

On the Chlorophyll a Retention Properties of Glass-Fiber GF/F Filters

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- HEDGES, J. I. 1992. Global biogeochemical cycles: Progress and problems. Mar. Chem. **39**: 67–93.
- ——, B. A. BERGAMASHI, AND R. BENNER. 1993. Comparative analyses of DOC and DON in natural waters. Mar. Chem. 41: 121–134.
- ———, AND P. L. PARKER. 1976. Land-derived organic matter in the surface sediments from the Gulf of Mexico. Geochim. Cosmochim. Acta 40: 1019–1029.
- JEFFREY, S. W. 1974. Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. Mar. Biol. 26: 101-110.
- ——, AND G. M. HALLEGRAEFF. 1987. Chlorophyllase distribution in 10 classes of phytoplankton—a problem for chlorophyll analysis. Mar. Ecol. Prog. Ser. 35: 293–304.
- KLEIN, B. 1988. Variations of pigment content in two benthic diatoms during growth in batch cultures. J. Exp. Mar. Biol. Ecol. 115: 237–248.
- LAMBERT, C. 1994. Chemical biomarkers as tracers of organic matter in the Gulf of Mexico. M.S. thesis, Lamar Univ. 70 p.
- LEAVITT, P. R., AND S. R. CARPENTER. 1990. Aphotic pigment degradation in the hypolimnion: Implications for sedimentation studies and paleolimnology. Limnol. Oceanogr. 35: 520–535.
- LEE, C., AND S. M. HENRICHS. 1993. How the nature of dissolved organic matter might affect the analysis of dissolved organic carbon. Mar. Chem. 41: 105–120.
- MILLIE, D. F., H. W. PAERL, AND J. P. HURLEY. 1993. Microalgal pigment assessments using high-performance liquid chromatography: A synopsis of organismal and ecological applications. Can. J. Fish. Aquat. Sci. 50: 2513–2527.
- Nelson, J. R. 1993. Rates and possible mechanism of light-dependent degradation of pigments in detritus derived from phytoplankton. J. Mar. Res. 51: 155–179.
- RANBY, B., AND J. F. RABEK. 1975. Photodegradation, photoxidation, and photostabilization of polymers. Wiley. REPETA, D. J. 1989. Carotenoid diagenesis in recent marine

- sediments: 2. Degradation of fucoxanthin to loliolide. Geochim. Cosmochim. Acta **53**: 699–707.
- SANTSCHI, P. H., AND OTHERS. 1995. Isotopic and biochemical evidence for the recent origin of colloidal organic matter in the ocean. Geochim. Cosmochim. Acta 59: 625–631.
- SHARP, J. 1973. Total organic carbon in seawater—comparison of measurements using persulfate oxidation and high temperature combustion. Mar. Chem. 1: 211-229.
- SHUMAN, F. R., AND C. J. LORENZEN. 1975. Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. 20: 580–586.
- SOKAL, R. R., AND F. J. ROLHF. 1981. Biometry, Freeman.
 STAUBER, J. L., AND S. W. JEFFREY. 1988. Photosynthetic pigments in fifty-one species of marine diatoms. J. Phycol. 24: 158–172.
- SUN, M., R. C. ALLER, AND C. LEE. 1991. Early diagenesis of chlorophyll-a in Long Island Sound sediments: A measure of carbon flux and particle reworking. J. Mar. Res. 49: 379–401
- Welschmeyer, N. A., and C. J. Lorenzen. 1985. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord and the central Pacific gyre. Limnol. Oceanogr. 30: 1–21.
- WILLIAMS, P. M., AND E. R. M. DRUFFEL. 1988. Dissolved organic matter in the ocean: Comments on a controversy. Oceanography 1: 14–17.
- WRIGHT, S. W., AND S. W. JEFFREY. 1987. Fucoxanthin pigment markers of marine phytoplankton analyzed by HPLC and HPTLC. Mar. Ecol. Prog. Ser. 38: 259–266.
- ——, AND OTHERS. 1991. Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Mar. Ecol. Prog. Ser. 77: 183–196.

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On the chlorophyll *a* retention properties of glass-fiber GF/F filters

Abstract—Extensive comparisons of the retention properties of glass-fiber GF/F and 0.2-µm membrane filters show that these two filter types retain equivalent amounts of Chl a. The experiments conducted were in the open ocean waters of the Pacific Ocean, from 46°N to 28°S, including waters from the equatorial divergence, the low latitude subtropical gyres, and higher latitudes. These results contradict a recent report that suggests that in some cases GF/F filters underestimate chlorophyll concentration by 4-fold when compared with 0.2-µm membrane filters. The data set also allowed examination of latitudinal gradients in integrated chlorophyll. Previously observed latitudinal gradients in the North Pacific were present but were much weaker than those found in the South Pacific.

Dickson and Wheeler (1993) reported that particulate matter collected by vacuum filtration of water samples from the North Pacific yielded significantly higher concentrations of chlorophyll a (Chl a) for 0.2-\mu Nuclepore filters compared to Whatman GF/F glass-fiber filters. In the most extreme case, at 28°N, 155°W, the 0.2-\mu filters retained four times the amount of Chl a retained on GF/F filters. If these results truly reflect the Chl a retention properties of GF/F filters, then the oceanographic community may have seriously underestimated Chl a and primary productivity in the sea, as most biological oceanographers routinely make measurements of Chl a and primary productivity with GF/F filters. We report here

several independent open ocean comparisons of these two filter types that show little or no difference between their retention properties. These data contradict the results of Dickson and Wheeler (1993) and support the use of GF/F filters for accurate estimates of Chl a and primary productivity in the sea.

During a recent series of cruises in the Pacific that sampled waters from the equatorial divergence, the low latitude subtropical gyres and higher latitudes, the Chl a retention capabilities of 0.2-μm and GF/F filters were compared (Fig. 1). In most cases Chl a and pheopigments were determined by the fluorometric technique using a Turner Designs model 10-005 R fluorometer that was calibrated with commercially available Chl a (Sigma Chem Co.). Samples for determination of plant pigments were filtered onto 25-mm-diameter Whatman GF/F filters and 0.2-µm Nuclepore or Poretics membrane filters and extracted in 90% acetone at -20° C for between 24 and 30 h (Venrick and Hayward 1984). Volume filtered ranged from 100 to 540 ml and vacuum ranged from 100 to 250 mm of Hg. Other than the modification of the extraction procedure, the method used was the conventional fluorometric procedure of Holm-Hansen et al. (1965) and Lorenzen (1966). On one cruise (Table 1) samples were analyzed for plant pigments by high-performance liquid chromatography (HPLC) following the procedures of Bidigare et al. (1989). The results show that for six separate cruises and two independent methods (fluorometric and HPLC), the two filters produce results that differ by only a few percent (Fig. 2), with a small positive bias toward GF/F filters.

Data collected by Dickson and Wheeler (1993) at 28°N, 155°W can be compared with data collected at the Hawaii Ocean Time-series (HOT) station ALOHA site over the past several years (Fig. 3). The HOT Chl a method is a derivative of the fluorometric techniques described above: samples collected on GF/F filters are allowed to extract at -20° C in 100% acetone for 7 d before reading on a fluorometer. The water-column values for the HOT site compare favorably with the 0.2-µm Nuclepore values (Fig. 3) but not with the GF/F filter values reported by Dickson and Wheeler suggesting that they might have had reduced efficiency in the collection of particles on GF/F filters or of extracting Chl a from the particles collected on GF/F filters. Recent primary productivity comparisons at station ALOHA also show that 0.2-µm Nuclepore and GF/F filters provide equivalent results for ¹⁴C assimilation (Fig.

A retrospective analysis of Chl *a* data for the North Pacific provides similar evidence. A site at 25°N, 155°W was visited repeatedly between 1968 and 1985 and Chl *a* analysis on GF/C filters, which have higher porosity than GF/F filters, was carried out. The mean depth-integrated Chl *a* for the 1980s (0–200 m) was 22.6 mg m⁻² and the range of 51 observations was 14.7–33.4 mg m⁻² (Hayward 1987). Correction for retention differences between GF/C and GF/F filters increases the values by 15% (Venrick and Hayward 1984). Dickson and Wheeler (1993) reported an integrated Chl *a* value (0–175 m) of <10 mg m⁻² for GF/F filters at 28°N, 155°W—a value that is

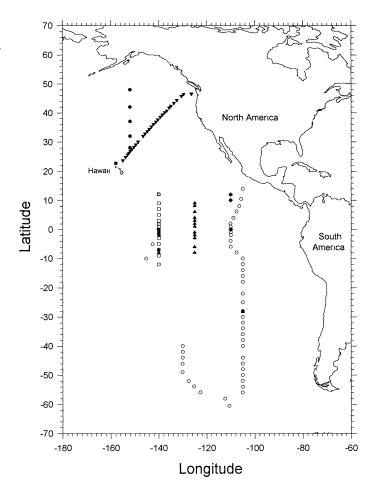


Fig. 1. Map showing the location of Chl *a* observations. Filled symbols represent locations of comparisons between GF/F and 0.2-µm filters: ●—locations sampled by Dickson and Wheeler (1993); ◆—locations of the equatorial Pacific NOAA-JGOFS spring 1992 cruise; ▲—locations of the equatorial Pacific NOAA-JGOFS fall 1992 cruise and the South Pacific NOAA-WOCE winter 1994 cruise; ●—locations of the equatorial Pacific NSF-JGOFS spring 1992 cruise; ■—the Hawaii Ocean Time-series (HOT) site; ▼—locations of underway sampling between Hawaii and Seattle on a NOAA summer 1994 cruise. Open symbols represent locations of integrated Chl *a* measurements on GF/F filters: O—locations of an NOAA-RITS cruise in winter 1989; □—locations of an NSF-JGOFS cruise in fall 1992.

outside the range of the 51 observations made in the 1980s with GF/C filters (Hayward 1987). The value reported by Dickson and Wheeler (1993) for 0.2-μm Nuclepore filters is close to 25 mg m⁻²—very similar to the mean GF/C value of 22.6 mg m⁻² (26.0 if corrected to GF/F) and to the mean of 4 yr of GF/F data from the HOT site (0–175 m) of 23.3 mg m⁻². The range of values for the 4 yr of HOT data is from 14.8–45.6 mg m⁻², again well above the GF/F value reported by Dickson and Wheeler. The mean depth-integrated Chl *a* during the PRPOOS experiment at 28°N, 152°W, using 0.45-μm Millipore H/A filters, was 26.5 mg m⁻² (Venrick et al. 1987). During PRPOOS one profile of Chl *a* was also made with GF/F filters and the integrated value for that

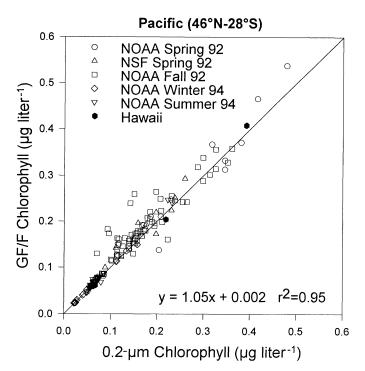


Fig. 2. Comparison of Chl a measurements made with Whatman GF/F and 0.2- μ m membrane filters during six separate cruises in the Pacific. The 1992 NOAA and the Hawaii cruises used Nuclepore filters; the other cruises used Poretics filters. Plotted with the data is y=x. A model 2 regression analysis showed that the slope was ($\pm 95\%$ C.L.) 1.05 ± 0.04 , the intercept was 0.002 ± 0.006 , and the correlation coefficient was 0.973. The positive GF/F bias is due primarily to the fall 1992 cruise; ANOVA shows that the fall cruise was the only set where Chl a was significantly greater with GF/F filters than with 0.2- μ m filters.

profile was 26.1 mg m $^{-2}$ —practically identical to the value reported with H/A filters.

Further evidence of the similar Chl a retention properties of GF/F and 0.2-\mu filters derives from an investigation of one of the most oligotrophic areas of the World Ocean: the South Pacific subtropical gyre. This area has typically 0.02 μ g liter⁻¹ Chl a at the surface and a Chl a maximum near 150 m (Fig. 5). Comparison of profiles from this region shows that these two filter types produce equivalent results even in this oligotrophic environment (Fig. 5). By combining observations from the South Pacific with observations in the equatorial and North Pacific, the ocean-scale latitudinal gradients in integrated Chl a can be examined (Fig. 6). A significant linear latitudinal gradient from the high latitude North Pacific to 15°N is evident (Fig. 7) and is not statistically different from that observed by Hayward and McGowan (1985). From 15°N to 20°S there are higher and more variable concentrations associated with the equatorial divergence (Fig. 6). At 20°S (and 105°W) there is a sharp drop in Chl a to the lowest values of the entire basin, and these remain low until 30°S where a steep gradient (relative to the North Pacific) begins. Chl a reaches a maximum between 50 and 55°S and a decrease is observed from 55 to 60°S. The lower Chl a concentrations in the oligotrophic South Pacific may be related to the size of the gyre, circulation patterns therein, and(or) the atmospheric transport of continental dust, all of which may result in a reduced supply of nutrients.

Dickson and Wheeler (1993) suggested that prochlorophytes may not be retained efficiently by GF/F filters and that this could be the cause of the underestimation they observed. Prochlorophytes are ubiquitous in the equatorial Pacific and comprise on the order of 35–40% of the standing stock of Chl a (Chavez et al. 1991; Bidigare

Table 1. Comparison of HPLC pigment analysis of material collected on either a 0.2- μ m Poretics or a Whatman GF/F filter during a NSF-JGOFS spring 1992 cruise to the equatorial Pacific. The results show that GF/F filters retained a slightly larger proportion of chlorophyll and zeaxanthin (zeax). Zeaxanthin is the dominant xanthophyll found in procaryotic picophytoplankton. Volume filtered was 100 ml for the equatorial station and 200 ml (0.2 μ m) and 540 ml (GF/F) for the other two stations.

	Depth	Zeax 0.2 μm	Chl <i>a</i> 0.2 μm	Zeax GF/F	Chl a GF/F	Zeax	Chl a		
Location	(m)	(μg liter ⁻¹)				GF/F	GF/F : 0.2 μm		
0°, 140°W	10	0.056	0.198	0.059	0.172	1.05	0.87		
	30	0.064	0.238	0.055	0.251	0.86	1.05		
	50	0.022	0.231	0.033	0.224	1.50	0.97		
1°S, 140°W	20	0.064	0.176	0.083	0.193	1.30	1.10		
	40	0.066	0.198	0.072	0.219	1.09	1.11		
	60	0.048	0.260	0.054	0.293	1.13	1.13		
2°S, 140°W	20	0.038	0.086	0.037	0.099	0.97	1.15		
	60	0.029	0.111	0.036	0.142	1.24	1.28		
	100	0.031	0.159	0.033	0.196	1.06	1.23		
					Mean SD <i>N</i>	1.13 0.19 9	1.10 0.13 9		

Table 2. Flow cytometric analysis of prochlorophytes (prochl) passing through GF/F filters (uncombusted and combusted) for waters from the Atlantic and Pacific Oceans. The results show that 0.2–5.8% of the population passed through uncombusted GF/F filters with a mean of 2.8%. (ND–not determined.)

		Depth				l ml ⁻¹ filtrate	% Prochl GF/F filtrate	
Cruise	Location	(m)	Prochl ml ⁻¹	n	Uncom	Com	Uncom	Com
RV Atlantis II, Nov 86	5°N, 82°W	60	1.6×10 ⁴	1	3.4×10 ²	ND	2.1	ND
		80	1.2×10 ⁴	1	5.7×10^{2}	ND	4.4	ND
B25, Feb 89	32°N, 64°W	15	6.4×10^{4}	1	4.6×10^{2}	ND	0.7	ND
		100	3.8×10^{3}	1	1.6×10^{2}	ND	4.2	ND
RV Moana Wave, Aug 91	10°N, 152°W	20	1.4×10^{5}	1	5.5×10^{3}	ND	3.9	ND
		80	1.9×10^{5}	2	1.1×10^{4}	9.1×10^{3}	5.8	4.8
RV Endeavor, Jan 92	27°N, 68°W	0	3.5×10^{4}	3	< 100	1.4×10^{2}	0.2	0.4
This study	21°15′N, 157°54′W	30	1.9×10^{5}	9	1.4×10^{3}	ND	0.7	ND
						Mean	2.8	
						SD	2.1	2.6
						n	8	2

and Ondrusek in press). HPLC analysis of pigments from the two filter types (Table 1) shows that they both retain equivalent amounts of zeaxanthin, the dominant xanthophyll found in procaryotic picophytoplankton (i.e. *Prochlorococcus* spp. and *Synechococcus* spp.). Flow cytometric analysis of GF/F filtrates from several open ocean environments shows that most of the prochlorophytes are

retained by this filter type (Table 2). The nominal porosity of GF/F filters is 0.7 μ m but the effective pore size of glass-fiber filters is substantially smaller (Sheldon 1972). Their effective pore size must be <0.5 μ m, since prochlorophytes are in the 0.54–0.67- μ m equivalent spherical diameter range (Morel et al. 1993) and are clearly

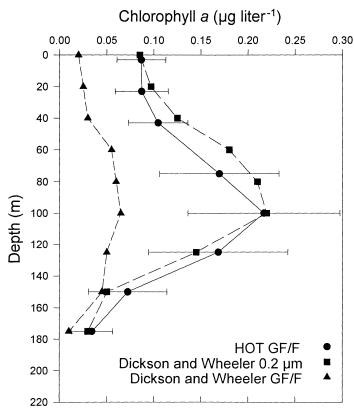


Fig. 3. Mean vertical Chl a profile at the Hawaii Ocean Time-series (HOT) station ALOHA (22°45′N, 158°W), based on 4 yr of data, plotted with the standard deviation, and vertical profiles reported by Dickson and Wheeler (1993) at 28°N, 155°W for $0.2-\mu m$ and GF/F filters.

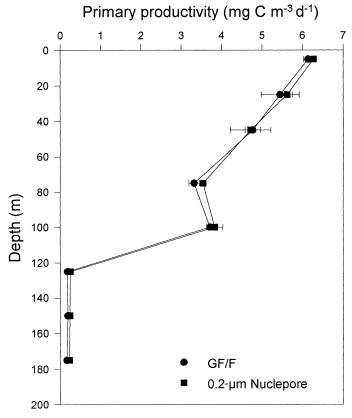


Fig. 4 Primary productivity measurements at station ALO-HA during cruise H-46 (April 1993) obtained with Whatman GF/F and 0.2- μ m Nuclepore filters showing that both filter types yield similar and not significantly different results (ANOVA at P > 0.05). Incubations followed the standard HOT protocols (Karl et al. 1990).

Table 3. Comparison between the methods described by Dickson and Wheeler (1993) (A,B) and a standard GF/F grind and extraction in acetone (C). Samples were collected 4.8 km off Honolulu Harbor at essentially the same location as PRPOOS station B (Laws et al. 1984). Filtrates from all treatments were analyzed by flow cytometry for picoplankton. Initial concentration of prochlorophytes (prochl) was 189,220 ml⁻¹, Synechococcus (Syn) 9,399 ml⁻¹, and picoeucaryotes (picoeu) 4,835 ml⁻¹. Given are means and standard deviations.

Treatment	Chl (µg liter ⁻¹)	Prochl ml ⁻¹ filtrate	% prochl filtrate	% Syn fil- trate	% picoeu filtrate
A. DW GF/F	0.408±0.010	$1,353\pm581$ $1,466\pm1,781$ $1,317\pm754$	0.72	0.00	0.38
B. DW 0.2 μm	0.392±0.008		0.77	0.91	0.51
C. GF/F	0.384*		0.70	0.07	0.51

^{*} Sample size = 2.

retained by GF/F filters (Table 2). Even though some of these organisms pass through GF/F filters (Table 2) similar numbers pass through 0.2- μ m filters (Table 3). Taguchi and Laws (1988) found that particles in the filtrate of 0.2- μ m Nuclepore filters could be retained by a GF/F filter and that consecutive filtration through three 0.2- μ m Nuclepore or three GF/F filters yielded the same concentration of Chl a. Similarly, Venrick et al. (1987) showed that GF/F filters retained more of the Chl a present in 0.45- μ m H/A Millipore filtrate than did 0.2- μ m Nuclepore filters.

The only major difference between the protocol described by Dickson and Wheeler (1993) and those used in Figs. 2, 3, and 5 is the application of MgCO₃ after the filtration. To evaluate whether the results presented by Dickson and Wheeler were due to this methodological difference, a set of samples collected in oligotrophic waters close to Hawaii was processed by conventional methods and by those used by Dickson and Wheeler. In addition, the original sample and the filtrates from the comparisons were analyzed by flow cytometry. We were un-

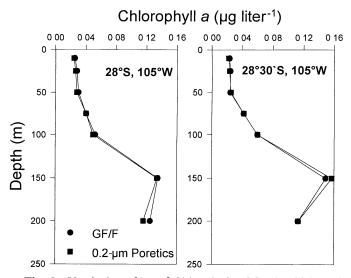


Fig. 5 Vertical profiles of Chl a during March 1994 made with GF/F and 0.2- μ m Poretics filters. The GF/F and 0.2- μ m Poretics filters yielded Chl a results that are not significantly different (ANOVA at P > 0.05).

able to reproduce the observations of Dickson and Wheeler. Our results show that all treatments yielded the same amounts of Chl a (Table 3) and that <1% of the prochlorophytes passed through GF/F filters. The average percentage of prochlorophytes that passed through GF/F filters, from a compilation of similar exercises in the Atlantic and Pacific Oceans, was 2.8% (Table 2). One can estimate the number of prochlorophytes required to explain the extreme case reported by Dickson and Wheeler in the chlorophyll maximum at 28°N, 152°W. Assuming 1 fg divinyl Chl a per cell for populations at the bottom of the mixed layer (Chavez et al. 1991), an underestimate of 0.15 μ g Chl a liter⁻¹ would imply a passage of 1.5 \times 105 cells ml⁻¹, two orders of magnitude larger than what we observed. Based on the results from the comparisons we must conclude that the results reported by Dickson

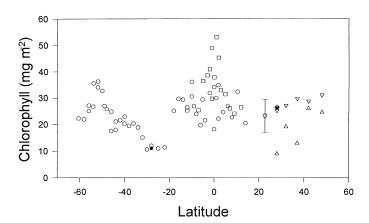


Fig. 6. Latitudinal distribution of depth-integrated Chl a from 50°N to 60°S in the Pacific Ocean. Plotted are observations during March 1991 reported by Dickson and Wheeler (1993) using 0.2- μ m Nuclepore (∇) and GF/F (\triangle) filters (0–175 m); mean from PRPOOS (\diamondsuit) (0–200 m) using 0.45- μ m H/A Millipore filters (Venrick et al. 1987) and one profile using GF/F (\square) filters (26.48 and 26.14 mg m⁻² respectively); the mean and standard deviation for 4 yr of HOT (O) data (0–175 m) using GF/F filters; observations from a JGOFS survey (\square) in August 1992 (0–150 m) using GF/F filters and the fluorometric techniques of Lorenzen (1966); observations during November 1989 (O) (0–175 m) on GF/F filters; and a profile during March 1994 (\blacksquare) at 28°30′S, 105°W (0–175 m) using 0.2- μ m Poretics filters (see Fig. 5).

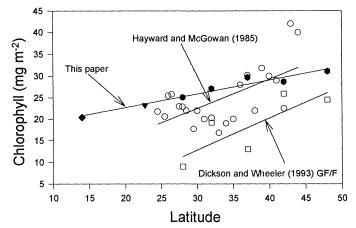


Fig. 7. Latitudinal gradients of depth-integrated Chl a extracted from the present data compilation, including the Dickson and Wheeler (1993) 0.2- μ m data (\bullet), the HOT mean (\blacktriangledown), and the northern extreme of the November 1989 data set (Fig. 6) (\bullet); for the Dickson and Wheeler (1993) GF/F data (\Box) and for data presented by Hayward and McGowan (1985) (O). Lines represent the regression between latitude and intergrated chlorophyll. With the exception of the Dickson and Wheeler GF/F data, the regressions are significant at P < 0.05. There is no significant difference between the slope or the intercept of the present compilation and that of Hayward and McGowan.

and Wheeler (1993) do not adequately represent the retention properties of GF/F filters and that GF/F filters can be used to accurately measure Chl a and primary productivity in the sea.

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References

- BIDIGARE, R. R., AND M. E. ONDRUSEK. In press. Influence of the 1992 El Niño on phytoplankton pigment distributions in the equatorial Pacific Ocean. Deep-Sea Res.
- ——, O. SCHOFIELD, AND B. B. PRÉZELIN. 1989. Influence of zeaxanthin on quantum yield of photosynthesis of *Synechococcus* clone WH7803 (DC2). Mar. Ecol. Prog. Ser. 56: 177–188.
- CHAVEZ, F. P., AND OTHERS. 1991. Growth rates, grazing, sinking and iron limitation of equatorial Pacific phytoplankton. Limnol. Oceanogr. 36: 1816–1827.
- DICKSON, M.-L., AND P. A. WHEELER. 1993. Chlorophyll a concentrations in the North Pacific: Does a latitudinal gradient exist? Limnol. Oceanogr. 38: 1813–1818.
- HAYWARD, T. L. 1987. The nutrient distribution and primary production in the central North Pacific. Deep-Sea Res. 34: 1593–1627.
- -----, AND J. A. McGowan. 1985. Spatial patterns of chlorophyll, primary production, macrozooplankton biomass, and physical structure in the central North Pacific Ocean. J. Plankton Res. 7: 147–167.
- HOLM-HANSEN, O., C. LORENZEN, R. HOLMES, AND J. STRICK-LAND. 1965. Fluorometric determination of chlorophyll. J. Cons. Cons. Int. Explor. Mer 30: 3–15.
- KARL, D. M., C. D. WINN, D. V. HEBEL, AND R. LETELIER. 1990. Hawaii Ocean Time series Program: Field and laboratory protocols. Univ. Hawaii.
- Laws, E. A., AND OTHERS. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. Limnol. Oceanogr. 29: 1161–1169.
- Lorenzen, C. J. 1966. A method for the continuous measurement of in vivo chlorophyll concentration. Deep-Sea Res. 13: 223–227.
- MOREL, A., Y.-H. AHN, F. PARTENSKY, D. VAULOT, AND H. CLAUSTRE. 1993. *Prochlorococcus* and *Synechococcus*: A comparative study of their optical properties in relation to their size and pigmentation. J. Mar. Res. **51**: 617–649.
- SHELDON, R. W. 1972. Size separation of marine seston by membrane and glass-fiber filters. Limnol. Oceanogr. 17: 494–498.
- TAGUCHI, S., AND E. A. LAWS. 1988. On the microparticles which pass through glass-fiber filter type GF/F in coastal and open waters. J. Plankton Res. 10: 999–1008.
- VENRICK, E. L., S. L. CUMMINGS, AND C. A. KEMPER. 1987. Picoplankton and the resulting bias in chlorophyll retained by traditional glass-fiber filters. Deep-Sea Res. 34: 1951–1956.
- ——, AND T. L. HAYWARD. 1984. Determining chlorophyll on the 1984 CalCOFI surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 25: 74–79.

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