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Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans?

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Abstract

The fraction of primary production lost to sinking (the export ratio) increases with productivity in the ocean and decreases slightly with productivity in lakes. To explore why this distinction exists, we compared marine and freshwater regressions relating chlorophyll concentrations in the euphotic zone to each of the three variables that define the export ratio: primary productivity, carbon sinking fluxes, and euphotic zone depth. Chlorophyll was found to predict these three variables well (r^2 = 0.54–0.90) in both lakes and the ocean. The differences between the marine and freshwater export ratio–productivity relationships stem primarily from a discrepancy in the primary productivity–Chl relationships. On average, a >10-fold difference in Chl-specific productivity exists between the most oligotrophic lakes (Chl = 0.2 mg^{-3}) and oceanic regions with similar Chl concentrations. This difference disappears at higher concentrations of Chl because primary productivity : Chl ratios increase with productivity in lakes. In addition, carbon sinking rates average 2–3-fold higher in the oceans than in lakes with similar concentrations of Chl. The trends of marine and freshwater export ratio-production can be qualitatively reproduced with Chl-based predictions of euphotic zone primary productivity, depth, and carbon sinking losses from regressions. Marine and freshwater ecosystems may differ systematically in the efficiency of nutrient recycling processes in the water column and in the nature of settling material.

The sinking of particles from the euphotic zone is an important fate of planktonic organic matter, nutrients, and contaminants. Up to half of annual planktonic production is lost to sinking in both marine and freshwater environments (Wassmann 1990; Bloesch and Uehlinger 1990; Baines and Pace 1994). As a

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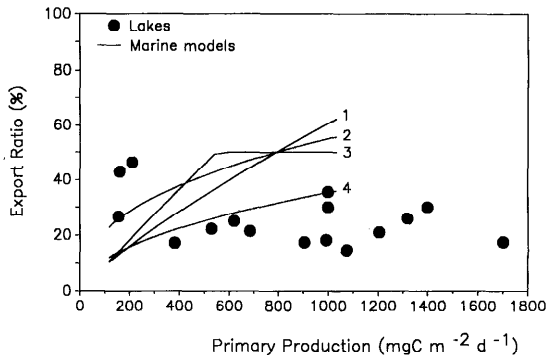


Fig. 1. Comparison of export ratio–euphotic zone primary production relationships in marine and freshwater environments. Predictions of marine models from Betzer et al. 1984 (model 1), Wassmann 1990 (model 2), Eppley and Petersen 1979 (model 3), and Pace et al. 1987 (model 4). Observations on freshwater systems from Bloesch and Uehlinger 1990 and Baines and Pace 1994.

consequence, this process exerts a strong influence on the behavior of aquatic ecosystems. The response of plankton and benthic communities to changes in nutrient and pollutant load depends, in part, on the sinking flux (Sigg 1985). The composition, biomass, and production of the plankton and benthos are influenced by the downward flux of nutrients (Graf et al. 1982; Reynolds 1984). The role of the ocean as a storage pool in the global carbon cycle is directly related to sinking export of planktonic primary production (Eppley and Petersen 1979; Pace et al. 1987). Considering the important role played by sinking fluxes, there is a need to characterize and explain the variability in the fraction of primary production that sinks from the water column. In this paper, we refer to this fraction as the "export ratio."

In oceanic environments, the export ratio appears to increase asymptotically with productivity (Eppley and Petersen 1979; Wassmann 1990). Productivity-related shifts in the forms of nitrogen predominantly used by marine phytoplankton corroborate this observation (Eppley and Petersen 1979). Oligotrophic marine phytoplankton obtain most of their nitrogen as reduced forms (ammonium, urea) produced by zooplankton excretion and microbial amino acid catabolism, while eutrophic communities depend more on oxidized forms of nitrogen (primarily nitrate) which diffuse or upwell from deep water. More nitrogen must sink from the water column in more productive areas to offset the relatively high influx of nitrate-N to maintain the near steady state in algal biomass which exists at annual scales in oceanic environments.

In lakes, the export ratio appears to decrease slightly as a function of primary productivity (Aksnes and Wassmann 1993; Baines and Pace 1994). This pattern contrasts with previous expectations (Reynolds 1984) but agrees with a relationship between benthic respiration and primary production (Hargrave 1973). Changes in either the sinking rate of suspended matter or the depth of the euphotic zone are not responsible for this pattern. The negative relationship between water transparency and chlorophyll concentrations (Carlson 1977) should result in greater losses of particles by sinking from the euphotic zone as productivity increases, and particle sinking rates do not vary systematically with primary production (Baines and Pace 1994). A possible alternative explanation is that the rate of algal turnover increases with lake productivity. Such a pattern would mean more phytoplankton biomass per unit of primary production in oligotrophic lakes than in eutrophic lakes. Consequently, the export ratio would tend to be higher in less productive lakes because there is a strong positive relationship between the sinking flux of organic C and the concentration of algal pigments among lakes.

Lakes and oceans clearly differ in the relationship between the export ratio and primary production (Fig. 1). This observation threatens the possibility of establishing generalizations across the two environments. Therefore it is desirable to determine why an analogy between lakes and oceans fails with regard to the fate of primary production. In this paper, we test for differences in particle sinking behavior, light attenuation, and algal turnover rates that could give rise to the observed difference between the limnetic and oceanic export ratio–primary production relationships. Patterns relating C sinking flux, primary productivity, and euphotic zone depth to chlorophyll concentrations are contrasted between the two environments. Our results should help focus future work on the biological underpinnings of the difference between the export ratio and primary production relationships for lakes and oceans.

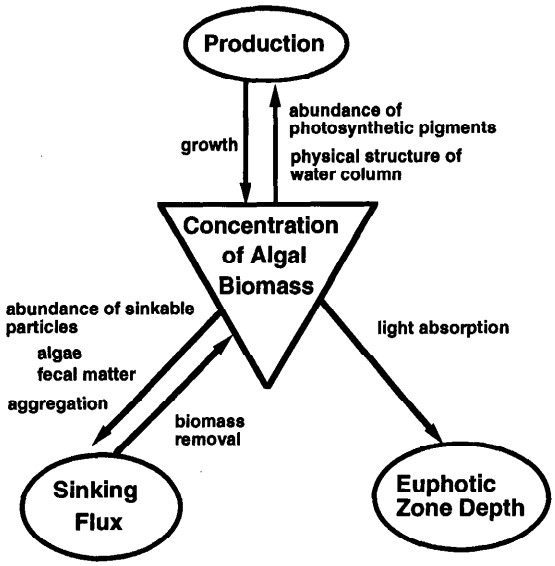


Fig. 2. Conceptual scheme where algal biomass is the nexus of a set of interdependencies among sinking fluxes, primary production, and water transparency.

Notation

Z	Euphotic zone depth, depth at which light is 1% of surface irradiance or net primary production = 0, m
D	Daylength, length of period between sunrise and sunset, h d^{-1}
I	Length of ^{14}C primary production incubation, h
PP	Primary productivity averaged over the euphotic zone, mg C m^{-3} h^{-1}
dPP	Primary productivity averaged over the euphotic zone on a daily basis, mg C m^{-3} d^{-1}
ΣPP	Primary production summed over the euphotic zone on a daily basis, mg C m^{-2} d^{-1}
Chl	Chl concentration averaged over the euphotic zone, mg Chl m^{-3}
ΣChl	Chl standing stock integrated over the euphotic zone, mg Chl m^{-2}
S	Sinking flux of C from the euphotic zone, mg C m^{-2} d^{-1}
A	Assimilation number or the efficiency of photosynthesis relative to Chl concentration (PP·Chl^{-1}) or (ΣPP·ΣChl^{-1}·D^{-1}), mg C (mg Chl)$^{-1}$ h^{-1}
e	Export ratio, the fraction of integrated primary production lost from the euphotic zone due to sinking, dimensionless

Approach and hypotheses

The export ratio (e) had three components: daily sinking flux (S), average volumetric daily primary productivity (dPP), and euphotic zone depth defined as the depth at which irradiance is 1% of the surface, or dPP = 0 (Z). A list of symbols and definitions is provided.

$$e = S \cdot \mathrm{dPP}^{-1} \cdot Z^{-1}. \quad (1)$$

We can quantify how primary productivity, sinking flux, and euphotic zone depth covary by determining how they change along a common gradient. Gradients in euphotic zone Chl concentration are the most promising candidates for such an analysis. Primary productivity (Smith 1979; Smith and Baker 1978; Hayward and Venrick 1982) and light extinction (Lorenzen 1970; Carlson 1977) are well related to Chl concentrations in both lakes and oceans. In lakes, sinking fluxes of C depend on water-column Chl concentrations or algal biomass (Baines and Pace 1994), although a similar relationship has yet to be established for marine environments. Thus, sinking flux, primary productivity, and euphotic zone depth can be seen as indirectly linked through the concentration of algal biomass (Fig. 2).

Because of the constraints imposed by Eq. 1 and given that the observed difference between the export ratio–production relationships in lakes and oceans holds generally, the relationships of sinking flux, primary productivity, and euphotic zone depth to euphotic zone Chl concentration should also differ in predictable ways between lakes and oceans. Three nonexclusive scenarios are expected, given the observed difference between the export ratio–productivity relationships in lakes and oceans. First, production increases more steeply with chlorophyll in lakes than in oceans. Algal standing stocks will differ between lakes and oceans of similar productivity, causing sinking fluxes and export ratios to differ as well. Second, sinking flux of organic C increases more steeply with chlorophyll in oceans than in lakes. Differences in the average sinking rate of particulate matter cause the export ratio to differ between lakes and oceans of the same productivity. Third, the decline in euphotic zone depth as chlorophyll increases is steeper in oceans than in lakes. Differences in the distance over which particles must sink cause the export ratio to differ among similarly productive lakes and oceans.

Methods

To test the above hypotheses, we compare freshwater and marine regressions which use

Table 1. Primary production and chlorophyll data summary. Units are mg m $^{-3}$ for Chl, mg C m $^{-3}$ h $^{-1}$ for primary production, and mg C (mg Chl *a*) $^{-1}$ h $^{-1}$ for assimilation number (*A*).

Source	*n*	Chl	Primary prod.	*A*	Site
Ocean					
Bienfang et al. 1984	19	0.30–3.26	0.15–11.4	0.25–5.67	N Pacific, Hawaii
Birrien et al. 1991	12	0.11–0.23	0.02–0.28	0.09–2.39	Iroise Sea, France
Bradford and Chang 1987	8	0.27–1.19	2.54–5.91	3.68–14.9	Westland, New Zealand
Chang and Bradford 1985	12	0.54–1.13	0.14–0.78	0.16–0.75	Westland
Glover et al. 1986	3	0.51–1.49	0.32–1.21	0.63–1.10	Gulf of Maine
Hanson et al. 1986	5	1.13–7.53	4.07–26.7	3.47–3.74	Ria de Arosa, Spain
HOT	19	0.10–0.25	0.17–0.65	0.83–3.61	N Pacific gyre, Hawaii
Joint et al. 1986	6	0.30–13.1	0.57–2.62	0.20–2.54	Celtic Sea, Ireland
Karl et al. 1991	18	0.41–10.7	0.22–6.78	0.34–1.21	Bransfield St., Antarctica
Laws et al. 1987	7	0.05–0.09	0.27–0.62	5.00–9.63	N Pacific gyre
Laws et al. 1989	8	0.05–0.14	0.25–0.39	2.38–7.09	N Pacific gyre
Mackenzie and Gillespie 1986	10	0.63–6.98	1.43–20.0	1.14–3.30	Tasman Bay, New Zealand
Riegman and Colijn 1991	36	0.13–13.0	0.25–5.90	0.37–17.0	Dogger Bank, North Sea
Videau 1987	5	1.22–3.43	2.64–11.3	2.16–5.41	NE Atlantic, France
Smith and Baker 1978	123	0.04–6.17	0.03–18.1	0.34–8.72	Caribbean, Sargasso Sea, central and NE Pacific
Lakes					
Smith 1979	83	0.28–96.0	0.05–145	0.13–5.71	N America, Europe, Philippines

euphotic zone Chl concentrations to predict euphotic zone primary productivity, the sinking flux of C from the euphotic zone or mixed layer, and the euphotic zone depth. Models from the literature were used to test for differences between marine and freshwater euphotic zone depth–Chl relationships. Our own data were combined with observations culled from the literature to relate euphotic zone primary productivity and carbon sinking flux with Chl concentrations. When collecting data from graphs, we used an image analysis system (Cue-2 Image Analyzer version 1.5, Olympus Co.).

Primary productivity–chlorophyll data—The freshwater data are from the literature review of Smith (1979) (Table 1). These data represent seasonal-annual means of euphotic zone primary productivity and Chl for lakes primarily in northern Europe and North America. Both productivity and Chl were expressed on a per cubic meter basis in the original paper. The daily productivity rates were converted to hourly units by dividing all data by 13 h because most of the data represent summer values. These productivity rates therefore represent average hourly primary productivity over the daytime period.

Marine euphotic zone primary productivity and Chl data were unaveraged individual observations collected from published studies and unpublished data from the Hawaii Ocean Time Series (HOT) station of the Global Ocean Flux Study (Table 1). These data are part of the emergent HOT Program database which is available with the worldwide Internet system and anonymous file transfer protocol (ftp). The data are in a subdirectory called */pub/hot* and the workstation's address is *hokulea.soest.hawaii.edu.*

Only primary productivity estimates that were integrated over the euphotic zone are included in the data. Estimations of productivity were first brought to daily units to make them comparable with the freshwater data. Half-day incubations were doubled. Short-term (2–6 h) incubations centered around noon were extrapolated to daily units as

$$dPP = (PP \cdot I) + [0.5 \cdot PP \cdot (D - I)]. \quad (2)$$

dPP and PP are the daily and hourly photosynthetic rates, respectively, I is the length of the incubation in hours, and D the daylength defined as the period from sunrise to sunset in hours. The left-hand portion of the equation estimates the production over the incubation period (I). The right-hand portion roughly approximates the production during the rest of the daylight period ($I - D$) by assuming only

half the rate of fixation exhibited during the incubation. This method is intended to correct for the lower irradiance before and after an incubation that straddles noon. The daylength used in the calculation was taken from the original paper or calculated from date and latitude.

When compared to independent observations of daily primary productivity (Chang and Bradford 1985; Bradford and Chang 1987), our estimates calculated from Eq. 2 and the estimated daylengths explained 95% of the variance in the observed data and yielded unbiased parameter estimates. Division of the final estimates of PP by the daylength in hours was required to correct for variations in daily irradiance resulting from latitudinal and seasonal differences. Division by euphotic zone depth and daylength increased the fit of the data. Assimilation number was calculated by dividing the euphotic zone productivity by the chlorophyll concentrations averaged over the euphotic zone.

Sinking flux–chlorophyll data—The freshwater observations of carbon sinking flux are those of Baines and Pace (1994). Fifteen stratified lakes of the northeastern U.S. were sampled 2–3 times in summer. Cylindrical sediment traps with internal height : diameter (aspect) ratios of 5 and containing a 0.75% saline layer in the bottoms were used to measure the sinking flux of C. Settled material was collected on glass-fiber filters (Whatman GF/F), and C was measured after combustion of the filters at 1,000°C in a Carlo-Erba CNS (model NA-1500) analyzer. This temperature is high enough to oxidize both organic and inorganic forms of C. However, because most of the lakes sampled are not prone to calcite precipitation, this method can be assumed to approximate organic C concentration. Water-column chlorophyll was measured with a Turner Designs fluorometer after extraction of the filters in basic methanol (1 ml 1 N NaOH liter^{-1} of methanol).

Marine data are from published studies and unpublished reports of the HOT study. An effort was made to include seasonally dynamic and productive coastal environments because these are likely to exhibit high export ratios (Wassmann 1990). Almost all the oligotrophic points are from the open Pacific near Hawaii.

Statistical analyses—Regressions were compared with ANCOVA in the General Linear Models procedure of SAS (Version 6.3). Euphotic zone Chl concentration was used as the continuous predictor and habitat type (marine or freshwater) as the noncontinuous predictor. *F*-tests were used to detect differences between the elevations and slopes of the marine and freshwater regressions. Model 1 regression parameters, predictions, and confidence limits were calculated with the REG procedure of SAS. The use of model 1 calculations is justified when prediction within the range of the data is the goal. When developing regressions, it was necessary to $\log_{10}$ transform all data to obtain normality and stabilize the variance.

Prediction of export ratio—The regressions developed were combined to predict the export ratio from euphotic zone Chl concentration and areal primary production. These predictions were compared with reports from the literature to determine whether the difference between marine and freshwater export ratio–primary productivity relationships can be accounted for by the relationships summarized here. This calculation is possible because all terms in the equation defining export ratio (*e*, Eq. 1) have been regressed against euphotic zone Chl concentration. Placing Eq. 1 into logarithmic terms, we get

$$\log e = \log S - (\log \mathrm{PP} + \log Z). \quad (3)$$

Equations predicting daily primary productivity, C sinking flux, and euphotic zone depth from euphotic zone Chl concentrations were substituted into Eq. 3. A hypothetical daylength of 12 h was assumed to convert predictions of hourly productivity to daily units. Regressions based on mean data were used when possible since we were interested in average system behavior. The Secchi disk depth predictions of Carlson (1977) were multiplied by 2.4 under the assumption that Secchi disk depth corresponds on average to the depth where light is 15% of incident irradiation. These predictions are based on surface chlorophyll and are therefore slightly biased since the ratio of surface to euphotic zone Chl is not constant along the trophic gradient. Marine euphotic zone Chl concentrations and euphotic zone depth are assumed to be related by a slope of 0.32 based on the findings of Lorenzen (1970).

We attempted to determine reasonable maximum confidence intervals for the mean predictions of the export ratio obtained by com-

Table 2. Summary of regressions of Chl on primary production for marine systems. Chl in mg m^{-3} (this study) or mg m^{-2} (Lorenzen 1970; Hayward and Venrick 1982; deLafontaine and Peters 1986). Production in mg C m^{-2} d^{-1} (Lorenzen 1970; deLafontaine and Peters 1986), mg C m^{-2} h^{-1} (Hayward and Venrick 1982), and mg C m^{-3} h^{-1} (this study). The model was $\log Y = a + (b \cdot \log\mathrm{Chl}) + [c \cdot (\log\mathrm{Chl})^{-2}]$.

Source	a	b	c	r^2	n	P-value
		Y = Euphotic zone production				
Ocean						
Lorenzen 1970	2.03	0.76	—	—	91	0.0001
Hayward and Venrick 1982	0.53	0.91	—	0.79	95	0.0001
deLafontaine and Peters 1986	1.49	0.70	—	0.42	225	0.0001
This study	0.17	0.83	—	0.56	289	0.0001
Lakes						
Smith 1979	−0.33	1.71	−0.27	0.89	83	0.0001
		Y = Assimilation No.				
Ocean						
Lorenzen 1970	*	−0.23	—	—	91	*
Hayward and Venrick 1982	0.53	−0.09	—	0.03	95	0.08
deLafontaine and Peters 1986	*	−0.30	—	—	225	*
This study	0.17	−0.17	—	0.05	289	0.0001
Lakes						
Smith 1979	−0.33	0.71	−0.27	0.32	83	0.0001

* Insufficient information to allow calculation.

bining regression models. The variance of the export ratio predictions (s^2) can be approximated from the variance of the predictions by assuming no covariance among the residuals. Under these conditions, the variances of the predictions are additive. Thus,

$$s^2 = s_{PP}^2 + s_S^2 + s_Z^2. \quad (4)$$

The terms s_{PP}^2, s_S^2, and s_Z^2 are the variances associated with the mean predictions of primary productivity, sinking flux, and euphotic zone depth calculated according to standard formulae (Draper and Smith 1981). The necessary statistics were not available to calculate the variances for predictions of euphotic zone depth, so this variance is assumed to equal the variance associated with the primary productivity predictions. The large fraction of variance explained by the euphotic zone regressions ($r^2 > 0.80$, Lorenzen 1970; Carlson 1977) suggests that our assumptions probably lead to an overestimate of the variance associated with these predictions. Variances around slope and intercept estimates were calculated under the same assumptions adopted when calculating the variance of mean predictions. Confidence intervals for mean predictions and parameter estimates were approximated by multiplying the square root of each variance by a t-value ($\alpha = 0.05$, two-tailed distribution) corresponding to the degrees of freedom of the sinking flux-Chl regressions because these regressions contributed the most variance and had the fewest degrees of freedom. For the marine predictions, t was 2.26 (df = 9); for freshwater, t was 2.16 (df = 13).

Results

Primary productivity–chlorophyll relationships—Two data sets were compiled for marine systems (Table 1). We culled 166 observations of marine euphotic zone primary productivity and Chl from 14 studies spanning a wide range of habitats. Productivity varied from 0.02 to 26.7 mg C m^{-2} h^{-1} and euphotic Chl ranged from 0.05 to 13.1 mg Chl m^{-3}. Another 123 observations were taken from a study by Smith and Baker (1978). From this study, only average Chl concentrations for the water column between the surface and the depth of one attenuation length (=1/diffuse attenuation coefficient) could be extracted. The euphotic zone average was calculated from the attenuation length average with a regression reported for the same data by Smith and Baker (1978). Euphotic zone productivity ranged from 0.04 to 6.2 mg Chl m^{-3} and 0.03 to 18.1 mg C m^{-3} h^{-1} primary productivity. A statis-

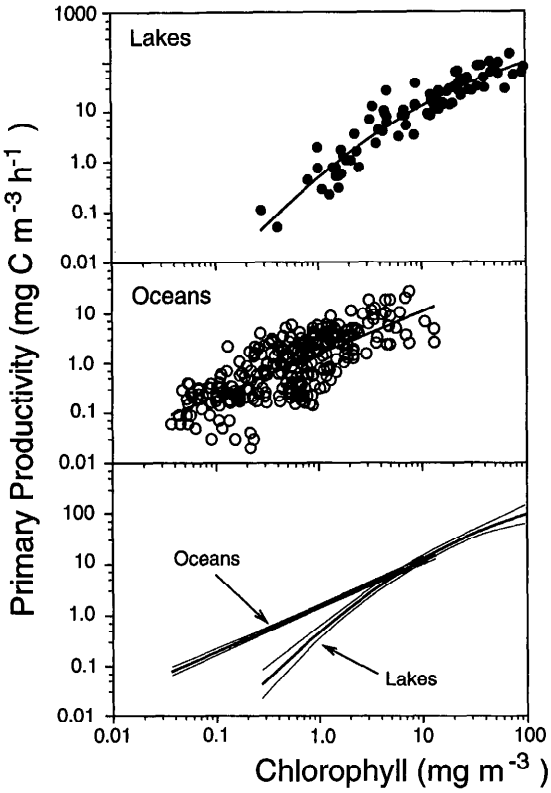


Fig. 3. Euphotic zone primary productivity vs. euphotic zone Chl in oceans and lakes. Solid lines in the upper panels represent the regressions. Both regressions are presented in the lower panel (thick lines) along with 95% C.I. for the mean prediction (thin lines). Regression equations given in Table 2.

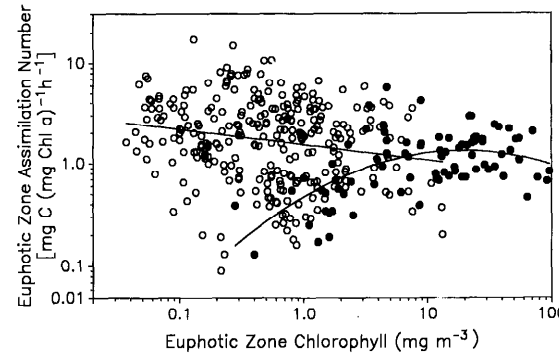


Fig. 4. Assimilation numbers averaged over the euphotic zone vs. euphotic zone Chl for marine (○) and freshwater (●) systems, data and regression lines. Regression equations given in Table 2.

tical comparison between the two data sets indicated only a marginally significant difference in the slope of the regression of primary productivity on chlorophyll ($P = 0.026$). Therefore, we combined the data sets when we compared the marine and freshwater regressions. The findings reported below do not depend on which marine data are compared to the lake data.

Differences exist in the ranges covered by the freshwater and marine data (Table 1). Lake Chl concentrations are generally higher than the marine estimates. On the other hand, primary productivity in lakes virtually encompasses the range found in the ocean. The lake and ocean data overlap in the range 0.28–13.1 mg m^{-3} for Chl concentrations and 0.05–26.7 mg C m^{-3} h^{-1} productivity.

The marine and freshwater regressions of primary productivity on Chl differ, confirming the first hypothesis (Table 2, Fig. 3). An ANCOVA revealed a highly significant difference between the slopes of the freshwater and marine linear models ($P < 0.0001$). However, the freshwater regression was nonlinear even after log transformation (Baines and Pace 1994). A quadratic model

$$\log PP = a + (b \times \log Chl) + [c \times (\log Chl)^2] \quad (5)$$

described the lake data significantly better than did a linear model (Table 2, Fig. 3, P-value for $c = 0.002$). This nonlinearity does not render the ANCOVA meaningless. The linear model overestimates the residual variance associated with the freshwater regression, making it much less likely to detect differences between the two slopes. Consequently, the ANCOVA based on the linear models can be taken as a conservative test for a difference in the relative steepness of the lake and ocean regressions.

The lake and ocean regressions differ most strongly at the oligotrophic end of the gradient. Euphotic zone primary productivity averages 11-fold higher in the ocean than in lakes when Chl = 0.3 mg m^{-3} (Fig. 3). The freshwater and marine regressions converge as productivity increases, ultimately intersecting near 5 mg Chl m^{-3}. At 13 mg Chl m^{-3}, freshwater productivity is predicted to be 1.4-fold higher than marine productivity.

The efficiency of production as measured by

Table 3. Data sources and description for Chl (mg m^{-3}) concentrations and organic C flux (mg C m^{-2} d^{-1}) in marine systems. For Hargrave and Taguchi (1978) and Peinert et al. (1982), means are weighted by the interval between sampling dates for chlorophyll and the deployment period for the sediment-trap flux estimates.

Study	*n*	Chl concn			Org C flux			Site
		Min	Mean	Max	Min	Mean	Max	
Ocean								
Fleeger et al. 1989			7.1			625		Auke Bay, Alaska 1985
			6.4			1,107		Auke Bay 1986
			8.6			544		Auke Bay 1987
			5.3			362		Auke Bay 1988
Hargrave and Taguchi 1978	8	1.4	2.2	3.2	89	219	270	Bedford Basin, Nova Scotia
Karl et al. 1991	18	0.3	1.9	7.4	40	143	373	Bransfield St., Antarctica
HOT	16	0.1	0.2	0.3	18	35	62	Central N Pacific
Lindahl 1991	15	3.0	19.7	37	656	1,948	5,879	Gullmar fjord, Sweden
Nelson et al. 1987	1		0.4			32		S California coast
Passow 1991	7	4.2	6.6	10.5	206	377	566	Baltic Sea
Peinert et al. 1982	10	1.4	2.1	5.3	70	281	767	Kiel Bight
Wassmann et al. 1990	4	1.9	4.6	7.3	49	388	835	Barents Sea
Marine totals	79	0.1	5.5	37	18	521	5,879	
Lakes								
Baines and Pace 1994	39	0.4	6.2	33.0	26	197	459	NE USA

the assimilation number increases with productivity in lakes, but decreases or does not vary with productivity in the ocean (Table 2, Fig. 4). On average, over the range of Chl held in common for the two data sets (0.3–13 mg m^{-3}), the marine assimilation numbers decline 2-fold [1.8–0.96 mg C (mg Chl *a*)$^{-1}$ h^{-1}] with a geometric average of 1.3. Assimilation numbers in lakes increase by almost 9-fold over the same range in Chl [0.17–1.34 mg C (mg Chl *a*)$^{-1}$ h^{-1}] and average 0.7 (50% of the marine estimates).

Sinking flux–chlorophyll relationships—The sinking flux data spanned a smaller range of Chl concentrations than the primary productivity data (Table 3). There were 79 marine observations from nine studies representing a wide range of environments. Chl ranges were similar in the lake and ocean data. However, C sinking flux varied much more widely in the ocean than in lakes. Studies of blooms are particularly prevalent in the marine data (Wassmann et al. 1990; Lindahl 1991; Fleeger et al. 1989). Such systems are generally believed to export large amounts of primary production (Wassmann 1990), so any tendency toward higher sinking fluxes in productive marine environments should be accentuated in this data set. The lake data have no observations from the spring period. Because the spring bloom is often dominated by diatoms which may exhibit high sinking rates, our sinking flux estimates may be relatively low. However, community sinking rates inferred from our flux estimates were not inconsistent with most observations of diatom sinking rates in the lit-

Table 4. Statistical analyses of the relationship between euphotic zone Chl and organic C sinking flux: $\log S = a + (b \cdot \log\text{Chl})$. ANCOVA tests for difference between the lake and ocean regression intercepts and slopes. Δa = difference between lake and ocean intercepts; Δb = difference between lake and ocean slopes.

Model	Regression results					ANCOVA results			
	a	*b*	*r*	*n*	*P*	Δa	*P*	Δb	*P*
Unaveraged data									
Ocean	2.09	0.79	0.82	79	<0.0001				
Lake	1.90	0.51	0.54	39	<0.0001	0.19	0.014	0.28	0.011
Means									
Ocean	2.09	0.81	0.90	11	<0.0001				
Lake	1.82	0.62	0.86	15	<0.0001	0.27	<0.0001	0.19	0.11

erature (Baines and Pace 1994). Consequently, we do not believe that the bias introduced into our flux estimates is very large.

The slope of the regression between POC sinking flux and Chl was greater for the marine data than for lakes but with only marginal statistical significance (Table 4, Fig. 5, $P = 0.011$). The slopes based on single observations differed by 0.28 units, whereas the slopes derived from the mean data differed by 0.19 units. The observed slope differences indicate that the difference between the two regression lines increases by between 1.5- and 2.0-fold for every 10-fold increase in Chl. This shift is small compared to that seen for the productivity–Chl relationships in which the difference between the lake and ocean predictions increases by 8.5-fold as Chl increases from 0.3 to 3 mg m^{-3}.

Sinking flux of C was higher at a given level of Chl in the ocean than in lakes (Fig. 5). For the regression based on unaveraged data, this difference averaged 2.2-fold; for the regression based on means, the average difference was 2.3-fold. This trend is seen most clearly in the mean data.

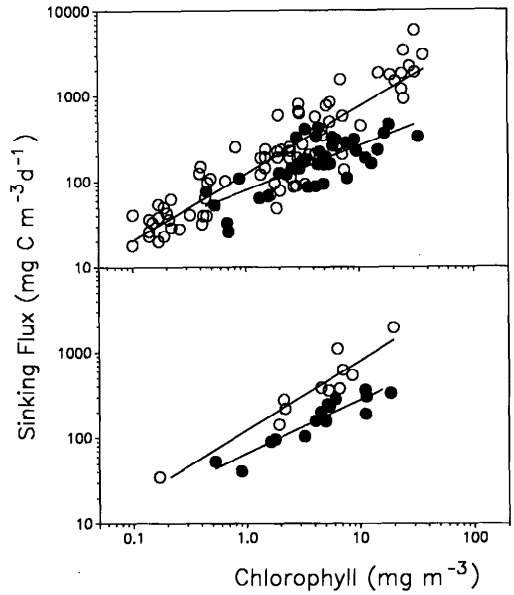


Fig. 5. Carbon sinking flux from the euphotic zone vs. euphotic zone Chl for marine (○) and freshwater (●) systems, data and regression lines. Upper panel—individual observations. Lower panel—mean observations. Regression equations given in Table 4.

Prediction of export ratio from chlorophyll—The export ratio is predicted to increase with Chl in the ocean and decrease with Chl in lakes (Table 5, Fig. 6). In the ocean, the export ratio increases by ~2-fold for every 10-fold increase in Chl. This increase is large relative to the confidence limits of the predictions and the slope is significant ($P < 0.01$, Table 5). In lakes, the export ratio is initially high, but quickly decreases. There is a hint that the export ratio may increase again at high Chl concentrations, but the limited range of the data used to construct the sinking flux regression makes it impossible to substantiate this trend at higher algal densities. The confidence intervals around the predictions of lake export ratio are large.

Discussion

Our results indicate that phytoplankton in oligotrophic lakes and oceanic areas differ in their Chl-specific productivity and that this difference largely causes the export ratio to increase with productivity in the ocean and to decrease with productivity among lakes. By comparison with the differences between the productivity–Chl relationships, the discrepancies between the sinking flux–Chl relationships for lakes and the ocean were small. More-

Table 5. Summary of parameters from regressions and derived models. Standard errors in parentheses. Parameters for Eq. 9 are determined by subtracting those of Eq. 7 and 8 from those of Eq. 6. Standard errors for Eq. 9 parameters calculated by taking the square root of the summed variances for the corresponding parameters in Eq. 6–8. Variances for Eq. 8 were assumed to equal those of Eq. 6 (*see text*).

	Ocean		Lake		
Eq.	*a*	*b*	*a*	*b*	*c*
(6) $\log S = a + (b \cdot \log Chl)$	2.09 (0.070)	0.81 (0.092)	1.82 (0.052)	0.62 (0.069)	
(7) $\log dPP = a + (b \cdot \log Chl) + [c \cdot (\log Chl)^2]$	1.25 (0.027)	0.83 (0.041)	0.78 (0.061)	1.71 (0.14)	−0.27 (0.077)
(8) $\log Z = a + (b \cdot \log Chl)$	1.51	−0.32	1.26	−0.68	
(9) $\log e = a + (b \cdot \log Chl) + [c \cdot (\log Chl)^2]$	−0.67 (0.08)	0.30 (0.11)	−0.22 (0.10)	−0.41 (0.21)	0.27 (0.08)

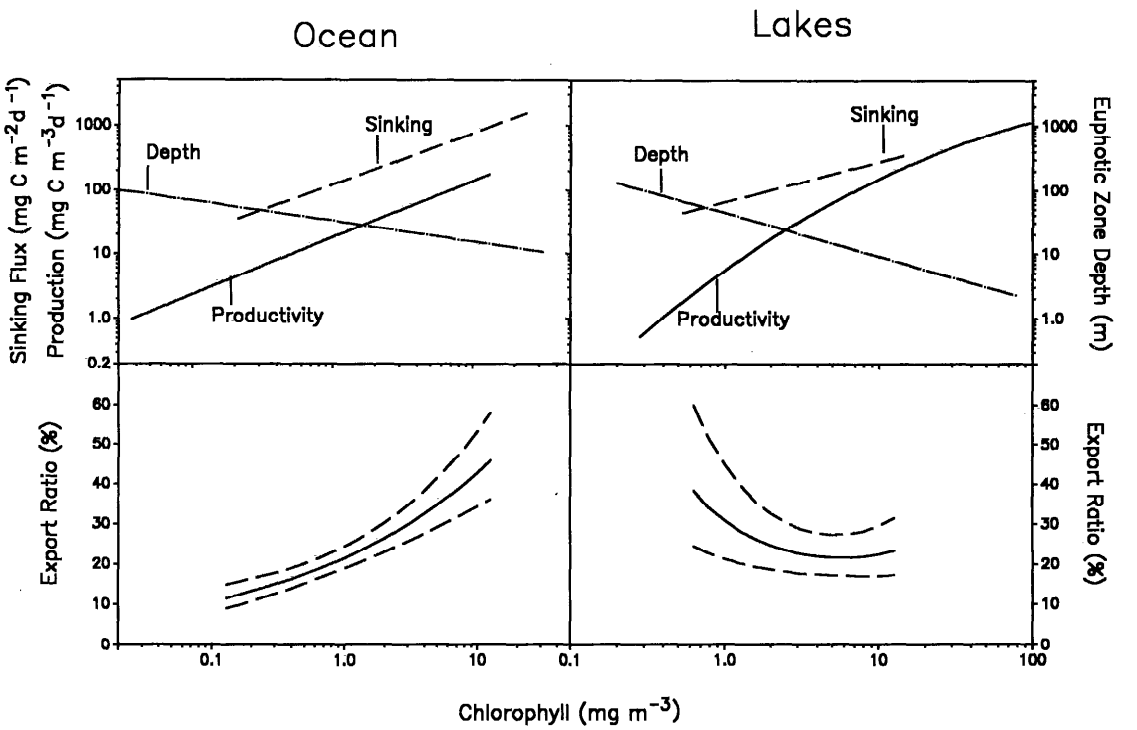


Fig. 6. Euphotic zone depth, primary productivity, C sinking loss, and export ratios vs. Chl concentrations. Upper panels—Chl-based regressions of euphotic zone primary productivity, depth, and C sinking losses vs. euphotic zone Chl concentrations in marine and freshwater systems. Lower panels—predictions (solid lines) with 95% mean prediction confidence intervals (broken lines) of the export ratio from Chl in marine and freshwater systems. Predictions and confidence intervals are derived from regressions in upper panels. Equations relating the export ratio to Chl are presented in Table 5.

over, according to Lorenzen (1970) and Carlson (1977), the decrease of the euphotic zone thickness with increasing surface Chl is more pronounced across lakes (slope = −0.68) than across oceanic regions (slope = −0.29). This pattern is opposite that required to explain why the export ratio–Chl relationships differ in lakes and the ocean. The productivity–Chl relationships, on the other hand, differed dramatically and in the manner hypothesized based on the export–Chl relationships. This difference seems robust. Several previous independent literature reviews have found that the slope of the regression of euphotic zone Chl on euphotic zone production ranges from 0.7 to 0.9 in the ocean (Table 2). We have adopted an intermediate slope of 0.83, based on data from our search and the data of Smith and Baker (1978). The freshwater data from Smith (1979) consists of means from 83 lake-years and therefore represents a database at least as substantial as that for marine systems.

The difference in the primary productivity–Chl relationship is sufficient to explain the qualitative difference between the export ratio–productivity relationships in lakes and the ocean. By predicting the export ratio from Chl concentrations with the models developed here, we obtain a negative relationship between Chl and the export ratio in lakes and a positive relationship in the ocean (Table 5, Fig. 6). The marine slope is statistically significant ($P < 0.01$) but the freshwater slope is not ($0.1 > P > 0.05$). Because Chl is shown to be related to productivity, these results correspond qualitatively with the observed differences between marine and freshwater export ratio–primary production relationships.

We compared export ratio predictions based on our models with literature reports based on direct observations of production and sinking export. To make this comparison, it was necessary to predict euphotic zone depth and primary productivity from Chl with the equation

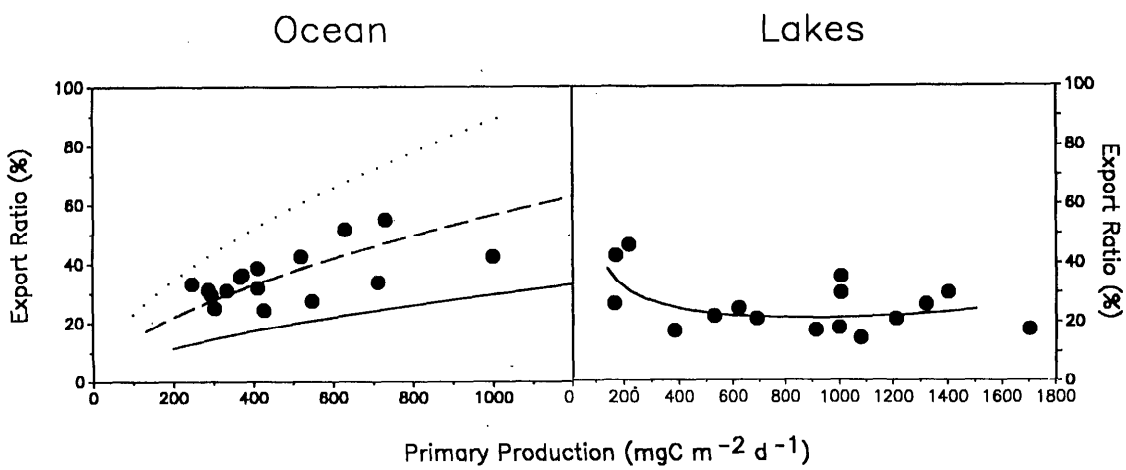


Fig. 7. Export ratio vs. euphotic zone primary production. Sinking flux, primary productivity, and euphotic zone depth were predicted from Chl and then used to compute the predicted primary production and export ratio. Left—marine observations (from Wassmann 1990) and predictions assuming the observed mean assimilation number (solid line) and 67% (broken line) and 50% (dotted line) of the observed mean assimilation number. Right—freshwater predictions (line) and observations (Baines and Pace 1994; Bloesch and Uehlinger 1990).

in Table 2 and from Lorenzen (1970) and Carlson (1977). The results must be considered preliminary as the propagation of error from the original models could not be computed. The predicted export ratios compare very well with observed lake data (Fig. 7). However, the marine export ratios are systematically underestimated by about half (Fig. 7), indicating that the predictions of our models do not apply to the validation data (derived from Wassmann 1990). Of the observations that are the basis of our primary productivity models, 79% were made at latitudes <50°N, whereas only 14% of the validation data were from latitudes <50°N. The average temperature of the areas represented in Wassmann's data are likely to be colder than that of the locales represented in our marine primary productivity-Chl data. Temperature is an important determinant of the phytoplankton photosynthetic capacity and has accounted for significant variability in previous regression analyses of primary productivity and Chl data (Eppley 1972; deLafontaine and Peters 1986). Lower temperatures would result in higher algal biomass per unit of primary production and, therefore, higher sinking fluxes per unit of productivity.

To explore the sensitivity of our predictions to temperature, we modified the Chl-production equation used to produce the predictions. Estimates of the Q_{10} for primary production range between 2 and 2.3—i.e. primary production will increase in an exponential fashion by 2–2.3-fold for every 10°C increase in temperature (Eppley 1972; deLafontaine and Peters 1986). Assuming a Q_{10} of 2, a decline of 6°C would lower the assimilation number by 33% and raise the export ratio prediction by 50%. This change is enough to account for the discrepancy between the predicted and observed export ratios (Fig. 7). A 10°C decline would lower the assimilation number by 50% and raise the predicted export ratio by 2-fold. Such an increase in the export ratio predictions would significantly overshoot the observed export ratios (Fig. 7). This analysis suggests that our predictions of export ratio could be sensitive to moderate temperature differences between the data sets used to produce and test the export ratio predictions.

Control of the export ratio along productivity gradients—The balance between sinking flux and primary productivity seems to determine how the export ratio will be related to productivity. In the ocean, sinking flux and primary productivity change at the same rate with increasing Chl (Fig. 6). Thus, the balance between the sinking flux and primary productivity does not change systematically with the level of productivity. The increase in export ratio with productivity in the ocean is forced primarily by the decline in euphotic zone depth with increasing productivity (Lorenzen 1970, Fig. 6), and the inverse relationship between

euphotic zone depth and export ratio (Eq. 1). In lakes, by contrast, primary productivity increases much more sharply with Chl than does sinking flux (Fig. 6). Over the range in Chl for which the productivity and sinking flux relationships overlap (0.5–17.0 mg m^{-3}), the regressions indicate that productivity increases on average 177-fold (from 0.13 to 23.2 mg C m^{-3} h^{-1}), whereas sinking flux increases on average only 9-fold (from 43 to 383 mg C m^{-2} d^{-1}). Therefore, the productivity : sinking flux ratio declines by almost 20-fold. A slope of −0.68 for the euphotic zone depth–Chl regression indicates an 11-fold decrease in euphotic zone depth. Combined, these results indicate that the export ratio should decline by ~2-fold over the range of our data.

Interpretations and hypotheses—Several hypotheses might explain why Chl-specific productivity differs between lakes and the ocean in areas with low standing algal biomass. These hypotheses concern methodology, effects on algal photosynthetic rates, and use of algal biomass by consumers. Although we cannot conclusively determine which of these hypotheses is most likely, it may be constructive to review some of them.

Generally, techniques for measuring primary production in lakes have not incorporated the "ultra-clean" methods used by many oceanographers to reduce contamination and poisoning by trace metals (Fitzwater et al. 1982). Some workers claim that such techniques can elevate primary production estimates 2–4-fold (Fitzwater et al. 1982; Laws et al. 1987), although others failed to find a statistical difference between standard and ultra-clean techniques (Marra and Heinemann 1984). Use of such techniques in freshwater oligotrophic environments may result in higher productivity estimates. However, the differences between the marine data of Smith and Baker (1978) and the freshwater data of Smith (1979) predates the widespread use of clean techniques in oceanography. Furthermore, productivity at low Chl concentration can differ by an order of magnitude on average between lakes and the ocean, which is much higher than the 2–4-fold increase in lake productivity estimates that might result from using ultra-clean techniques. Nonetheless, the effect of contamination on primary production estimates in oligotrophic lakes warrants investigation.

The productivity of a given amount of phytoplankton biomass may differ between lakes and the ocean for several reasons. Some chemical aspect of oligotrophic lakes (e.g. metal concentration) may poison phytoplankton or exact some extra metabolic investment. More intense mixing in the ocean may lead to more temporally variable light fields, which can elevate photosynthetic rates compared to less variable situations (Marra 1978). In oligotrophic lakes in the temperate zone, the phytoplankton community may not be as well adapted to chronically low nutrient conditions as are their oceanic counterparts because greater seasonal variability in temperature, light, or nutrient concentration could select for traits other than fast relative growth at very low nutrient concentrations. Finally, bacteria may derive a higher fraction of their C and energy needs from allochthonous sources in oligotrophic lakes than in eutrophic lakes or the ocean (del Giorgio and Peters 1993). Because bacteria can successfully compete with phytoplankton for critical nutrients (Currie and Kalff 1984), the result may be less nutrient availability to the phytoplankton.

Even if phytoplankton photosynthetic rates differ between oligotrophic lakes and oceanic areas, it is still perplexing that relatively high Chl concentrations are maintained in oligotrophic lakes over seasonal scales despite low Chl-specific productivity. If, for the sake of argument, we assume a C : Chl ratio of 50 : 1, the turnover time of algal C in lakes is >10× longer (16.5 d) than in the ocean (1.5 d) when average euphotic Chl concentrations are 0.3 mg m^{-3}. The slow turnover exhibited by oligotrophic phytoplankton over seasonal scales in lakes suggests that freshwater herbivores are less efficient than their marine counterparts at harvesting phytoplankton biomass when phytoplankton concentrations are very low. The basis for this difference is unclear. Some marine filter feeders (e.g. appendicularian and thaliacean tunicates, and pteropod molluscs) harvest very small (< 10 μm) particles efficiently even at very low concentrations (Alldredge and Madin 1982), but in most systems these animals are sporadically abundant. In any case, the much lower Chl concentrations observed in oceans than in lakes could reflect the efficiency of the herbivore communities more than the supply of nutrients.

Implications for predictive models—This study may hold implications for large-scale predictions of sinking fluxes in the ocean. Models that have been developed for this purpose have assumed that sinking fluxes should be closely related to water-column productivity and the depth of the water column (Martin et al. 1987). This approach presumably derives from the equation of "new production" to sinking export by Eppley and Petersen (1979). However, models developed to predict sinking export from primary production often have low predictive precision and appear to differ substantially from each other (Fig. 1). Using primary production as a predictor presents logistical problems as well, because estimating primary production over large areas of the sea is a considerable task. Algorithms designed for use with satellite imaging will improve the scope of primary production determinations, but there are questions about the precision of such indirect estimates. Chlorophyll, on the other hand, is determined more directly by satellite and seems to be well related to sinking fluxes of C, even when most of that flux may not be algal cells. It seems reasonable to propose the use of chlorophyll as a more precise and logistically feasible predictor of sinking fluxes.

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