Siliceous microplankton such as radiolarians, silicoflagellates, and diatoms were examined for their fluxes in order to interpret temporal production changes in the upper ocean. The eastern subarctic Pacific was chosen as the study region for its high biological productivity as well as a large amplitude of seasonality. Automated time-series sediment traps were deployed at two different locations in the Gulf of Alaska during 1982–1986 and 1985–1986. Temporal fluxes of siliceous microplankton showed large seasonal and interannual productivity changes during the course of the four-year long and one-year long field experiments. Most significantly, a severe suppression in production of biota occurred during late 1983 and most of 1984, reflecting a drastic reduction in the mixing of upper water layers, and causing less nutrient supply. Temporal fluxes of *Neodenticula seminiae*, a dominant pennate diatom contributing greater than 70% of diatom flux assemblages in valve number, paralleled with that of total mass, indicating that this taxon is a productivity indicator. Radiolarian diversity indices and nassellarian fluxes are anti-correlated. Their temporal changes also match with all other relevant productivity parameters examined. Temporal flux pattern of *Ceratospyris borealis*, a nassellarian radiolarian, resembles quite well with that of *N. seminiae*, suggesting that this species is also a promising paleoproduction indicator.

1. Introduction

Siliceous plankton makes up one of the major marine microfossil groups. They differ markedly from the counterpart calcareous plankton in production, preservation, and diagenesis. Most importantly, production of the siliceous plankton tends to associate with areas of high biological productivity such as coastal and equatorial upwelling regions and subpolar seas (Lisitzin, 1972; Schrader and Schuette, 1981). Calcareous plankton, on the other hand, tends to prosper better in the vast areas of central oceanic gyres and less productive parts of the world oceans. The siliceous plankton can provide a wealth of information on pelagic biological productivity. The pelagic productivity is largely governed by physical forcing such as vertical mixing in the upper layers which regulates nutrient supply from the subsurface layers. The supply rates of the nutrients more or less govern the annual biological productivity. The physical forcing is largely dictated by seasonal and interannual climate changes. Therefore, in a crude sense, a time-series research for the pelagic productivity is to study climate changes. This research can be applied to a variety oceanographic as well as paleoclimatic investigations.

One of the best ways to obtain seasonally varying plankton production is to deploy bottom tethered automated time-series sediment traps for a length of period (Honjo and Doherty, 1988). The eastern subarctic Pacific (Fig. 1) was chosen to study particle fluxes, employing the sediment traps by a US-Canadian program (Honjo, 1984) since biological productivity in the region is fairly high (Koblentz-Mishke et al., 1970; Berger et al., 1987; Longhurst et al., 1995) and oscillates seasonally due to the annual climate cycles. There had been a Canadian Weather Station PAPA in the central Gulf of Alaska for a long time prior to the emergence of satellite imagery technology and hence, a wealth of hydrographic information is available in the region (Anderson et al., 1977).

Many studies in the program, using the same sediment trap samples from this region, have been carried out concerning shell-bearing plankton and chemical parameters (Druffel et al., 1986; Haake et al., 1993). The plankton studies include on diatoms (Takahashi, 1986, 1987a, 1994; Takahashi et al., 1989, 1990), silicoflagellates (Takahashi, 1987b, 1989), Radiolaria (Takahashi, 1987c), and planktonic foraminifera (Reynolds and Thunell, 1985, 1986; Sautter and Thunell, 1989). In the 1987 radiolarian paper, I have reported the fluxes at Station PAPA during 1982–
1984, which was for the first two years of the consequent four full years of the trap samples. In that paper, some of the useful radiolarian taxon fluxes were discussed, but a comprehensive overview of total radiolarian fluxes or with other siliceous plankton fluxes were not included. Here, I will discuss an overview of radiolarian fluxes and other relevant siliceous microplankton fluxes at Station PAPA for four years and at Station C for one year. Although flux data available from Station C are only for one year, they provide useful information concerning spatial variability of the fluxes within the Gulf of Alaska. They enhance the validity of the four year long flux data at Station PAPA.

2. Materials and Methods

A PARFLUX type sediment trap (Honjo and Doherty, 1988) was deployed at 3800 m depth at Station PAPA (50°N, 145°W; water depth: 4200 m) during September 1982 through August 1986 for four full years. An additional trap was deployed at 1000 m depth at Station PAPA during March 1983 through September 1983 and May 1985 through April 1986 for a total of one and a half years in two separated periods (Table 1). Another trap was deployed at 3500 m at Station C (49.5°N, 138°W; water depth: 3900 m) during May 1985 through April 1986 for one full year (Fig. 1: Honjo, 1984; Honjo et al., 1995; Wong et al., 1995). All of the sampling intervals were synchronized so that direct comparisons among samples from different depths or stations were possible (Table 1).

High resolution flux data, with two week intervals from 3800 m trap depth at Station PAPA, were available for most of the 1982–1986 four-year period. Eighty three trap samples from PAPA 3800 m were available. There are, however, two exceptions that no trap sample from 3800 m is available in two intervals; they are (1) a hiatus period between 24 August 1984 and 21 November 1984 for about three months due to the cruise schedule; and (2) a hiatus period between 1 February 1986 and 25 May 1986 for about four months due to the malfunction of the traps and a change-over of the traps during the spring 1986 cruise to the region. Details of the sampling intervals and exact duration of the sampling hiatuses have been reported earlier (Takahashi, 1987b, 1989). The data just before and after the first hiatus in 1984 cannot be connected due to absence of data. The second sampling hiatus was filled with a set of substituted data (see below).
Table 1. Sampling increments of 143 sediment trap samples from Stations PAPA and C in the Gulf of Alaska in the eastern subarctic Pacific, 1982–1986. Number of samples from each station/depth are: 83 from PAPA 3800 m; 36 from PAPA 1000 m; and 24 from C 3500 m.

<table>
<thead>
<tr>
<th>Station /Deployment #</th>
<th>Depth (m)</th>
<th>Duration of each sample (days)</th>
<th>Beginning date of the sequential samples with the same increment</th>
<th>Ending date of the sequential samples with the same increment</th>
<th># of samples with the same sampling increment</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAPA I 3800</td>
<td>3800</td>
<td>15</td>
<td>23 September 1982</td>
<td>7 March 1983</td>
<td>11</td>
</tr>
<tr>
<td>PAPA I 3800</td>
<td>3800</td>
<td>11</td>
<td>7 March 1983</td>
<td>18 March 1983</td>
<td>1</td>
</tr>
<tr>
<td>PAPA II 1000, 3800</td>
<td>1000, 3800</td>
<td>16</td>
<td>27 March 1983</td>
<td>5 October 1983</td>
<td>12</td>
</tr>
<tr>
<td>PAPA III 3800</td>
<td>3800</td>
<td>16</td>
<td>14 October 1983</td>
<td>23 April 1984</td>
<td>12</td>
</tr>
<tr>
<td>PAPA IV 3800</td>
<td>3800</td>
<td>14</td>
<td>13 May 1984</td>
<td>5 August 1984</td>
<td>6</td>
</tr>
<tr>
<td>PAPA IV 3800</td>
<td>3800</td>
<td>4</td>
<td>5 August 1984</td>
<td>24 August 1984</td>
<td>5</td>
</tr>
<tr>
<td>PAPA VI 3800</td>
<td>3800</td>
<td>12</td>
<td>21 November 1984</td>
<td>12 April 1985</td>
<td>12</td>
</tr>
<tr>
<td>PAPA VII 1000, 3800**</td>
<td>1000, 3800</td>
<td>14</td>
<td>10 May 1985</td>
<td>25 October 1985</td>
<td>12</td>
</tr>
<tr>
<td>C 3500</td>
<td>3500</td>
<td>14</td>
<td>10 May 1985</td>
<td>25 October 1985</td>
<td>12</td>
</tr>
<tr>
<td>PAPA VIII 3800**</td>
<td>1000, 3800</td>
<td>12.5–14.5*</td>
<td>13 November 1985</td>
<td>23 April 1986</td>
<td>12</td>
</tr>
<tr>
<td>C 3500</td>
<td>3500</td>
<td>12.5–14.5*</td>
<td>13 November 1985</td>
<td>23 April 1986</td>
<td>12</td>
</tr>
<tr>
<td>PAPA IV 3800</td>
<td>3800</td>
<td>14</td>
<td>27 April 1986</td>
<td>12 October 1986</td>
<td>12***</td>
</tr>
</tbody>
</table>

*They vary within this range, depending on the sample. For details see Takahashi (1989).
**Only first six samples at PAPA 3800 m were available due to malfunction of the traps.
***Of these only six samples were available due to malfunction of the traps (see Takahashi, 1989).

Other available samples include 36 trap samples from Station PAPA at 1000 m in two separate periods (27 March 1983–5 October 1983; and 10 May 1985–23 April 1986) and 12 trap samples from Station C at 3500 m (10 May 1985–23 April 1986). A summary of the total of 143 samples used in this study, including sampling increments, is given in Table 1.

Furthermore, a part of the trap data from 1000 m at Station PAPA are used to fill the 1986 sampling hiatus of 3800 m depth at Station PAPA. Previous observations suggest that biogenic sinking particles in this region sink rapidly at 175 m d−1 to 200 m d−1 in an aggregate form rather than a discrete form (Takahashi, 1986, 1987a, b, 1989; Takahashi et al., 1989, 1990). These studies clearly demonstrate that siliceous plankton assemblages captured at 1000 m depth are also captured about one sampling period later at 3800 m depth at Station PAPA. The similarity of the assemblages include, not only species composition, but also abundance, strongly indicating vertical fluxes of accelerated sinking particles. Not much of flux loss due to dissolution en route has been observed and hence, the 1000 m data are comparable with that of 3800 m, except that there is a temporal delay of particle arrivals (Takahashi, 1986). Therefore, it is reasonable to use the 1000 m data and simply shift one sample onward to fill the sampling hiatuses. The substituted data are for seven samples. Temporal changes of fluxes are illustrated, using all the actual 84 samples/data and seven substituted data plotted together, making 91 datum points in all.

A trap sample was sieved through a stainless steel screen with 63 µm mesh and split to an appropriate aliquot size. The split sample was filtered through Gelman® membrane filters with a nominal pore size of 0.45 µm. The filtered sample was desalted with distilled water and dried in an oven at 50°C for more than one hour. The dried sample on the filter was subjected to prepare a microslide; Cargile® type B immersion oil was applied to render the filter prior to sealing with a No. 1 cover slip secured with Devcon® 5-minutes epoxy at four corners.

Prior to species enumeration, detailed taxonomic investigation concerning identity of each taxon was conducted, using light microscopes and a scanning electron microscope. Such a taxonomic investigation constitutes the basis of the present taxon-quantitative flux study. Siliceous microplankton groups were counted under an Olympus compound microscope at various magnifications, depending on each of the taxonomic groups or species, always with 10× wide field eye pieces. For instance, most of the diatom study was conducted, using 20×, 40×, and 60× objective lenses, whereas 10× and 20× objective lenses were commonly used for the radiolarian study. Furthermore, a 20× objective lens was used for silicoflagellates. Each of the taxa encountered were counted and tabulated to derive total fluxes of each taxonomic groups.

Diversity indices, using Shannon and Weaver formula (Pielou, 1969), were calculated for radiolarians.

3. Results

Temporal fluxes of spumellarian, nassellarian, phaeodarian radiolarians at Station PAPA for four years
Fig. 2. Four-year long fluxes of (a) three subgroups of Radiolaria (Nassellaria, Spumellaria, and Phaeodaria), (b) total silicoflagellates, and (c) total diatoms at 3800 m depth at Station PAPA in the Gulf of Alaska during September 1982 through August 1986. See the methods section for details of actual measurements.
Fig. 3. One-year long fluxes of (a) three subgroups of Radiolaria (Nassellaria, Spumellaria, and Phaeodaria), (b) total silicoflagellates, and (c) total diatoms at 3500 m depth at Station C in the Gulf of Alaska during May 1985 through April 1986.
during 1982–1986 are illustrated (Fig. 2a). Order Nassellaria represents the most abundant radiolarian subgroup flux in shell number, followed by Class Phaeodarea and Order Spumellaria. The same trend is also seen at Station C where one year long radiolarian flux data are available (Fig. 3a). It is important to compare the flux data from Station C in order to validate the long time-series data at Station PAPA and assess spatial variability of the fluxes. A significant seasonal variability is observed in the four year radiolarian fluxes at Station PAPA. Typically, the radiolarian fluxes increase during spring and taper down toward winter, but their flux levels and exact timings varied substantially from one year to another. In addition to the seasonal changes, there is a significant interannual change of the radiolarian fluxes. In particular, fluxes in 1984 displayed the lowest maximum of the four year data with a single significant peak (i.e., $>20 \times 10^3$ shells m$^{-2}$d$^{-1}$). Although there is the three month sampling hiatus during 24 August through 21 November 1984, no significant flux maximum during this hiatus can be inferred from the subsequent flux patterns (see more developed argument in the discussion section). The radiolarian fluxes at Station C showed a similar flux fluctuation for one year (Fig. 3a) to the corresponding time intervals at Station PAPA. In detail, the Station C data are significantly lower than that of Station PAPA (Table 2). Station C flux data represent only 55% of total radiolarian fluxes of Station PAPA. Furthermore, fluxes of Ceratospyris borealis at Station C, a nassellarian radiolarian species, similarly show 52% of Station PAPA. Note that the radiolarian flux maximum observed at Station PAPA in March–April 1986 did not occur at Station C in March–April 1986.

Total silicoflagellate fluxes are illustrated for Station PAPA (Fig. 2b) and Station C (Fig. 3b). Analogous to the radiolarians, total silicoflagellates showed significant seasonal and inter-annual flux excursions in the four years at Station PAPA. Generally, temporal increases and decreases of the silicoflagellate fluxes occurred analogous to those of total radiolarians. One notable difference, however, is that the amplitude of silicoflagellate fluxes is substantially greater than that of the radiolarian fluxes. Furthermore, a difference between the low 1984 silicoflagellate flux maximum and high flux maxima (i.e., 1982-83, 1985-86) is one order of

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean (No. shells m$^{-2}$d$^{-1}$)</td>
<td>S.D.</td>
<td>Mean (No. shells m$^{-2}$d$^{-1}$)</td>
</tr>
<tr>
<td>Total diatoms</td>
<td>$8.99 \times 10^6$</td>
<td>$9.84 \times 10^6$</td>
<td>$12.2 \times 10^6$</td>
</tr>
<tr>
<td>Neodenticula seminiae</td>
<td>$8.36 \times 10^6$</td>
<td>$8.43 \times 10^6$</td>
<td>$9.40 \times 10^6$</td>
</tr>
<tr>
<td>Total silicoflagellates</td>
<td>$128 \times 10^3$</td>
<td>$138 \times 10^3$</td>
<td>$96.0 \times 10^3$</td>
</tr>
<tr>
<td>Distephanus speculum</td>
<td>$65.2 \times 10^3$</td>
<td>$92.7 \times 10^3$</td>
<td>$72.9 \times 10^3$</td>
</tr>
<tr>
<td>Total Radiolaria</td>
<td>$25.3 \times 10^3$</td>
<td>$14.3 \times 10^3$</td>
<td>$35.2 \times 10^3$</td>
</tr>
<tr>
<td>Ceratospyris borealis</td>
<td>$184$</td>
<td>$142$</td>
<td>$181$</td>
</tr>
</tbody>
</table>

*For diatoms the following units are applicable: valves m$^{-2}$d$^{-1}$.

Table 2. Mean fluxes (No. shells m$^{-2}$d$^{-1}$) and standard deviations of total diatoms, total silicoflagellates, total Radiolaria, and one of the representative taxa from each of the taxonomic groups for four years during September 1982–August 1986 at Station PAPA 3800 m and for one year during May 1985–April 1986 at Station PAPA 3800 m and Station C 3500 m. Compared values between the two stations are given in percentage.
magnitude whereas that of total Radiolaria is only factor of two, reflecting short a production time of the autotrophs vs. heterotrophs which must depend on the primary producers. Moreover, the mean silicoflagellate flux is only slightly higher at Station PAPA than that of Station C (82%) during 1985–1986 (Table 2). Destephanus speculum, the dominant silicoflagellate species, showed a similar flux level at Station C (77%) compared to Station PAPA.

Time-series change in amplitude and seasonality of total diatom fluxes at Stations PAPA and C (Figs. 2c and 3c) are fairly similar to those of silicoflagellates with a significant inter-annual variability. Although exact timing varies, total diatom fluxes showed recurrent spring maxima every year around March–May. Timings of fall maxima tend to vary more significantly than that of spring maxima. Flux maxima with their magnitude comparable to the spring ones occurred in the fall: October 1982, and September 1985. An early maximum occurred in July 1983. An insignificant maximum occurred in November 1984, although there is no data during late August through late November.
I have chose to discuss details of the fluxes of the following representative taxa for their excellent covariance: *Neodenticula seminae* (Simonsen and Kanaya, 1986), which is a dominant pennate diatom; and *Ceratospyris borealis* (Bailey, 1856), which is a nassellarian radiolarian (Figs. 4 and 5). In my earlier studies (e.g., Takahashi 1987a; Takahashi et al., 1989) *N. seminae* was determined as one of the best productivity indicators. Therefore, *C. borealis* can also be considered as a representative productivity taxon of Radiolaria.

All radiolarian, silicoflagellate, and diatom flux data from May 1985–April 1986 showed almost consistently lower values at Station C than those at Station PAPA (Fig. 2; Table 2). The same trend is also observed for *N. seminae* as well as *C. borealis* (Figs. 4 and 5). Fall flux maximum of silicoflagellates at Station C occurred in November. This maximum is delayed one sample interval compared to that of Station PAPA. No obviously discernible delay in fall flux peaks between the two stations can be recognized for Radiolaria. Spring flux increases already began in late March 1986 at Station PAPA for most taxa observed including total Radiolaria, total silicoflagellates, total diatoms, *N. seminae*, and *C. borealis*. Such a spring increase was not observed at Station C within available data through early April 1986 (Fig. 5).

Radiolarian diversity indices and nassellarian fluxes are generally anti-correlated (Fig. 6). Although not illustrated, a similar trend is observed between total radiolarian fluxes and radiolarian diversity indices (see details in the Discussion section). Because the nassellarian fluxes are slightly better anti-correlated with radiolarian diversity indices than total radiolarian fluxes, the former was chosen to be dealt here.

4. Discussions

Based on the siliceous microplankton fluxes, general productivity regime observed at Station PAPA is higher than that of Station C. This trend is seen in all siliceous microplankton groups without any exceptions (Table 2). *N. seminae* showed approximately twice as much fluxes at Station PAPA than that of Station C. This taxon is the dominant diatom species in the region (Sancetta, 1982; Takahashi, 1994) which contributes significant amount of carbon to total diatoms (Takahashi, 1987a). Considering similar contributions by *N. seminae* to total diatoms at both stations, diatom carbon export production is significantly higher at Station PAPA than that of Station C. Furthermore, Obayashi et al. (1997) showed dominant contributions of diatoms to total phytoplankton assemblages in the Gulf of Alaska based on phaeo-pigment analyses from nine longitudinal E-W seasonal cruises across the subarctic Pacific.

Station PAPA is located further offshore, relative to Station C. As stated earlier, the sediment trap data showed the higher productivity at the former than the latter. Such a difference in productivity between Stations PAPA and Station C cannot readily be discerned by examining most published productivity maps (Koblentz-Mishke et al., 1970; Berger et al., 1987; Longhurst et al., 1995). In fact, they illustrate that the productivity levels are nearly equal at the two stations. These maps were compiled for large scale synoptic views of world productivity and hence, not necessarily applicable to meso scale comparison. Nevertheless, the biological productivity trend, assessed from the sediment trap material clearly showed a marked difference in productivity at the two stations. It is concluded that the productivity assessment done here, employing the high resolution sediment trap material, is a detailed and faithful
representation of what actually occurred in the region.

A comparison with siliceous plankton flux data being generated in a currently on-going program indicates that the productivity in the Gulf of Alaska is slightly lower than that of the central subarctic Pacific. This is based on five-year long fluxes of organic carbon and total mass fluxes (49°N, 174°W: Takahashi et al., 1997) and the four-year long fluxes of diatoms at Station SA (Takahashi et al., 1996). Furthermore, these data from the pelagic subarctic Pacific are substantially lower than those obtained from the Bering Sea. The Bering Sea is roughly twice as much productive than Station SA in terms of biogenic particle fluxes measured at Station AB (53.5°N, 177°W) in the Aleutian Basin (Takahashi et al., 1996, 1997). Such a difference in the marginal sea and pelagic environment within the subarctic Pacific region is expected, considering water circulation and morphology of the ocean basins. In fact, distribution of nutrient concentrations in the Bering Sea (Tsunogai et al., 1979) and in the central subarctic Pacific (Maita and Toya, 1986) clearly supports this view.

Both Neodenticula seminae and Ceratospyris borealis (Figs. 4 and 5) can be represented as productivity indicators in the upper ocean at least in the eastern subarctic Pacific. This is because their fluxes parallel with organic carbon and mass fluxes (Table 3), which is further substantiated by the following two facts. N. seminae is a dominant diatom taxon in the fluxes of the region, normally well exceeding 70% of total diatom assemblage in valve number (Takahashi, 1986, 1987a; Takahashi et al., 1990). Flux maxima of this diatom species occurred during spring and fall when both organic carbon and total mass fluxes increase. The seasonal flux pattern of N. seminae is well correlated with total mass fluxes ($r = 0.88$, $N = 85$), while that with organic carbon is intermediary correlated ($r = 0.56$, $N = 85$) (Table 3; Takahashi, 1986). The N. seminae fluxes are also correlated with nutrient and light regimes of the upper layer. Hence, this taxon is a biological productivity indicator (Takahashi et al., 1989).

The seasonal flux pattern of C. borealis resembles that of N. seminae remarkably well at both Stations PAPA and C (Figs. 4 and 5). Among ninety seven radiolarian species examined at Station PAPA only C. borealis showed such a good correlation ($r = 0.67$) with the diatom taxon. Considering that the signal-to-noise-ratios for the radiolarian counts are lower than those for diatoms due to radiolarian’s low abundance in the prepared slides, causing larger statistical errors, the excellent match in Fig. 4 is well taken even though the apparent correlation coefficient is not as good as it could be. This radiolarian species, belonging to spyrids, represents about 1% of total radiolarian fluxes, but its abundance in surface sediments increases up to a few percent. This is because the preservation of this taxon in sediments is generally as good as other spyrid radiolarians due to robust nature of its skeletons. Because of such an excellent preservation one can readily use this taxon with the fidelity productivity signals in down core studies. Without the preservation, one cannot use the signals, if they were not there. Furthermore, spyrids have numerous Cenozoic ancestors and well utilized for biostratigraphy (Sanfilippo et al., 1985). As a new paleoproductivity tracer, this taxon is quite promising for future investigations.

Superclass Radiolaria can be sub-grouped into three taxonomic subgroups: Order Nassellaria, Order Spumellaria, and Class Phaeodarea (Anderson et al., 1997; Takahashi and Anderson, 1997). Nassellarian fluxes are best anti-correlated with radiolarian diversity indices ($r = -0.62$) among three subgroups and total radiolarians ($r = -0.55$). Both Spumellaria ($r = 0.00$) and Nassellaria ($r = -0.17$) showed almost no correlation at all with the radiolarian diversity indices, suggesting that much of the correlation signals reside within Nassellaria. This is partially due to the diverse nature of Nassellaria with 50 taxa compared to 20 spumellarian and 27 phaeodarian taxa.

Since the radiolarian diversity index represents a measure of a spread of taxonomic composition and relative quantity of each taxon in an assemblage, it is expected that the index increases as flux decreases. When radiolarians feed well on prey items, generally during spring and fall when productivity increases, relative contributions of nassellarians increase substantially (Figs. 2a, 3a and 5). This is attributed to numerous small-sized nassellarians whose fluxes parallel with those of phytoplankton. They include Lithomelissa setosa, Phormacantha hystrix, and Lophophoa sp. aff. L. apiculata. They are most likely feeding on small phytoplankton, bacteria, and/or detritus (Anderson, 1983) and quick in responding to feeding opportunities. Their growth rates are presumably higher than large-sized taxon. Therefore, their flux increases can be analogously as fast as those of phytoplankton. This can be

<table>
<thead>
<tr>
<th>Total diatoms</th>
<th>Neodenticula seminae</th>
<th>Total silicoflagellates</th>
<th>Distephanus speculum</th>
<th>Total Radiolaria</th>
<th>Nassellaria</th>
<th>Spumellaria</th>
<th>Phaeodaria</th>
<th>Ceratospyris borealis</th>
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<tr>
<td>0.88</td>
<td>0.88</td>
<td>0.60</td>
<td>0.58</td>
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<td>0.42</td>
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<td>0.34</td>
<td>0.27</td>
<td>0.30</td>
<td>0.53</td>
</tr>
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<td></td>
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<td></td>
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<td></td>
<td>0.27</td>
<td>0.27</td>
<td>0.53</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Table 3. Correlation coefficients $r$ between fluxes of total mass or organic carbon of Honjo (1984) vs. major siliceous taxonomic groups and representative species at PAPA 3800 m during 1982–1986.
inferred from the flux data with temporal resolution of about two weeks.

The mirror image of the nassellarian fluxes and radiolarian diversity indices during 1985 and 1986 (Fig. 6) represents a basic seasonal pattern. This should be looked at with a notion of specific hydrographic conditions prevailed during the late 1983 and much of 1984, possibly an El Niño effect (Takahashi, 1987a, c). According to an examination of available vertical hydrographic data such as σt values, the mixing in the upper layer was significantly restricted down to about 80 m depth during this time period (Takahashi et al., 1989), causing less supply of subsurface nutrients. Such restricted supplies of nutrients lead to a suppression of normal biological production, eventually leading to lower fluxes than normal years. The suppressed fluxes are seen in almost all the taxa examined. For instance, N. seminae shows a very small flux maximum during May 1984, approximately one order of magnitude lower than other years (Fig. 4). C. borealis as a radiolarian, on the other hand, represents a flux maximum in June 1984 which is only about a factor of two to four lower than other years (Fig. 4). Such a marked contrast in differences between the maxima and minima of diatom and radiolarian fluxes is likely caused by distinction in nutrition behaviors. Direct absorption of nutrients by the autotroph such as N. seminae may be expected whereas C. borealis as a heterotroph may be preying food items such as plankton or detritus. Furthermore, the relatively high radiolarian diversity indices such as 1.0 during the latter half of 1983 and most of 1984 are attributed to the flux suppression explained above. The general high indices conform with general low fluxes of total radiolarians, total diatoms, and total silicoflagellates (Fig. 2).

Although there is very limited amount of information on N. seminae standing stock in the euphotic zone, it is worthwhile to proceed even with a back of envelope calculation for comparing its fluxes with the standing stock. Taylor and Waters (1982) reported N. seminae standing stock of ~2.8 × 10^6 cells m^-2 in March 1969 and ~2.3 × 10^7 cells m^-2 in May 1969 in the upper 100 m water column near Station PAPA. Booth (1981) reports that N. seminae standing stock is an order of 10^4 l^-1 at the surface based on 36 American Mail Line cruises across the eastern subtropical Pacific covering spring through early summer. This surface value can be translated to 1 × 10^9 m^-2, assuming equal concentration down to 100 m depth.

Four year mean flux values of N. seminae at Station PAPA 3800 m for April, June, and April through June were obtained and shown below. This is to compare with the standing stock data of Taylor and Waters (1982) as well as spring through early summer values from Booth (1981), even though their sampled years are different from my trap data. Since Taylor and Waters (1982) did not specify dates for the March and May samples, the middle of March and May, respectively, are simply assumed. Based on the sinking speed of 175 to 200 m d^-1 (Takahashi, 1986, 1987a, b, c, 1989), the March and May standing stocks should reflect vertical fluxes at Station PAPA 3800 m in the middle of April and June. The entire April (15 April ± 15 days) and May (15 May ± 15 days) flux values were taken to allow errors involved in the computations for April and May. The entire April, May and June flux data were used to calculate a mean flux value for spring through early summer. The obtained values are: April: 11.6 × 10^6 valves (5.8 × 10^6 cells) m^-2 d^-1; June: 10.4 × 10^6 valves (5.2 × 10^6 cells) m^-2 d^-1; and April through June: 11.4 × 10^6 valves (5.7 × 10^6 cells) m^-2 d^-1. These mean flux values are conservative since 1984 data are low due to the unusual flux suppression which occurred (Takahashi et al., 1989), as discussed earlier.

Compared values between the standing stock and flux ranges from 0.21% to 23%. It means that 0.21% to 23% of standing stock values in the upper water are observed in the daily flux at 3800 m about a month later. In this comparison an assumption of no dissolution loss during their descent is used. In practice it would not necessarily hold true, but on the contrary, it will provide a clue for loss due to dissolution en route. Considering errors involved in these computations, such as an assumption of equal standing stock down to 100 m and in different years, these values appear reasonable; let’s say that about a few percent of standing stock would be observed in the daily flux at depth.

Cell dimensions of N. seminae are available: 6.6 × 25.1 × 8.6 µm, N = 92 (Takahashi, 1987a). Approximately one half of N. seminae cells are still in chain form in the flux (Takahashi et al., 1985). Thus, the small size of this species may not always be an influential factor for the discussion below. Michaels and Silver (1988) showed that small-sized phytoplankton was not effectively converted to sinking particles, while net phytoplankton are important contributors to the sinking materials. I tend to view that this taxon is actually acting like a net phytoplankton because of the chain form. In the future it is necessary to obtain other net phytoplankton standing stocks and compare them with their fluxes. The validity of Michaels and Silver’s conclusion has to be confirmed or rejected, depending on the future detailed time-series comparisons of standing stock and fluxes.

5. Conclusions

In first order analysis, the seasonal flux pattern of total Radiolaria resembles that of total silicoflagellates and total diatoms in terms of timing of flux peaks and valleys. However, there is a fundamental difference between flux levels of Radiolaria, which are protozoan, and silicoflagellates and diatoms, which are phytoplankton. Specifically, the differences between high and low flux values are considerably greater in the phytoplankton than the protozoan, reflecting growth ecology of the respective plankton groups.

All siliceous plankton groups showed significantly
higher fluxes at Station PAPA than Station C. Such a difference is attributed to hydrography of the regions. A higher biological production was recognized at Station PAPA than Station C.

Temporal fluxes of *Neodenticula seminae*, a dominant pennate diatom contributing greater than 70% of diatom flux assemblages in valve number, paralleled with that of total mass flux. This indicates that the seasonal flux pattern of this taxon resembles that of sum of many other taxa. Thus, this taxon can be considered as a productivity indicator.

Siliceous shell-bearing microplankton fluxes can be used to reconstruct temporal changes in biological productivity in the upper oceans. This can be justified by: (1) export production of organic carbon represents a trend of biological productivity; and (2) siliciclastic plankton and total mass fluxes parallel each other. Change in radiolarian diversity index shows as a mirror image with that of nassellarian or total radiolarian fluxes, much of the signals in Nassellaria itself. Total radiolarian diversity in fossil record can be used to assess paleoproductivity. Nassellarian radiolarians are more promising than spumellarian radiolarians since they tend to respond quickly to feeding opportunities than other groups. The best example of a radiolarian productivity indicator is *Ceratospyris borealis*, a spyrid radiolarian. Temporal flux pattern of this taxon is nearly the same as that of *Neodenticula seminae*, the dominant diatom taxon with productivity signals in the subarctic Pacific. Spyrids are generally well preserved in Cenozoic fossil record and thus further detail studies of *C. borealis* and other taxa in the family are needed in order to advance our understanding of paleoproductivity.

Silicoflagellate fluxes parallel with that of *N. seminae* and they are useful as well for productivity studies. The 1984 flux suppressions observed for diatoms and radiolarians are also seen in the silicoflagellate fluxes.

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