

Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station ALOHA

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ABSTRACT: Planktonic diatoms are important agents of vertical transport of photosynthetically fixed organic carbon to the ocean's interior and seafloor. Diatom fluxes to the deep sea were studied for 2 yr using bottom-moored sequencing sediment traps located in the vicinity of the Hawaii Ocean Time-series (HOT) program station 'ALOHA' (22° 45' N, 158° W). The average flux of empty diatom frustules was around 2.8×10^5 cells $m^{-2} d^{-1}$ in both years, except in late summer when it increased approximately 30-fold. Flux of cytoplasm-containing diatom cells was much lower (about 8×10^3 cells $m^{-2} d^{-1}$) but increased 500-fold in late July 1992 and 1250-fold in August 1994. *Mastogloia woodiana* Taylor, *Hemiaulus hauckii* Grunow and *Rhizosolenia* cf. *clevei* var. *communis* Sundström were the dominant diatom species observed during the July 1992 event, with the former 2 species again dominant in August 1994. The 1994 summer flux event occurred about 3 wk after a documented bloom of *H. hauckii* and *M. woodiana* in the mixed-layer and a simultaneous increase in vertical flux of these species. This surface flux signal was clearly detectable at 4000 m, suggesting rapid settling rates. A further indication of very high sinking speeds of the diatoms was the much larger proportion of cytoplasm-containing cells in the bottom-moored traps during the 2 summer events. Cells of *H. hauckii* and *R. cf. clevei* var. *communis* frequently contained endosymbiotic cyanobacteria with heterocysts (cf. *Richelia*), similar to the cells of these species in the mixed-layer. Our data show for the first time that diatoms containing nitrogen-fixing cyanobacteria contribute directly to the vertical flux of organic matter to the deep sea in the oligotrophic regions. The peak of diatom flux coincided with a significant flux increase of biogenic silica in both years. During periods of rapid sinking, the vertical flux of diatom assemblages out of the uppermost water column seems to be more important than the diatom flux out of the deep chlorophyll maximum layer (DCML). Aggregate formation may be responsible for the fast sinking of the diatoms.

KEY WORDS: Biogenic silica · Bottom-moored sediment traps · Deep sea · Diatoms · Vertical particle flux

INTRODUCTION

Diatoms appear to be a very important phytoplankton group for new production in the ocean (Brzezinski & Nelson 1995, Dugdale et al. 1995, Dugdale & Wilkerson 1998). Vertical flux of particulate organic matter (POM) into the ocean's interior arises in the form of fecal pellets, carcasses of zooplankton, detritus and intact phytoplankton cells. Bottom deposition of diatom cells and other phytodetritus have been

observed even at abyssal depths (Billett et al. 1983, Smith et al. 1996).

In the subtropical oligotrophic (low standing stocks of nutrients and biomass) gyres, diatom populations do not achieve high cell abundances, unlike prokaryotes and eukaryotic nanoflagellates which dominate the phytoplankton populations in these areas (Olson et al. 1990, Letelier et al. 1993, Malone et al. 1993, Campbell et al. 1997). Among the microphytoplankton, the filamentous cyanobacterium *Trichodesmium* spp. has received special attention, partly due to their striking presence at the sea surface under certain environmental conditions and partly due to their quantitative role in the biogeochemistry of oligotrophic oceans because

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of their ability to fix dinitrogen (Karl et al. 1992, 1997, Letelier & Karl 1996, Capone et al. 1997). However, it has been suggested by Goldman (1988, 1993) that the role of diatoms in oligotrophic gyres might be more important for new production and export of particulate carbon than previously thought. Goldman hypothesized that episodic injections of new nutrients into the deep chlorophyll maximum layer (DCML) near the base of the euphotic zone would lead to rapid diatom growth and a coupled export flux. Support is lent to this proposal of the role of deep-living diatoms by recent investigations which revealed that about half of the biogenic silica production occurred within the nitracline in the Sargasso Sea in spring (Brzezinski & Kosman 1996) and, furthermore, that occasional increases took place of biogenic silica concentrations in the DCML in the central North Pacific (Brzezinski et al. 1998).

In a separate paper (Scharek et al. 1999) we investigated diatom cell abundances in the water column and the flux out of the euphotic zone in the framework of the Hawaii Ocean Time-series (HOT) research program. The HOT study was established at a site north of Hawaii that is characteristic of larger regions of the subtropical North Pacific gyre (Karl & Lukas 1996). We did not find any episodic growth of diatoms in the DCML but did observe an enigmatic increase of diatom abundance in the mixed-layer in July. This diatom population was responsible for the greatest flux of diatoms out of the euphotic zone found during that 1 yr study. However, it was not clear whether the observed increase of diatom biomass and flux was a seasonal or an episodic phenomenon. Furthermore, if the periods of diatom growth proposed by Goldman (1988) were shorter than the approximately monthly intercruise periods, they may have been missed. Therefore, the important question whether these increases of diatom biomass and vertical flux would have any significance for the flux of material to the deep sea and the ocean floor remains to be answered. We present here the results of our work on the flux of diatoms and biogenic silica during 2 yr with bottom-moored sediment traps which sampled continuously with a 17 to 18 d time resolution. Deep-sea diatom fluxes were quantified at either 2800 m (1992/93) or 4000 m (1993/94). Our results show that, in the oligotrophic subtropical North Pacific gyre, diatoms are more important for the vertical flux of POM than previously assumed.

MATERIALS AND METHODS

An array of bottom-moored sequencing sediment traps was deployed twice during our study period as 1 component of the HOT research program. The array consisted of 4 PARFLUX (McLane Research, Model MK 7-21) individual traps, positioned at 800, 1500, 2800 and 4000 m; the approximate bottom depth was 4800 m. Each conical trap had a collection area of 0.5 m² and 21 individual sample cups which rotated into position according to a predetermined, programmed time schedule. The collection surface was covered by baffles with 25 mm diameter cells (Honjo & Doherty 1988, Karl et al. 1996). The cups were filled with a buffered (0.1% sodium borate) formalin solution (concentration 3%) which was slightly hypersaline (5 g NaCl l⁻¹ surface seawater) to prevent diffusive loss of preservative and sample material. The array ALOHA I was deployed at 22° 57.3' N, 158° 06.2' W and the collection period was from June 8, 1992 to June 8, 1993. Each individual cup sampled for 17.4 d. ALOHA II was deployed at 23° 06.7' N, 157° 55.8' W, with a collection period from September 13, 1993 to September 30, 1994 and 18.2 d collection time per individual cup (Fig. 1).

After recovery of the traps, samples were wet sieved through a 1 mm Nitex mesh. Next, a rotating splitter device was used for quantitative separation into 4 aliquots (Honjo 1980). Subsamples from each of the 21 sample cups were analyzed for biogenic silica with the sequential leaching technique described by DeMaster (1981). Soluble reactive silicate was measured in the

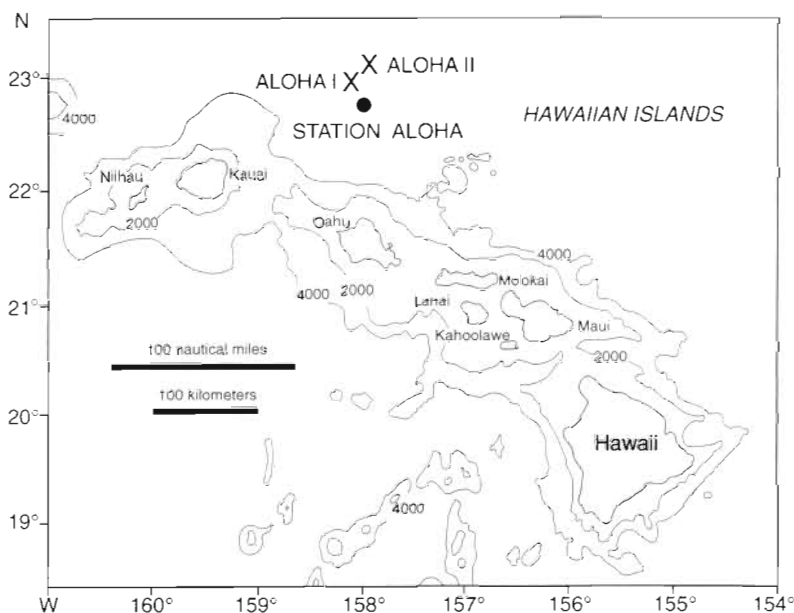


Fig. 1. Map showing locations of the moorings ALOHA I and ALOHA II, as well as of the HOT study site (Stn ALOHA). Bathymetry contours are indicated in meters

brine solution of the traps (Strickland & Parsons 1972) and used to correct for the total biogenic silica concentrations. Dissolved reactive silicate derived from dissolution of the biogenic silica during trap exposure; typical post-recovery concentrations ranged from 200 to 600 μM , and between 10 and 60% of the biogenic silica had dissolved into the brine.

Likewise, subsamples were taken from each of the 21 sample cups for the qualitative and quantitative determination of diatom flux of the 2800 m trap from array ALOHA I and of the 4000 m trap from ALOHA II. We chose to analyze the 4000 m trap and not the 2800 m trap of the array ALOHA II because of trap malfunction on the second deployment. Mass flux and other biochemical parameters (particulate carbon, nitrogen and phosphorus) show that the flux patterns during these time intervals were similar at the 2 depths (Karl et al. 1996, Karl unpubl.). Cell counts of the diatom assemblages were carried out to the genus and, when possible, to the species level, with a Zeiss inverted microscope equipped with bright field and phase contrast objectives using the method of Utermöhl (1958). Diatom cells were characterized for presence or absence of plasma content and damage of frustules. Recognizable half frustules were counted, divided by 2 and added to the number of intact empty cells of the respective taxa. Besides the diatoms, other protists with silica skeletons (radiolaria, silicoflagellates) and trichomes of *Trichodesmium* spp. (cyanobacteria) were also enumerated.

RESULTS

Vertical fluxes of diatom cells

Vertical fluxes of full and empty diatom cells showed 2 maxima during our study period: the first one during the ALOHA I sampling period from July 13 to July 30, 1992; and the second one during the ALOHA II sampling period from August 6 to August 24, 1994 (Fig. 2). In 1992 (ALOHA I), the flux peak carried on into the first half of August (sampling interval from July 30 to August 16). In 1994 (ALOHA II), the diatom flux was somewhat enhanced during the sampling interval preceding the flux peak (July 19 to August 6). During the maxima, the flux of empty diatom frustules increased approximately 30-fold and cytoplasm-containing cell flux increased 500-fold in late July 1992 and 1250-fold in August 1994 (compared to the average flux during the low flux periods in the respective year of mooring deployment). The July 1992 maximum represented 74 and 46% of the annual fluxes of full and empty diatoms (calculated for the respective year of mooring deployment). The August 1994 maximum carried 88

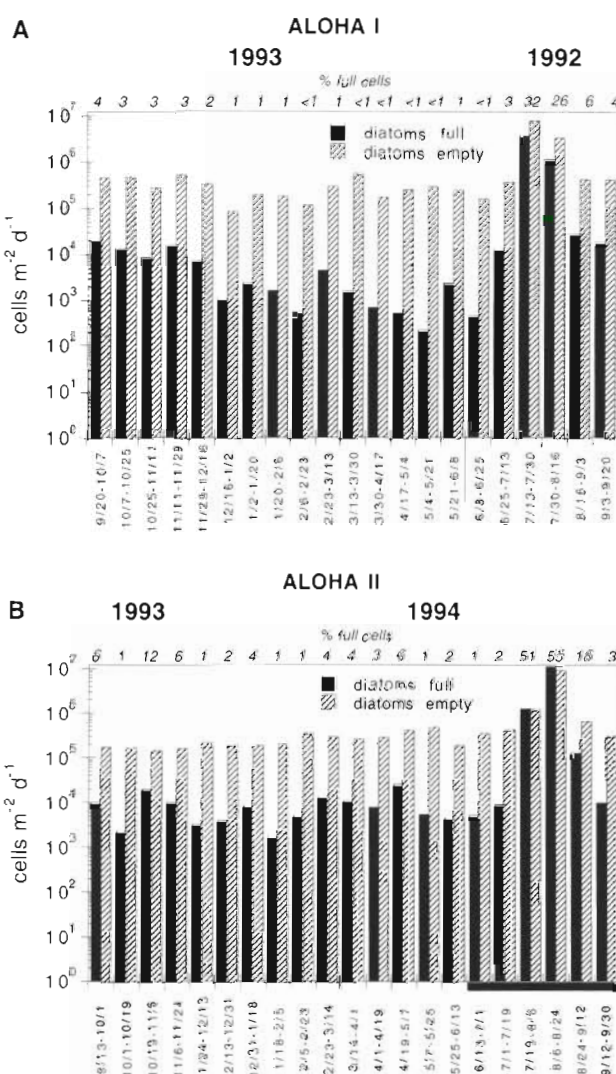


Fig. 2. Vertical fluxes of full and empty diatom frustules ($\text{cells m}^{-2} \text{d}^{-1}$, in logarithmic notation): (A) flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (B) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). Indicated above each graph are full cell percentages of total diatom frustules. Sequences of sampling intervals of ALOHA I are arranged according to corresponding days of the year for comparison (mo/d); the black horizontal bar indicates the period when the upper water column had been sampled simultaneously for diatoms in approximately monthly intervals during ALOHA II deployment

and 57% of the annual fluxes of full and empty frustules. Considering the increased fluxes during the sampling intervals immediately after (in 1992) or before (in 1994) the maxima (see above), 97% of the annual flux of cytoplasm-containing cells sank in summer 1992 and 98% in summer 1994; the percentages for the flux of empty frustules were 66% in summer 1992 and 65% in 1994

The observed pattern indicates that these pulses of diatom cells were fairly discrete events and lasted 5 wk at most. It is further remarkable that the ratio of full to empty cells was much higher during these peaks than during the rest of the year, especially for the 1994 peak (ALOHA II) when the flux of full frustules at 4000 m was greater than the flux of empty frustules (Fig. 2).

The downward flux of diatoms to the deep sea consisted nearly entirely of *Mastogloia woodiana* Taylor and *Hemiaulus hauckii* Grunow during the peak export events of 1992 and 1994. These 2 species accounted for 99 % of the full cells and 94 % of the empty cells (Fig. 3). During the rest of the year, the downward flux of cytoplasm-containing diatom cells, which was much lower, consisted mainly of these 2 species as well; however, they were only partly responsible for the flux of empty cells (Figs. 2 & 3). At Stn ALOHA, the principal habitat of these 2 species is the mixed-layer rather than the DCML (Scharek et al. 1999).

Rhizosolenia cf. *clevelandi* var. *communis* Sundström contributed less than 1 % to the numbers of diatom cells in the traps, but its flux patterns during both years resembled the patterns previously described for *Mastogloia woodiana* and *Hemiaulus hauckii*. However, only during the peak in 1992 (ALOHA I) did we observe cytoplasm-containing cells of this species. Downward flux patterns of empty cells were similar during both years (Fig. 4). Other rare species of the genera *Hemiaulus* and *Mastogloia*, *H. sinensis* Greville, *H. membranaceus* Cleve and *M. rostrata* (Wallich) Hustedt, revealed similar seasonal variations to those observed for the dominant species *M. woodiana* and *H. hauckii* during both deployments (Table 1). The habitats of these non-dominant species as well as their seasonal distribution and export patterns out of the euphotic zone resemble those of *M. woodiana* and *H. hauckii* at Stn ALOHA (Scharek et al. 1999).

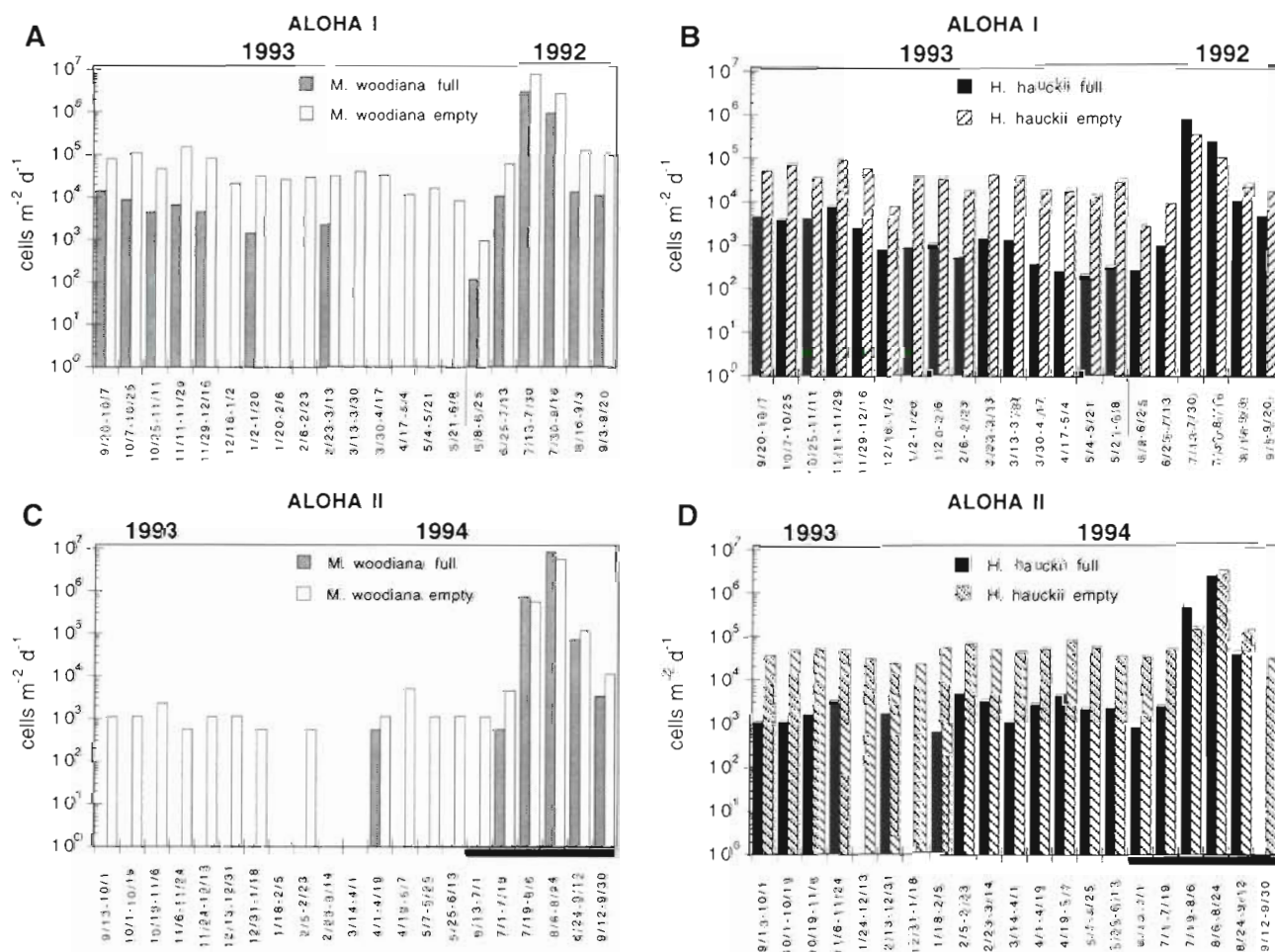


Fig. 3. Vertical fluxes of full and empty frustules of *Mastogloia woodiana* and *Hemiaulus hauckii* (cells $\text{m}^{-2} \text{d}^{-1}$, in logarithmic notation): (A) and (B) flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (C) and (D) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

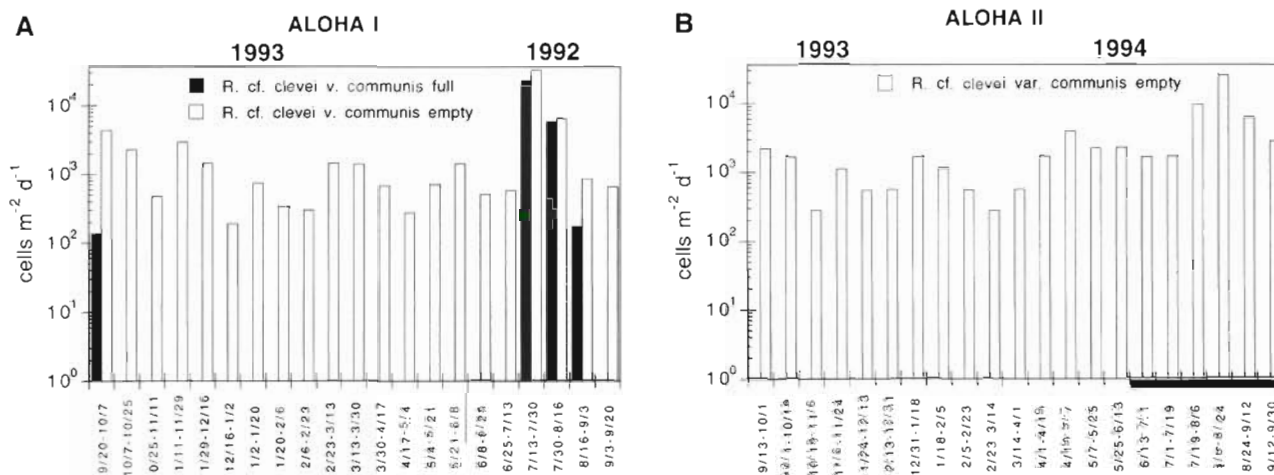


Fig. 4. Vertical fluxes of full and empty frustules of *Rhizosolenia cf. clevei* var. *communis* (cells $\text{m}^{-2} \text{d}^{-1}$, in logarithmic notation): (A) flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (B) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

Other species of the genus *Rhizosolenia* and related taxa (*Proboscia* spp. and *Guinardia cylindrus* [Cleve] Hasle comb. nov.) did not show distinct summer maxima of vertical flux to depth. Weak summer or late summer signals of vertical flux to great depths were partly detected with some species whose spatial and temporal surface distribution and export patterns at Stn ALOHA were different from the species already discussed (Fig. 5, Table 1). We attribute these small summer flux increases to particle 'sweeping effects' of the dominant diatom species and other organic material sinking out from the upper layer during the summer flux pulse (Smetacek 1985).

Hemiaulus hauckii, *Rhizosolenia clevei* var. *communis* and *Guinardia cylindrus* regularly were encountered with *Richelia*-type (cyanobacteria) endosymbionts in the traps. These *Richelia* possessed heterocysts which enable them to fix dinitrogen (Villareal 1991). Furthermore, aggregates of *H. hauckii* chains or *H. hauckii* chains with *Mastogloia woodiana* attached were found in the traps during both summer maxima.

Aggregate formation could have facilitated rapid sinking of the diatoms. High sinking speeds were also indicated by the microscopically observable silification status of the frustules of *Hemiaulus hauckii* and *Mastogloia woodiana* during the sampling intervals comprising the flux maxima (July 13 to August 16, 1992 and July 19 to August 24, 1994). Full and empty frustules of the dominant species (*H. hauckii* and *M. woodiana*) and also of other diatoms originating from the mixed-layer appeared to be more heavily silicified and more intact. They resembled the cells observed in the mixed-layer in summer 1994 (Scharek et al. 1999).

During the rest of both years most frustules appeared weakly silicified and often partly dissolved.

Very few trichomes of the cyanobacterium *Trichodesmium* spp. were present. Only during the flux maximum in 1992 (ALOHA I, 2800 m) were some observed. We did not find any trichomes during the ALOHA II deployment (4000 m) either during the summer flux maximum or during the rest of the year (Table 1). *Trichodesmium* spp. occur in high abundances in summer at Stn ALOHA (Letelier & Karl 1996) and their habitat, seasonal abundance and export patterns are very similar to those of the dominant diatom species *Hemiaulus hauckii* and *Mastogloia woodiana* (Table 1). However, *Trichodesmium* spp. are known to undergo rapid autolysis in the upper ocean (Scharek et al. 1999). Evidently, they do not contribute significantly to the deep-sea flux. We attribute the occurrence of the trichomes in the deep trap ALOHA I (2800 m) to the previously mentioned particle 'sweeping mechanism'.

Vertical flux of biogenic silica

Peaks of biogenic silica flux into the traps coincided with the peaks of diatom flux in both years (Fig. 6). For an estimation of the contribution of intact empty and full diatom frustules to the flux of biogenic silica we assumed an average Si content of 2 pmol diatom cell⁻¹. This cellular Si content is meant as an approximation since the sizes of the 2 dominant and the other diatom species were different and data on cellular Si content measurements with cultures of the 2 dominant diatoms are not available. For our assumption we refer to

Brzezinski (1985), where Si contents for diatoms of similar sizes and degrees of silification are presented. Thus, during the ALOHA I sampling (1992/93, 2800 m), intact diatom frustules provided about 1 to 4 % of the of particulate biogenic silica flux (uncorrected for soluble reactive silica in the brine due to dissolution in the traps, see 'Materials and methods'), except during the summer flux peak. From July 13 until July 30, 1992, 44 % of the biogenic silica originated from intact diatom frustules. For the period between July 30 and August 16, this percentage was 18 % (Fig. 7). During the ALOHA II deployment (1993/94, 4000 m), intact diatom cells contributed 10 % of the particulate biogenic silica (uncorrected, see above) from July 19 until August 6, 1994 and 31 % from August 6 until August 24. These percentages were only about 1 to 3 % during the rest of the year (Fig. 7). The proportional contributions of the frustules might have been even less during the low flux periods because of their lower silification status which we observed microscopically. Thus, biogenic silica removal rates via flux of intact diatom frustules appear to be low, except during the summer export events.

The summer increases of biogenic silica flux were mainly due to diatoms and not to radiolarian skeletons because vertical fluxes of radiolaria to 2800 m (ALOHA I) and 4000 m (ALOHA II) were not higher during the summer events, although they contributed to biogenic silica flux in general (Fig. 8). Fragments of diatoms and radiolaria could be observed microscopically in every sediment trap sample. They may have originated from zooplankton grazing (sloppy feeding or disintegration of fecal pellets) or from frustule or skeleton dissolution during sinking, the latter may be promoted by digestion of organic matter in the diatom cell

Table 1. Microphytoplankton species (diatoms, cyanobacteria, silicoflagellates) found in the bottom-moored sediment traps (ALOHA I and ALOHA II) at Stn ALOHA. Indicated are flux patterns during 1992/93 in 2800 m and during 1993/94 in 4000 m reference depths. For comparison, habitats and temporal distribution and export patterns out of the euphotic zone (measured in floating traps in 165, 315 and 515 m reference depths; Scharek et al. 1999) are given. *Hemiaulus hauckii* and *Rhizosolenia cf. clevei* var. *communis* regularly contained cyanobacterial (cf. *Richelia*) endosymbionts (DCML: deep chlorophyll maximum layer; EZ: euphotic zone)

	Flux pattern in 2800 m 1992–93 temporal variation	Flux pattern in 4000 m 1993–94 temporal variation	Main habitat in EZ	Distribution pattern in EZ temporal variation	Export pattern out of EZ temporal variation
High abundance in deep traps and EZ					
<i>Hemiaulus hauckii</i> Grunow	summer max.	summer max.	mixed-layer	summer max.	summer max.
<i>Mastogloia woodiana</i> Taylor	summer max.	summer max.	mixed-layer	summer max.	summer max.
Low abundance in deep traps, high abundance in EZ					
<i>Trichodesmium</i> spp. (cyanobacteria)	few trichomes only during summer max.	none observed	mixed-layer	summer/ late summer max.	late summer max.
Low abundance in deep traps and EZ					
Other <i>Hemiaulus</i> spp.	full cells only during summer max.	full cells only during summer max.	mixed-layer	summer/ late summer max.	summer max.
<i>Mastogloia rostrata</i> (Wallich) Hustedt	summer max., full cells only during summer max.	summer max., full cells only during summer max.	mixed-layer	late summer max.	summer/ late summer max.
<i>Rhizosolenia cf. clevei</i> var. <i>communis</i> Sundström	full cells only during summer max.	summer max. of empty cells	mixed-layer	no max. observed	summer/ late summer max.
<i>Cylindrotheca closterium</i> (Ehrenberg) Lewin & Reimann	few cells only during summer max.	few cells only during summer max.	mixed-layer and DCML	no max. observed	late spring max.
<i>Nitzschia bicapitata</i> group	slight increase after summer max.	no max. observed	mixed-layer and DCML	no max. observed	no max. observed
<i>Thalassionema cf. bacillare</i> (Heiden & Kolbe) Kolbe	full cells only after summer max.	full cells only during summer max.	DCML	no max. observed	no max. observed
<i>Pseudonitzschia</i> spp.	no max. observed	no max. observed	DCML	spring max.	early summer max.
<i>Dictyocha</i> spp. (cryophyte)	weak summer increase	no max. observed	mixed-layer and DCML	no max. observed	no max. observed

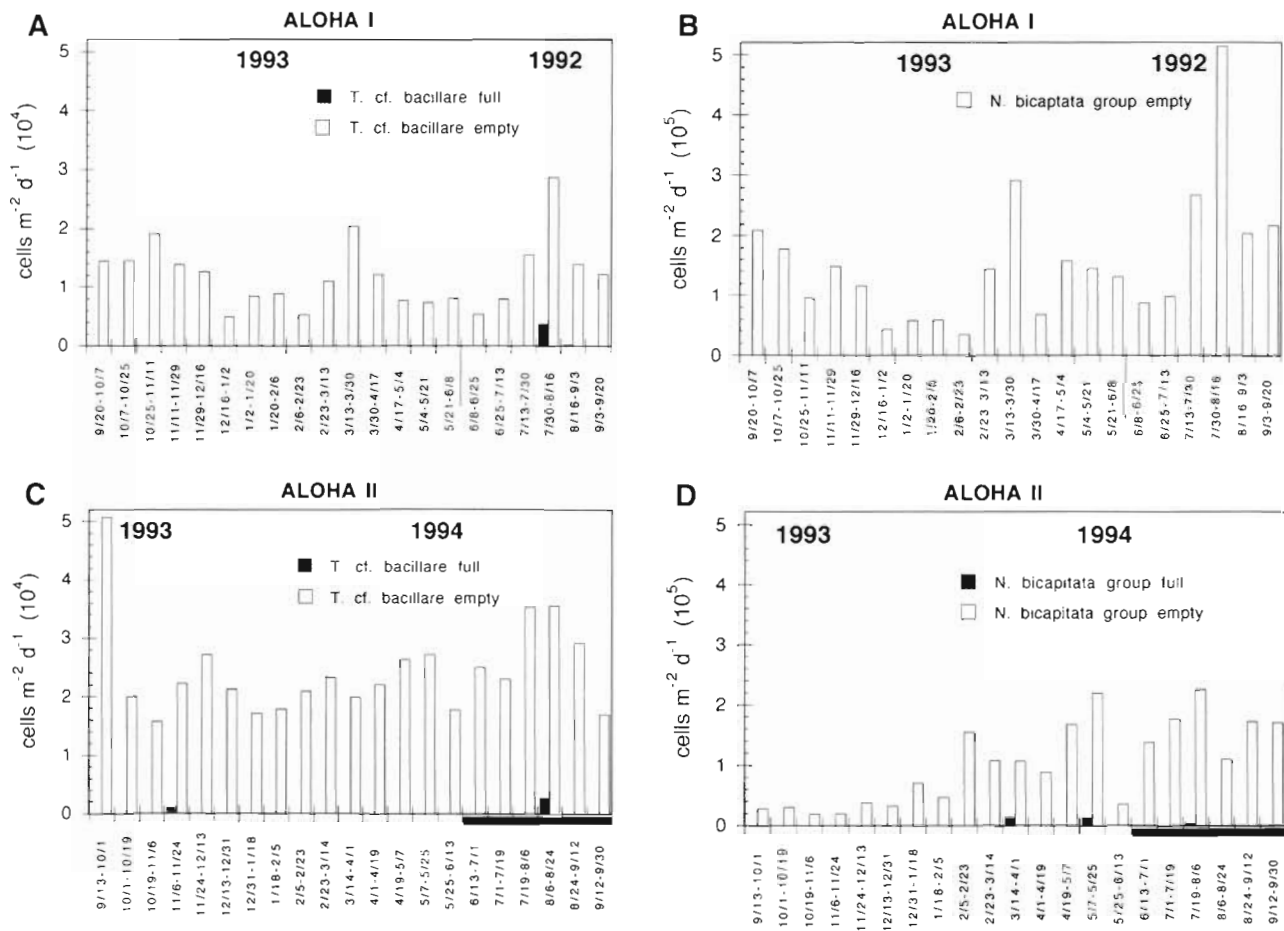


Fig. 5. Vertical fluxes of full and empty frustules of *Thalassionema cf. bacillare* and *Nitzschia bicapitata* group (cells m⁻² d⁻¹): (A) and (B) flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (C) and (D) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

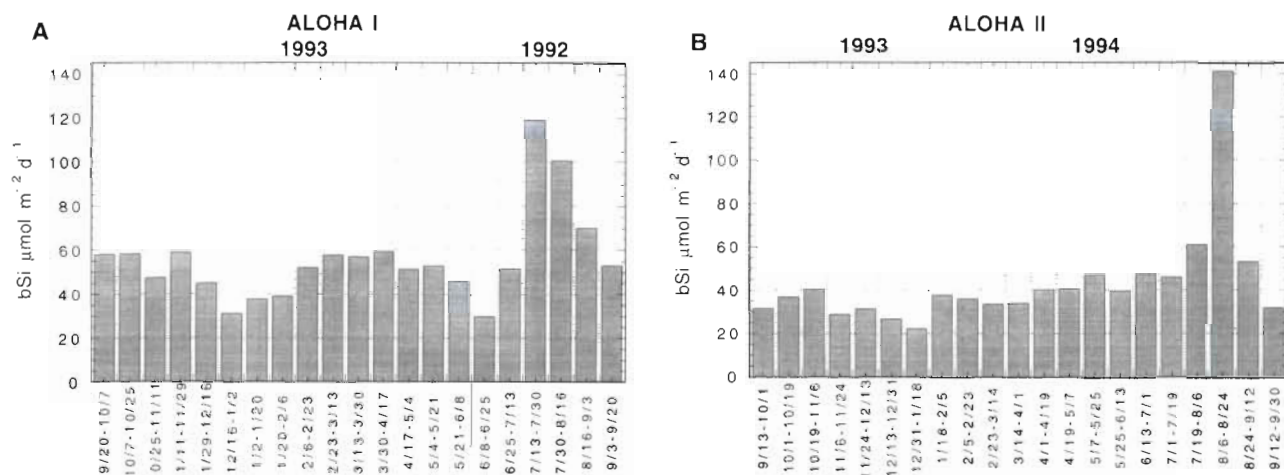


Fig. 6. Vertical fluxes of biogenic silica (bSi, μmol m⁻² d⁻¹): (A) biogenic silica flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (B) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

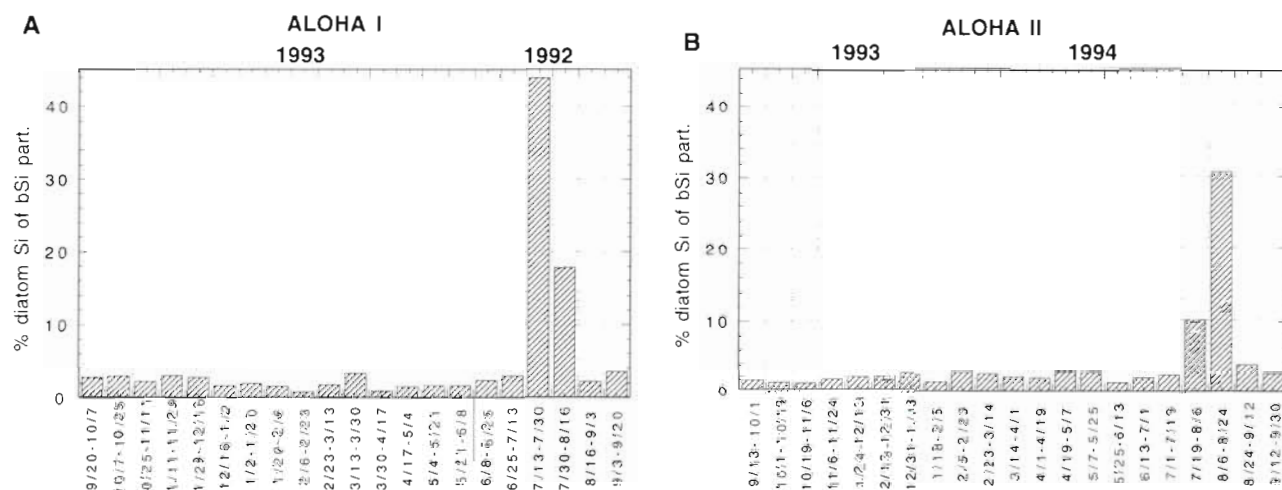


Fig. 7. Estimated percentage contribution of intact diatom frustules (full and empty cells) to the vertical fluxes of biogenic silica (biogenic silica assumed, $2 \text{ pmol diatom cell}^{-1}$). (A) Percentages of particulate biogenic silica (uncorrected) at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (B) percentages of particulate biogenic silica (uncorrected) at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

wall by bacteria. These fragments appear to be responsible for a considerable part of the silica flux during both years.

DISCUSSION

The most remarkable result of our study is the 2 summer maxima of diatom flux to the deep ocean during the 2 full year periods of trap sampling. These 2 events were clearly different from the regular sinking pattern of particulate matter not only because of the quantity but also the quality of the material arriving in the deep

ocean. Thus, it was only during these peaks that the flux of full frustules was high and that only 2 species accounted for more than 94 % of the diatom cell counts. In addition, it was evident that during these events the diatom frustules were more silicified and intact than in the rest of the samples. These features are characteristics of sinking events recorded in coastal waters (von Bodungen et al. 1981).

The material arriving in the deep ocean was fresh and resembled samples taken from the mixed-layer in July 1994. Complementary work in the upper water column at Stn ALOHA (Fig. 1) from June 1994 through July 1995 indicates that the July/August 1994 flux

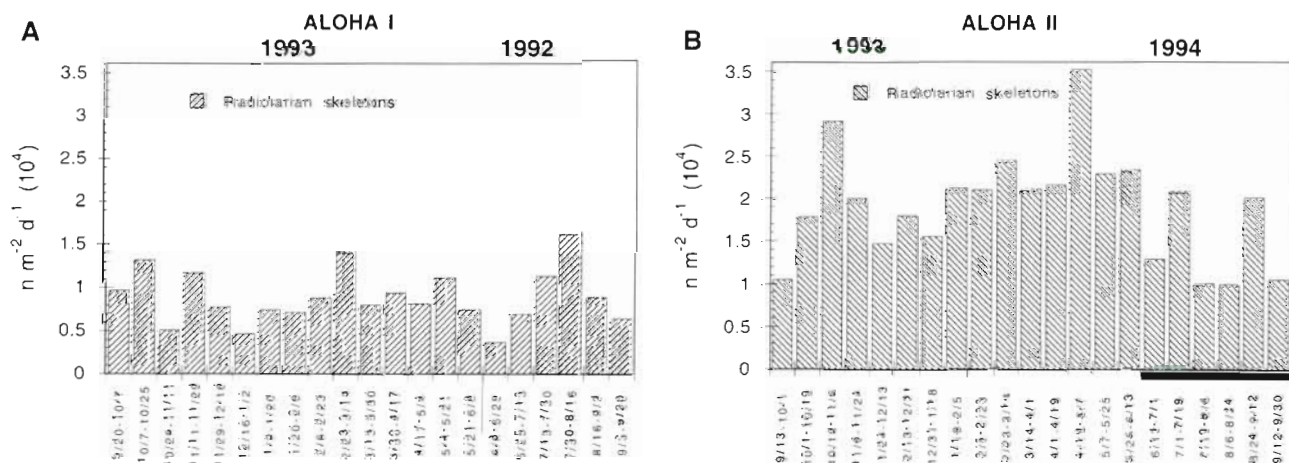


Fig. 8. Vertical fluxes of radiolarian skeletons (numbers $\text{m}^{-2} \text{d}^{-1}$): (A) flux at 2800 m reference depth during the ALOHA I sampling (June 8, 1992 to June 8, 1993); (B) flux at 4000 m reference depth during the ALOHA II sampling (September 13, 1993 to September 30, 1994). For further explanations of notation see Fig. 2

maximum we observed at 4000 m (ALOHA II) occurred about 3 wk after a distinct bloom of diatoms in the mixed-layer, dominated by the species *Mastogloia woodiana* and *Hemiaulus hauckii*. This accumulation was accompanied by a simultaneous flux increase of these species out of the surface layer (measured at 165, 315 and 515 m reference depths; Scharek et al. 1999). If we assume that the deep sediment trap signal was a consequence of the mixed-layer proliferation of *M. woodiana* and *H. hauckii* 3 wk before, then we can estimate settling rates of ca 100 to 200 m d⁻¹. These settling speeds can only be achieved if the diatoms sink as aggregates. In a compilation of measured settling speeds of marine snow, Diercks & Asper (1997, their Table 1) give speeds for diatom aggregates of 100 to 150 m d⁻¹. Indeed, in spite of the 'rough' treatment (for aggregate preservation) of the samples from the bottom-moored traps, we observed aggregates in the traps during both events. Elevated diatom sinking speeds were further indicated by the large proportion of diatom cells still containing cytoplasm and by the presence of undegraded pigments (data not presented).

Although some of the characteristics described above are typical of sinking events recorded elsewhere (Billett et al. 1983, Smetacek 1985, von Bodungen et al. 1986, Smith et al. 1996), it is remarkable that, in this case, they took place in the 'invariant' oligotrophic North Pacific gyre. There is a basic difference making the events at our study site diverge from most of those described in the literature; diatoms make up at most 5% of the total phytoplankton biomass in our study area (e.g. Letelier et al. 1993, Venrick 1993, Andersen et al. 1996), and even during the observed summer proliferation of July 1994, their biomass did not, conservatively estimated, represent more than 20% of the total phytoplankton (Scharek et al. 1999). For most of the HOT program core parameters routinely measured, this July cruise was not particularly distinct from the cruises before or after. Only weak signals could be observed for selected geochemical parameters because it was a change not of the entire phytoplankton population but of only 1 component (for the HOT-JGOFS core data set see: <http://hahana.soest.hawaii.edu>). Similarly, rapid settling of biogenic silica to the ocean interior following an annual winter/spring diatom bloom has been observed in another oligotrophic gyre ecosystem, the Sargasso Sea. In contrast to the oligotrophic North Pacific gyre the Sargasso Sea bloom appears to be a regular event following winter mixing (Deuser et al. 1981, Nelson & Brzezinski 1997). In other areas where sinking events take place, diatom blooms with high chlorophyll concentrations develop (von Bodungen et al. 1981, 1986, Smetacek 1985, Kiørboe et al. 1994). For vertical fluxes of particulate carbon, high biomass blooms of certain species and

their subsequent sinking are logically important. Thus, it could appear that in our study area diatoms cannot play an important role in biogeochemical cycles because of their low abundance. However, our results suggest that diatoms are important vectors in the vertical transport of organic matter to the deep ocean in the North Pacific gyre. The only time from June 1994 through July 1995 that a proliferation of a diatom population had been observed in the euphotic zone (Scharek et al. 1999), a clear maximum of organic matter was recorded shortly thereafter thousands of meters below.

The evidently high settling rates of diatoms during both flux events (1992 and 1994) must have resulted in a lower degree of POM remineralization on its way to the sea bed, and thus in lower carbon-to-nitrogen and carbon-to-phosphate ratios of the sinking POM, in contrast to the rest of the year when particulate material sank more slowly and was exposed to degradation over longer periods of time. Yet, the estimated contribution of diatom carbon derived from intact cells to total particulate carbon (PC) flux was relatively small: about 8% (estimation based on 15 pmol C per diatom cell; Brzezinski 1985) during the summer flux maximum at the end of July 1992, decreasing to 4% at the beginning of August (Karl et al. 1996). Intact diatoms were 0.1% or less of the PC in the rest of the ALOHA I samples. However, more transformed carbon of diatom origin, not considered in these estimations, probably sank to greater depths in the form of detritus, bacteria or fecal pellets originating from zooplankton grazing on diatoms in the upper layers.

Determinations of the ¹⁵N isotopic signatures of the sinking material are consistent with an atmospheric source of new nitrogen during the summer export event of 1992. The delta ¹⁵N (relative to air N₂) value of the particulate material was 1.53‰ at 1500 m, well below the annual mean of 3.10‰ (Karl et al. 1997). The nitrogen isotopic signature obtained from the bulk of exported material cannot distinguish between nitrogen fixed by diatom endosymbionts (Villareal 1991), *Trichodesmium* spp. (Taylor et al. 1973) or other cyanobacteria (e.g. *Synechococcus* spp. [Mitsui et al. 1986]). However, our data indicate that, in contrast to the diatoms, *Trichodesmium* spp. do not reach the deep ocean intact (Table 1). Yet, we expect that part of the sinking transformed POM originates from *Trichodesmium* spp. and thus contributes to the ¹⁵N depleted isotope signal in summer.

Our results suggest that intact diatom frustules contributed considerably to the increase of biogenic silica flux observed during the 2 summer export events. The biogenic silica flux during each year was similar to the fluxes found in other open-ocean areas not influenced by upwelling (Noriki & Tsunogai 1986: northeastern

Pacific; Fischer et al. 1988: Weddell Sea; Nair et al. 1989: Arabian Sea; Wefer & Fischer 1993: southeastern Atlantic; Jickells et al. 1996: northeastern Atlantic; Honjo et al. 1995: Pacific north and south of equatorial upwelling; Fischer et al. 1996: subtropical North Atlantic; Deuser et al. 1981, Sayles et al. 1996: Sargasso Sea). Even though the reference depths of the sediment traps differed in each of these studies, all traps were deployed in relatively deep water (>696 m). A rapid loss of sinking biogenic silica with depth is not generally observed in deep-sea environments (Walsh et al. 1988, Jickells et al. 1996). Our average biogenic silica fluxes (56 and 43 $\mu\text{mol m}^{-2} \text{d}^{-1}$ of ALOHA I and ALOHA II, calculated for each respective year of trap deployment) concur with the average flux in the Sargasso Sea (Sayles et al. 1996, at 3200 m at a site close to Bermuda). In these 2 oligotrophic, subtropical gyre systems the overall biogenic silica fluxes to great depths appear to be similar.

Continuous sampling over 2 full years with bottom-moored sequencing sediment traps enabled us to detect episodic events of diatom deep flux, even those of relatively short duration. Goldman (1988) proposed flux events as a consequence of diatom growth which could occur episodically in the lower portion of the euphotic zone due to injection of new nutrients from below. Depth-integrated inventories of $[\text{NO}_3^- + \text{NO}_2^-]$ in the surface water of Stn ALOHA (0 to 100 m) revealed 2 'spring events' (February 1993 and February 1994) of such injections during the 2 yr of ALOHA I and ALOHA II sampling (Karl et al. 1996). Indeed, the flux of particulate carbon revealed a weak increase at all sampling depths, in 800 and 1500 m in February and in 2800 and 4000 m in March, in the ALOHA I trap (Karl et al. 1996). But these nutrient mixing events obviously do not result in an enhanced diatom export because no spring increase of diatom cell flux and biogenic silica flux from either the mixed-layer or from the DCML assemblage was evident during ALOHA I or ALOHA II sampling (Figs. 2 & 6). In spring 1986, Taylor (1989) measured flux of organisms at 30, 120 and 200 m with floating sediment traps deployed close to the position of Stn ALOHA. Similarly, no increase of diatom flux out of the euphotic zone was detected after a spring storm, despite a flux increase of particulate carbon. It appears that in the vicinity of Stn ALOHA the mechanism of spring nutrient injection into the euphotic zone does not give rise to a response of the system, resulting in an important enhancement of vertical diatom flux. However, in summer 1995 Brzezinski et al. (1998) found indications of eddy pumping under a diatom bloom north of Stn ALOHA, which was similar to the bloom in the summer of 1994 (Scharek et al. 1999). They suggested that diatom production is locally enhanced by mesoscale eddies.

The mixed-layer diatom assemblage appears to be more important than the DCML assemblage for vertical carbon fluxes, therefore indicating a different mechanism than the one proposed by Goldman (1993) to explain the diatom signal in the deep ocean. Another argument reinforcing the idea of not completely random sinking events taking place in the North Pacific gyre is our finding of a diatom flux increase to the deep ocean in summer in both years. The summer fluxes during these 2 yr and indications of similar patterns in following years (Karl unpubl.) may suggest a seasonal phenomenon. In this context we have to take into consideration that the deployments of ALOHA I and ALOHA II fall into a period of abnormal climate conditions, i.e. a series of individual ENSO (El Niño-Southern Oscillation; Wyrтки 1975) episodes (1991 to 1992, 1993, 1994; Goddard & Graham 1997). But, as mentioned above, a very similar diatom bloom to the one in the summer of 1994 (Scharek et al. 1999) was observed in the following summer, somewhat north of our investigation area (Brzezinski et al. 1998). If mesoscale eddies do promote these diatom blooms (Brzezinski et al. 1998) it would be important to investigate the eddy frequency in the North Pacific gyre in relation to the different seasonal and climatic conditions. Scharek et al. (1999) discussed reasons for a summer proliferation of the 2 species *Hemiaulus hauckii* and *Mastogloia woodiana*. The simultaneously increased concentrations of the N_2 -fixing *Trichodesmium* spp. during the summer months at Stn ALOHA (Letelier & Karl 1996) indicate that the N_2 -fixing capacity of the *H. hauckii* endosymbionts may play a significant role. Factors that may have favored diatom growth in summer include a possible increase of iron in the upper stratified layers, which is particularly limiting for diatoms (Sunda & Huntsman 1995, Muggli & Harrison 1997) and for the N_2 -fixing processes carried out by cyanobacteria (Paerl et al. 1994). Yet, Brzezinski et al. (1998) did not find elevated lithogenic silica concentrations (normally originating from airborne dust which presumably also adds iron to the surface waters) in the diatom bloom of summer 1995. Also, the apparently very high affinity of *H. hauckii* and *M. woodiana* with silicic acid (Brzezinski et al. 1998), an element relatively depleted in near surface waters of the North Pacific gyre, probably favors these over other diatom species. However, as these blooms obviously always occur during summer, we speculate that the mentioned factors only spur the proliferation of *H. hauckii* and *M. woodiana* in combination with calm conditions.

Still, the question why these fast sinking events occurred remains unanswered. It seems that the main reason for the apparently very high sinking speeds must be the occurrence of aggregation processes. According to a coagulation model (Jackson 1990,

Kjørboe 1993) and considering conditions very favorable to aggregation such as a small-scale turbulence of medium intensity (in contrast to low turbulence in a highly stratified ocean), with a cell radius of 100 μm (taking into account the chain formation of *Hemiaulus hauckii*), a coefficient of stickiness of 0.15 (found for a highly sticky species such as *Skeletonema costatum*; Kjørboe et al. 1990) and a growth rate of 2 divisions d^{-1} , the concentrations of diatoms were 1 to 2 orders of magnitude below the critical concentration necessary for cell aggregation processes to become important. This holds true provided transparent exopolymer particles (TEP), which can favor diatom aggregate formation (Alldredge et al. 1993), were not abundant. An alternative explanation to this coagulation model would be that the small-scale turbulence was so low in the mixed-layer during July that it did not break and separate the various chains formed by *H. hauckii* during their growth. Thus, they could have thrived as colonies. The loss of buoyancy of the chains and their subsequent sinking could have been triggered by factors influencing diatom physiology. Depletion of macronutrients (N, P, Si) or iron can trigger diatom sinking (Bienfang et al. 1982, Waite et al. 1992, Muggli et al. 1996). The waters of the subtropical North Pacific gyre are chronically depleted in macronutrients and the N:P stoichiometries of surface ocean particulate and dissolved matter pools suggest that phosphate could be the limiting element (Karl et al. 1997), although the silicate necessary for diatom growth cannot be ruled out as the limiting element. Silicate limitation could become more significant in the case of concurrent iron limitation since Hutchins & Bruland (1998) and Takeda (1998) demonstrated enhanced consumption of Si versus N and P by iron-limited diatoms.

In summary, the summer diatom flux increases that we measured at depth show for the first time that diatoms have a geochemical importance for vertical transport of POM in the oligotrophic subtropical North Pacific gyre. They transport particulate silica, carbon and nitrogen rapidly to great depths; the latter partly originates as new nitrogen fixed by free-living and endosymbiotic cyanobacteria. These endosymbiont-carrying diatoms (*Hemiaulus* spp. and *Rhizosolenia* spp.) also occur in warm oligotrophic areas of the Atlantic, the Indian Ocean, the Mediterranean and in the Red Sea (Sundström 1984, Kimor et al. 1992, Villareal 1992, 1994). It has already been proposed that these diatom endosymbionts provide a considerable contribution to overall N_2 fixation in oligotrophic waters (Mague et al. 1974, Venrick 1974, Villareal 1991, 1992). Now it remains to be investigated whether similar export processes occur in other open-ocean regions. The global significance of *Trichodesmium* spp. N_2 -fixers in oligotrophic seas has recently been

emphasized by Capone et al. (1997). Our results provide evidence that diatoms, partially fueled by endosymbiotic N_2 -fixers, might also play an important role in the biogeochemistry of oligotrophic oceans.

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