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Time-series fluxes of Radiolaria in the eastern subarctic Pacific Ocean

Kozo TAKAHASHI*

Abstract Four-year long fluxes of total radiolarians, three major radiolarian subgroups, and selected radiolarian species were examined for their intra-annual and interannual changes in temporal production in the eastern subarctic Pacific Ocean. The study region was chosen for its high biological productivity and a large amplitude of seasonality. Automated time-series sediment traps were deployed at Station PAPA in the Gulf of Alaska during 1982 through 1986. Temporal fluxes of radiolarians showed large seasonal and interannual changes in their productivity during the course of the field experiment. Fluxes of *Lithomelissa setosa*, a nassellarian taxon, displayed a distinct spring seasonal pattern that was not recorded in any other siliceous microplankton fluxes in the region. Therefore, this unique taxon is useful as a spring season indicator for a variety of applications in productivity studies. The temporal flux pattern of *Ceratospyris borealis*, a nassellarian radiolarian, resembles quite well with that of *N. seminae*, a dominant diatom taxon with strong productivity signals, suggesting that this radiolarian species is a promising productivity indicator. Radiolarian diversity indices and total radiolarian fluxes are anti-correlated, indicating the total Radiolaria as a productivity indicator. Their temporal changes also match with all other relevant productivity parameters examined.

Key words: Radiolaria, flux, seasonal change, productivity, subarctic Pacific

Introduction

Radiolaria are heterotrophic microzooplankton ubiquitous in pelagic oceans. In the subarctic Pacific radiolarians comprise up to 56 wt % organic carbon export production of an entire siliceous microplankton (Takahashi, unpublished) and up to 70 wt % of biogenic opal export production (Takahashi, 1991). Although these maximal values are extremes and mean values are substantially lower than these, a relative importance of Radiolaria in carbon and opal export production of whole siliceous plankton assemblage is evident from this.

Radiolaria can provide a wealth of information on pelagic biological productivity since this group is comprised of highly diversified assemblage dwelling different depth zones. Radiolarian fluxes vary seasonally as well as interannually based on an earlier radiolarian flux study for the initial two years at Station PAPA (Takahashi, 1987a). One of the best ways to collect seasonally varying plankton production is to deploy bottom tethered automated time-series sediment traps for a long 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) 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 oceanographic 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 shell-bearing plankton studies include diatoms (Takahashi, 1986, 1987b, 1994; Takahashi et al., 1989, 1990), silicoflagellates (Takahashi, 1987c, 1989), Radiolaria (1987a), and planktonic foraminifera (Reynolds and Thunell, 1985, 1986; Sautter and Thunell, 1989). In the 1987 radiolarian paper I have reported flux data from first two year worth of the fluxes at Station PAPA. In that paper some of the useful radiolarian taxon fluxes were discussed, but a comprehensive overview of total radiolarian fluxes or with other

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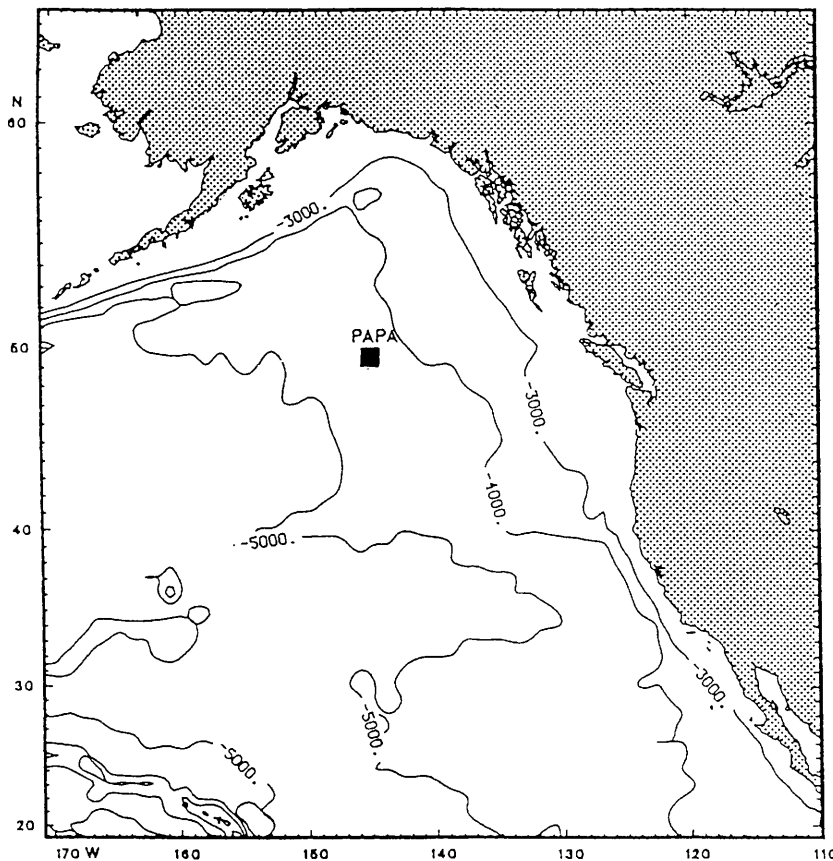
Fig. 1. A map showing the location of the sediment trap station in the Gulf of Alaska, the eastern subarctic Pacific Ocean.

siliceous plankton fluxes were not included. Here I will discuss an overview of total radiolarian taxon fluxes and relevant radiolarian fluxes in the light of results obtained for siliceous phytoplankton and other biogeochemical fluxes at Station PAPA for four years during 1982-1986.

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 with sampling intervals of 12 to 16 days (Fig. 1: Honjo, 1984). 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 with sampling intervals of 12.5 days to 16 days. Sampling intervals at the two different depths were synchronized so that direct comparisons between the two depths could be readily made. A trap sample was sieved through a stainless 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 at least one hour. The dried filter was subjected to prepare 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, a detailed taxonomic investigation concerning identity of each taxon was conducted using a compound light microscope and a scanning electron microscope. Radiolarian taxa were counted under an Olympus compound microscope using a 10x, 20x, or 40x objective lense and wide field eye pieces at total magnifications ranging from 100x to 400x. Each of the taxa encountered were counted and tabulated to derive total radiolarian fluxes as well as three radiolarian subgroups: Spumellaria, Nassellaria, and Phaeodaria.

High resolution flux data from 3800 m trap depth at Station PAPA are available every two week intervals for most of the 1982-1986 four-year period. Details of the sampling intervals and exact duration of the sampling hiatuses have been reported earlier (Takahashi, 1987c,
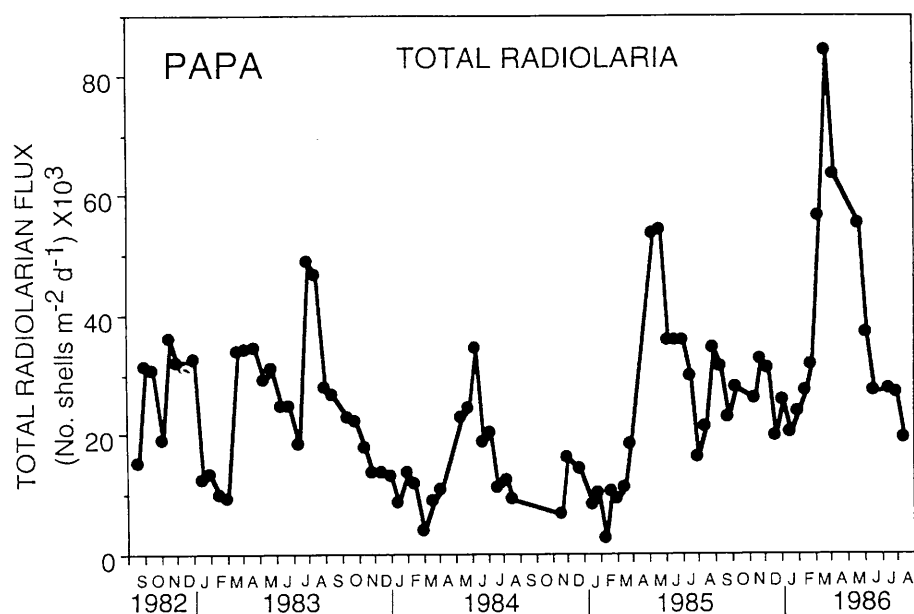
Fig. 2. Four-year long fluxes of total Radiolaria at 3800 m at Station PAPA in the Gulf of Alaska during September 1982 through August 1986. See the methods section for details of actual measurements for Figs. 2, 3, 6, and 7.

1989). Total of eighty four available samples from 3800 m were studied.

Obtained trap data from 1000 m were combined together with data from 3800 m at Station PAPA in order to make a composite of four-year long total radiolarian fluxes and other computed values such as percent and diversity indices. This is mainly to fill a four-month long sampling hiatus of 1 February through 25 May 1986 at 3800 m depth at Station PAPA due to a malfunction of the trap. The following statement justifies this substitution. 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, 1987b, c, 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 tightly coupled vertical fluxes of accelerated sinking particles from the upper depth to deep ocean. Not much of loss due to dissolution en route has been observed and hence the 1000 m data are comparable with that at 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 hiatus. The substituted data are for seven samples. Temporal changes of fluxes are illustrated using

all the actual 84 samples/data and seven substituted data spliced together.

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

Results

Significant intra-annual as well as interannual flux variabilities were observed for total radiolarian fluxes (Fig. 2). Typically two seasonal flux maxima, during spring and fall, occur in a year. The spring flux maxima tend to be greater than the fall maxima. However, this is not always the case as in 1983. Timing of the spring maxima varied significantly as early as in March 1986 and as late as in June 1984. Winter flux minima were observed around January and February. Timing for the winter minima tends to be more stable than variable timing of spring and fall maxima. In addition to the seasonal changes, there is a significant inter-annual change of the radiolarian fluxes. In particular, the fluxes in 1984 displayed the lowest values in the four year record and the fall flux maximum in November 1984 was essentially insignificant relative to the base level. Although the three month sampling hiatus took place during August through November 1984, no significant flux maximum during this hiatus can be inferred from the subsequent flux patterns.

Total of 101 radiolarian taxa were encountered in the flux samples at Station PAPA (Table 1). The included number of taxa in each of the high level taxonomic groups

Table 1. List of the 101 radiolarian taxa encountered in this study. The included number of taxa in each of the high level taxonomic groups are: Order Spumellaria: 22; Order Nassellaria: 50; and Class Phaeodarea: 29.

Superclass Radiolaria Müller
  Class Polycystinea Ehrenberg
    Order Spumellaria Ehrenberg
      Acrosphaera spinosa (Haeckel)
      Cenosphaera minuticaula
      Cenosphaera bellula
      Cenosphaera sp. [ellipsoidal form]
      Rhizoplegma boreale (Cleve)
      Cladococcus cervicornis Haeckel
      Hexacontium hostile (Cleve)
      Stylosphaera group
      Dorydruppa bensoni Takahashi
      Echinoma group
      Heliodiscus asteriscus Haeckel
      Heterosphaera sp. A
      Tetrapyle sp.
      Saturnalis circularis Haeckel
      Tholospira group
      Tholospira? juvenile group
      Spongodiscus spp.
      Spongodiscus sp. C
      Stylodictya multispina (Haeckel)
      Stylochlamydium venustum (Bailey)
      Spongurus sp.
      Circodiscus-Spongopyle group

    Order Nassellaria Ehrenberg
      Tetraplecta pinigera (Haeckel)
      Pinigera sp.
      Clathromitra pterophormis (Haeckel)
      Cladoscenium ancoratum (Haeckel)
      Deflandrella cladophora
      Phormacantha hystrix (Jorgensen)
      Peridium sp. A
      Lophospyris juvenile form group
      Lophospyris pentagona quadris group (Haeckel)
      Lophophaena sp. aff. *L. apiculata*
      Lithomelissa setosa Jorgensen
      Canthrospyris platybursa Haeckel
      Ceratospyris borealis (Bailey)
      Tetraphormis rotula (Haeckel)
      Arachnocorys ? dubius Dorgiel
      Eucecryphalus spp.
      Corocaryptra? sp.
      Cornutella profunda Ehrenberg
      Peripyramis circumtexta Haeckel
      Litharachnium tentorium Haeckel
      Pterocanium? sp. A
      Pterocanium diplotriaea (Dorgiel)
      Pterocanium diplotriaea (Dorgiel) juvenile
      Pterocanium korotonevi (Dorgiel)
      Pterocanium korotonevi (Dorgiel) juvenile
      Psuedodictyophimus gracillipes (Bailey)
      Artostrobus annulatus (Bailey)
      Conarachnium polyacanthum (Popofsky)

      Conarachnium sp.
      Stichopilium bicorne Haeckel
      Dictyophimus crisiae Ehrenberg
      Cyrtopera languncula Haeckel
      Lipmanella dictyoceras (Haeckel)
      Cycladophora davisiana Ehrenberg *cornutoides* Petrushevskaya
      Cycladophora davisiana davisiana Ehrenberg
      Cycladophora davisiana aff. *cornutoides*
      Theocalyptra bicornis (Popofsky)
      Theocalyptra sp.
      Pterocorys zancleus (Müller)
      Eucyrtidium teucheri Haeckel
      Eucyrtidium acuminatum (Ehrenberg)
      Lamprocyrtis hannai (Campbell and Clark)
      Spirocyrtis subscalaris (Haeckel)
      Botryostrobus aquilonaris (Bailey)
      Botryostrobus auritus/australis (Ehrenberg) group
      Phormostichoartus corbula (Harting)
      Siphocampe arachnea (Ehrenberg)
      Artobotrys borealis (Cleve)
      Acrobotrys spp.
      Carpocanium papillosum (Ehrenberg)

  Class Phaeodarea Haeckel
    Protocystis thomsoni (Murray)
    Protocystis naresi (Murray) [flat]
    Protocystis naresi (Murray) [round]
    Protocystis tridens (Haeckel) [large]
    Protocystis tridens? (Haeckel) [small]
    Protocystis tridentata Borgert
    Protocystis harstoni (Murray)
    Protocystis auriculata Takahashi
    Protocystis sp. A
    Challengerosium avicularia Haecker
    Challengeron ornithocephala (Reshetnyak)
    Challengeron vicina (Reshetnyak)
    Entocannula infundibulum Haeckel
    Entocannula subglobosa
    Euphysetta elegans Borgert
    Euphysetta staurocodon Haeckel
    Euphysetta neptuni (Borgert)
    Borgertella caudata (Wallich)
    Lirella melo (Cleve)
    Lirella tortuosa Takahashi
    Lirella sp. [gooseberry shape]
    Lirella bullata (Stadum and Ling)
    Porospathis holostoma (Cleve)
    Conchellium capsula Borgert
    Conchopsis compressa Haeckel
    Haeckeliana porcellana Murray
    Castanellids
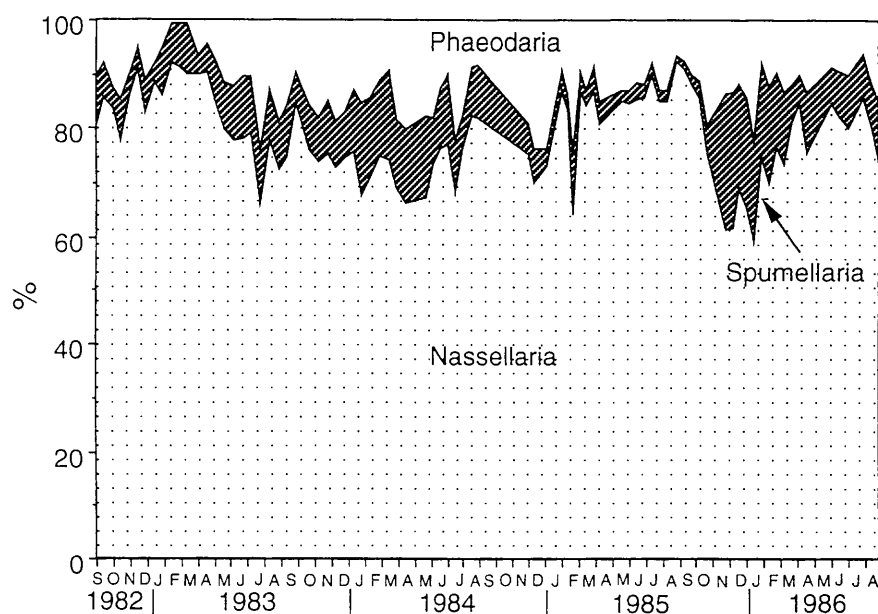   Circoporids
    Aulosphaeridae group

Fig. 3. Percent contributions of Nasse-llaria, Spumellaria, and Phaeodaria in the four-year long fluxes at 3800 m at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.

Table 2. Mean flux and percent contributions by three radiolarian subgroups and representative radiolarian species at 3800 m at Station PAPA in the eastern subarctic Pacific during September 1982 through August 1986.

	Mean Flux Shells m^{-2} d^{-1}	S. D. Shells m^{-2} d^{-1}	Mean % Contribution in Total Radiolaria	S. D. %
Nassellaria	20,177	12,139	78.9	8.0
Spumellaria	2,056	1,645	8.6	5.3
Phaeodaria	3,042	1,865	12.5	5.1
Total Radiolaria	25,275	14,345	100.0	-
Lithomelissa setosa	689	1,235	2.4	3.9
Ceratospyris borealis	184	142	0.8	0.6

are: Order Spumellaria: 22; Order Nassellaria: 50; and Class Phaeodarea: 29. The Nassellaria contribute the most not only in species composition, but also in flux value. Percent contributions in shell flux number of spume-llarian, nassellarian, phaeodarian radiolarians are illustrated (Fig. 3). Order Nassellaria represent the most abundant radiolarian high level taxonomic group followed by the Class Phaeodarea and Order Spumellaria (Anderson et al., in press; Takahashi and Anderson, in press). Mean percent contributions to total Radiolaria for the three groups are: Nassellaria: 78.9 %; Spumellaria: 8.6 %; and Phaeodarea: 12. 5% (Table 2).

Among many radiolarian taxa Lithomelissa setosa Jorgensen (1900) and Ceratospyris borealis (Bailey, 1856)

are two taxa presenting characteristic seasonal trends. L. setosa displayed clear spring maxima in every single year during the four-year trap deployments (Figs. 4, 5). The maximum values varied significantly from the lowest 1984 to the highest 1983, ranging one order of magnitude. C. borealis showed both spring and fall flux maxima (Fig. 6). The fall flux maxima are not always readily discernible and they tend to be lower than the spring maxima. Higher counting errors are involved for C. borealis than those for phytoplankton taxa (see below). This is due to presence of less C. borealis population in a given microslide than general phytoplankton taxa.

Diversity indices and radiolarian fluxes are generally anti-correlated (Fig. 7). Nassellarian fluxes are slightly
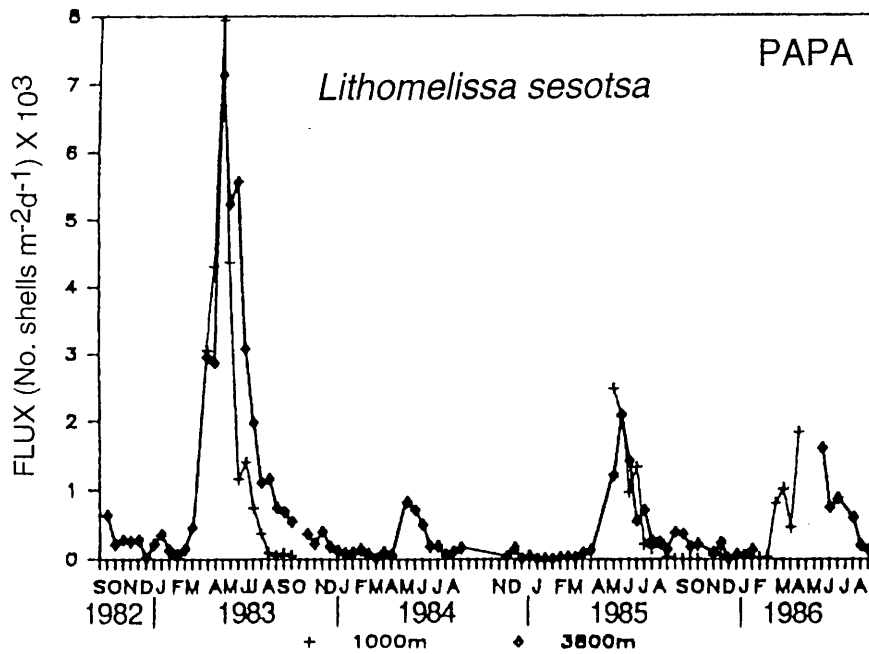
Fig. 4. Four-year long fluxes of *Litho-melissa setosa* Jorgensen at 3800 m and 1000 m at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.
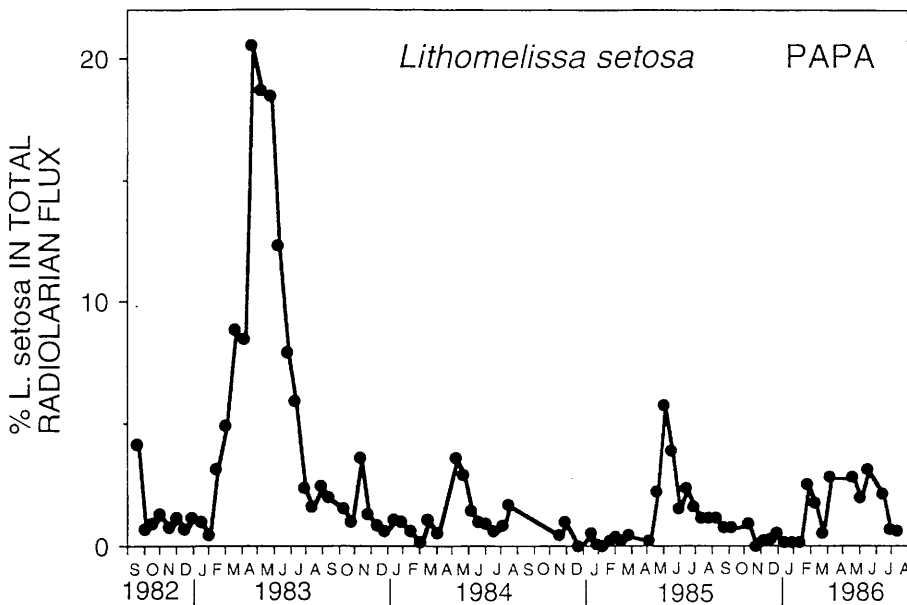

Fig. 5. Percent contribution of *Litho-melissa setosa* Jorgensen in total radiolarian fluxes at 3800 m at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.

better anti-correlated with diversity indices (r = -0.62) than total radiolarians.

Discussions

The seasonality with spring flux maxima shown by *Lithomelissa setosa* is quite unique (Fig. 4) among all the siliceous microplankton taxa, including 101 radiolarian, 18 diatom, and 7 silicoflagellate taxa. No other species, including the phytoplankton, displayed such a seasonality, making this species as a very distinguished spring seasonal

indicator among them. A pronounced spring production of this species occurred even in 1984 when a significant productivity suppression persisted due to poor upper water mixing which lead to poor nutrient supply (Takahashi et al., 1989). As noted earlier, the difference between 1983 and 1984 *L. setosa* flux maximum values is one order of magnitude. This compares well with many siliceous phytoplankton fluxes. For instance, fluxes of *Coscino-discus marginatus*, a centric diatom, varied one order of magnitude from its minimum to maximum (Takahashi et
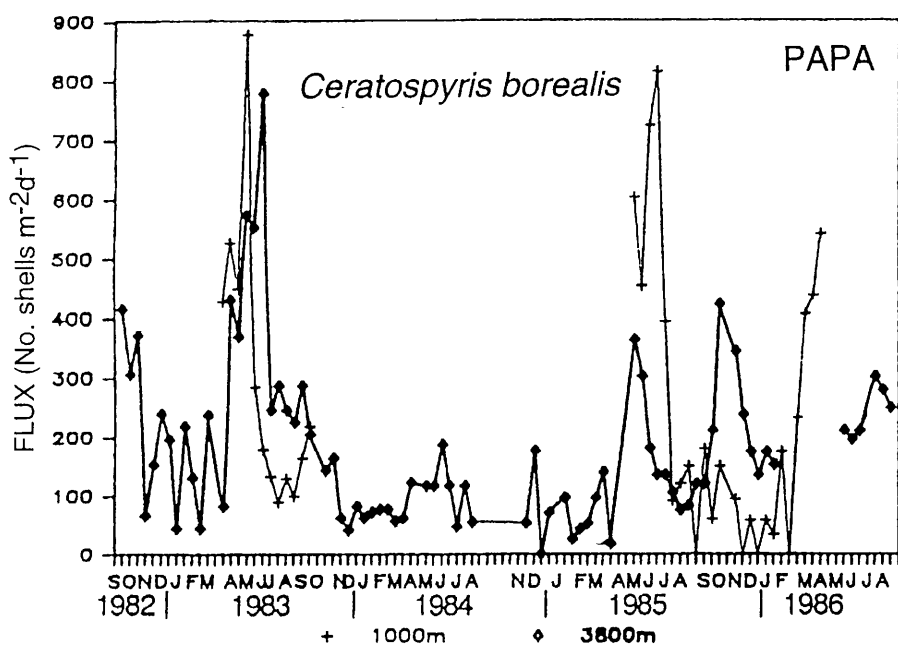
Fig. 6. Four-year long fluxes of *Ceratospyris borealis* (Bailey) at 3800 m and 1000 m at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.
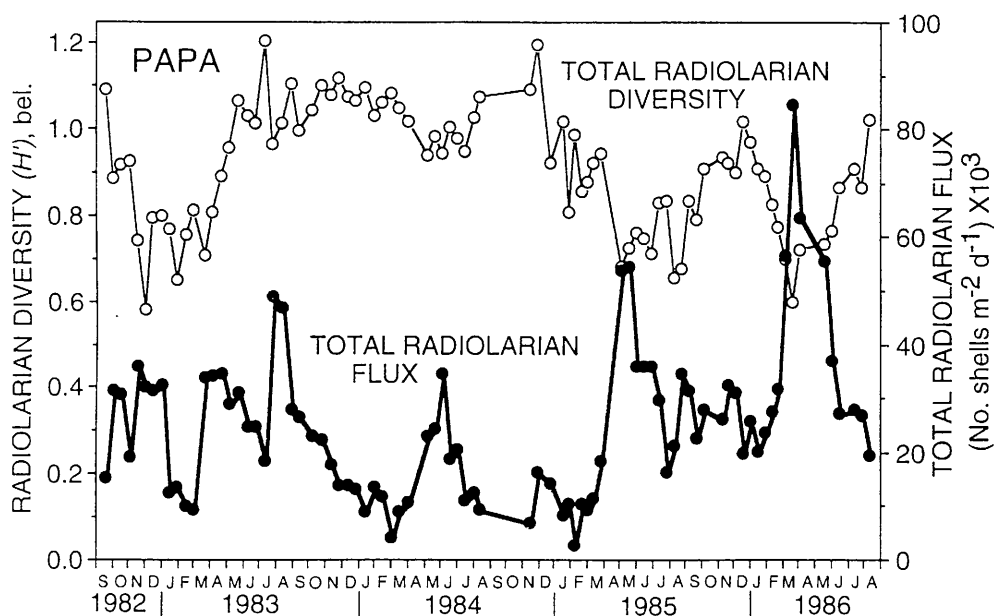

Fig. 7. Four-year long fluxes of total Radiolaria and radiolarian diversity indices at 3800 m depth at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.

al., 1989). While fluxes of typical phytoplankton productivity indicators such as a diatom *Neodenticula seminae* and a silicoflagellate *Distephanus speculum* varied two orders of magnitude (Takahashi et al., 1989), the one order of magnitude flux variation of *L. setosa* as a radiolarian is significant. Such a significant flux excursion might be caused by a probable rapid growth of small-sized radiolarian taxon *L. setosa*. Small nassellarian taxa are known to feed on bacteria, phytoplankton, and/or detritus rather than preying on zooplankton observed for some large-

sized spumellarians (Anderson, 1983). The population of *L. setosa* can feed on these items as they grow, taking advantage of a favorable environmental condition responsively in spring. For a comparison one should examine total radiolarian fluxes whose maxima vary only a factor of two from one year to another (Fig. 2).

L. setosa can also be argued for a spring season contributor numerically. Although not a very conspicuous member, *L. setosa* is one of the few radiolarian species consistently contributing to total radiolarian fluxes in shell
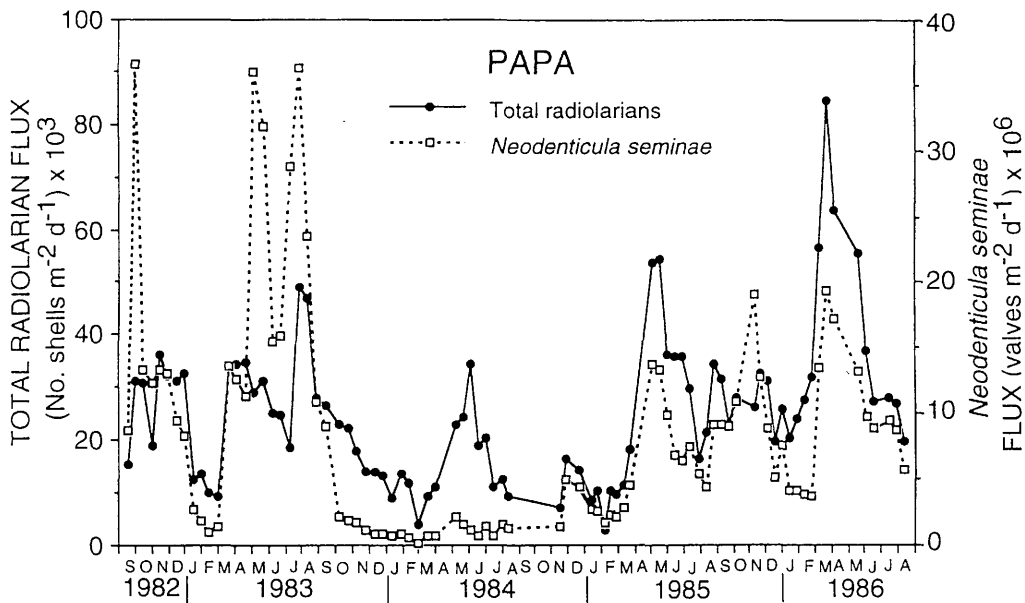
Fig. 8. Four-year long fluxes of total Radiolaria and *Neodenticula seminae* (Simonsen and Kanaya), a dominant pennate diatom, at 3800 m depth at Station PAPA in the Gulf of Alaska during September 1982 through August 1986.

number. A mean contribution of *L. setosa* was 2.4 % (S.D. = 3.9 %) with a maximum of 21% of total Radiolaria (28 April- 14 May 1983: Sample # 15) in the four year fluxes (Fig. 5; Table 2). Annual maximum contributions by *L. setosa* in other years are: 3.6 % in 1984 (23April-13 May: Sample #37); 5.8 % in 1985 (7 June-21 June: Sample #63); and 3.2 % in 1986 (22 June-6 July: Sample #89) (Fig. 5). Major contributions of this species are centered around spring season every year and percentages in the remaining seasons are around one percent or so. It is of interest to reconstruct such a spring seasonal production based on *L. setosa* in down core materials in the future work.

Ceratospyris borealis is another unique radiolarian taxon, displaying both spring and fall flux maxima (Fig. 6). Flux patterns of this species parallel with that of *N. seminae*, a dominant diatom taxon (Fig. 7). It is conceived here that both *N. seminae* and *C. borealis* represent general biological productivity in the upper ocean at least in the eastern subarctic Pacific. This is 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 occur during spring and fall when both organic carbon and total mass fluxes increase. The seasonal flux patterns of *N. seminae*, organic carbon, and total mass fluxes are well correlated (Takahashi et al., 1996a, b). 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 remarkable resemblance of *C. borealis* seasonal flux pattern (Fig. 6) with that of *N. seminae* (Fig. 8) is a testimony that this radiolarian species can also be used as a productivity indicator in paleoceanographic and other applications. Among the one hundred and one radiolarian taxa examined at Station PAPA only *C. borealis* showed such a good correlation (r=0.67) with the diatom taxon. Considering that signal to noise ratios are lower for the radiolarian counts than those for diatoms due to radiolarian's low abundance in the prepared slides causing larger statistical errors, the excellent match in the figure is well taken even though the apparent correlation coefficient is not as good as what is wished. This radiolarian species belonging to spyrids represents on the average only 0.8 % (S.D.=0.6 %) of total radiolarian fluxes in shell number (with a maximum of 3.1 % in 15 June-1 July 1983 [Sample #18]) (Table 2), but its abundance in surface sediments increases up to several percents. Preservation of this taxon in sediments is generally good as other spyrid radiolarians due to robust nature of its skeletons due to preferential dissolution of other fragile taxa. Spyrids have numerous Cenozoic ancestors and are well utilized for biostratigraphy (Sanfilippo et al., 1985). As a new paleoproductivity tracer this taxon is quite promising for future investigations.

Nassellarian fluxes are best anti-correlated with radio-larian diversity indices (r = -0.62) among three major groups and total radiolarians (r = -0.55) (Fig. 7). Both Spumellaria (r = 0.00) and Phaeodarea (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 diverse nature of Nassellaria with 50 taxa compared to 22 spumellarian and 29 phaeodarian taxa.

Since the radiolarian diversity index represents a measure of a spread in taxonomic composition as well as relative quantity of each taxon in an assemblage it is expected that the index increases as flux decreases. This is because that when radiolarians can feed well on prey items, generally during spring and fall when productivity increases, relative contributions of nassellarians increase substantially (Fig. 3). This can be attributed to numerous small-sized nassellarians whose fluxes parallel with those of phytoplankton. They include *Lithomelissa setosa*, *Phormacantha hystrix*, and *Lophophaena* sp. aff. *L. apiculata*. They are probably feeding on small phytoplankton, bacteria, and/or detritus (Anderson, 1983) and quick in responding to feeding opportunities. Therefore, their flux increases are as fast as those of phytoplankton at least in the flux data with temporal resolution of about two weeks.

It is interpreted that a mirror image of the nassellarian fluxes and radiolarian diversity indices during 1985 and 1986 (Fig. 8) represent 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 Nino effect (Takahashi, 1987a, b; Takahashi et al., 1989). That is, according to an examination of available vertical hydrographic data such as σ_t values the water mixing in the upper layer was quite restricted during this time period causing less supply of subsurface nutrients. Such restricted supplies of nutrients to the mixed layer lead to a suppression of normal biological production in the upper layers, which eventually lead to lower downward fluxes than normal years. The suppressed fluxes are seen in almost all the taxa examined. For instance, *N. seminae* shows a quite small flux maximum during May 1994, approximately one order of magnitude lower than that of other years (Fig. 8). *C. borealis* as a radiolarian, on the other hand, represents a flux maximum in June 1984 which is only about a factor of

two lower than other years. Such a marked contrast in flux amplitudes of the diatom and radiolarian fluxes is likely caused by a distinction in nutrition behaviors. Direct adsorption of nutrients by the autotroph is expected whereas the radiolarian as a heterotroph is preying food items such as small phytoplankton or detritus. Such a secondary trophic nature of the radiolarian feeding may explain why the radiolarian fluxes vary less than the siliceous phytoplankton. Furthermore, the relatively high radiolarian diversity indices during the latter half of 1983 and most of 1984 are attributed to the flux suppression explained above. The general high indices conform with the general low fluxes of total radiolarians (Fig. 2).

The radiolarian fluxes at Station PAPA can be compared with those being generated in a currently on-going program in the central subarctic Pacific and the Bering Sea. Sediment traps have been deployed at pelagic sediment trap Station SA (49°N, 174°W) and marginal sea Station AB (53.5°N, 177°W) since August 1990 through August 1995 (Takahashi et al., 1996a, b). Among many measured parameters three-year long total radiolarian fluxes are available in a preliminary form (Itaki and Takahashi, 1995). They are: Station SA: 13.9 x 10^3 shells m^{-2} d^{-1}; and Station AB: 17.5 x 10^3 shells m^{-2} d^{-1}. These values are significantly lower than that observed at Station PAPA: 25. 2 x 10^3 shells m^{-2} d^{-1}. This trend is different from that observed for diatom, mass, and organic carbon fluxes measured at these sites discussed below. Further comparisons at species level as well as acquisition of additional two-year fluxes of radiolarians at Stations SA and AB will be specifically required to conclude the productivity value of radiolarian fluxes. Furthermore, relative contributions of three radiolarian subgroups are rather similar at all of the three stations.

According to measured data for total mass, organic carbon, and diatom fluxes, biological productivity in the Gulf of Alaska is slightly lower than that in the central subarctic Pacific. This is based on five-year long fluxes of organic carbon and total mass fluxes at Station SA (Takahashi et al., 1996a) and four-year long fluxes of diatoms (Takahashi et al., 1996b). 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 at Station SA in terms of biogenic particle fluxes measured at Station AB (53.5°N, 177°W) in the Aleutian Basin (Takahashi et al.,

1996a, b). Such a difference in the marginal sea and pelagic environments is expected considering water circulation and morphology of the ocean basins. The above cited radiolarian fluxes at Station AB are 21 % greater than that at Station SA, conforming the general productivity trend increasing from outside toward inside of the Bering Sea.

Conclusions

Total radiolarian fluxes showed significant interannual and intra-annual variabilities at Station PAPA, reflecting changes in environmental conditions which occurred in the ocean. The extent of annual maximum flux levels varied factor of two in the four-year record. Radiolarian fluxes generally increased during spring and fall; and their timings varied substantially depending on the year. The spring flux maxima tend to be greater than fall maxima. The temporal pattern of the total radiolarian fluxes parallels with that of siliceous phytoplankton groups, suggesting that Radiolaria as a whole also can be considered as a productivity indicator. Details of the flux changes, however, are different from the siliceous phytoplankton, indicating their own characteristic signals.

Nassellaria contributed on the average 79 % of total radiolarian fluxes followed by 13 % by Phaeodaria and 9 % Spumellaria in shell flux number. Change in radiolarian diversity index shows a mirror image with that of nassellarian or radiolarian fluxes, much of the signals in Nassellaria themselves. Radiolarian diversity in fossil record can be used to assess paleoproductivity. Nassellarians are generally more promising productivity indicators than spumellarians 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 belonging to Nassellaria. Temporal flux pattern of this taxon is nearly the same as that of *Neodenticula seminae*, the dominant diatom taxon in the subarctic Pacific. Spyrids are generally well preserved in Cenozoic fossil record. Further detailed studies of *C. borealis* and other taxa in the family are encouraged in order to advance our understanding of paleoproductivity.

Spring seasonal signals are carried by *Lithomelissa setosa* belonging to Nassellaria, demonstrating characteristic spring flux maxima even in 1984 when a wide spread suppression of siliceous plankton production

occurred in the region. It is concluded that the signals examined for radiolarian fluxes are more robust than those for siliceous phytoplankton counterparts such as diatoms and silicoflagellates. This is probably due to radiolarian's wide spread feeding habits as well as depth zones.

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