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Seasonal fluxes of silicoflagellates and *Actiniscus* in the subarctic Pacific during 1982–1984

by Kozo Takahashi¹

ABSTRACT

A seasonal flux study of silicoflagellates and *Actiniscus* was conducted at subarctic Pacific Station PAPA (50N, 145W; water depth 4200 m) during September, 1982 through August, 1984 using PARFLUX high resolution time series sediment traps deployed at 1000 m and 3800 m depths. The time series sediment trap samples were collected for 4 to 16-day periods depending on the samples; most of the samples were collected for 14 to 16-day periods. From a depth of 3800 m, a total of 47 samples represents a nearly two-year continuous record of the fluxes of silicoflagellate and *Actiniscus* taxa. An additional 12 samples from 1000 m represent a 6-month period, providing synchronized time series samples with the deeper depth which is essential to understand particle sinking processes.

Seven silicoflagellate taxa, several variants of silicoflagellates, and *Actiniscus pentasterias* (Ehrenberg) group were examined. A total of more than 32×10^3 specimens were identified to species level and counted in this study. *Distephanus speculum* (Ehrenberg) and *Dictyocha mandrai* Ling are the dominant taxa, generally contributing >75% of the flux assemblages. Considerable intra-annual and interannual flux variability was observed with the range of total silicoflagellate flux varying from 5×10^3 to 700×10^3 skeletons $m^{-2}day^{-1}$ during the two years. Seasonal flux patterns of *D. speculum* and its closely related taxa are internally consistent and they conform with the productivity signals shown by diatom, total mass, or opal fluxes. The seasonal flux pattern of *D. mandrai* exhibits its own unique late fall/early winter signals with most of the cumulative flux concentrated during this season in year 1.

The sinking mechanism of silicoflagellates is large aggregates which sink faster than discrete specimens. Silicoflagellates generally sink faster than marine snow mediated diatom assemblages. The larger influence of fecal material may be responsible for the observed faster sinking speeds than those of diatoms. No significant dissolution of silicoflagellate assemblages occurs in the water column due to innate protection and to accelerated sinking. Most of the silicoflagellates supplied to the sea floor are subsequently dissolved, and only 1% of the total supply is preserved in the surface sediments, with considerably altered assemblages.

1. Introduction

Silicoflagellates are marine chrysophytes which dwell in the euphotic zones of essentially all parts of the world oceans. Their microplankton size skeletons (20–80 μm) are composed of biogenic opal which can be preserved in the sedimentary fossil record.

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The numerical abundance of silicoflagellates in siliceous plankton standing stocks is generally less than that of diatoms and is followed by radiolarians. Due to the small mass of silicoflagellate skeletons, their contribution to SiO_2 flux is no more than a few percent, but numerous skeletons in fluxes make them good tracers for the vertical transport mechanisms of settling particles (Takahashi, 1987a). Some silicoflagellate taxa are considered to be useful as environmental indicators such as for high productivity and oligotrophic waters (Murray and Schrader, 1983; Takahashi, 1987a). The recent rapid progress in using silicoflagellates as a tool to interpret the fossil record yields a promising future for reconstructing paleotemperature variation (e.g., Ciesielski, 1975) and paleoproductivity (e.g., Schrader and Baumgartner, 1983) studies.

In a previous paper (Takahashi, 1987a), silicoflagellate fluxes at meso- and bathypelagic depths were assessed at four different environments ranging from the temperate oligotrophic Atlantic to the tropical eutrophic Pacific in which temperate to tropical species were dealt with. In that paper, not only were detailed vertical processes examined but also indicator species for productivity and oligotrophic environments were proposed. A time-series flux assessment throughout the year was not conducted in the previous study in the low latitudes where relatively small seasonal changes in productivity were expected.

The objectives of this paper are as follows. As the fossil records generally exhibit mixed signals from different seasons with unknown ratios between them, it is difficult to assess summer or winter conditions accurately by studying fossils alone. If we can understand the seasonal variations of supply rates of microfossils to the sea floor, accurate paleoenvironmental assessments will be possible. It is important to study year to year variability of the supply rate in the short term as well as in the long term. For these reasons it is desirable to conduct a high resolution time-series vertical flux study of silicoflagellate assemblages in an area where primary production is seasonally highly variable. Furthermore, it is crucial to understand the processes of fossil preservation in the sedimentary record, in particular, early diagenesis in the water column. Less than a few percent of biogenic opal is generally preserved in surface sediments and the bulk of the supply is dissolved in the vicinity of the sea floor (Takahashi, 1983, 1986), indicating the significance of such a dissolution mechanism to the fossil record. It is likely that all of the preserved fossils go through some level of dissolution process in corrosive water with respect to biogenic opal. Without a better understanding of the dissolution/preservation processes, it is difficult to link the present with the past. Therefore, a part of this study is focused on the effects of dissolution.

Since silicoflagellate flux is a function of organic production in the overlying euphotic zone (Takahashi, 1987a), flux studies on materials collected from the bathypelagic zone will provide productivity signals, a part of which will be subsequently preserved in the fossil record. Therefore, one can expect the results of this study to be of value for interpretive paleoproductivity. Whether temperature signals

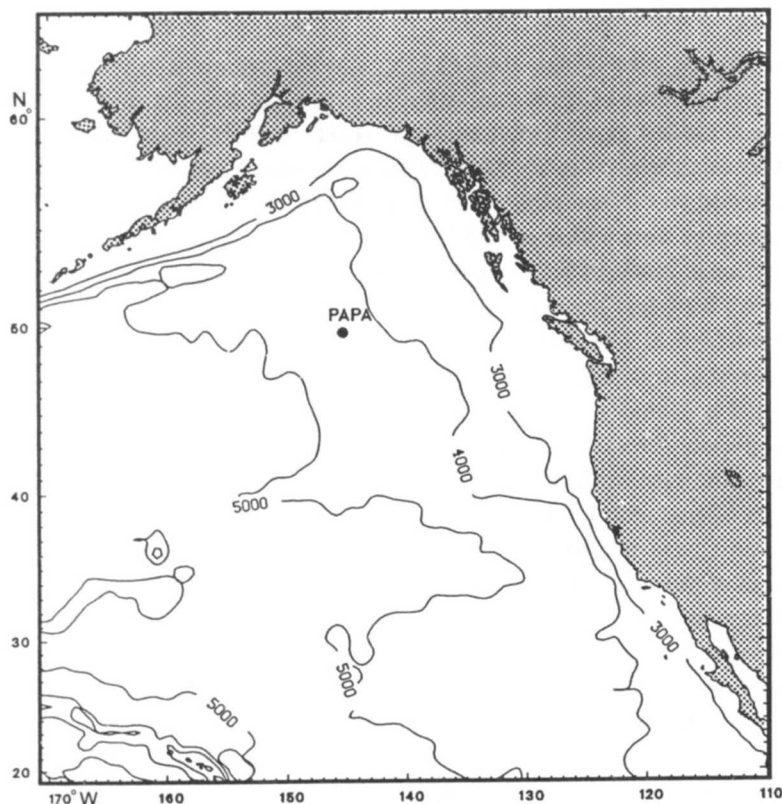


Figure 1. A map showing the location of PARFLUX sediment trap Station PAPA with bathymetric contours in meters.

(e.g., Ciesielski, 1975) can be derived from the flux assemblages or not will decide the potential use of silicoflagellates for future paleotemperature studies.

The results of a detailed high resolution time-series vertical flux study of silicoflagellates during 2 years from September, 1982 to August, 1984 at Station PAPA (Fig. 1; 50N, 145W; water depth 4200 m) located in the Alaskan current gyre are presented. Station PAPA was the site of Canadian Weather Station P and numerous hydrographic data were collected there from 1956 to 1981 (Anonymous, 1981; Tabata and Peart, 1985; and unpublished observations by the Institute of Ocean Sciences, Patricia Bay, British Columbia). The study of a continuous 2-year flux record provides an opportunity to learn the extent of intra-annual and interannual variabilities in present-day sedimentation rates. A pair of sediment trap samples collected simultaneously from two depths for 6 months enable us to clarify vertical sinking processes.

The *Actiniscus pentasterias* group was also studied because of its similar size and abundance to silicoflagellates and is included in this report. *Actiniscus pentasterias* is a dinoflagellate which secretes a pair of siliceous endoskeletons in the cell (Orr and Conley, 1976). No ebridians occurred in the material studied.

2. Methods

An automated time series PARFLUX Mark 5 sediment trap was deployed at 3800 m for 4 periods of 6 months each for a total of 2 years. Forty-seven samples (September, 1982–August, 1984; PAPA I, II, III, and IV) were collected by bottom tethered mooring array (Table 1). An additional trap was deployed at 1000 m for a 6-month period and its sampling intervals were synchronized with those of the 3800 m trap; 12 samples were collected (PAPA II). The Mark 5 sediment trap has a conical collection funnel made of polypropylene with a surface opening of 1.167 m² which is covered with a 94-cell honeycomb baffle. The funnel is connected to a rotating disk located underneath. The disk has 12 screw-on sample containers (250 ml each) and turns according to a preprogrammed schedule set into a command microprocessor (Honjo, 1984; Honjo and Wong, 1985). The containers had sodium azide as a microbial poison. A total of 59 time series sediment trap samples were collected for 4 to 16-day periods; most of the samples were collected for 14 to 16-day periods (Table 1). Dissolution of opal within the sample containers during the deployment and storage in the laboratory was not significant as shown by dissolved silicon measurements of supernatant of the samples (Manganini and Honjo, 1985).

The microslide preparation method used in this work is similar to that employed for a diatom study (Takahashi, 1986). Briefly, a sample is sieved through 1000 μm and 63 μm mesh stainless screens. Both 63–1000 μm and <63 μm size fractions are split into four aliquots using an Erez-Honjo precision liquid rotary splitter (Honjo, 1978) with an accuracy error of less than 5%. The splitting is repeated until a desirable aliquot size was obtained, requiring several repetitions. Because silicoflagellate fluxes varied greatly with seasons, the aliquot size had to be changed often in consecutive samples. An appropriately split aliquote of 63–1000 μm was wet sieved through 250 μm and 125 μm mesh screens. The size-fractioned aliquot of the appropriate sample size (see Takahashi, 1985, for details) is filtered through a 47 mm HA Millipore® grid membrane filter with a nominal 0.45 μm pore size using a rectangular stainless steel filtration funnel with a 19 × 42 mm opening. The filter is rinsed with distilled water to remove salts and then dried in an oven. After trimming off the excess margins, the dried filter is mounted with Cargile® type B immersion oil on a standard glass microslide. The oil-immersed filter is left overnight in a clean box in order to drive air bubbles out of the biogenic particles. A cover glass is placed over the oil with Devcon® 5-minute epoxy adhesive on four corners of the cover glass to secure the sample on the slide.

Silicoflagellate counts were performed with a light transmission microscope with wide-field, 10× eyepiece lenses and a 20× S Plan Apochromat objective lens with a total magnification of 200×. Silicoflagellate flux values reported in this paper are the sum of four size fractions actually studied: <63 μm , 63–125 μm , 125–250 μm , and 250–1000 μm . Detailed counts and fluxes for each size fraction of silicoflagellate species, as well as detailed methods and statistics, are reported elsewhere (Takahashi,

Table 1. Sampling intervals for PAPA I—IV deployments of PARFLUX time-series sediment trap experiment at subarctic Pacific Station PAPA. Dates represent opening and closing times of sample cups placed with a tight seal under the conical PARFLUX Mark 5 traps (surface area = 1.167 m²). For deployment II there are two synchronized depth samples from 1000 m and 3800 m of each sequenced sample number.

Deployment	Sample #	Date open	Date closed	Duration (days)
PAPA I 3800 m	#1	Sep. 23, 1982	Oct. 8, 1982	15
	#2	Oct. 8,	Oct. 23	15
	#3	Oct. 23	Nov. 7	15
	#4	Nov. 7	Nov. 22	15
	#5	Nov. 22	Dec. 7	15
	#6	Dec. 7	Dec. 22	15
	#7	Dec. 22, 1982	Jan. 6, 1983	15
	#8	Jan. 6	Jan. 21	15
	#9	Jan. 21	Feb. 5	15
	#10	Feb. 5	Feb. 20	15
	#11	Feb. 20	Mar. 7	15
	#12	Mar. 7	Mar. 18	11
PAPA II 1000 m & 3800 m	#13	Mar. 27	Apr. 12	16
	#14	Apr. 12	Apr. 28	16
	#15	Apr. 28	May 14	16
	#16	May 14	May 30	16
	#17	May 30	June 15	16
	#18	June 15	July 1	16
	#19	July 1	July 17	16
	#20	July 17	Aug. 2	16
	#21	Aug. 2	Aug. 18	16
	#22	Aug. 18	Sept. 3	16
	#23	Sept. 3	Sept. 19	16
	#24	Sept. 19	Oct. 5	16
PAPA III 3800 m	#25	Oct. 14	Oct. 30	16
	#26	Oct. 30	Nov. 15	16
	#27	Nov. 15	Dec. 1	16
	#28	Dec. 1	Dec. 17	16
	#29	Dec. 17, 1983	Jan. 2, 1984	16
	#30	Jan. 2	Jan. 18	16
	#31	Jan. 18	Feb. 3	16
	#32	Feb. 3	Feb. 19	16
	#33	Feb. 19	Mar. 6	16
	#34	Mar. 6	Mar. 22	16
	#35	Mar. 22	Apr. 7	16
	#36	Apr. 7	Apr. 23	16

Table 1. (Continued)

Deployment	Sample #	Date open	Date closed	Duration (days)
PAPA IV 3800 m	#37*	Apr. 23	May 13, 1984	14
	#38	May 13	May 27	14
	#39	May 27	June 10	14
	#40	June 10	June 24	14
	#41	June 24	July 8	14
	#42	July 8	July 22	14
	#43	July 22	Aug. 5	14
	#44	Aug. 5	Aug. 9	4
	#45	Aug. 9	Aug. 13	4
	#46	Aug. 13	Aug. 17	4
	#47	Aug. 17	Aug. 21	4
	#48	Aug. 21	Aug. 24, 1984	4

*No sample/data due to malfunction

1985). Because samples were prepared for both silicoflagellate and radiolarian studies, four different size fractions were examined, but most silicoflagellate and *Actiniscus* specimens are located in the $<63 \mu\text{m}$ fraction. Thus, most of the counting effort was spent on the $<63 \mu\text{m}$ fraction. One slide per size fraction of each sample was studied for census. One to nine traverses of vertical strips (along the minor axis of a microslide) per slide were studied for counts. Each strip represents $15.1 \times 10^6 \mu\text{m}^2$ which is equal to $1/35.9$ (or 2.786×10^{-2}) of an entire filtered area of the membrane filter on a slide. Raw counts for a sample combining all of the four slides ranged from 74 to 1558 per sample with a mean of 552. Possible major sources of errors in silicoflagellate counts reported here include (i) sample splitting, (ii) imperfect distribution of filtered silicoflagellates, and (iii) counting errors. The second category of the sources of errors is determined to be the largest, based on statistical assessments performed on the representative samples. The first and third categories caused less than 5% of the errors, each. Overall reproducibility for silicoflagellate flux assessment reported here is considered better than 85%.

Diversity indices of silicoflagellate assemblages were computed using the following Shannon and Weaver formula (Pielou, 1969),

$$H' = - \sum_{i=1}^n P_i \log P_i \quad (1)$$

where H' is the diversity index in a "bel" or a "decimal digit" unit (Pielou, 1969), P_i is the proportion of the i th species of the total population dealt with, and n is the number of species. The nine most abundant counting groups of silicoflagellates, whose seasonal fluxes are illustrated in later sections, were used for the diversity index computations.

The sinking speeds of individual silicoflagellate species were obtained by examining

seasonal flux maxima and minima of 1000 m and 3800 m data. In order to find the best matching lag time between the two depth data sets, a crosscorrelation method was applied (e.g., Davis, 1973). In this method, we first compute a correlation coefficient, r , between data from the two depths without shifting any data (Lag 0). This provides a direct data comparison between the two depths. If sinking time between the two depths is less than the sample resolution, a strong correlation coefficient is obtained. Second, the 3800 m data are shifted by one sample to the preceding sample dates (to the left) and a correlation coefficient r is computed (Lag 1). By shifting the 3800 m data further left to earlier sample dates and computing the coefficients, one can get a continuous trend of crosscorrelation.

3. Results

Seven silicoflagellate taxa, their several variants, and the *Actiniscus pentasterias* group were encountered during the census (Plates 1 and 2; Appendix). More than one species of *Actiniscus* were encountered; they were lumped together as a group. Detailed taxonomic discussions with illustrations of the taxa used in the paper will be published elsewhere.

The counts were converted into flux and reported as the number of individuals $m^{-2}d^{-1}$ (Appendix). Highly variable fluxes of silicoflagellate and *Actiniscus* taxa were observed, both intra-annually and interannually, during the 1982–1984 period (Figs. 2–4). *Distephanus speculum* and *Dictyocha mandrai* are major contributors to the flux of silicoflagellates throughout the period studied. The combined flux of the two species is generally greater than 75% ($\bar{x} = 83\%$, $\sigma = 8\%$) of the total silicoflagellate flux. During August, 1984, the combined flux decreased to about 67% of total silicoflagellates.

Essentially all silicoflagellates encountered during the census were not associated with fecal pellets. The number of fecal pellets found in the samples was so small that they rarely turned up during the census.

a. Seasonal flux variability in year 1 (September, 1982–September, 1983). The intensity of the flux of silicoflagellates varied significantly from species to species. For example, a maximum flux of *Distephanus speculum* (Plate 1, Figs. 1, 2; Plate 2, Fig. 4) reached 543×10^3 individuals $m^{-2}d^{-1}$ in October, 1982, at 3,800 m while that of *Distephanus quinquangellus* was only 5×10^3 individuals $m^{-2}d^{-1}$ (Figs. 2a, 2b). Seasonal flux patterns of silicoflagellate species can be assessed by comparing timing and relative intensity of flux maxima and minima. All species show 3 to 5 major flux maxima at 3,800 m during year 1. The 5 seasonal maxima are: October, December (1982), March, May, and August (1983). A general similarity of the flux patterns of species within a genus is observed in *Distephanus* and *Dictyocha*, respectively. The flux of *Distephanus* presents rather intensive maxima during October, March, and August.

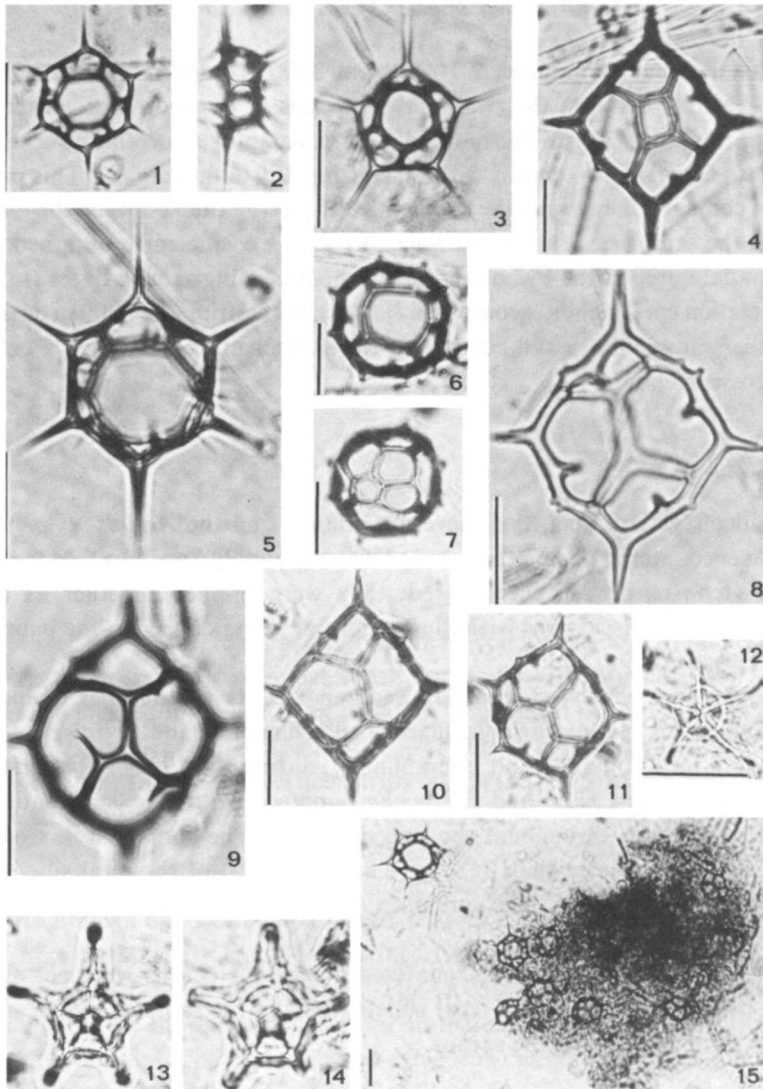


Plate 1. Light micrographs of silicoflagellate species from Station PAPA. All scale bars equal 20 μm . The scale of Figures 2, 13, and 14 are the same as that in Figure 1. Sources of the micrographs are from maximum flux time periods at 3,800 m illustrated in Figures 2–4. (1, 2) *Distephanus speculum* (Ehrenberg), apical view (1) and side view (2). Radial spine length and ratios of apical/basal ring diameters tend to vary whereas the shapes of the apical ring (mostly circular) and the basal ring (mostly equilateral hexagon) tend to be uniform. (3) *Distephanus quinquangellus* Bukry and Foster. (4) *Distephanus boliviensis* (Frenguelli). (5) *Distephanus boliviensis* (Frenguelli). (6) *Distephanus octangulatus* Wailes, regular form with one apical window. (7) *Distephanus octangulatus* Wailes. A form with three apical windows. Forms with two or more apical windows were enumerated separately from the regular form with an apical window. (8) *Dictyocha mandrai* Ling, regular form. (9) *Dictyocha mandrai* Ling, form with variable shaped apical rods. (10) *Dictyocha messanensis* ? f. *spinosa* (Lemmerman). Size and orientation of supporting spines vary considerably. (11) *Dictyocha mandrai* f. *pentagona*. (12–14) *Actiniscus pentasterias* group. (15) An organic aggregate containing many specimens of *D. speculum*. Compare the size of a discrete specimen of *D. boliviensis* in the upper left with that of *D. speculum*. Sample #22 (18 August–3 September, 1983), 3,800 m.

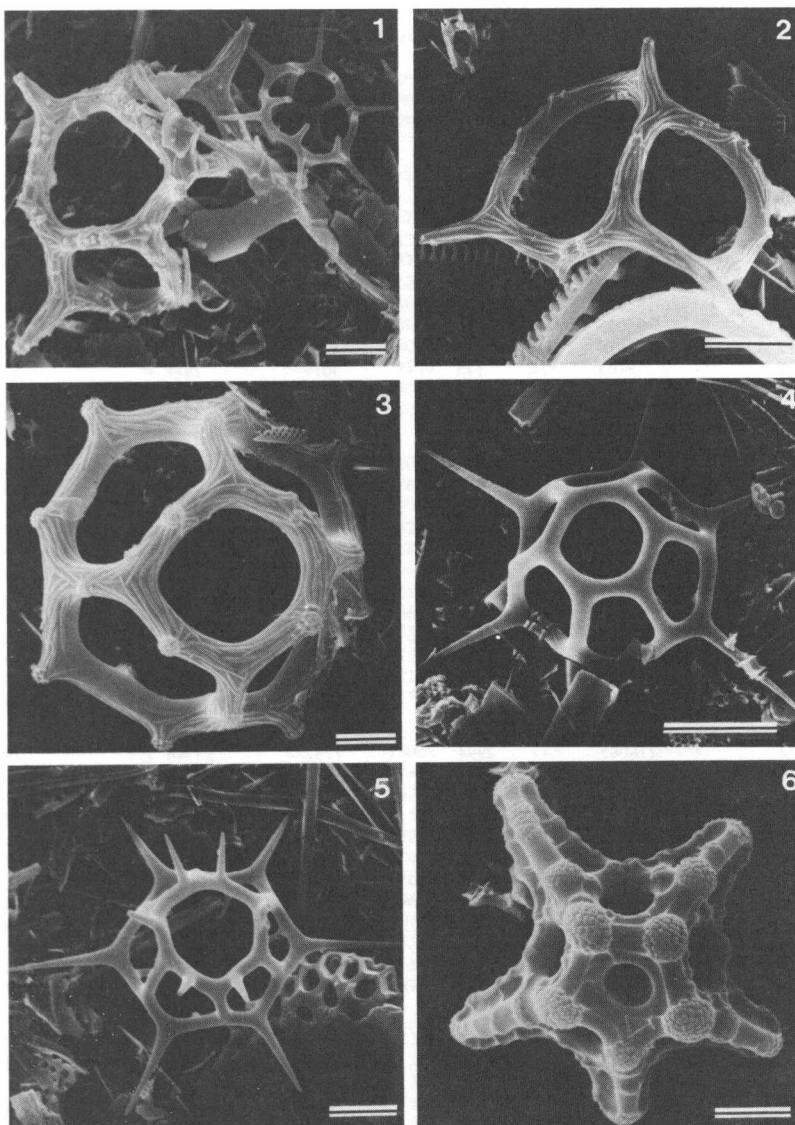


Plate 2. Scanning electron micrographs of silicoflagellate species from Station PAPA. All scale bars equal 10 μm . All specimens were collected from 3,800 m. (1) *Dictyochoa mandrai* Ling, apical view, Sample #23 (3 Sept.–19 Sept., 1983). Note wavy ornamentation on skeletal surface which was not observed in low latitude sediment trap material (Takahashi, 1987a). A small specimen on upper right is *D. speculum* for size comparison. (2) *Dictyochoa mandrai* Ling, side view, #25 (14 Oct.–30 Oct., 1983). Note that apical spine is relatively short compared to *D. messanensis* ? *spinosa* illustrated in the low latitude study. (3) *Distephanus octangulatus* Wailes, apical view, #2 (8 Oct.–23 Oct. 1982). Note wavy surface ornamentation. (4) *Distephanus speculum* (Ehrenberg), oblique apical view, #25 (14 Oct.–30 Oct., 1983). Note small size and smooth circular shape of apical ring without any spines and compare it to (5). Overall size of this taxon is relatively small compared to *D. mandrai* which is illustrated in (1). (5) *Distephanus boliviensis* (Frenguelli), apical view, #23 (3 Sept.–19 Sept., 1983). Note several spines projecting from apical ring. Shape of its apical ring is a polygon. (6) *Actiniscus pentasterias* (Ehrenberg), apical view, #14 (12 April–28 April, 1983).

APPENDIX

Time-series fluxes (No. m⁻²d⁻¹) of silicoflagellate taxa and *Actiniscus* at 1000 m (for 6 months) and at 3800 m (for 2 years) at the Subarctic Station PAPA during 1982–1984.

Deployment/Depth Sample No.	<i>Distephanus speculum</i>	<i>Distephanus quinquangellus</i>	<i>Distephanus boliviensis</i>	<i>Distephanus octangulatus</i>	<i>Distephanus octangulatus</i> (>1 apical window)
PAPA I 3800 m					
#1	206710	508	3588	3115	0
#2	542606	5303	16590	19793	306
#3	287841	2188	13230	9721	840
#4	239182	2940	7718	10229	840
#5	200830	1479	10343	7070	44
#6	208040	2984	14980	12644	0
#7	182858	2100	19163	8068	840
#8	95025	420	8024	7560	420
#9	37319	0	3719	5775	394
#10	19163	175	3019	2888	44
#11	8400	0	1094	2888	0
#12	7186	0	858	3873	143
PAPA II 1000 m					
#13	313943	779	5619	24364	0
#14	125430	123	2953	17924	123
#15	63166	0	6768	20549	246
#16	40729	0	5094	14421	1575
#17	23404	0	5636	7998	0
#18	13978	0	6276	11419	394
#19	30823	0	21503	8882	0
#20	61481	1316	10866	6003	439
#21	184412	1436	9352	4430	0
#22	180105	2994	7588	2625	0
#23	117800	779	6276	1313	0
#24	104798	1436	6891	1436	0
PAPA II 3800 m					
#13	276085	2994	7752	23544	779
#14	150409	2092	3897	13700	123
#15	108941	779	5742	12387	1313
#16	115257	656	3568	16735	0
#17	67555	656	5988	17924	656
#18	42034	0	4159	7949	788
#19	46168	517	4897	10951	911
#20	59357	0	7373	6757	3510
#21	172854	1878	12022	14778	3510
#22	303803	4387	20026	8143	877
#23	97210	369	15135	7957	123
#24	46590	246	1792	3633	439
PAPA III 3800 m					
#25	41630	1162	3589	2892	164
#26	34413	0	2789	3281	492
#27	23626	164	1641	2338	0
#28	16243	164	2010	1805	0
#29	13659	0	1148	1189	0
#30	11218	0	1528	1641	0
#31	8244	164	1005	523	0
#32	9865	0	872	656	0
#33	6214	0	1548	338	0
#34	9249	174	882	1702	164
#35	16509	390	2789	1764	0
#36	12141	0	2953	1354	0
PAPA IV 3800 m					
#37	No sample				
#38	23298	0	5438	1594	0
#39	31407	0	6000	844	0
#40	18657	0	3375	1125	0
#41	9141	47	1688	1219	188
#42	10500	188	1875	609	0
#43	1031	0	1734	656	0
#44	2625	0	1969	164	0
#45	1969	0	3117	164	0
#46	656	0	2297	328	164
#47	1313	0	328	1477	0
#48	820	0	492	656	0

APPENDIX (Continued)

<i>Dictyocha mandrai</i>	<i>Dictyocha mandrai</i> (with variable apical rods)	<i>Dictyocha mandrai</i> f. <i>pentagona</i>	<i>Dictyocha messanensis</i> ? <i>spinosa</i>	<i>Distephanus crux</i> ?	Total Silicoflagellates	<i>Actiniscus pentasterias</i> group
10509	219	0	840	1059	226967	37441
94789	1855	1899	0	5915	689055	158708
75355	744	420	700	3404	394486	60813
101159	770	420	1260	2520	367037	99759
178877	2914	420	2739	3404	408293	73491
280403	551	2275	1260	3824	527380	65958
233039	1059	1680	8864	2144	459813	78978
110408	840	1260	10920	1260	236136	49228
73413	263	350	8094	1094	130419	20125
37231	0	88	4900	219	67725	17588
30844	0	0	5075	525	48825	13169
27172	0	203	6066	286	45786	11643
34454	0	0	23093	0	402252	18991
38884	0	0	17678	0	203116	37407
27112	0	0	13905	0	131746	43765
44715	0	0	16242	0	122776	133801
16636	0	0	15873	0	69548	53207
15554	0	0	9844	394	57858	52026
17046	0	123	6881	439	85696	89795
47398	3740	123	8898	1755	142019	105236
40525	5414	123	7219	1313	254223	77358
31583	1313	656	1559	1148	229571	27030
23134	779	656	3281	0	154018	33306
21739	779	0	3527	0	140606	41919
69319	492	369	13084	123	394541	26251
36997	1025	656	7465	0	216364	20098
44708	123	779	6276	1313	182361	34700
38884	0	0	11526	656	187283	59967
45816	656	656	19278	1313	160499	62961
33740	0	0	5488	0	94158	49515
44101	123	394	7063	788	115913	47793
74145	3633	1001	9636	2001	167412	120575
75456	10144	0	10776	2001	303418	144914
52583	5511	2755	5511	1755	405353	76135
37653	1313	0	6153	1436	167349	55947
20775	781	0	2755	219	77231	30914
21125	1148	164	1340	335	73550	23552
20303	656	328	205	41	62510	21247
14684	1477	0	369	369	44667	15627
11362	656	0	533	328	33101	16243
13084	820	0	656	0	30558	12387
10921	328	0	554	10	26200	12746
7004	164	0	513	328	17945	11956
10203	328	10	10	174	22118	14489
7824	328	0	338	0	16591	11013
15135	328	0	513	10	28158	15022
6583	21	0	267	21	28343	7404
7465	0	0	697	0	24610	9639
14766	0	0	844	0	46689	33751
21282	0	0	1594	0	61127	19313
18329	0	188	563	47	42283	10313
10828	0	0	609	234	23954	9703
8625	47	0	563	0	22501	10266
5953	94	0	141	0	10219	13969
3445	0	0	492	0	8696	9024
5250	0	0	328	0	10828	12633
2625	0	0	492	164	6727	12141
6563	164	0	328	164	10336	10008
2953	0	0	0	0	4922	7219

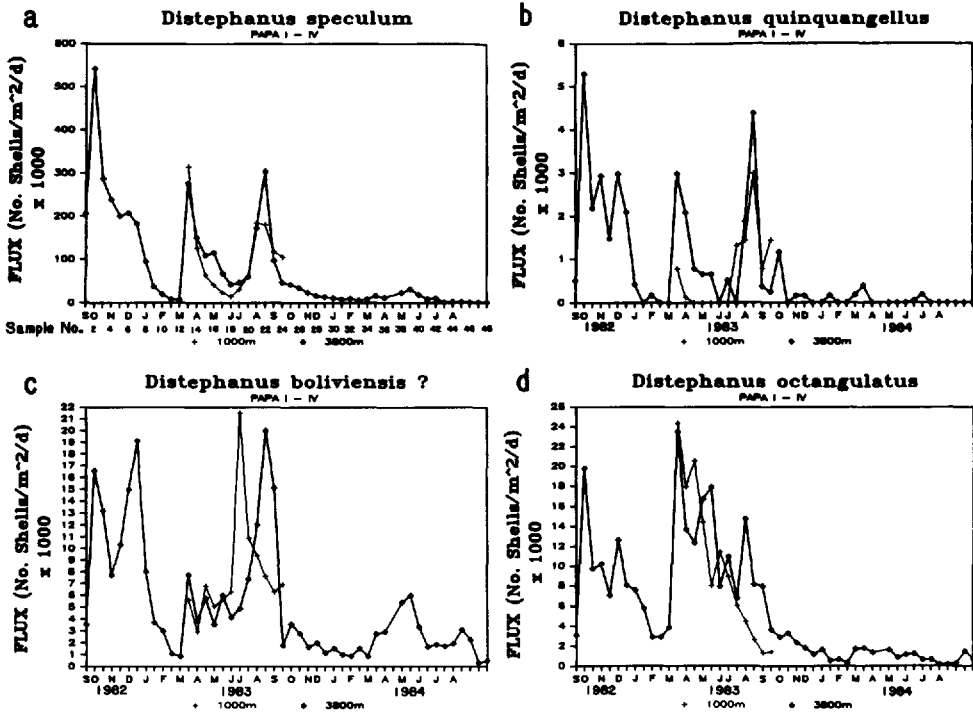


Figure 2. Two year time-series fluxes of four species of *Distephanus* at 3800 m. The fluxes at 1000 m are only for six months.

The December maximum is the fourth highest maximum in all *Distephanus* species, with the exception of *Distephanus boliviensis* (Fig. 2c; Plate 1, Fig. 5; Plate 2, Fig. 5) which shows a second highest maximum in December. A flux maximum in *Distephanus octangulatus* (Fig. 2d; Plate 1, Figs. 6, 7; Plate 2, Fig. 3) is observed in May, but is not as well defined in other species of the genus. Overall, the seasonal flux patterns observed in four species of *Distephanus* are similar enough (with a possible exception of *D. octangulatus*; see later discussion of cluster analysis) relative to patterns observed for *Dictyocha* as well as for diatoms, and thus the fluxes of the 4 species can be grouped together.

Dictyocha mandrai (Fig. 3a; Plate 1, Fig. 8; Plate 2, Figs. 1, 2) is numerically a dominant species in the genus (Fig. 3). It shows a well-defined maximum in December but the intensities of the other maxima in year 1 are relatively low. Two variants of *D. mandrai*, a form with variable-shaped apical rods (Fig. 3c) and a form with a pentagonal basal ring (*D. mandrai pentagona*), show high flux values in August. Besides the August peak, *D. mandrai pentagona* shows high flux maxima during October and December. *Dictyocha messanensis* ? *spinosa* (Fig. 3b) shows an intense maximum in May which is rather unique compared with other silicoflagellate species observed in year 1 except for *D. octangulatus*.

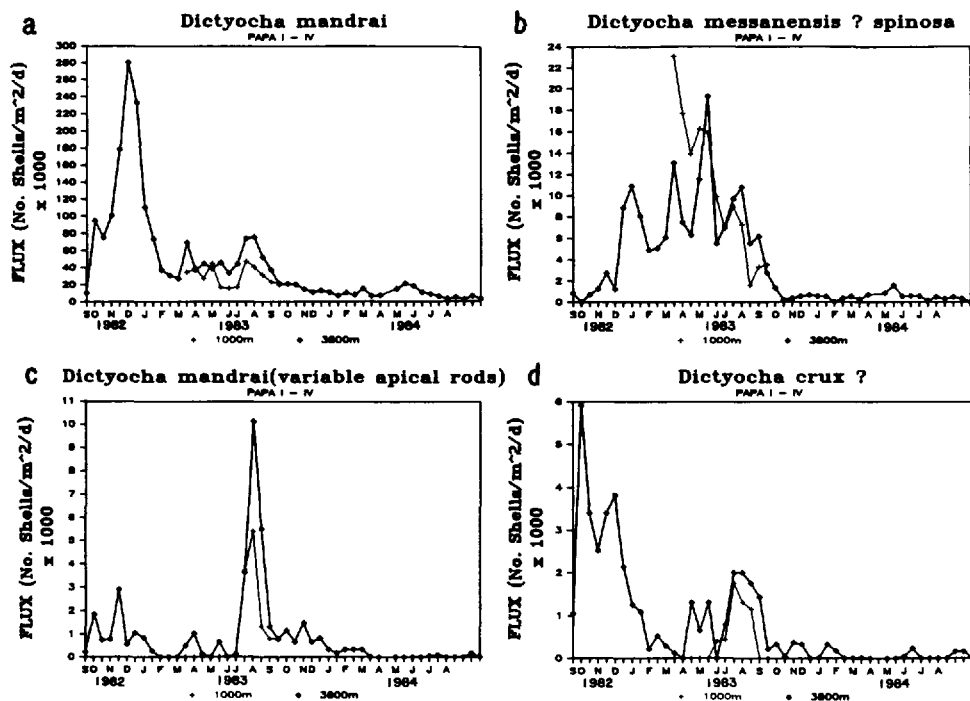


Figure 3. Two year time-series fluxes of *Dictyocha mandrai*, its closely related forms, and *Distephanus crux* ? at 3800 m and 1000 m.

The seasonal flux pattern of *Distephanus crux* ? (Fig. 3d) resembles that of the *Actiniscus pentasterias* group (Fig. 4a). The flux patterns of the two taxa are more similar to those of diatoms (Takahashi, 1986) than to the above mentioned silicoflagellate species. The pattern of *Distephanus crux* ? has some affinity with that of the remainder of the *Distephanus* taxa (see cluster analysis section). This is of interest and casts doubt about the artificial classification of this taxon as *Distephanus* because of the presence of an apical window, a requirement of the genus. The doubt is based on the similarity of basal ring shape (including variability; from *Dictyocha mandrai* type to *Dictyocha messanensis* type) and size in the studied assemblages; thus one would expect the seasonal flux pattern to be more similar to that of *Dictyocha*. *Actiniscus* shows seasonal fluxes of up to 160×10^3 individuals $m^{-2}d^{-1}$, which is two orders of magnitude higher than that of *Distephanus crux* ?. The flux of *Actiniscus* is numerically comparable to that of *Dictyocha mandrai*.

b. Seasonal flux in year 2 (September, 1983–August, 1984) and its comparison to the year 1 record. The relatively high flux values observed at the beginning of year 2 is part of the August maximum in year 1 which tails off in September/October in year 2. Most silicoflagellate taxa show only one flux maximum in year 2 which occurred in

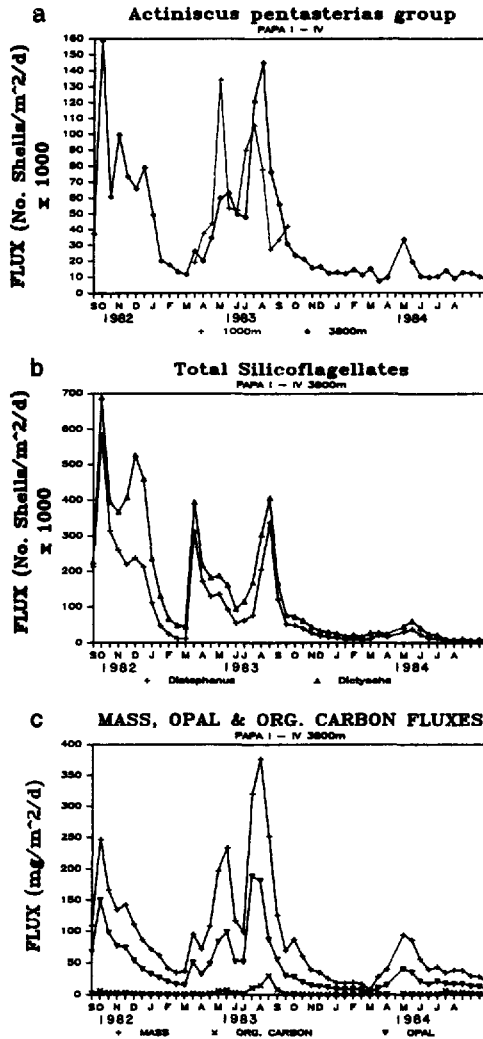


Figure 4. (a) Two year time-series fluxes the *Actiniscus pentasterias* group at 3800 m and 1000 m. (b) Two year time-series fluxes of *Distephanus* and *Dictyochoa* (plotted cumulatively) at 3800 m. (c) Organic carbon, opal, and mass (plotted noncumulatively) at 3800 m. These data are taken from Honjo (1984).

May (Figs. 2–3). The May peak in year 2 is smaller, by approximately a factor of 10, than the major peaks in year 1. A similar trend in decrease of flux peak intensity from year 1 to year 2 is observed in *Actiniscus* (Fig. 4a), opal and mass (Fig. 4c), and diatoms (Takahashi, 1987b).

c. *Vertical fluxes at 1000 m and 3800 m trap depths.* Species flux observed at the two different trap depths are graphically compared (Figs. 2, 3, 4a). During March through

September, 1983, where two-depth trap data are available, two prominent flux maxima occurred which can be compared with each other. March flux maxima at 3800 m and March flux values at 1000 m of many species tend to show similar levels, especially in *Distephanus*. Exact comparisons of the March maxima between the two depths in terms of lag time is difficult due to lack of the 1000 m data prior to sample No. 13. Comparisons of flux maxima during August, however, are possible. Zero sample lag for August maximum was recognized for *D. quinquangellus* and *D. mandrai* variable form, and one sample lag for *D. speculum*, *D. mandrai*, *D. messanensis* ? *spinosa* and *D. crux* ?, and three sample lags for *D. boliviensis* and *D. octangulatus*. It is noteworthy that many species with lags 0 and 1 are relatively small in size (e.g., *D. speculum*: basal diameter = 18.5 μm , S.D. = 2.3 μm , $N = 100$) and that two species with lag 3 are selectively large (e.g., *D. boliviensis*: basal diameter = 24.6 μm , S.D. = 3.4 μm , $N = 4$).

4. Discussion

The seasonal fluxes observed for each of the 5 species of *Distephanus* (Figs. 2a–d, 3d) represent unique patterns by themselves. Although details of the patterns are different from one another, the overall configurations are similar so they can be generalized as a group. In the case of year 1, they generally show a pronounced October maximum followed by March and August maxima and an additional December maximum. This type of seasonal flux pattern of *Distephanus* does not exactly conform to patterns shown by other silicoflagellate and diatom species. The closest seasonal flux pattern to that of *Distephanus* is Type 1 of diatoms (Takahashi, 1986). However, in detail most species of *Distephanus* show strong March peaks and generally insignificant flux maxima in May, while the diatoms in Type 1 show insignificant or small March peaks and well-defined May peaks. The relative intensity of October and August peaks in relation to the remaining peaks within a species is similar in both *Distephanus* and the diatom species. Although the intensity is generally not so high, the December peak of *Distephanus* is unique in its occurrence in the early winter season.

There is a definite correlation between the increases of *Distephanus* (and many diatom species) fluxes and the short term decrease of silicate concentrations in surface waters (Reynolds and Thunell, 1985), suggesting that these organisms are productivity indicators. Both of these processes take place within a time scale of 2 weeks or less. The uptake of silicates by these indicators (especially diatoms, a major phytoplankton component) effectively decreases the ambient silicate concentration temporarily until the bloom is completed. It is possible that this bloom is succeeded by nonsiliceous phytoplankton blooms which would explain why nitrate concentration in surface waters does not follow the same trend (Reynolds and Thunell, 1985). Correlation between *Distephanus* (in conjunction with diatoms) blooms and silicate concentrations are observed for time intervals corresponding to the March, May, and August maxima

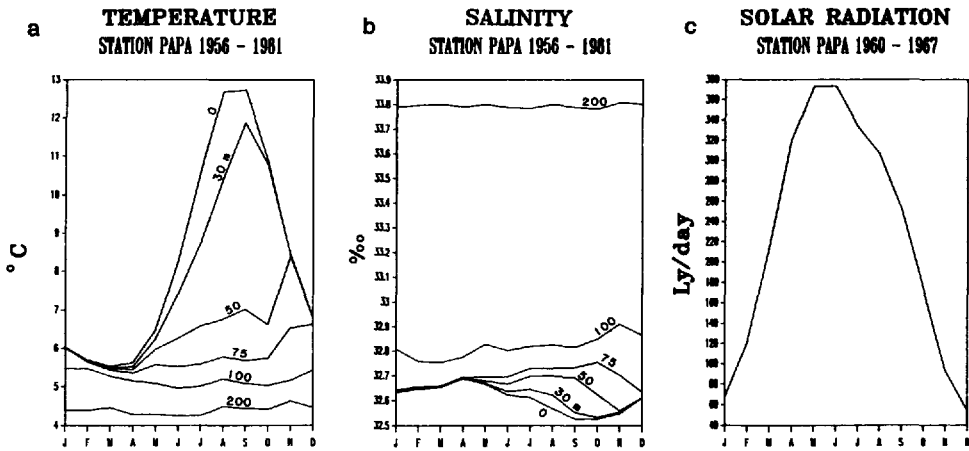


Figure 5. Time-depth plots of monthly averaged (a) temperature (1956–1981 data); (b) salinity (1956–1981); and (c) daily solar radiation at the sea surface (1960–1967) at Station PAPA. The numbers above each line are water depth in meters. The temperature and salinity data are from Tabata and Peart (1985). The figure of solar radiation is redrawn from Anderson *et al.* (1977).

of the fluxes. An exception is the September–October period when the silicate concentration keeps increasing with time as a result of convective mixing caused by atmospheric cooling.

That 54% of *D. mandrai* annual flux in year 1 occurred during a 3-month period, from October to January, is an important fact, especially for paleo-oceanographic implications. If specimens of *D. mandrai* from different seasons are equally preserved, fossil records represent mostly fall/winter signals and few signals from other seasons. The specimens that are supplied to the sea floor in high flux seasons may actually be preserved better than those supplied in low flux seasons due to rapid burial with accompanying large amounts of biogenic opal. The unique timing of this pronounced maximum is considered to be a response to given environmental conditions. Although slightly earlier than that of *D. mandrai*, a similarly offsetting flux maximum from the October opal flux maximum is shown by the diatom species, *Coscinodiscus marginatus* (Takahashi, 1986). From fall through early winter, the water temperature in the euphotic layer (maximum is in September) decreases gradually through March or April, depending on depth. During that time, little salinity change is observed; incident solar radiation decreases until December (Fig. 5). Nutrient levels are continuously increasing from August minima to winter maxima (Anderson *et al.*, 1977; Wong and Honjo, 1984). The flux maximum observed in December at 3800 m results from late November production in the euphotic zone (see a later section on sinking speeds). The late November production of *D. mandrai* corresponds with (1) relative high levels of available nutrients, (2) relatively low but adequate levels of incident solar radiation for

this species, and (3) intermediate levels of water temperature ($\sim 8.5^{\circ}\text{C}$ at the surface) (Fig. 5), and is perhaps related to biological competition.

The fact that there is no December or August flux maximum in year 2 for any silicoflagellate species leads to questions on the range of year to year variability. The records from year 2 appear to deviate from the other 3 years, as suggested by unpublished mass flux data for years 3 and 4 which show that the flux maxima at 3800 m occurred about October/November, March/May, and August/September (Honjo, pers. comm., 1986). The causes of the large year 1 to year 2 flux variability observed have not yet been determined; this will require long-term time-series flux studies as well as detailed analyses of environmental parameters. The possible effects of the 1982–1983 large El Niño event in the Pacific low to middle latitudes should not be overlooked (Takahashi, 1987b).

The silicoflagellate flux maxima often occurs slightly later than that of diatoms, about 2 weeks, as shown by the November/December and August peaks of year 1 and the May peak of year 2. This suggests that diatoms respond more quickly to favorable environmental conditions than silicoflagellates do. Biological competition may be an important factor in offsetting the flux maxima. Alternatively, a difference in the doubling times of cell populations of diatoms and silicoflagellates may be responsible for the offset in the fluxes. However, in the light of the wide range of diatoms sizes (i.e., 3 orders of magnitude), and in their morphology and physiology, the alternative is an unlikely explanation.

a. Species affinity among silicoflagellate taxa. Seasonal flux patterns and flux values (individuals $\text{m}^{-2}\text{day}^{-1}$) are 2 major signals in the time-series flux record. Of these, the seasonal flux pattern can be used to clarify taxonomic affinities among silicoflagellate species. Cluster analysis (e.g., Davis, 1973) is a useful technique for this definition. To maximize comparison of the patterns and to estimate the effect of flux values, correlation coefficients were used (rather than using Euclidian distance) for constructing a dendrogram (Fig. 6). Most of the obvious similarities and differences in the patterns can be readily extracted without using a cluster technique. However, some subtle differences and similarities which cannot be detected by visual observation can be numerically expressed by this technique.

D. speculum and *D. quinquangellus* are the most closely clustered groups among the species studied. The major morphological difference is the shape of the basal ring, whether hexagonal or pentagonal. Some authors attribute these two forms to two varieties of a single species (e.g., Ciesielski, 1975), while others regard them as two distinct species (e.g., Bukry, 1973). As the pentagonal (or very rarely, heptagonal) form is usually rare, it is often lumped together with the dominant hexagonal form. As the seasonal flux patterns for both forms are very similar, they suggest that two taxa could actually represent a single species. However, until conclusive evidence based on further biological information becomes available, it is probably wise to separate these

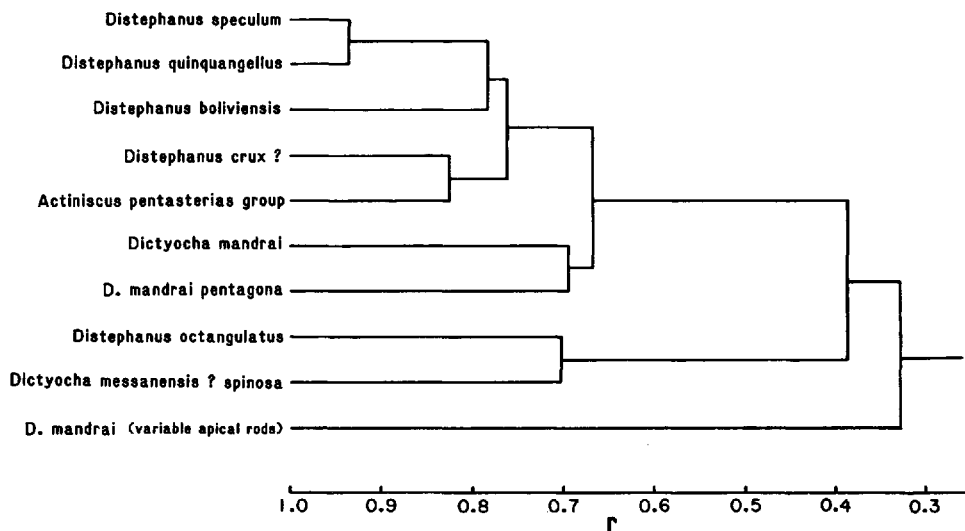


Figure 6. Dendrogram of Silicoflagellates and *Actiniscus* seasonal flux patterns constructed by the averaging method, using arithmetic averaging of correlation coefficients.

two forms because lumping of split counts can be easily done while the reverse is usually not possible.

It is noteworthy that the seasonal pattern of *Distephanus octangulatus* shows a relatively close affinity with that of *Dictyocha messanensis? spinosa* ($r = 0.70$) despite different generic assignment, in addition to those of *Distephanus speculum* ($r = 0.73$) and *Distephanus quinquangellus* ($r = 0.70$). Although *D. octangulatus* is placed in the genus *Distephanus*, its morphology and size are vastly different from all other species in the genus. The skeletal surface ornamentation observed on *D. octangulatus* also occurs in species assigned to the genus *Dictyocha*, but not in species in *Distephanus* except for the former (Plate 2). This implies that the generic assignment of *D. octangulatus* should be reconsidered.

The unique high August maximum presented by the variety of *D. mandrai* with variably shaped apical rods (Fig. 3c) caused the extreme position of this counting group in the dendrogram (Fig. 6). I consider this form as part of *D. mandrai* and not as an independent subspecies. The variably shaped skeletons occur throughout the year, but are more common during the 1983 summer season when other fluxes such as total mass and diatoms are also significantly high. The August maximum of this form of *D. mandrai* may result from high nutrient concentrations and high temperatures. Such variable morphology in the skeletons of *D. mandrai* has been observed in coastal waters of the Gulf of San Matias (Frenguelli, 1935) and in Lake Hiruga, Japan, where salinity varies seasonally from 13 to 27‰ in surface waters (Shitanaka, 1983). Nutrient levels in these coastal environments are apparently higher than those in

Table 2. Correlation coefficient r between silicoflagellate taxa and mass, opal, and organic carbon fluxes at 3800 m for two year record.

Taxon	Mass	Opal	Organic carbon
<i>Distephanus speculum</i>	0.62	0.66	0.44
<i>Distephanus quinquangellus</i>	0.56	0.55	0.51
<i>Distephanus boliviensis</i>	0.66	0.63	0.61
<i>Distephanus octangulatus</i>	0.68	0.66	0.33
<i>Distephanus octangulatus</i> (>1 apical window)	0.77	0.78	0.51
<i>Distephanus crux</i> ?	0.64	0.70	0.35
<i>Dictyocha mandrai</i>	0.38	0.40	0.14
<i>Dictyocha mandrai</i> (variable apical rods)	0.76	0.70	0.73
<i>Dictyocha messanensis</i> ? <i>spinosa</i>	0.55	0.48	0.32
Total Silicoflagellates	0.63	0.66	0.41
<i>Actiniscus pentasterias</i> group	0.90	0.92	0.57

pelagic realms and may be responsible for the variable shapes of the skeletons. The salinity change is very small at Station PAPA (Fig. 5b).

b. Relations with other fluxes and factors. Seasonal flux patterns of silicoflagellates are similar in general but different in detail from those of diatoms (Takahashi, 1986). For example, the March flux maximum of silicoflagellates is as high as that of August, whereas diatom flux shows a rather low maximum in March relative to a high August maximum. This greatly contributes to the level of correlation coefficients between silicoflagellate species and total mass, opal, or organic carbon fluxes (Table 2). All coefficients for total mass and opal are significant at the 99% level and thus silicoflagellates are considered to co-occur with other productivity components. However, the coefficients are not as good as those between diatoms and total mass or opal fluxes (Takahashi, 1986) which are not totally independent of one another. Since silicoflagellates contribute an insignificant amount compared to opal flux (<0.4% using $0.34 \text{ ng shell}^{-1}$ of Takahashi, 1987a), the coefficient reflects a relationship between two independent variables. The relatively poor coefficient of correlation with organic carbon reflects the labile nature of organic carbon which is largely recycled in the upper parts of the water column.

In order to understand factors controlling fluxes of silicoflagellate species it is necessary to reduce a large number of flux patterns into small groups so that we can correlate the patterns with environmental parameters. Results of *R*-mode factor analysis (Table 3) show in factor 1 high scores of *D. speculum* and *D. quinquangellus* and intermediate scores for *D. boliviensis*, *D. octangulatus* and *D. crux* ?. Factor 1 is interpreted as the productivity factor since fluxes of these species show relatively high

Table 3. Matrix of varimax rotated factor score.

Taxon	Factors			
	1	2	3	4
<i>Distephanus speculum</i>	0.877	0.195	0.157	0.216
<i>Distephanus quinquangellus</i>	0.856	0.153	0.205	0.230
<i>Distephanus boliviensis</i>	0.486	0.191	0.300	0.410
<i>Distephanus octangulatus</i>	0.567	0.761	0.087	0.176
<i>Distephanus crux</i> ?	0.578	0.096	0.187	0.461
<i>Dictyocha mandrai</i>	0.257	0.204	0.079	0.890
<i>Dictyocha mandrai</i> (variable apical rods)	0.182	0.159	0.958	0.081
<i>Dictyocha mandrai pentagona</i>	0.388	0.158	0.120	0.354
<i>Dictyocha messanensis</i> ? <i>spinosa</i>	-0.061	0.962	0.150	0.092
Variance	2.969	2.282	1.168	1.473

correlation with total mass, opal fluxes (Table 2) as well as productivity indicator diatom species. Factor 2 is related to high light intensity and *D. messanensis* ? *spinosa* and *D. octangulatus* show high scores. Factors 3 and 4 whose high scores are represented by *D. mandrai* variable form and *D. mandrai*, respectively, show seasonal relationships with summer and fall/winter respectively in year 1 but not in year 2. Acquisition of longer term flux records than two years will be required to clarify these trends.

c. *Sinking processes.* The time necessary for silicoflagellates in aggregates to sink through the water column from 1000 m to 3800 m is approximately equal to, or shorter than, the sample time interval of 16 days as shown by cross-correlation analysis (Figs. 2-3; Table 4). Cross-correlation seeks the best match of flux maxima and minima

Table 4. Correlation coefficient r between 1000 m and 3800 m data sets for silicoflagellate taxa and *Actiniscus* using the cross-correlation method. Results of sample lag 0, 1, and 2 are listed. The highest r values in the cross-correlation are underlined. Note that the value for total silicoflagellates at lag 0 is the highest. This is due to the effect of amplifying signals and to cancelling noises in silicoflagellate species flux.

Taxon	Sample lag		
	0	1	2
<i>Distephanus speculum</i>	<u>0.84</u>	0.50	-0.05
<i>Distephanus quinquangellus</i>	<u>0.60</u>	0.32	0.12
<i>Distephanus octangulatus</i>	0.69	<u>0.74</u>	0.73
<i>Distephanus crux</i> ?	0.68	<u>0.71</u>	0.32
<i>Dictyocha mandrai</i>	<u>0.57</u>	0.34	-0.41
<i>Dictyocha messanensis</i> ? <i>spinosa</i>	<u>0.61</u>	0.42	0.36
Total Silicoflagellates	<u>0.85</u>	0.45	-0.09
<i>Actiniscus pentasterias</i> group	0.46	<u>0.69</u>	0.36

between the two depths and determines appropriate time lags. The examined silicoflagellate species showed that time lag 0 and lag 1 led the above sinking time. This corresponds to 175 m day^{-1} or greater sinking speed, and implies accelerated sinking relative to single particle sinking of 1.4 m day^{-1} of silicoflagellates (Takahashi, 1987a). The three most abundant species, *D. speculum*, *D. mandrai*, and *D. messanensis* ? *spinosa*, show the highest correlation coefficient between 1000 m and 3800 m depths with 0 sample lag (Table 4), suggesting much faster sinking speeds than 175 m day^{-1} . This may be a realistic approximation, because of their smaller size range, silicoflagellates are grazed more efficiently by herbivores than diatoms are. Within silicoflagellate taxa, as noted in the Results section, relatively small sized species tend to sink faster than those of larger size, suggesting a possibility of differential grazing by herbivores. The herbivores are probably excreting readily disintegrated fecal matter (but not pellets) that sinks faster than marine snow. Silicoflagellate transport via biogenic aggregates (Plate 1, Fig. 15) was also documented in the equatorial Atlantic and Pacific (Takahashi, 1987a), which supports the above observation. Perhaps both transport mechanisms via fecal matter and marine snow are responsible for the fluxes observed.

Although it was hypothesized earlier that two copepod species of *Neocalanus* were primary grazers in the subarctic Pacific, the hypothesis has not been vigorously tested yet (Frost *et al.*, 1983). In light of such unsettled grazers and the present observation of insignificant numbers of fecal pellets in the flux, we must consider other grazing candidates such as salps more critically than before.

We note that the *Actiniscus pentasterias* group, dinoflagellates, shows a maximum coefficient at lag 1 which is sufficiently different from the coefficient at lag 0 while two species of silicoflagellates with maximum coefficient at lag 1 show similar coefficients at lag 0. The *A. pentasterias* group's sinking mechanism is more like that of diatoms rather than that of silicoflagellates based on results of cross correlations.

Similar values of flux assemblages at 1000 m and 3800 m at sample lag 0 or lag 1 indicate that the effect of dissolution of sinking silicoflagellates is insignificant. The abundance patterns of the assemblage (in percent) at 1000 m are also repeated at 3800 m with a slight time offset (Fig. 7). If significant uniform dissolution and/or species preferential dissolution occurred, the flux values and percentages of soluble and resistant taxa would be different at 3800 m and at 1000 m. That no significant differences are observed suggests that sinking silicoflagellates are unaffected by dissolution.

d. Use of percent signals. Despite considerable change in flux values from year 1 to year 2, the patterns of relative abundance of silicoflagellate species in the flux did not change very much (Fig. 8a). The detailed values of the percentages differ in the 2-year record, but the overall patterns are similar so that the percent signals may be used for a variety of applications, including comparisons with percentages preserved in fossils.

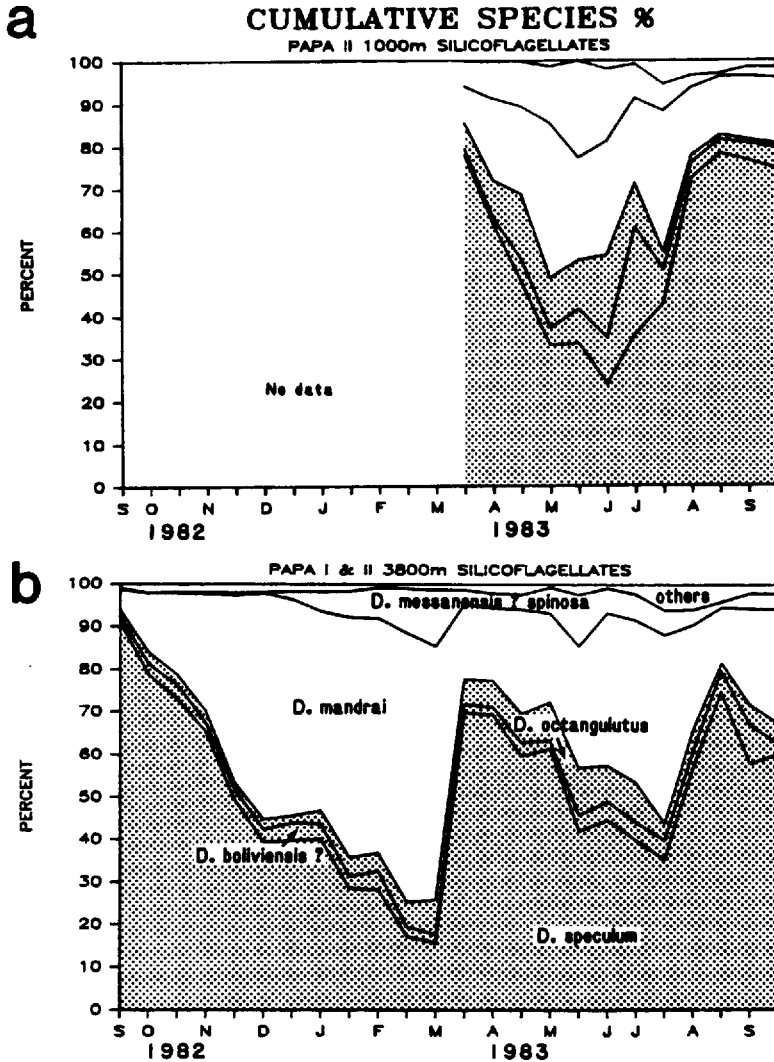


Figure 7. Cumulative percents of silicoflagellate species flux: (a) at 1000 m, May–Sept., 1983; (b) at 3800 m, Sept. 1982–Sept. 1983. Legends for a and b are the same. Shaded areas represent *Distephanus*.

Essentially, *D. speculum* and *D. mandrai* contribute to the largest of the percent values while the remaining species contribute a small percentage of the assemblages. For correlation analysis it is necessary to take a logarithm of fluxes because they tend to vary by orders of magnitude with time whereas percentages vary within a factor of ten. A good correlation of percent *D. speculum* with the logarithm of *D. speculum* flux is seen ($r = 0.80$) while a fair anti-correlation of percent *D. mandrai* with the logarithm of *D. speculum* flux is evident ($r = -0.64$). These values are significantly high

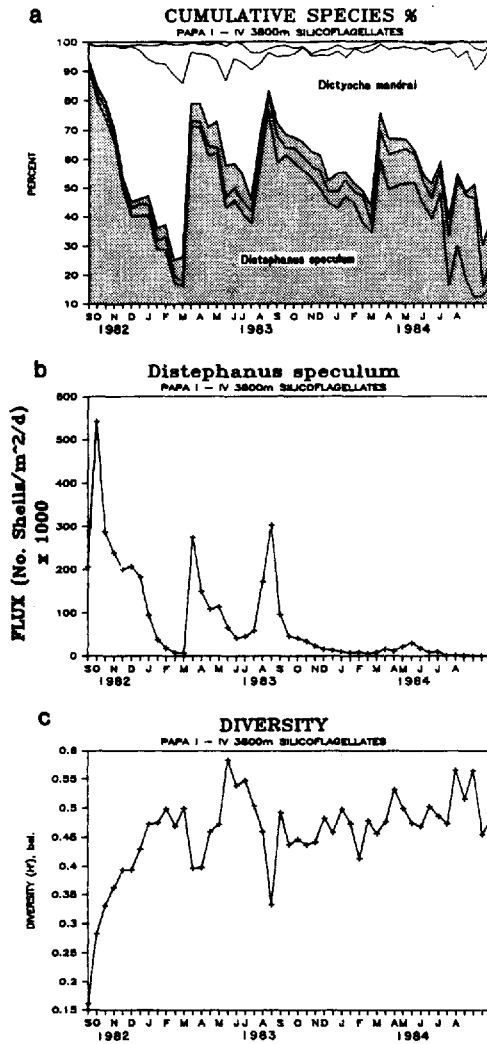


Figure 8. (a) Silicoflagellate cumulative percent data for two years. Legends are the same as in Figure 7. (b) Fluxes of *Distephanus speculum* for two years at 3800 m. (c) Plot of silicoflagellate diversity index at 3800 m vs. time. Note that index values are antirelated with both fluxes and % *D. speculum*.

considering that critical values at 95% and 99% levels with 45 degrees of freedom are 0.288 and 0.372, respectively (Rohlf and Sokal, 1969). The flux of *D. speculum* in a given interval of time can be predicted once we have a percent value.

$$\log_{10} F_{Ds} = 0.0318 P_{Ds} + 2.99 \tag{2}$$

where F_{Ds} and P_{Ds} are flux and proportion of *D. speculum*, respectively.

e. Diversity index. Diversity indices computed using the Shannon and Weaver formula show antirelations with % *D. speculum* ($r = -0.67$) and with *D. speculum* fluxes ($r = -0.72$). The data suggest that low index values are related to high fluxes of *D. speculum* (and total silicoflagellates) and high % *D. speculum*. The high index values are related to low fluxes of *D. speculum* and low % *D. speculum*. Moreover, the index values and % *D. mandrai* tend to be parallel (Figs. 8a, c) with a correlation coefficient of 0.46.

f. Actiniscus as a productivity indicator. The flux of the *Actiniscus pentasterias* group is well correlated with the total mass flux (Table 2) and thus can be used to predict it.

$$F_{\text{mass}} = 0.00203 F_{\text{Ap}} + 14.9 \quad (3)$$

where F_{mass} and F_{Ap} are fluxes of total mass and the *Actiniscus pentasterias* group, respectively. The total mass flux predicted using the *Actiniscus pentasterias* group flux data with the above regression equation, conforms with the observed total mass flux (Fig. 9). The application of this group in paleoproductivity assessment depends on future studies on downcore preserved samples. *Actiniscus* is frequently well preserved, often better than silicoflagellates, in many parts of the world (e.g., Dumitrica, 1973; Perch-Nielsen, 1975; Orr and Conley, 1976; Takahashi, unpublished) and deserves attention.

g. Relationship with fossil records in surface sediments. A few percent or less of silicoflagellates that arrive at the sea floor are preserved in the surface sediments of the study area. To compute the percent of skeletons preserved, the following values were used: 10^5 skeletons per gram⁻¹ of dry sediment (Poelchau, 1976), dry density of 0.8 g cm^{-3} , sedimentation rate of $1 \text{ cm } 10^3 \text{ yr}^{-1}$ (see Takahashi, 1986, for details). Use of these values yields 8×10^4 skeletons $\text{cm}^{-2} 10^3 \text{ yr}^{-1}$ that have accumulated in the surface sediments. A mean flux for the 2 year period yields $143,261$ skeletons $\text{m}^{-2} \text{ day}^{-1}$ which is equivalent to 5.23×10^6 skeletons $\text{cm}^{-2} 10^3 \text{ yr}^{-1}$. This means that 1.5% of the silicoflagellates in the flux are preserved. Since Poelchau's (1976) values are actually slightly less than 10^5 skeletons g^{-1} of sediment, approximately 1% of silicoflagellates are preserved. This value is similar to the percentage of diatoms (2%) preserved in the sediments in the same area (Takahashi, 1986). Silicoflagellate dissolution (~99% in this case) mostly occurs at the sediment/water interface or in the sediments as shown elsewhere (Takahashi, 1987a); this is also true for other siliceous microfossils (Takahashi, 1983, 1986).

A large discrepancy is observed between species proportion in the flux and in surface sediments (Table 5). This discrepancy may be superficial resulting from different methods used for analysis. In particular, Poelchau's (1976) concentration technique involving settling and decantation may have biased the proportions between species. More likely, however, it reflects the preferential dissolution of susceptible taxa. For

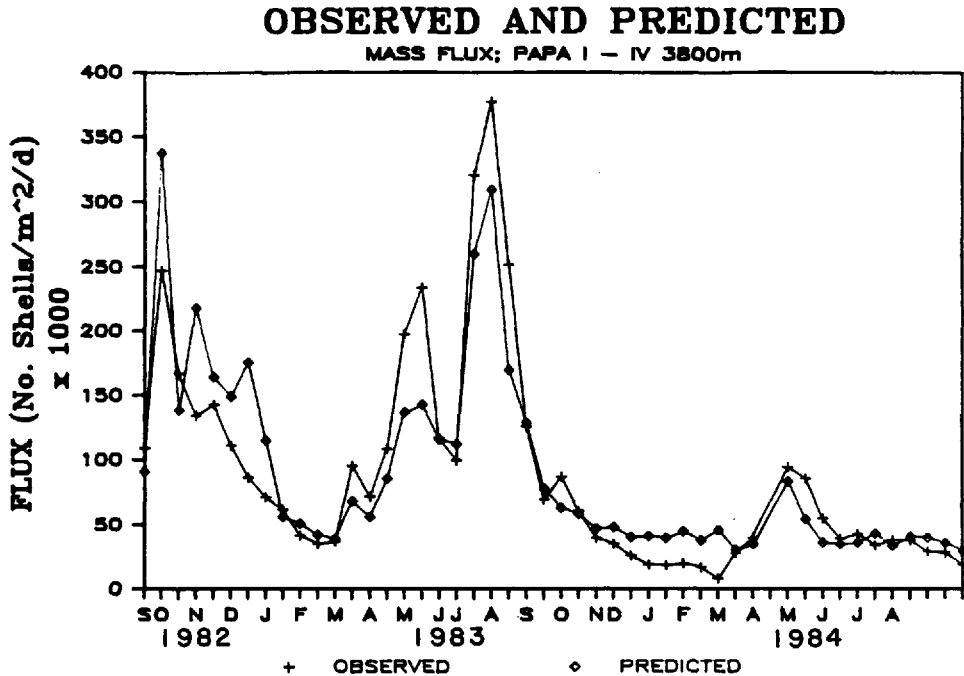


Figure 9. Observed (Honjo, 1984) and predicted total mass fluxes at 3,800 m, Station PAPA, 1982–1984. The predicted values were computed using the *Actiniscus pentasterias* group fluxes and a linear regression equation for total mass and *A. pentasterias* group fluxes.

instance, the sum of *D. speculum* and its variants is about 50% in the flux and only 10% occurs in the sediments. *Distephanus speculum* (and *D. quinquangellus*) is one of silicoflagellate taxa of the study area with the smallest and thinnest skeleton. Thus it is likely to be preferentially dissolved relative to other taxa with more robust skeletons. There is a good correlation between the dissolution index (Johnson, 1974) and the thickness of opal skeletons (Takahashi and Hurd, unpublished). *Dictyocha mandrai*, *D. messanensis* ? *spinosa* and *Distephanus octangulatus* are larger and more robust than *D. speculum* and thus are relatively better preserved. In the case of such preferential dissolution/preservation, for example, 99.8% of *D. speculum* and 98.5% of *D. mandrai* flux to the sea floor would have to be dissolved to acquire the values in the sediment. Alternatively, components of present-day production may be different from that in the surface sediments which represent the past several hundred years or more, causing such a high percent of *D. mandrai* (60%). Detailed down core studies in the future are needed to evaluate all of these three possible explanations.

5. Summary and conclusions

The high resolution time-series flux study of silicoflagellates showed considerable intra-annual and interannual flux variabilities within the studied 2-year period at

Table 5. Comparison of relative abundances in flux and surface sediment assemblages in the study area. The percentages in flux are listed taking mean values of the two year record. The surface sediment data are taken from Poelchau (1976).

Taxon	% in Flux	% in surface sediments
<i>Distephanus speculum</i>	47	10
<i>Distephanus boliviensis</i>	6	—
<i>Distephanus octangulatus</i>	5	15
<i>Distephanus crux</i> ?	1	—
Total <i>Distephanus</i>	59	25
<i>Dictyocha mandrai</i>	37	60
<i>D. mandrai</i> (variable apical rods)	1	—
<i>Dictyocha messanensis</i> ? <i>spinosa</i>	3	15
Total <i>Dictyocha</i>	41	75

pelagic Station PAPA in the northeastern North Pacific. Seasonal flux patterns tend to differ between morphologically distant species groups while the patterns are similar within a morphologically confined group.

Silicoflagellate flux is generally numerically dominated by two major taxa, *Distephanus speculum* and *Dictyocha mandrai*, which contribute on the average 83% ($6.7\% < \sigma < 10.1\%$ at 95% confidence limits) of the total sinking assemblages. *D. speculum* is considered to be a productivity indicator based on its affinity of the seasonal flux pattern to the total mass, opal, and diatom flux patterns. Seasonal patterns show by *Distephanus speculum* and its two other closely related species are similar to the seasonal pattern of diatom flux Type 1, which is a productivity indicator. *D. mandrai* carries its unique late fall/early winter signals. More than half of the cumulative annual flux of this species occurred in a three month period (October, 1982–January, 1983), implying a significance to the fossil record.

The silicoflagellate seasonal flux patterns are generally similar enough to those of total mass, opal, and diatoms so that an assessment of surface water opal or total mass productivity using silicoflagellates is possible. Moreover, the silicoflagellate flux is nearly an independent measure from opal due to its insignificant mass contribution to opal. Although general patterns are similar, as mentioned above, details of silicoflagellate seasonal flux deviate from opal, whose main contributor is diatoms, providing unique signals. Some of the silicoflagellate flux maxima tend to be temporally offset from diatoms by one sample interval, indicating a different response to environmental changes from that of diatoms.

The level of flux changes significantly from year 1 to year 2. Despite such annual flux variations in the 2-year record, the annual patterns of species percents are similar for the two years, suggesting a possible use of percent data for productivity assessment.

Sinking speeds of silicoflagellates are determined to be approximately 175 m day^{-1} or greater based on cross-correlation analysis of the synchronized 1000 m and 3800 m

samples. Generally, silicoflagellates sink faster than diatoms. Both fecal material and marine snow are likely mechanisms for the observed accelerated sinking speeds. No significant dissolution of silicoflagellate skeletons occurs in the water column due to protection and accelerated sinking via aggregates. Therefore, species composition and absolute flux of each species in the sinking assemblages at 1000 m and 3800 m are similar, with or without the slight temporal offset.

Approximately 1% of silicoflagellates supplied to the sea floor are preserved and the bulk of the supplied skeletons are dissolved in the sediments. The preferential dissolution of *D. speculum*, a solution susceptible taxon, relative to *D. mandrai*, a solution resistant taxon, is a probable reason for the preserved species percentages in the surface sediments of the study area.

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