophyll maximum, thermocline, nitracline) as determined by CTD casts prior to deployment of the mini-VPR.

Vertical distribution and depth-integrated abundance of colonial Radiolaria were obtained by extracting images from the video tapes using a computer-assisted image analysis system (Davis *et al.*, 1996). The volume of water imaged by the camera was calculated from the volume of water in focus and the recording time (Davis *et al.*, 1992a) while correcting for any video-frame overlap. Images of colonies were matched with the Sealogger depth profile record and colony abundances were binned into 10 m depth intervals. A CTD cast was performed just prior to each VPR deployment for comparison of colony vertical distribution to hydrographic features.

Central capsule abundance within each colony was estimated from colony surface area, employing an average central capsule density (9.12 central capsules mm<sup>-2</sup> of colony surface) determined from high magnification photomicrographs of a variety of diver-collected radiolarian species. Surface areas of colonies were estimated by measuring colony dimensions directly from video images and applying equations for standard geometric shapes (sphere, cylinder, etc.). The outer gelatinous matrix of the colonies was excluded from these measurements because this material is highly variable with the physiological state

of the colony (Swanberg, 1979). Abundances of central capsules were converted to carbon biomass using a conversion factor of 133 ng carbon central capsule<sup>-1</sup> (Michaels *et al.*, 1995).

After each VPR tow an oblique net tow was made from the surface to 150 m using a half meter 202 µm plankton net equipped with a General Oceanics™ flowmeter. The net was lowered at a rate of 12 m min<sup>-1</sup> while the ship was moving ahead at 1 knot. At the end of each tow the net was immediately rinsed with sea water and the cod end sample was preserved in 2% buffered formalin and stored at 4°C. Samples were prepared for counting using a modified method of Sachs (Sachs, 1964). Duplicate 25 ml splits of a net tow were centrifuged at 3300 g for 5 min. and the supernatant was removed and replaced with 50% hydrogen peroxide. After 48 h, samples were filtered onto 0.45 µm, 47 mm Sela™ silver filters, rinsed several times with distilled water and combusted at 450°C for 4–6 h. Counts of radiolarian skeletons were performed directly on each filter using a Wild™ M10 microscope.

All colonial Radiolaria that we have collected in our past studies possessed intracellular symbiotic algae with high photosynthetic rates (Caron *et al.*, 1995). We estimated the potential contribution of primary production by symbiotic algae in the colonial Radiolaria observed in this study by multiplying radiolarian abundance by an average value of 1700 pg C central capsule<sup>-1</sup> h<sup>-1</sup>. This value was derived for symbionts associated with a variety of colonial Radiolaria in the Sargasso Sea near Bermuda (Caron *et al.*, 1995). Symbiont productivity associated with colonial Radiolaria in this study was compared to average total production (463 mg C m<sup>-2</sup> day<sup>-1</sup>) from Station ALOHA (22°45'N, 158°W) during 1989–1995 (Karl *et al.*, 1996).

## RESULTS

### Video images of colonial Radiolaria

The mini-VPR was effective for obtaining detailed images of colonial Radiolaria *in situ* (Figure 2a–h). The colonies appeared as transparent-to-translucent matrices, with the central capsules appearing as highly reflective structures. These images were sufficiently clear to estimate colony dimensions, and in most cases individual central capsules could be distinguished within the gelatinous matrix of the colonies. Images obtained from the mini-VPR were almost of the quality obtained in the laboratory using dissecting microscopy and darkfield illumination of diver-collected specimens (Figure 2i–k).

### VPR estimates of colonial Radiolaria

The average abundance of colonies across the transect as determined from the mini-VPR images was greater than

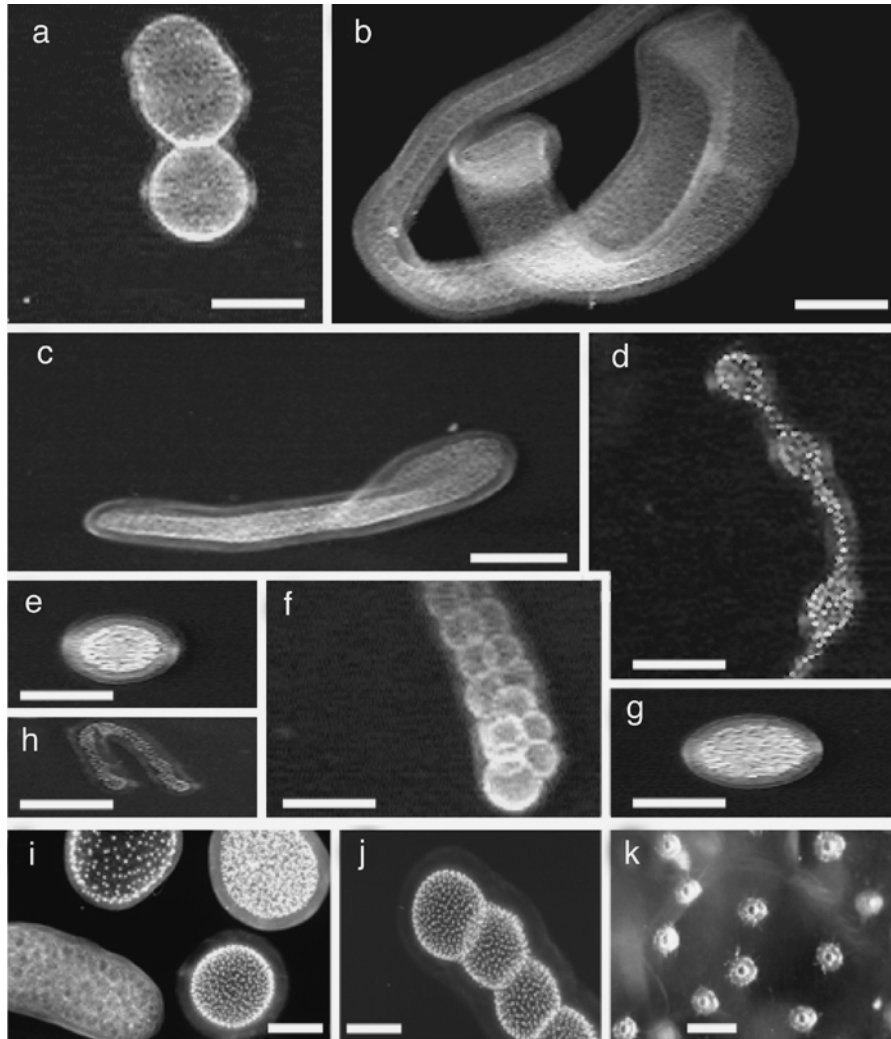
8 colonies m<sup>-3</sup> in the top 150 m of the water column at stations where depth profiles were performed (Table I, Figure 3). Abundances up to 30 colonies m<sup>-3</sup> were observed at specific depths at several stations. Colony abundance ranged from 2.8–11.0 colonies m<sup>-3</sup> in the upper 150 m with the lowest abundance occurring at the most easterly depth profile station (Station 13). Average central capsule abundance estimated from images of colony surface area ranged from 2130 to 13 300 central capsules m<sup>-3</sup> in the upper 150 m. The highest single value from a single depth was obtained at station 9 where the abundance exceeded 10<sup>5</sup> central capsules m<sup>-3</sup> (Figure 4f). The depth of maximum colony abundance at our sampling stations varied from the surface to 65 m while maximal central capsule abundance extended to 85 m. Abundances just below the surface were not obtained because bubbles associated with the disturbance of the surface obscured the video images.

The vertical distributions of colonies along the transect appeared to be associated with several hydrographic features (deep chlorophyll maximum, pycnocline, mixed layer), but no single feature explained all of the vertical profiles. Colony abundance at Stations 1, 2, 3 and 6 (157°9'W–142°20'W) was greatest above or at the pycnocline or within the mixed layer (Figure 3a–d). Maximal abundance of colonies at Stations 7, 9, 10 and 11 (140°12'W–126°44'W) occurred over a range of depths from near the surface to below the mixed layer but they generally remained above the depth of the chlorophyll maximum (Figure 3e–h). A peak in the vertical distribution of colonies was observed within the California Current (Station 13) at the depth of the chlorophyll maximum (55 m; Figure 3i) but otherwise the distribution was fairly uniform from the surface to 150 m at that station.

Average abundance of central capsules in the upper 150 m converted to carbon biomass varied by a factor of 2.6 over the entire transect in the North Pacific gyre (overall range of 101–265 mg C m<sup>-2</sup>; Stations 1–12, Table I). Depth-integrated biomass in the southern California Current was 42.5 mg C m<sup>-2</sup> (Station 13; Table I).

### Net tow estimates of colonial Radiolaria

The abundance of skeleton-bearing Radiolaria (central capsules of colonies, and solitary species) determined from the plankton net tows between the surface and 150 m at stations across the transect ranged from 2.8 to 43.3 Radiolaria m<sup>-3</sup> (Table I). The lowest abundance of radiolarian skeletons occurred at the most easterly end of the transect within the California Current. Abundances of central capsules of colonial Radiolaria determined from video images averaged 380× the abundances obtained from nets for stations where both types of counts were performed (Table I; range 130–760×).



**Fig. 2.** Representative colony morphologies captured by the mini-VPR in the central North Pacific (**a–h**), skeleton-bearing polycystine radiolarian (**a, d–g**), *Collozoum* sp. (**b, c, h**) and photomicrographs taken in the laboratory of specimens collected by divers near Bermuda (**i–k**), *Collozoum* sp. (**i**, upper left), *Collozoum* sp. (**i**, lower left), two unidentified polycystine radiolarians (**i**, upper and lower right), skeleton-bearing polycystine radiolarian (**j**). The central capsules (small white dots) are embedded near the periphery of the colonies. High magnification of the central capsules of *Siphonosphaera cyathina* (**k**). (**a–h**, bar = 0.5 cm; **i, j**, bar = 0.25 cm; **k**, bar = 250  $\mu\text{m}$ ).

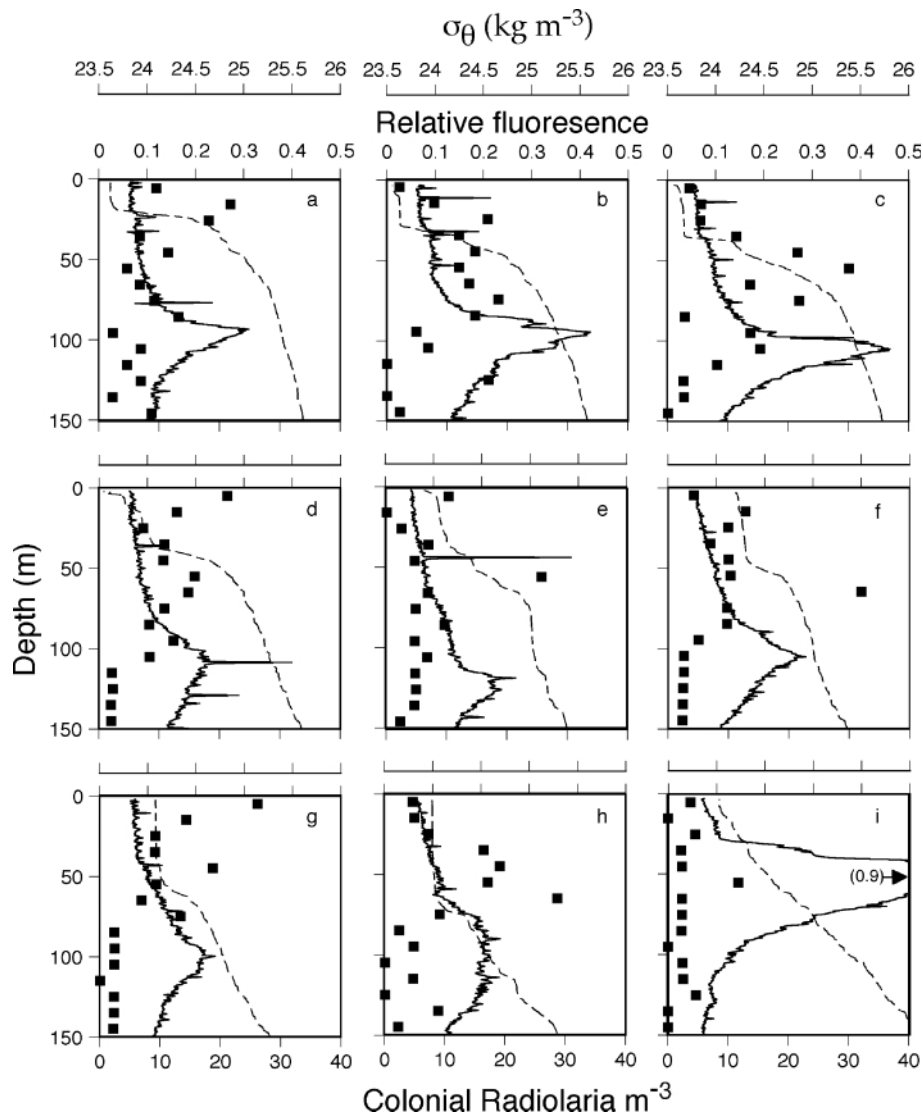
### Primary productivity of symbiont-bearing colonial Radiolaria

Colonial Radiolaria inhabiting surface waters possess large numbers of intracellular symbiotic dinoflagellates. Depth-integrated primary productivity by these symbiotic algae was estimated based on abundances of central capsules (from analysis of the video images) and previous estimates of primary production of the intact host–symbiont association (expressed as carbon per central capsule) (Caron *et al.*, 1995). Symbiont primary production in the upper 150 m ranged from 6.5 to 40.7 mg C m<sup>-2</sup> day<sup>-1</sup> (average 23.6; Table II). Comparison of these values with

a long-term record of primary production at Station ALOHA north of Oahu, Hawaii indicated that symbiont production constituted an average of 5.1%.

### DISCUSSION

Our results indicate that previous studies have significantly underestimated colonial radiolarian abundance and biomass because extant methodology has been ineffective for assessing the standing stocks of the skeletonless forms of these large protozoa. The use of our non-destructive sampling to quantify colonial radiolarian



**Fig. 3.** Plots of average colonial radiolarian abundance (squares) in 10 m depth intervals, relative *in situ* fluorescence (solid lines) and sigma-*t* (dashed lines) from stations 1 (**a**), 2 (**b**), 3 (**c**), 6 (**d**), 7 (**e**), 9 (**f**), 10 (**g**), 11 (**h**), 13 (**i**).

abundance indicates that these species constitute a major fraction of total radiolarian abundance and biomass in areas of the oligotrophic ocean. Central capsule abundances from VPR images exceeded by more than two orders of magnitude the estimates of skeleton-bearing Radiolaria from net tows performed along the same transect. In addition, our abundance values obtained from video images exceeded published reports of total, skeleton-bearing Radiolaria (solitary and colonial forms) for a study conducted in the North Pacific east of our transit line at the same latitude by more than one order of magnitude (Kling and Boltovskoy, 1995), and were similar to or greater than the abundances of skeleton-bearing

Radiolaria from extremely productive regions of the equatorial Pacific (Table I). The enumeration of skeleton-bearing Radiolaria from chemically digested and high-temperature-combusted preserved samples substantially underestimates total radiolarian abundance by excluding these skeletonless forms.

The average abundance of colonies in the upper 150 m of the water column across this west to east transect varied by less than a factor of 2 until reaching the California current. Colonial radiolarian abundance on the eastern end of our transect line may have declined due to a change in the water masses and consequent shift in the assemblage to colder water species. Surface water

*Table I: Radiolarian abundance and biomass estimated from analysis of mini-VPR images and from plankton tows by light microscopy*

Location/ Station Number	Depth (m)	Colonies (m <sup>-3</sup> )	Skeleton-bearing Radiolaria from plankton tows (m <sup>-3</sup> )	Central capsules from mini-VPR images (m <sup>-3</sup> )	Biomass (mg C m <sup>-2</sup> )
BATS <sup>a</sup>	0–150				2.8
Eastern	0–101		34		
Equatorial	0–150		25		
Atlantic					
Eastern North	0–200		578		
Pacific <sup>c</sup>	0–200		291		
Central	0–200		9810		
Equatorial	0–200		2940		
Pacific <sup>d</sup>	0–200		1000		
Equatorial	0–120		2430		0.99
Pacific <sup>e</sup>	0–120		5670		2.61
This study					
1	0–150	8.6	39.7	7940	158
2	0–150	9.3	30.5	8940	178
3	0–150	10.5		9540	190
4	118 (*)	2.9		714	
4	154 (**)	3.7		4230	
5	5	12.6		9290	
5	30 (***)	8.0		5440	
6	0–150	9.9	43.3	5540	110
7	0–150	6.7	22.3	5070	101
8	0–150	11.1	20.2	10300	205
9	0–150	7.4	36.4	13300	265
10	0–150	11.0	13.7	5880	117
11	0–150	7.8	16.7	8400	167
12	6	3.3		2020	
12	118 (*)	3.1		2350	
13	0–150	2.8	2.8	2130	42.5

Discrete samples were collected at the deep chlorophyll maximum(\*), the nitracline (\*\*), and the thermocline (\*\*\*)

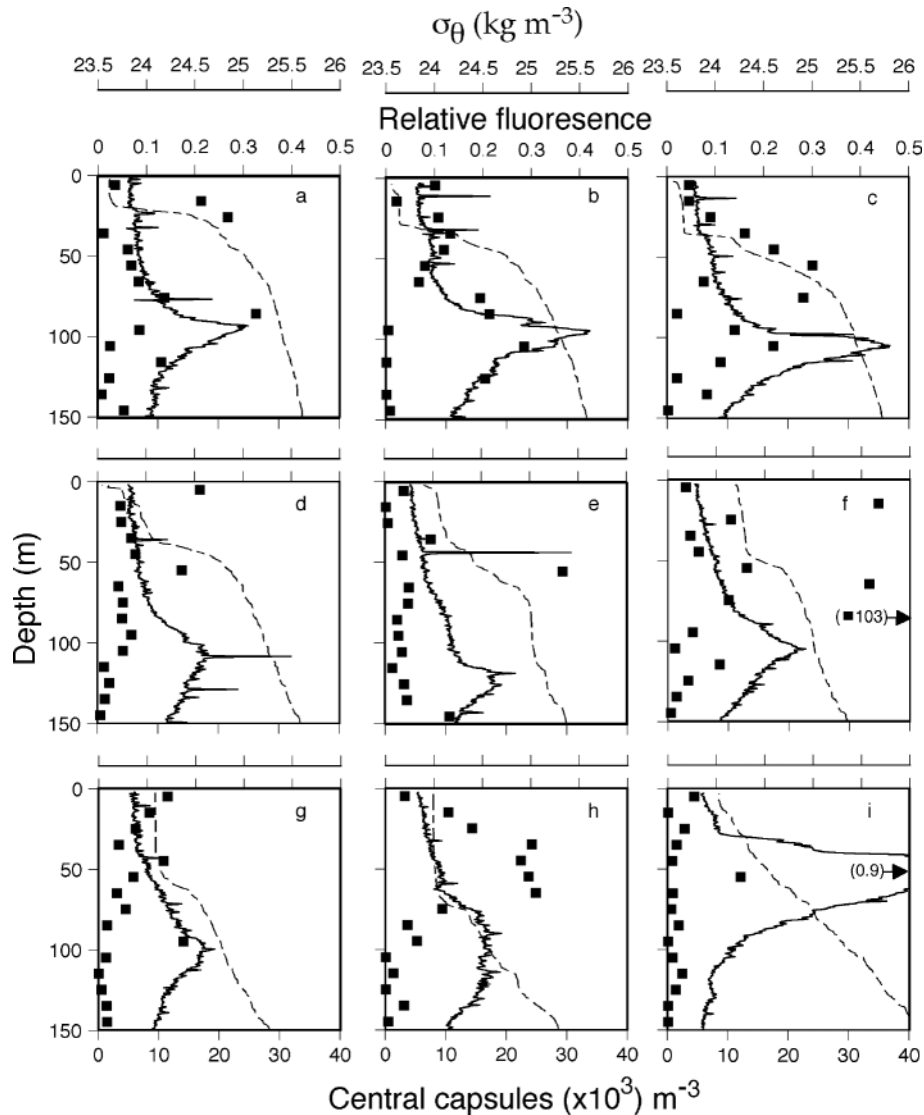
<sup>a</sup>(Michaels *et al.*, 1995); <sup>b</sup>(Dworetzky and Morley, 1987); <sup>c</sup>(Kling and Boltovskoy, 1995); <sup>d</sup>(Renz, 1976); <sup>e</sup>(Stoecker *et al.*, 1996).

temperatures decreased from 22.6 to 17.7°C across these latter stations.

Vertical distribution and peaks in abundance of colonial Radiolaria at individual stations may be related to changes in water density, temperature or may simply reflect optimal light conditions for the symbiotic algae or optimal feeding conditions for the Radiolaria (Figure 3). Our results indicated near-surface and subsurface peaks at several stations. Subsurface peaks appeared to occur coincidentally with the pycnocline (Figure 3a,c,e,f) and deep chlorophyll maximum (Figure 3i). Near-surface peaks in abundance also occurred (Figure 3d,g). Colonial

Radiolaria occasionally reach very high abundances near the air–water interface during periods of extreme calm or at the convergence of Langmuir circulation cells (Khmel'eva, 1967; Swanberg, 1983; Caron *et al.*, 1995). Our video images do not take these highly elevated abundances into account because of the interference of bubbles in the video images. Therefore, the 0–10 m depth integral at some of our stations may have contained higher abundances than the values reported here.

In comparison to reported values, our estimates of colonial radiolarian biomass indicate that these species comprise a previously overlooked but potentially important



**Fig. 4.** Plots of average radiolarian central capsule abundance (squares) in 10 m depth intervals, relative *in situ* fluorescence (solid lines) and sigma *t* (dashed lines). Panels same as in Fig. 3.

component of living biomass in oligotrophic oceans. Our estimates of colonial radiolarian biomass in the central North Pacific gyre exceed by more than two orders of magnitude the only other previous estimates of living radiolarian biomass reported for an oligotrophic station at the Bermuda Atlantic Time Series (BATS) site in the Sargasso Sea and for a study in the eastern Equatorial Pacific (Table I). The latter study noted that colonial Radiolaria were underestimated [or specifically excluded (Stoecker *et al.*, 1996)] but included solitary Radiolaria. Our values were similar to previous reports of the standing stock of living biomass in the  $> 200 \mu\text{m}$  size fraction, up to 10% of the

living microbial biomass  $> 2 \mu\text{m}$ , and 6–12% of the total living biomass in the Atlantic and Pacific (Table III).

Similarly, photosynthesis by the intracellular symbionts of colonial Radiolaria may constitute a significant source of primary productivity in highly oligotrophic oceans. We estimate that the contribution of symbiont primary productivity associated with colonial Radiolaria may exceed previous estimates by an order of magnitude (Caron *et al.*, 1995), and could contribute up to  $\approx 9\%$  of the total primary productivity in the eastern North Pacific gyre (Table II). Taken together, these results indicate a significant biogeochemical role for colonial Radiolaria in

*Table II: Estimated contribution of radiolarian symbionts to total primary productivity in the upper 150 m along the transect in the North Pacific*

Station Number	Symbiont primary production (mg C m <sup>-2</sup> day <sup>-1</sup> )	Per cent of total primary production
1	24.3	5.2
2	27.4	5.9
3	29.2	6.3
6	16.9	3.6
7	15.5	3.3
8	31.5	6.8
9	40.7	8.8
10	18.0	3.9
11	25.7	5.6
13	6.5	1.4

open ocean ecosystems. In addition, these findings raise the possibility that species diversity of Radiolaria has been underestimated by the exclusion of skeletonless colonial species from biogeographical studies of these protists.

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*Table III: Depth-integrated (150 m) biomass of plankton size classes*

Study <sup>a</sup>	Location	Size fraction (µm)	Biomass (mg C m <sup>-2</sup> )
(Buck <i>et al.</i> , 1996)	25°–45°N Atlantic	>2	1830 <sup>e</sup>
(Roman <i>et al.</i> , 1995)	31°50'N, 64°10'W (BATS)	>2	1122 <sup>c</sup>
"	"	>2	1257 <sup>d</sup>
(Beers <i>et al.</i> , 1982)	North Pacific central gyre	2–200	1185 <sup>f</sup>
(Beers and Stewart, 1969)	California Current	>202	177 <sup>b</sup>
(Roman <i>et al.</i> , 1995)	31°50'N, 64°10'W (BATS)	>200	414 <sup>c</sup>
"	"	>200	590 <sup>d</sup>
(Buck <i>et al.</i> , 1996)	25°–45°N Atlantic	total living biomass	4485 <sup>g</sup>
(Roman <i>et al.</i> , 1995)	31°50'N, 64°10'W (BATS)	total living biomass	4061 <sup>c</sup>
"	"		2254 <sup>d</sup>
This study	Central North Pacific		101–265

<sup>a</sup>All data were integrated to 150 m; <sup>b</sup>assuming carbon is 40% of dry weight; mean of five stations; <sup>c</sup>March/April, mean of six stations; <sup>d</sup>August, mean of five stations; <sup>e</sup>auto- and heterotrophic nano- and microplankton; mean of 12 stations; <sup>f</sup>seasonal mean from five locations; <sup>g</sup>mean of 12 stations.



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