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PART I

Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre

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Abstract

The abundance of diatoms in the water column and the downward vertical flux of diatom cells from the euphotic zone were investigated during a time series of 11 monthly cruises (June 1994–July 1995) to Station ALOHA (22°45′N, 158°00′W) as one component of the Hawaii Ocean Time-series (HOT) Program. The diatom community was studied using light microscopy and by high-performance liquid chromatographic (HPLC) pigment analyses. Distinct diatom assemblages were found in the mixed-layer and in the Deep Chlorophyll Maximum Layer (DCML). Diatom cell abundances in the water column were generally low during the year, except in July 1994, when they increased in the upper euphotic layer. Two lightly silicified species (*Hemiaulus hauckii* [Grunow] and *Mastogloia woodiana* [Taylor]) were mainly responsible for this increase. Other less abundant diatom species present in the mixed-layer assemblage showed a similar temporal pattern. *H. hauckii* contained *Richelia*-type endosymbionts with heterocysts and was presumably able to fix dinitrogen. Both species of diatoms also were an important component of the vertical diatom flux out of the euphotic zone, which, likewise, was highest in July 1994. During this maximum export period, aggregates of these two species were collected in the drifting sediment traps. In the DCML, diatom abundances and export were low throughout the year, with the exception of one genus (*Pseudonitzschia*) for which a slight concentration increase was observed in spring. Reflecting the observed diatom cell abundance and vertical flux, fucoxanthin concentrations (a pigment marker for diatoms) did not indicate any significant increase of diatom pigment biomass in the DCML during the year. Ratios of diadinoxanthin to chromophyte pigments suggested that the phytoplankton cells sinking out of the euphotic zone in midsummer originated from the mixed-layer. The

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attenuation of the pigment vertical fluxes with depth was significantly lower for fucoxanthin, indicating a generally slower decay of diatom flux with depth compared with other phytoplankton groups. Our findings suggest that, in the subtropical North Pacific Ocean, summer conditions seem to favor the development of selected species of diatoms in the mixed-layer and that these assemblages appear to be more important with regard to export production than those in the DCML. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

In recent years considerable variability in phytoplankton productivity and standing stock, particle flux and picoplankton population abundances has been observed in subtropical ocean gyres (Venrick et al., 1987; Lohrenz et al., 1992; Malone et al., 1993; Michaels et al., 1994; Campbell and Vaulot, 1993; Karl et al., 1995, 1996; Campbell et al., 1997). However, these observations did not invalidate the conceptual view of these environments as being relatively stable. In these areas, the phytoplankton populations, dominated by small prokaryotes and nanoflagellates (Olson et al., 1990; Malone et al., 1993; Letelier et al., 1993; Campbell and Vaulot, 1993), are tightly coupled with their microzooplankton predators resulting in an efficient recycling of carbon and related bioelements. These microbial loop intensive ecosystems preclude the existence of a traditional biological pump (Volk and Hoffert, 1985) and typically export less than 10% of the particulate organic matter initially fixed through primary production (Lohrenz et al., 1992; Karl et al., 1996).

However, Goldman (1988, 1993) suggested that diatoms, typically in very low cell abundances, might play an important role in new production and export of particulate organic carbon in oligotrophic oceanic habitats. Some models suggest that diatoms are the main phytoplankton producers of sinking particulate organic matter in oceanic habitats (Michaels and Silver, 1988; Dugdale et al., 1995). Thus, despite their low abundances in the open ocean, diatoms could be disproportionate important for the export of particulate organic matter. Goldman proposed that possible episodic injections of new nutrients into the lower portion of the euphotic zone, the layer where in oligotrophic gyres the deep chlorophyll maximum layer (DCML) is located, would lead to rapid diatom cell growth and coupled export. The aim of our study was to test this hypothesis, originally formulated for the oligotrophic Sargasso Sea, in the oligotrophic North Pacific Gyre in the framework of the Hawaii Ocean Time-series (HOT) program (Karl and Lukas, 1996).

Investigations were conducted during approximately monthly cruises for a period of one year in order to detect possible short-term episodic or seasonal events of diatom growth. Diatom cell abundances in the water column and diatom cell flux out of the euphotic zone were investigated with water samples obtained with CTD-rosette casts and samples from floating sediment traps, respectively. Our results provide a revised view of the role of diatoms in oligotrophic oceanic habitats. We found that, in agreement with Goldman's hypothesis, diatoms are important for new production and carbon export. In contrast to the suggested importance of the assemblages at the base of the euphotic zone (Goldman, 1988, 1993), however, the

diatoms from the mixed-layer were mainly responsible for the export of particulate organic carbon.

2. Material and methods

2.1. Sampling

Samples were obtained during a series of eleven cruises from June 1994 to July 1995 to Station ALOHA (22°45′N, 158°00′W; Table 1). Seawater samples were collected in the water column from pre-determined depths using polyvinylchloride sample bottles attached to a rosette frame and equipped with a CTD system and a fluorescence sensor (Karl and Lukas, 1996). Sample depths extended between 5 and 165 m (Table 1), thus about reaching the calculated average depth of the euphotic zone at Station ALOHA (0.05% surface PAR at 173 m; Letelier et al., 1996). Two subsamples were transferred to 250 ml brown glass bottles and fixed with hexamethylenetetramine-buffered 20% (vol/vol) formaldehyde to a final concentration of 0.6% (vol/vol; Throndsen, 1978). For the enumeration of cyanobacterial endosymbionts in selected diatom species, the fluorochrome DAPI (Porter and Feig, 1980) was added to one set of samples, because bright field or phase contrast microscopy cannot distinguish accurately the endosymbionts within *Hemiaulus* spp. (Heinbokel, 1986). These samples were subsequently filtered onto 0.8 μm Nuclepore filters (filtration volume 250 ml), mounted on microscopic slides and frozen at −20°C.

Floating sediment traps were deployed at 165, 315 and 515 m for 72 h (Karl and Lukas, 1996). Single traps were designated for each parameter in order to obtain enough material. Two traps were assigned for the collection of diatoms, two for biogenic silica, and four for phytoplankton pigments. Thus, there were eight traps at each depth (except for cruises HOT 54 and HOT 55, when only two traps were assigned for pigments). The traps were filled with a hypersaline (50 g NaCl l^{-1} added to surface seawater) formaldehyde solution (final concentration 0.37% vol/vol), except for two of the four pigment traps, which were deployed with the same hypersaline solution but without fixative. Only these two non-fixed traps assigned for pigments were screened with a 335 μm Nitex mesh during deployment. We chose to screen the non-fixed traps in order to avoid the entrance of swimmers and subsequent grazing on the fresh particulate organic material in the traps during deployment, as our primary purpose in these field experiments was to characterize the photosynthetic pigments. Although some particulate material, e.g. aggregates, can be excluded by this treatment (Karl and Knauer, 1989), we did not observe statistical differences (Wilcoxon matched pairs test) between fixed (unscreened) and non-fixed (screened) pigment samples. However, HOT 54 and HOT 55 samples were not included in this test because there were no non-fixed (screened) pigment traps (Table 1).

After retrieval of the trap array, the contents of the traps assigned for diatoms were concentrated onto 0.8 μm Nuclepore filters with negative pressure to ca. 100 ml and fixed with hexamethylenetetramine buffered 20% (vol/vol) formaldehyde to a final concentration of 0.6% (vol/vol). The contents of the biogenic silica traps (ca. 1.5 l)

Table 1
General information regarding cruises and investigations carried out at Station ALOHA (22°45′N, 158°00′W) between June 1994 and July 1995. Depth of the DCML was obtained by the fluorescence sensor during the CTD down-cast. Mixed-layer depths are based on a 0.125 unit potential density criterion (Levitus, 1982). Mean mixed-layer depths and standard deviation of the means were determined from multiple casts on each cruise (generally, $n > 15$)

Cruise	Cruise dates	Samples and experiments		Mean mixed-layer depth, ± S.D. (m)
		Water column, sample depths (m)	Floating sediment traps (165, 315, 515 m)	
HOT 54	June 17–22, 1994	5, 40, 60, 80, 125[a], 165	Only formaldehyde-fixed pigment traps	37 (6)
HOT 55	July 22–27, 1994	5, 40, 70, 80, 130[a], 165	Only formaldehyde-fixed pigment traps	55 (8)
HOT 56	Aug. 28–Sept. 2, 1994	5, 10, 20, 30, 40, 60, 80, 120[a], 165	Non-formaldehyde-fixed pigment traps only in 165 m	54 (8)
HOT 57	Sept. 21–26, 1994	5, 10, 20, 30, 40, 70, 80, 110[a], 165		52 (6)
HOT 58	Oct. 13–18, 1994	5, 10, 20, 30, 40, 70, 80, 110[a], 165	In 515 m only non-formaldehyde-fixed pigment traps	61 (13)
HOT 59	Nov. 17–22, 1994	5, 10, 20, 30, 40, 80, 100[a], 165	No sediment traps deployed	91 (7)
HOT 60	Febr. 4–9, 1995	5, 10, 20, 30, 40, 60, 80, 115[a], 165		53 (12)
HOT 61	March 2–7, 1995	5, 10, 20, 30, 40, 60, 80, 105[a], 165	No sediment traps deployed	42 (9)
HOT 62	April 4–9, 1995	5, 10, 20, 30, 40, 60, 80, 125[a], 140[a], 165	Shallowest traps deployed in 180 m, one bSi trap (180 m) lost	51 (9)
HOT 63	May 5–10, 1995	5, 10, 20, 35, 50, 80, 115[a], 165		45 (11)
HOT 64	July 28–Aug. 2, 1995	5, 25, 40, 90, 100[a], 150	Traps only in 165 m, for diatom species composition	42 (8)

[a] Sample depths within the deep chlorophyll maximum layer (DCML).

were filtered onto Nuclepore filters and frozen at −20°C. We chose a poresize of 0.8 μm in order to facilitate passage of the brine solution through the filters. We estimate the contribution of the non-retained < 0.8 μm size fraction to total settling biogenic silica particles to be only a few percent, because biogenic silica particles in this size range have negligible settling velocities (Conley and Scavia, 1991). Pigment traps were filtered with positive pressure onto Whatman GF/F filters and subsequently stored in liquid nitrogen until analysis.

2.2. Sample analyses

Diatom cells concentrated onto Nuclepore filters were examined for cyanobacterial endosymbionts using a compound microscope (Zeiss) equipped with UV epi-illumination and the respective filter sets for fluorescence of DAPI and autofluorescence of chlorophyll and phycoerythrin.

Diatom cell counts were performed using an inverted microscope (Zeiss) equipped with bright field and phase contrast objectives according to the method of Utermöhl (1958; settling volume 100 ml). Diatom cells were identified to genus and, if possible, to species. Plasma content and damage of frustules were recorded, and cell sizes were measured. Recognizable half frustules were counted, divided by two and added to the number of intact empty cells of the respective taxa. Besides diatoms, other protists with silica skeletons (radiolaria and silicoflagellates) and trichomes of *Trichodesmium* spp. (cyanobacteria) were enumerated. Phytoplankton pigments were measured using high performance liquid chromatography according to Latasa et al. (1996) and Andersen et al. (1996). Biogenic silica was measured with the sequential leaching technique described by DeMaster (1981).

3. Results

3.1. Diatom cell concentrations in the water column

The microphytoplankton (>20 μm) assemblages in the mixed-layer were different from those in the DCML throughout the year. This difference was reflected not only by the distribution of diatom species but also by the distribution of *Trichodesmium* spp. trichomes in each layer (Tables 2 and 3).

A similar distinction between a shallow and a deep water phytoplankton assemblage was found by Venrick (1982, 1988, 1992) at other locations in the subtropical North Pacific Ocean near 28°N, 155°W. In addition, some diatom key species defined by Venrick (1988) for the shallow and deep assemblages were found in the same assemblages in this study (Table 2).

Concentrations of diatom cells were generally low throughout the year. No spring increase was observed in the mixed-layer (Fig. 1). In the DCML, a slight increase in concentration was observed for only one genus, *Pseudonitzschia*, in March (Table 2). However, we recorded a conspicuous increase in diatom concentration particularly in the mixed-layer during the July HOT 55 cruise (Fig. 1). Primarily responsible for this

Table 2
Most important diatom species occurring at Station ALOHA from June 1994 until July 1995; likewise microphytoplanktonic cyanobacteria and silicoflagellates are presented. Respective habitats, minimum and maximum abundances of full cells, and seasonal distribution and export patterns with minimum and maximum fluxes of full cells are indicated

	Main habitat	Distribution pattern temporal variation	Cells l^{-1} mixed-layer (5 m) min.–max.	Cells l^{-1} DCML min.–max.	Export pattern temporal variation	Exported cells m^{-2} d^{-1} (avg. in 165 m) min.–max.
Mastogloia woodiana	Mixed layer[a]	Max. July 1994	< 10–2340	< 10–20	Max. July 1994	< 100–4,017,450
Hemiaulus hauckii	Mixed layer[a]	Max. July 1994	< 10–960	< 10–30	Max. July 1994	< 100–1,231,725
Small fusiform pennate (20 × 3.5 μm)	Mixed layer	Max. July 1995, max. Nov. 1994	< 10–510	< 10–20	Max. July 1995	< 100–7728
Mastogloia rostrata	Mixed layer[a]	Max. Aug./Sept. 1994	< 10–90	< 10– < 10	Max. July 1994, Aug./Sept. 1994	< 100–7670
Hemiaulus other spp.	Mixed layer	Max. Sept. 1994, max. July 1995	< 10–10	< 10– < 10	Max. July 1995	< 100–2135
Rhizosolenia cf. *clevei* var. *communis*	Mixed layer	No distinct maximum observed	< 10–40	< 10– < 10	Max. July 1994, Aug./Sept. 1994	< 100–1629
Guinardia cylindrus	Mixed layer	No distinct maximum observed	< 10–50	< 10– < 10	No distinct maximum observed	< 100– < 100
Rhizosolenia other spp./ *Proboscia* spp.	Mixed layer and DCML	No distinct maximum observed	< 10– < 10	< 10–30	Max. June 1994, July 1994	< 100–1046
Cylindrotheca closterium	Mixed layer and DCML	No distinct maximum observed	< 10–430	< 10–270	Max. May 1995	< 100–2,041,953
Nitzschia bicapitata group	Mixed layer and DCML	No distinct maximum observed	< 10–190	< 10–60	No distinct maximum observed	< 100–94,562
Thalassionema cf. *bacillare*	DCML[a]	No distinct maximum observed	< 10– < 10	< 10–50	No distinct maximum observed	397–13,022
Pseudonitzschia spp.	DCML[a]	Max. March 1995	< 10– < 10	< 10–380	Max. June 1994	< 100–46,841
Trichodesmium spp. (cyanobact.)	Mixed layer	Max. July 1994, Aug./Sept. 1994	< 10–670 trich.	< 10– < 10 trich.	Max. Aug./Sept. 1994	< 100–120,540
Dictyocha spp. (crysophyte)	Mixed layer and DCML	No distinct maximum observed	< 10–110	< 10–130	No distinct maximum observed	4612–25,236

[a] Classified by Venrick (1988) as key species for the specific habitat in the subtropical North Pacific Ocean.

Table 3
Abundances of *Trichodesmium* spp. trichomes in the euphotic zone from June 1994 through July 1995 expressed as depth integrals for either the mixed layer (0 m to base of mixed layer) or the deep layer (base of mixed layer to 165 m); the latter includes the DCML. The respective mixed-layer depths and zones of the DCML are indicated in Table 1. Furthermore, vertical flux of trichomes in the two respective traps at 165, 315, and 515 m. No traps could be deployed during HOT 59 and HOT 61; during HOT 64 traps were only deployed at 165 m

		Trichodesmium trichomes							
Cruise	Cruise dates	(m^{-2}) euph. zone mixed-layer	(m^{-2}) euph. zone deep layer	Flux ($m^{-2}\,d^{-1}$) 165 m I	Flux ($m^{-2}\,d^{-1}$) 165 m II	Flux ($m^{-2}\,d^{-1}$) 315 m I	Flux ($m^{-2}\,d^{-1}$) 315 m II	Flux ($m^{-2}\,d^{-1}$) 515 m I	Flux ($m^{-2}\,d^{-1}$) 515 m II
HOT 54	June 17–22, 1994	0	0	0	0	0	0	0	0
HOT 55	July 22–27	8,358,335	600,000	0	0	0	0	0	0
HOT 56	Aug. 28–Sept. 2	11,948,637	160,909	135,205	105,875	11,287	13,910	9777	795
HOT 57	Sept. 21–26	2,520,000	0	1419	1242	0	3282	0	0
HOT 58	Oct. 13–18	75,000	0	9005	0	0	0	948	0
HOT 59	Nov. 17–22	100,000	0	n. d.	n. d.	n. d.	n. d.	n. d.	n. d.
HOT 60	Febr. 4–9, 1995	150,000	550,000	812	1083	2257	0	0	0
HOT 61	March 2–7	0	0	n. d.	n. d.	n. d.	n. d.	n. d.	n. d.
HOT 62	April 4–9	0	0	11,058 (180 m)	0 (180 m)	0	1663	0	0
HOT 63	May 5–10	2,925,000	0	2290	4090	0	0	0	0
HOT 64	July 28–Aug. 2	900,000	0	0	0	n. d.	n. d.	n. d.	n. d.

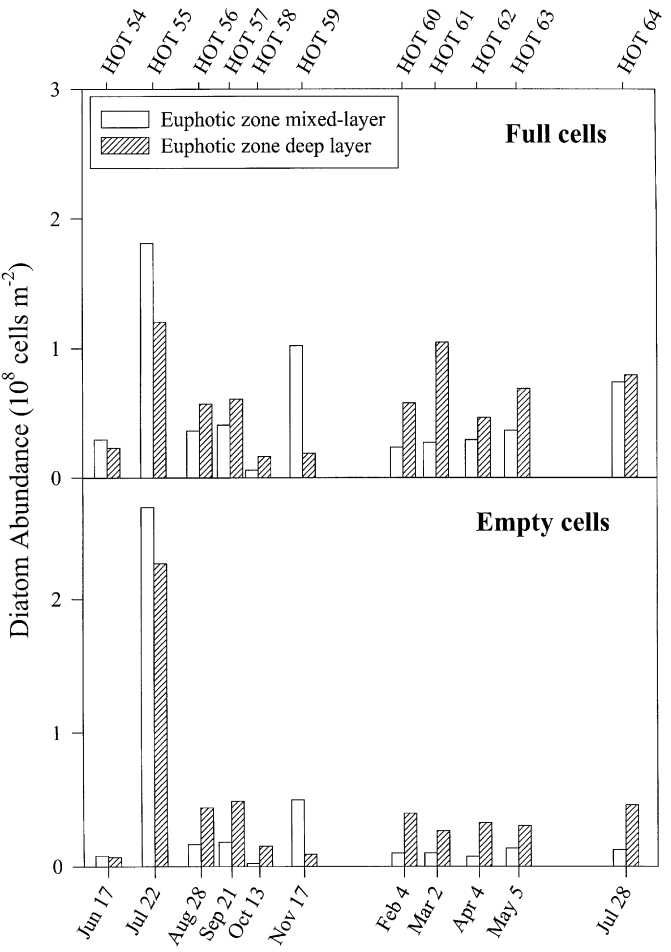


Fig. 1. Diatom cell abundance in the euphotic zone from June 1994 through July 1995, expressed as depth integrals for either the mixed-layer (0 m to base of mixed-layer) or the deep layer from the base of the mixed-layer to 165 m; the latter includes the DCML. The respective mixed-layer depths and zones of the DCML are indicated in Table 1. The upper graph shows full, the lower graph shows empty frustules.

increase were the species *Hemiaulus hauckii* [Grunow] and *Mastogloia woodiana* [Taylor] (Fig. 2). These two species were clearly more abundant in the mixed-layer than in the DCML (Wilcoxon matched pairs test; $p < 0.05$; $n = 11$ pairs). Both diatom species are lightly silicified. Mixed-layer concentrations of other less abundant species of the genus *Hemiaulus* and *Mastogloia* were also slightly elevated in late summer 1994 and July 1995 (Table 2). Moreover, numbers of *Trichodesmium* spp., which were primarily found in the mixed-layer, also increased in July and August/September 1994 (Tables 2 and 3).

One year later (July 1995; HOT 64 cruise), total diatom abundance in 0–165 m was somewhat elevated, but not due to an increase of *Hemiaulus hauckii* and *Mastogloia*

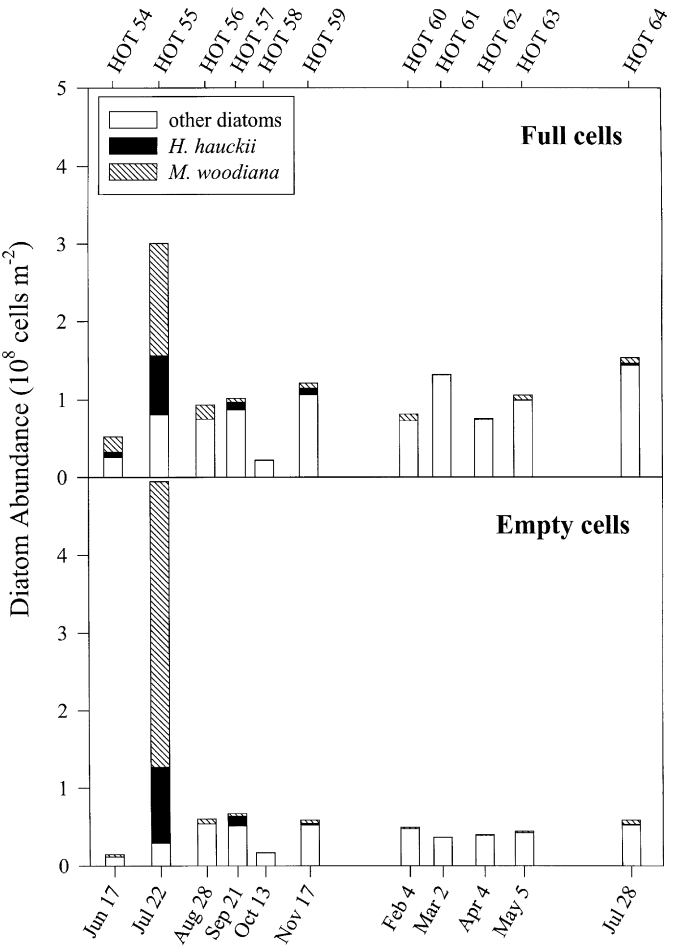


Fig. 2. Abundances of *Hemiaulus hauckii*, *Mastogloia woodiana* and all other diatoms in the water column from June 1994 through July 1995 expressed as depth integrals from 0 to 165 m. Upper and lower graph as in Fig. 1.

woodiana (Fig. 2). Mixed-layer diatom abundances were third highest in that month and second highest in November 1994. In both months a small fusiform pennate diatom was dominant in the mixed-layer assemblage and was responsible for 37 and 26% of the mixed-layer diatom cell stock in July and November (Table 2).

Investigation of water column samples using epifluorescence microscopy revealed that during the whole year nearly all plasma containing cells of *Hemiaulus hauckii* carried one or two *Richelia*-type endosymbionts with heterocysts. Most cells of the less abundant species of the genus *Hemiaulus* (*H. sinensis* and *H. membranaceus*) also contained endosymbionts. Occasionally, *Richelia*-type cells were observed as epiphytes on centric diatom cells, mainly *Chaetoceros* spp. Cells of *Mastogloia woodiana*

were sometimes detected in aggregates together with coccoid cyanobacteria of a diameter of approximately 5 μm.

3.2. Phytoplankton pigments in the water column

Phytoplankton pigment measurements corroborated the diatom distribution patterns. Concentrations of fucoxanthin (Fuco) were low throughout the year (Fig. 3). The increases of the pigment markers 19′-hexanoyloxyfucoxanthin (Hex-fuco), 19′-butanoyloxyfucoxanthin (But-fuco), and divinyl chlorophyll *a* (DV chl*a*) at the DCML horizon indicated that *Haptophyceae*, *Pelagophyceae* and *Prochlorophyceae*, respectively, were the main contributors to the elevated pigment biomass in that layer (Fig. 3). Fuco concentrations were low in the DCML, with two small maxima during HOT 61 and HOT 64. As these peaks coincided with elevated Hex-fuco and But-fuco concentrations and did not correspond with an increase in diatom numbers, they should be attributed to the distribution of *Haptophyceae* and *Pelagophyceae*. Both classes contain Fuco as a minor pigment, as well as other accessory pigments.

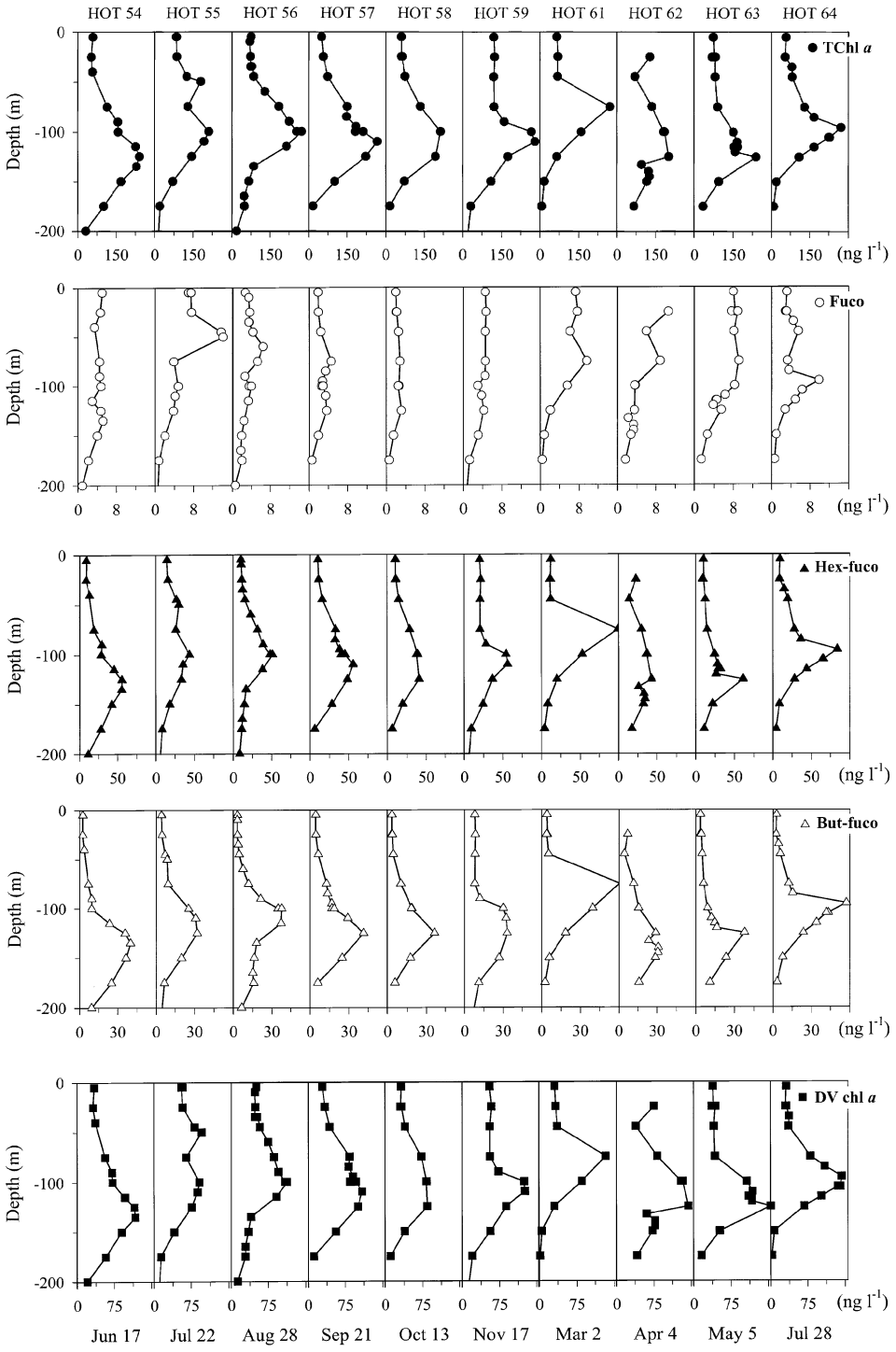
During HOT 55 (July 1994), concentrations of Fuco increased three-fold in the lower part of the mixed-layer (Fig. 3). The concentrations of the pigment markers of the other two chromophyte groups (Hex-fuco and But-fuco), in contrast, did not show a parallel change (Fig. 3). As explained above, diatom cell concentrations in the mixed-layer were also enhanced; thus, the Fuco peak in July was evidently caused by an increase of diatom biomass.

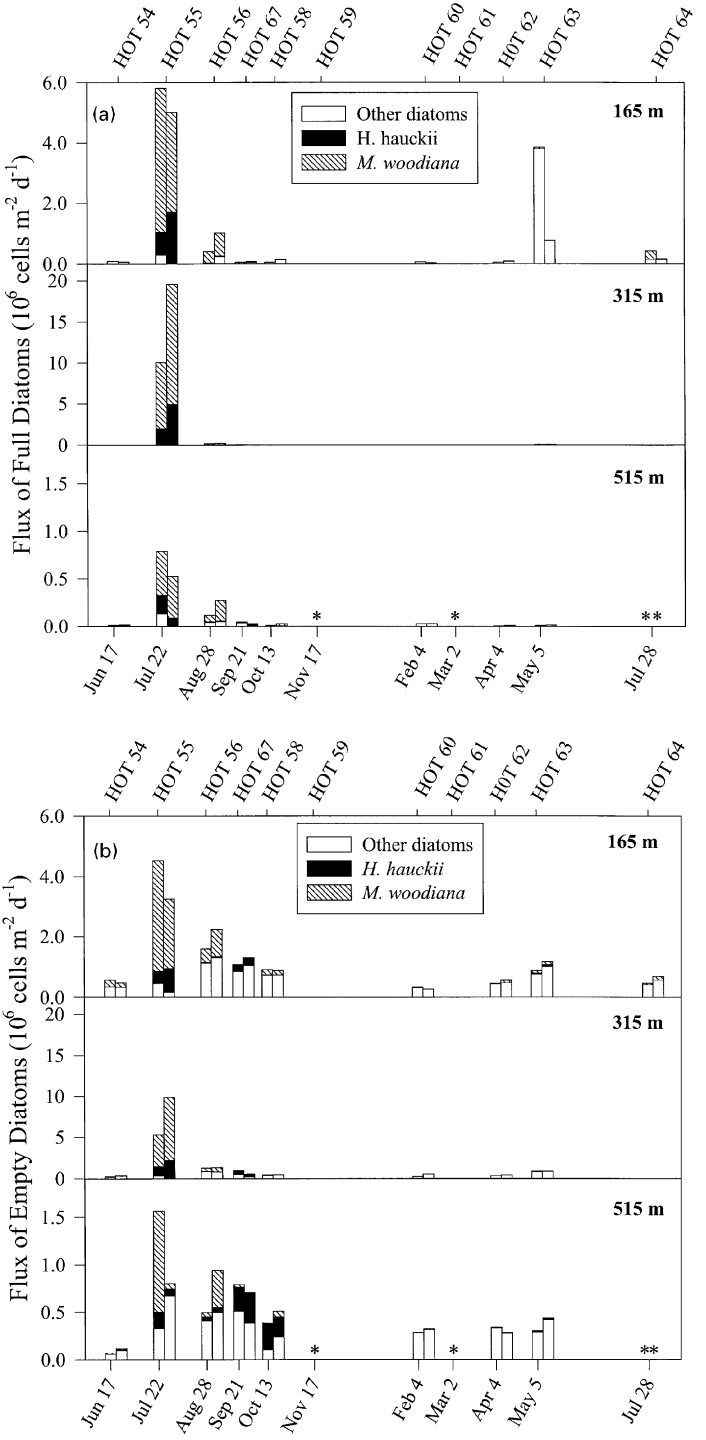
3.3. Vertical flux of diatom cells

The vertical flux of diatom cells and frustules out of the surface layer reflected water column diatom abundances and, therefore, was highest in July 1994 (HOT 55) at all collection depths (165, 315 and 515 m). Coincident with the species distribution in the water column, *H. hauckii* and *M. woodiana* were also the most abundant species of diatoms in the sediment traps during this period (Fig. 4). Microscopic observations showed that part of the cells of these two species were removed from the mixed-layer as aggregates.

Vertical flux of most of the other less abundant diatom species of the mixed-layer assemblage and of *Trichodesmium* spp. increased during summer or late summer (Tables 2 and 3). In May 1995 (HOT 63 cruise) high cell fluxes of *Cylindrotheca closterium* were observed, but solely in the shallowest sediment traps of 165 m depth, making up 88% (average) of total diatom cell flux (Fig. 4 and Table 2). However, this species, whose habitat was both the mixed-layer and the DCML, did not reveal elevated concentrations in the water column in this month.

Fig. 3. Concentrations of phytoplankton pigments in the water column from 0 to 200 m from June 1994 through July 1995. The graphs show from top to bottom: TChl *a* (total chlorophyll *a*: monovinyl chlorophyll *a* plus divinyl chlorophyll *a*), Fuco, Hex-fuco, But-fuco and DV chl *a*.


HOT 54
HOT 55
HOT 56
HOT 57
HOT 58
HOT 59
HOT 61
HOT 62
HOT 63
HOT 64
TChl a
Fuco
Hex-fuco
But-fuco
DV chl a
Depth (m)
0
-100
-200
0 150
0 8
0 50
0 30
0 75
(ng l-1)
Jun 17
Jul 22
Aug 28
Sep 21
Oct 13
Nov 17
Mar 2
Apr 4
May 5
Jul 28


HOT 54
HOT 55
HOT 56
HOT 67
HOT 58
HOT 59
HOT 60
HOT 61
H0T 62
HOT 63
HOT 64
(a)
Other diatoms
H. hauckii
M. woodiana
165 m
315 m
515 m
Flux of Full Diatoms (10^6 cells m^-2 d^-1)
Jun 17
Jul 22
Aug 28
Sep 21
Oct 13
Nov 17
Feb 4
Mar 2
Apr 4
May 5
Jul 28
(b)
Flux of Empty Diatoms (10^6 cells m^-2 d^-1)

From the DCML only the cell numbers of *Pseudonitzschia* spp. increased in March 1995 (HOT 61). This genus showed a small maximum in vertical flux in June 1994 (HOT 54; Table 2). Unfortunately, we could not determine whether there was an increase of total particulate matter flux in late autumn or early spring because traps could not be deployed during the cruises HOT 59 and HOT 61 due to inclement weather (Table 1).

3.4. Vertical flux of phytoplankton pigments

In general, the export flux of Fuco from the surface layer was low throughout the year. However, there was a clear maximum of Fuco flux in July 1994 (HOT 55), coincident with the maximum observed in the mixed-layer of the water column (Figs. 3 and 5). This maximum flux of Fuco did not correspond to a general increase in the fluxes of the pigment markers Hex-fuco, But-fuco and DV chl *a* (Fig. 5). Consequently, it appears that diatoms are selectively removed from the water column. The observed Fuco flux pattern corroborated the diatom cell counts in the traps.

We used the ratio of diadinoxanthin (Diadino; chromophyte photoprotectant pigment; Demers et al., 1991) to the sum of the chromophyte light harvesting pigments (But-fuco, Hex-fuco, Fuco) as an indicator of the origin of the trap material. These ratios were typically between 0.2 and 0.3 in the upper mixed-layer of the water column, in contrast to the relatively low ratios observed at the DCML (<0.1; Fig. 6). During the peak diatom flux event of July, these ratios were elevated at all trap collection depths (Fig. 6), suggesting that the phytoplankton cells sinking out of the euphotic zone were derived from the mixed-layer and not from the DCML.

Attenuation of the vertical flux of total chlorophyll *a* (TChl *a*: monovinyl chlorophyll *a* plus divinyl chlorophyll *a*) and pigment markers Fuco, But-fuco, and Hex-fuco with depth can be described as a function of depth with the negative exponential function

$$F_z = F_{165}\, e^{-a(z-165)},$$

where F_{165} is the estimated pigment flux at 165 m, "*a*" is the estimated attenuation coefficient and z is depth. The nonlinear model was adjusted by using a quasi-Newton algorithm to minimize the loss function (least squares; Christian et al., 1997). The coefficients "*a*" were in general smaller for Fuco than for the pigment markers of other phytoplankton taxonomic groups and for TChl *a* (Table 4). Bonferroni pairwise comparisons ($n = 23$, 1 outlier removed) showed significant differences ($p < 0.05$) of "*a*" Fuco from "*a*" of the other two pigment markers (But-fuco and Hex-fuco) but not between the "*a*" of But-fuco and Hex-fuco ($p > 0.05$). This implies longer

Fig. 4. Vertical flux of full and empty diatom frustules from June 1994 through July 1995 presented as fluxes of *Hemiaulus hauckii*, *Mastogloia woodiana* and all other diatoms. (a) fluxes of full cells in the two replicate traps at 165, 315, and 515 m; (b) fluxes of empty frustules at the same depths. No traps could be deployed during HOT 59 and HOT 61 (indicated by one asterisk); during HOT 64 traps were only deployed at 165 m (two asterisks).

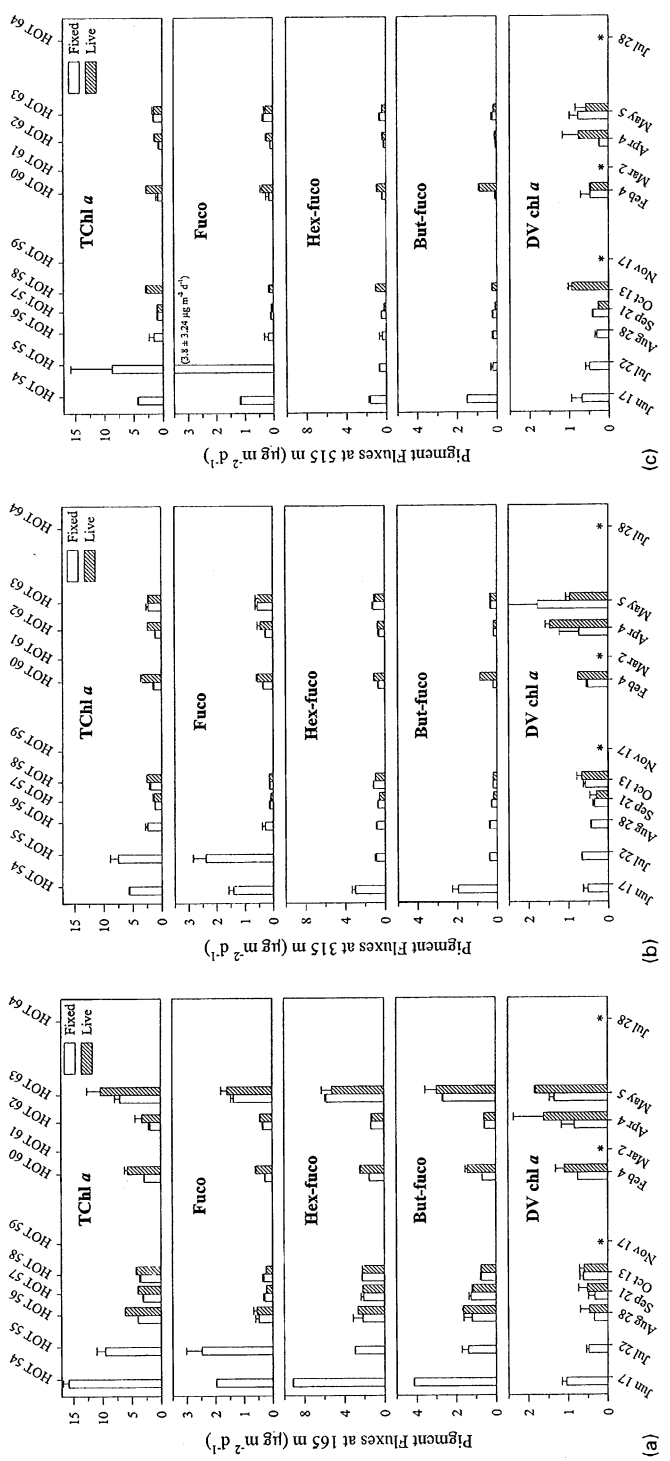


Fig. 5. Vertical fluxes of pigments at 165 (a), 315 (b), and 515 m (c), from June 1994 through July 1995 (cruises HOT 54 through HOT 64). Each figure shows from top to bottom: fluxes of TChl *a*, Fuco, Hex-fuco, But-fuco, and DV chl *a*. The hatched columns show the fluxes measured in the traps without fixative ("live", screened), the empty columns show the fluxes in the traps with fixative (unscreened); means of two traps +1 standard deviation are given. No pigment traps were deployed during HOT 59, HOT 61 and HOT 64 (indicated by an asterisk).

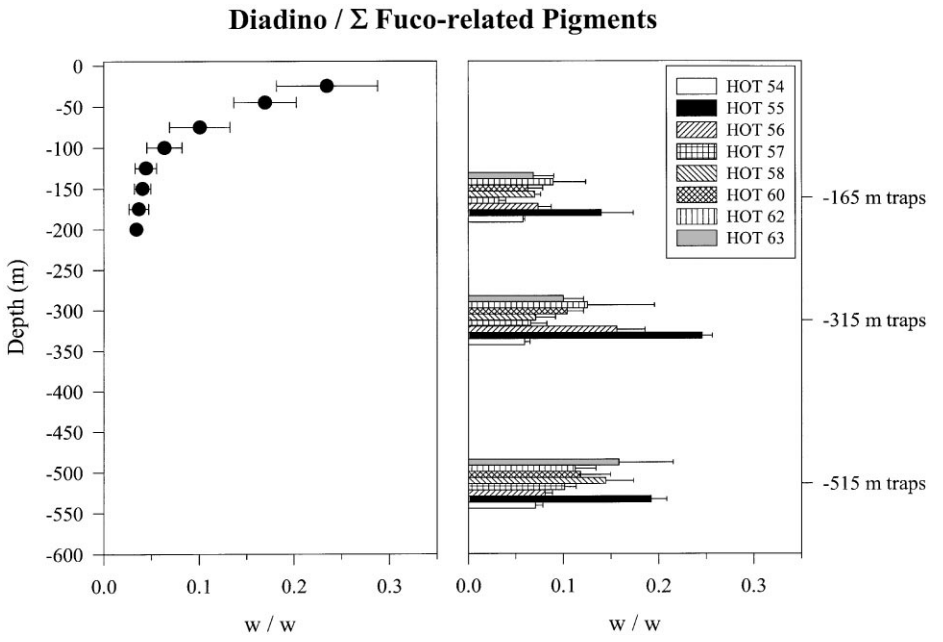


Fig. 6. Ratios of Diadino to the sum of chromophyte pigment markers (Fuco, But-fuco, Hex-fuco) in the water column from 0 to 200 m from middle of June 1994 through end of July 1995 (left panel) and in the sediment traps at 165, 315, and 515 m, from June 1994 through May 1995 (right panel). Error bars represent 1 standard deviation.

solubilization length scales of particulate organic matter originating from diatoms, which could be a consequence of faster sinking speeds, higher resistance to microbial attack, or both.

3.5. *Vertical flux of biogenic silica*

Vertical flux of biogenic silica out of the surface layer was highest throughout the summer at all trap depths (165, 315, and 515 m; Fig. 7A). In order to estimate the contribution of intact diatom frustules (empty and full cells) to the flux of biogenic silica out of the euphotic zone, 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 two dominant and the other diatom species were different. Data of cellular Si content measurements with cultures of the two dominant species are unfortunately not available. We refer to Brzezinski (1985), where Si contents for diatoms of similar sizes and degrees of silification are presented. Our assumption of 2 pmol cell^{-1} is likely conservative; thus it does not overestimate the silica contribution of the intact diatom frustules.

In July, intact diatom frustules provided 14, 32 and 4% of the silica flux at 165, 315 and 515 m, respectively; during the rest of the year these percentages were between <1 and 7% (Fig. 7B). In contrast to the sharp diatom flux maximum, the maximum

Table 4
Parameters estimated for the best fit of the nonlinear model $F_z = F_{165}\, e^{-a(z-165)}$, using a quasi-Newton algorithm. The model describes the attenuation of vertical flux of TChl a and pigment markers Fuco, But-fuco, and Hex-fuco as a function of depth, where F_{165} is the pigment flux at 165 m in ng $m^{-2}\, d^{-1}$, a (m^{-1}) is the attenuation coefficient and z is depth (Christian et al., 1997). Seed values of the unknowns were the average fluxes at 165 m for F_{165} and 0.001 for the attenuation coefficient a. a Fuco are significantly different from a But-fuco and a Hex-fuco ($p < 0.05$; Bonferroni pairwise comparison)

			Fucoxanthin				19′But-fucoxanthin				19′Hex-fucoxanthin				Total chlorophyll a			
Cruise	Cruise dates	n	F_{165} (seed)	F_{165} (estimate)	a	r^2	F_{165} (seed)	F_{165} (estimate)	a	r^2	F_{165} (seed)	F_{165} (estimate)	a	r^2	F_{165} (seed)	F_{165} (estimate)	a	r^2
HOT 54	June 17–22, 1994	6	1976	1932	0.00165	0.92	4128	3997	0.00353	0.92	9120	9025	0.00645	0.98	15789	15412	0.00526	0.93
HOT 55	July 22–27	5	2474	2576	0.00112	0.44	1385	1376	0.00780	0.92	2940	2889	0.00641	0.94	9566	9793	0.00227	0.80
HOT 56	Aug. 28–Sept. 2	6	475	468	0.00303	0.65	1190	1182	0.00760	0.85	2155	2134	0.00606	0.75	3937	3888	0.00286	0.86
HOT 57	Sept. 21–26	12	242	239	0.00520	0.85	1197	1193	0.01058	0.97	2077	2058	0.00696	0.96	3422	3342	0.00521	0.89
HOT 58	Oct. 13–18	10	272	261	0.00360	0.66	732	724	0.00778	0.90	2127	2064	0.00348	0.85	3801	3546	0.00158	0.43
HOT 60	Febr. 4–9, 1995	9	466	493	0.00090	0.18	1167	1105	0.00244	0.31	2080	2017	0.00384	0.74	4754	4576	0.00257	0.47
HOT 62	April 4–9	12	373	398	0.00214	0.49	554	550	0.00796	0.98	1248	1245	0.00475	0.96	2531	2545	0.00279	0.48
HOT 63	May 5–10	12	1462	1444	0.00568	0.94	2787	2786	0.01472	0.97	5491	5480	0.01053	0.97	8645	8566	0.00782	0.85
Mean			968	976	0.00291		1643	1614	0.00780		3405	3364	0.00606		6556	6459	0.00379	
S.D.			877	892	0.00181		1207	1174	0.00383		2635	2618	0.00222		4510	4462	0.00210	

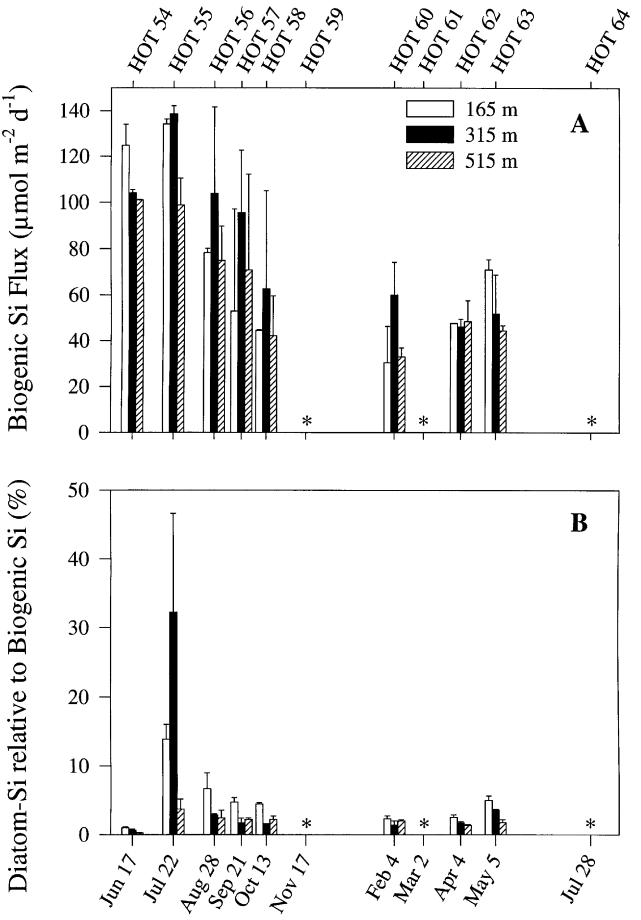


Fig. 7. (A) Vertical fluxes of biogenic silica at 165, 315, and 515 m. (B) Estimated percentage contribution of intact diatom frustules (full and empty cells) to the vertical fluxes of biogenic silica at 165, 315, and 515 m (biogenic silica assumed, 2 pmol diatom cell^{-1}). Indicated for each depth are the mean of two traps +1 standard deviation. No biogenic silica traps were deployed during HOT 59, HOT 61 and HOT 64 (indicated by an asterisk).

of biogenic silica flux during the July 1994 cruise (HOT 55; Fig. 7A) was relativly weak, which may reflect the degree of silification of the sinking diatom species. Aside from intact frustules, debris of diatom frustules was always present in the trap samples. The respective and possibly changing contributions of diatom frustule debris to the biogenic silica flux during each trap exposure could not be estimated. Still, we found that the increased diatom cell flux in July 1994 was obviously not averaged out by a minimum of vertical flux of radiolarian skeletons during the summer flux event (Fig. 8).

We assume that, during the year, the pattern of the carbon contribution of intact diatom cells to the flux of particulate organic carbon, and the pattern of the silica contribution of intact diatom frustules to the flux of biogenic silica, were similar. Since

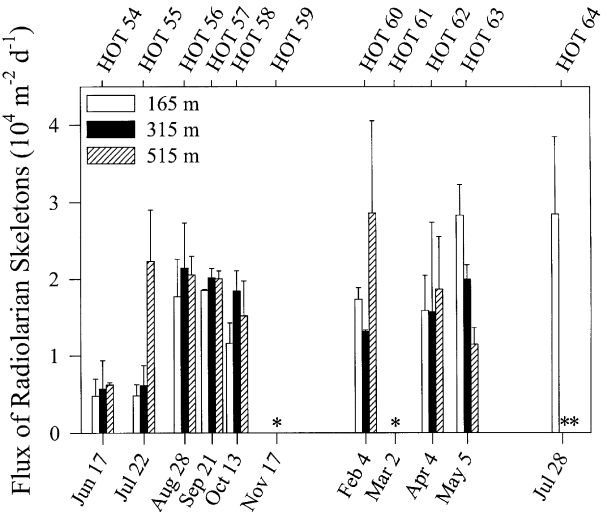


Fig. 8. Vertical flux of radiolarian skeletons from middle June 1994 until end July 1995. Indicated for each depth are the mean of two traps +1 standard deviation. No traps were deployed during HOT 59 and HOT 61 (indicated by one asterisk); during HOT 64 traps were only deployed at 165 m (two asterisks).

a considerable part of the flux of diatom frustules occurred as empty cells (Fig. 4), we conclude that intact diatoms contributed more to the vertical flux of biogenic silica than to the vertical flux of particulate carbon.

4. Discussion

4.1. Phytoplankton assemblages

The distribution of pigments in the water column between June 1994 and July 1995 confirmed the year long dominance of picoeukaryotic and prokaryotic phytoplankton at Station ALOHA, as described by Letelier et al. (1993). Likewise, they reported very low concentrations of Fuco, the pigment marker of diatoms (Fig. 3). It is remarkable that the Fuco maxima were almost always found in the upper layers, which was contrary to the vertical distributions of the dominant light-harvesting pigments, such as Hex-fuco, But-fuco, DV chl *a* and TChl *a*, with maxima at the DCML. The fact that the increase of pigment concentrations in the DCML is mainly due to an increase of pigment per cell (Falkowski and La Roche, 1991; Latasa et al., 1992; Campbell and Vaulot, 1993) could lead to an underestimation of the importance of diatoms in the upper water column. On the other hand, the three-fold increase of Fuco in the lower mixed-layer during HOT 55 was not a photoadaptive response, because there was a similar increase in the abundance of diatom cells as determined by light microscopy.

Our results, obtained during a one year period, provide a seasonal perspective to the predominantly summer observations of Venrick (1982, 1988, 1990, 1992) for a

station north of our study site. The two different assemblages of microplankton found throughout the year in the mixed and deep layers resembled those described by Venrick for the eastern basin of the North Pacific gyre, a result that provides a justification for time and space extrapolation of our results to a much larger area of the North Pacific. In this context, the most outstanding result of our investigations was the maximum concentration of diatom species *H. hauckii* and *M. woodiana*, present in the mixed-layer during the summer of 1994. Both species are large (>20 μm), and *H. hauckii* is chain-forming, in contrast to the delicate, needle-like pennate diatoms found in the DCML. The large oceanic diatom species proposed by Goldman et al. (1992) and Goldman (1993) to be responsible for episodic production and vertical flux in the Sargasso Sea, were present only in the mixed-layer at Station ALOHA. Furthermore, the species composition of diatoms sinking out of the euphotic zone clearly showed their origin from the mixed-layer and not from the DCML.

Observations from previous and following years at Station ALOHA suggest that the event of July 1994 is a seasonal phenomenon rather than an episodic incident (see Goldman 1988, 1993). And it appears that during our cruise in July1995 (HOT 64) *H. hauckii* and *M. woodiana* concentrations and export had not yet increased, because at the end of the following month Brzezinski et al. (1998) observed a mixed-layer bloom of these two species north of Hawaii. It seems that summer conditions favor the proliferation of species with certain physiological characteristics. Thus, *H. hauckii* carried cyanobacteria with heterocysts (cf. *Richelia*) as endosymbionts in very high frequencies. Other cyanobacteria (*Trichodesmium* spp.) had a maximum abundance in the mixed-layer in summer and late summer and a maximum in vertical flux in late summer (Tables 2 and 3). On Station ALOHA *Trichodesmium* spp. is known to occur in higher densities in summer, and "extended periods of water column stratification" seem to favor colony development of this genus (Karl et al., 1992; Letelier and Karl, 1996). Laboratory studies indicate suboptimal photosynthetic performance of some cyanobacteria under fluctuating irradiance (Ibelings et al., 1994). The lack of mixing (fluctuating irradiance) during calm periods may explain in part the success of cyanobacteria (and cyanobacteria-carrying diatoms) in stable stratified conditions at Station ALOHA.

The capability of *Trichodesmium* and *Richelia* endosymbionts in *Hemiaulus hauckii* (and other phytoplankton) to fix dinitrogen (Taylor et al., 1973; Villareal, 1991) may have important consequences in the biogeochemical fluxes of the area. For example, diatoms could benefit either from their endosymbionts or from fixed nitrogen leaching out of *Trichodesmium* spp. (Karl et al., 1992). In fact, at Station ALOHA nitrogen fixation seems to be an important mechanism of new production and nitrogen supply to the phytoplankton community (Karl et al., 1997). It also appears to play a role in particulate matter export, because Karl et al. (1996) have documented the presence of an export peak to the deep ocean in late summer – early fall.

The reasons for the particular proliferation of two diatom species as *H. hauckii* and *M. woodiana* are not clear yet. The iron requirements for diatoms exceed those of other phytoplankton groups and increase at sub-saturating growth irradiances (Sunda and Huntsman, 1995, 1997; Muggli and Harrison, 1997). Sunda and Huntsman (1995, 1997) have also shown that the growth of small cells is favoured under iron

limitation. Consequently, these authors hypothesize that small cells should dominate the DCML in open-oceanic waters because of the reduced light and low dissolved inorganic iron concentrations found at these depths. At Station ALOHA, iron concentrations will be highest in the surface, because the main source of iron is atmospheric deposition, and in summer, when the mixed-layer is shallowest (Table 1). The combination of relatively high iron concentrations and high photon fluxes might favour the growth of large diatoms, a result consistent with the predictions of Sunda and Huntsman (1997).

By virtue of their silica-impregnated cell wall, diatoms have a silicate requirement that is not shared by most other groups of marine phytoplankton. Soluble reactive silica concentrations at Station ALOHA are very low, and it is not possible to obtain accurate measurements using standard methods. Brzezinski et al. (1998) found widespread substrate limitation of silica production in the central North Pacific, except for the already mentioned bloom of *H. hauckii* and *M. woodiana* they observed at the end of August 1995 north of Hawaii. This bloom displayed very low half saturation constants (K_s around 0.55 μM). Evidently, diatom bloom formation can be accomplished only by those species of the mid-ocean gyre assemblages that have a high affinity for silicic acid or low Si cell quota.

4.2. Vertical flux

Microscopic observations of the microphytoplankton allowed us to follow the dynamics of the different diatom species in the water column and during transit to the deep ocean as sinking particles. During the flux event, we saw in the sediment traps a numeric dominance of species from the mixed-layer relative to species from the DCML. The similarity of the Diadino to chromophyte-light-harvesting-pigments ratios in the upper layers and in the traps (Fig. 6) provided further evidence that the sinking diatoms were derived from the mixed-layer. In spite of the high flux of diatoms during July 1994, the proportion of sinking full diatom cells at 165 m in relation to the standing stock we determined in the euphotic zone (0–165 m) was 1.8% d^{-1}, slightly larger than the ca. 0.5% d^{-1} observed during the rest of the year (except cruise HOT 63, average 2.2% d^{-1}). Thus, a massive sinking typical of the end of coastal diatom blooms did not occur. In addition, the specific export rate (d^{-1}) of empty cells was not enhanced. However, this could be a sampling artefact, as export events are likely to have a shorter lifetime than the roughly monthly sampling resolution used in this study. The export peak of *Cylindrotheca closterium* observed in May 1995 (HOT 63; Fig. 4) could have been an event like this. On the other hand, the high variability of cell flux in the two 165 m traps and the absence of a peak in the traps below points to a high degree of patchiness of this *C. closterium* flux.

The mechanism of diatom cell removal from the surface layers is still not resolved. The diatom aggregates found in the traps in July 1994 might have been responsible for the enhanced export out of the mixed-layer. The proliferation and sinking of *Trichodesmium* spp. colonies and trichomes in late summer (Table 3) did not increase the proportion of sinking diatoms, thus reinforcing the idea that the export mechanisms for each group are independent.

On an annual basis, the export of biogenic silica at 165 m was 23.7 mmol $m^{-2} yr^{-1}$ during our investigation period. This resembles the rate Brzezinski and Nelson (1995) measured on the BATS Hydrostation S at 150 m (47.6 mmol $m^{-2} yr^{-1}$), if we substract the contribution of a winter diatom bloom that was responsible for 62% of the Hydrostation S annual flux. The peak of diatom cells sinking at Station ALOHA in July 1994 is not clearly recognizable in the biogenic silica flux pattern. The estimated flux contribution of intact diatom silica frustules to the total flux of biogenic silica varies between each trap depth because of the variable flux of cells. This variability could be caused by aggregate formation of the dominant species. Unfortunately, the export of particulate carbon and particulate organic nitrogen could be measured only at 150 m for the July 1994 cruise (http://hahana.soest.hawaii.edu), and the fluxes at this depth suggest a low removal rate of particulate organic matter by intact diatoms. Nevertheless, the estimated contributions to the biogenic silica flux are based on numbers of intact cells and are probably an underestimation, because a possible transport of broken diatom frustules (e.g. in mesozooplankton fecal pellets) was not considered.

In contrast to other phytoplankton groups, the diatoms seem to stay more intact while sinking (Table 4). The similarity between the structures of Fuco and Fuco-related compounds (like But-fuco and Hex-fuco) supports similar biochemical destruction rates for these pigment markers. Thus, the lower attenuation coefficients "*a*" for Fuco than for But-fuco and Hex-fuco imply that the role of diatoms in the transport of organic matter is more conspicuous at greater depths, because lower "*a*" coefficients mean less decay. This is also indicated by the greater importance of Fuco flux with depth (Fig. 5). The mean attenuation coefficient "*a*" we calculated for TChl *a* (Table 4) is nearly as high as these coefficients for particulate nitrogen and particulate phosphorus at Station ALOHA; and our mean coefficient "*a*" for Fuco is nearly as low as the coefficient for particulate carbon (Christian et al., 1997). These similarities confirm the importance of diatoms as a vector for vertical carbon flux to the deep sea.

Although at Station ALOHA the maximum flux of diatoms out of the surface layer did not result in a large particulate organic carbon and biogenic silica flux, we suggest that their impact at great depths will be more pronounced because of their slower decay and faster sinking speeds, in comparison to the numerically dominant picophytoplankton. Our results show that *H. hauckii* and *M. woodiana* could be very effective vectors of material export at Station ALOHA, and their abundance in the water column may determine the export fluxes of particulate organic matter into the deep ocean.

Already in 1974, Venrick hypothesized that nitrogen fixation by the *Rhizosolenia-Richelia* symbiosis may promote blooms of other phytoplankton in the subtropical North Pacific gyre (Venrick, 1974). It is noteworthy that the *Rhizosolenia* blooms she observed coincided with blooms of *H. hauckii*, but by that time the latter were not known to potentially contain *Richelia* in high frequencies (Heinbokel, 1986). The excretion of recently fixed nitrogen by *Richelia* in a *Rhizosolenia-Richelia* symbiosis was indeed noted in cultures by Villareal (1990). He also proposed that the *Hemiaulus*-cyanobacteria symbiosis is a potentially important site of nitrogen fixation in oligotrophic seas (Villareal, 1992, 1994). The data presented here expand these notions. We found that diatom cell abundance and assemblage compositon can vary

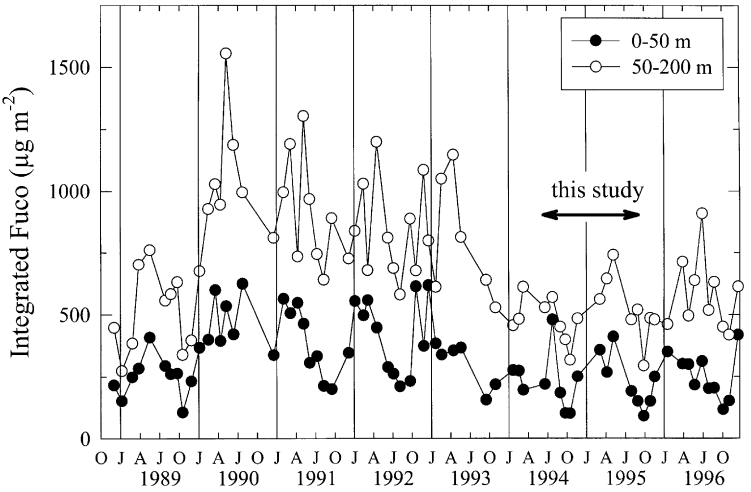


Fig. 9. Integrated stocks of Fuco for the depth regions 0–50 and 50–200 m at station ALOHA from 1988 to 1996.

considerably during the year in the central gyre of the North Pacific. Diatom growth and export took place in the mixed-layer at Station ALOHA, in contrast to the hypothesis of Goldman (1988, 1993), who suggested that nutrient injections at the base of the euphotic zone could be the responsible mechanism for diatom growth and export in the oligotrophic ocean. Moreover, we report that diatom cell proliferation and accumulation occurred under stratified conditions, contrary to the traditional view of diatom cell proliferation following a mixing event. The nitrogen fixation capacity of the endosymbionts of *H. hauckii* can explain part of these ecological particularities because of their potential to use "new" nitrogen. However, it is clear that there should be more reasons for the diatom proliferation in the mixed-layer.

At Station ALOHA, vertical carbon flux out of the surface layer and the ratio between primary production and export decreased since the beginning of 1992 (Karl et al., 1996), and since middle of 1993 Fuco stocks, notably in the deeper layers, appear to be lower than during 1990–1992 (Fig. 9). The question remains open whether the assemblages and seasonal dynamics of the autotrophic biogenic Si producers also have changed. Our results suggest that key species with certain physiological, morphological and life history characteristics are selected by the seasonally and interannually changing environment of the North Pacific subtropical gyre (Karl et al., 1995, 1997; Verity and Smetacek, 1996). Which selection factors are the most important and which organism properties are decisive await further investigation.

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