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Role of herbivory in controlling phytoplankton abundance: annual pigment budget for a temperate marine fjord

N. A. Welschmeyer [1] and C. J. Lorenzen [2]

[1] **Biological Laboratories, Harvard University; Cambridge, Massachusetts 02138, USA**
[2] **School of Oceanography, University of Washington; Seattle, Washington 98195, USA**

Abstract

An annual pigment budget was constructed for Dabob Bay, Washington (USA) by comparing the downward vertical loss of phytoplankton pigments (chlorophyll and pheopigments) to the production of chlorophyll within the euphotic zone. The vertical flux of pigments was measured with sediment traps deployed at intervals of 1 to 6 wk over a 2.5 yr period yielding 763 d of trap exposure (28 November 1978 – 16 June 1981). The production rate of chlorophyll was calculated from measurements of algal specific growth rates, chlorophyll (chl) crops, primary production (as carbon) and appropriate C:chl ratios. Sixty one to 77% of the annual chlorophyll production was accounted for by the vertical flux of pheopigments resulting from herbivorous zooplankton grazing (macrozooplankton). Algal sinking, represented by downward chlorophyll flux, accounted for only 5 to 6% of the annual chlorophyll production. The remaining fraction of chlorophyll production was estimated to be consumed by small herbivores (microzooplankton), whose fecal material contributes to the suspended pool of pheopigments found in the euphotic zone. The suspended pheopigments are continuously removed by photodegradation. In Dabob Bay, the major process controlling phytoplankton abundance is zooplankton grazing and it appears that the ultimate fate of most phytoplankton is to be consumed by herbivores.

Introduction

Planktonic and terrestrial ecosystems are often contrasted with respect to the gross differences in the standing stocks and turnover rates of the primary producers and the relative importance of herbivory as a factor in controlling plant biomass (Hairston *et al.*, 1960; Crisp, 1964; Odum, 1971; Parsons, 1976). On land, the long turnover times (years) and large stocks of massive woody tissue provide compelling evidence of the generally accepted notion that the impact of herbivores plays a relatively small role in limiting the contemporary crop of plants. The short turnover times (days) of phytoplankton, however, do not necessarily result in the accumulation of large algal standing crops. High phytoplankton production rates may be sustained for extended periods (weeks), although *in situ* changes in algal biomass may be smaller than expected or altogether undetectable. The conventional (and logical) explanation, is that newly produced algal biomass is removed nearly as fast as it is produced, either by herbivory, algal cell-sinking, or physical mixing-advection.

In planktonic systems where seasonal blooms may occur, the characteristic increase in herbivore stocks and coincident demise in phytoplankton biomass provide indirect support for the notion that herbivory is a major process controlling the abundance of phytoplankton. This concept has a considerably long history (Harvey *et al.*, 1935; Fleming, 1939; Riley, 1946). It is somewhat discouraging, however, that the products of experimentally determined herbivore filtration rates and herbivore standing stocks do not necessarily yield community grazing rates adequate to compensate the growth of phytoplankton; for a review see Haney (1973). In such cases, it could be argued that sinking and mixing account for the remaining mass balance, or that the estimated algal growth rates were too high and/or grazing rates were too low. The latter is understandably a possibility when one considers the difficulty of assessing the total community grazing activity of diverse zooplankton assemblages that include both protozoans and metazoans. In either case, statements regarding the importance of herbivory as a controlling factor of phytoplankton abundance remain weakly tested.

The presumed importance of herbivory as a major loss process to phytoplankton is not universal. The freshwater literature is replete with examples suggesting that sinking is the major loss process to phytoplankton (see Hutchinson, 1967; and Walsby and Reynolds, 1980; for reviews). Indeed, sinking has been viewed as a major process influenc-

ing seasonal succession in freshwater phytoplankton communities (Knoechel and Kalff, 1975; Kalff and Knoechel, 1978; Reynolds *et al.*, 1982). In contrast, the hypothesis that grazing controls phytoplankton in the oceans, and the accompanying corollary, that most primary production is consumed by herbivorous grazers, is often used as a first assumption in marine food-chain models (Ryther, 1969; Paloheimo and Dickie, 1970; Steele, 1974).

Several examples of major cell-sinking losses have also been noted in shallow coastal marine environments (Smetacek *et al.*, 1978; Malone and Chervin, 1979; Malone *et al.*, 1983). The losses seem most acute during the demise of blooms and are often associated with algal, resting-spore formation (Davis *et al.*, 1980; Garrison, 1981).

It is clear that the relative importance of grazing and sinking may change order in an episodic fashion, especially in seasonally variable environments. Therefore, generalizations pertaining to the overall net importance of specific loss processes must be carefully evaluated.

Under steady-state conditions, the impact of a given loss process can be assessed by comparing the loss rate to the intrinsic rate of growth of the phytoplankton. If, for instance, the instantaneous growth rate of phytoplankton approximately equals the herbivorous grazing rate, and if the *in situ* change in algal biomass is zero then, by mass balance, other loss processes must be assumed to be minimal. The concept is simple, the measurements are not (Eppley, 1980; Frost, 1980). Non steady-state conditions introduce further complications. Under conditions of large seasonal variations, the experimental determination of biological rate processes (typically conducted over periods of hours) does not necessarily reflect the net overall impact of the given processes. Obviously, on the rise of a phytoplankton bloom, grazing rates must be relaxed with respect to phytoplankton growth. However, during bloom cessation, grazing rates are not necessarily required to meet or exceed phytoplankton growth; sinking, mixing and advection must also be considered. In order to scale the net impact of herbivory, daily experiments must be repeated with a frequency adequate to filter-out large seasonal variations, thus yielding the overall average rates.

Cushing (1976) has provided evidence for the compensation of phytoplankton growth by zooplankton grazing in Lake Erken. The results of that study are the product of a large data base (weekly sampling of the whole water column over 1 yr) whose continuity has been difficult to replicate in marine environments. The problems of advection are also minimized in lake systems compared to most marine systems. The study has not, however, gone uncriticized (Knoechel, 1977; Lewis, 1977).

We have attempted to quantify the overall impact of herbivorous grazing in a temperate marine fjord (Dabob Bay, Washington, USA) by measuring the downward vertical flux of phytoplankton pigments continuously over two annual cycles. The zooplankton populations of Dabob Bay are dominated by copepods which have been shown to quantitatively degrade chlorophyll *a* to pheopigments (Shuman and Lorenzen, 1975). That is, each mole of chlorophyll *a* grazed has been shown to reappear as a mole of pheophorbide *a* in zooplankton fecal material (Shuman and Lorenzen, 1975). The flux of pheopigments contained in rapidly-sinking herbivore fecal pellets was measured continuously with sediment traps. The use of sediment traps removes some of the problems normally associated with the requirement to sample adequately through space and time. Traps passively catch the remnants of biological activity at the surface (in this case, sinking herbivore fecal pellets tagged with pheopigments), thus subsuming the events occurring within the euphotic zone and integrating the results over space and time.

By comparing the average annual downward flux of pheopigments to the average annual chlorophyll (chl) production (via growth rate estimates, ^{14}C primary production estimates and appropriate C:chl ratios), a simple budget was constructed describing the fraction of primary production that was consumed by fecal-pellet-producing herbivores. Results of the study are presented here.

Materials and methods

The study site (Dabob Bay, Washington, USA) and sediment traps have been described previously (Lorenzen *et al.*, 1981; Welschmeyer *et al.*, 1984; Welschmeyer and Lorenzen, 1985). The sediment traps were deployed and recovered at intervals ranging from 6 to 47 d. Traps were positioned at a depth of ca. 60 to 70 m (depth of water column being 110 m). Occasionally, traps were also included at a number of depths from 20 to 100 m, to insure that the flux measured at 60 to 70 m was representative of the pigment flux leaving the euphotic zone.

The traps contained a saline solution (NaCl) which was used to reduce flushing of the collected trap contents. At the time of deployment, solid NaCl was placed at the bottom of the traps (80 g, pet-store animal-lick) and the traps were filled with filtered seawater. The brine formed upon dissolution of the salt lick. The brine also appeared to act as a pigment preservative. Trap material stored in the dark (8 °C) over periods from 1 to 380 d showed little degradation of chlorophyll or pheopigments; exponential decay rates were $-0.009\ d^{-1}$ and $-0.018\ d^{-1}$, respectively ($n = 54$, not significantly different from zero) (Welschmeyer, 1982). No decay corrections were therefore applied to the flux calculations (cf. Iseki *et al.*, 1980). Some trap preservatives, specifically chloroform, have been suggested to convert chlorophyll to pheopigments (Smetacek *et al.*, 1978). Algal cultures stored in our traps, both with and without brine, showed no difference in the ratio of chlorophyll:pheopigments.

Throughout the 2.5 yr study (934 d), we obtained 763 d of continuous trap exposure, representing ca. 82% of the total observational period (28 November, 1978 – 16 June, 1981).

Pigment standing crops and primary production were measured during each visit to the bay. Pigments were determined fluorometrically immediately on board ship using

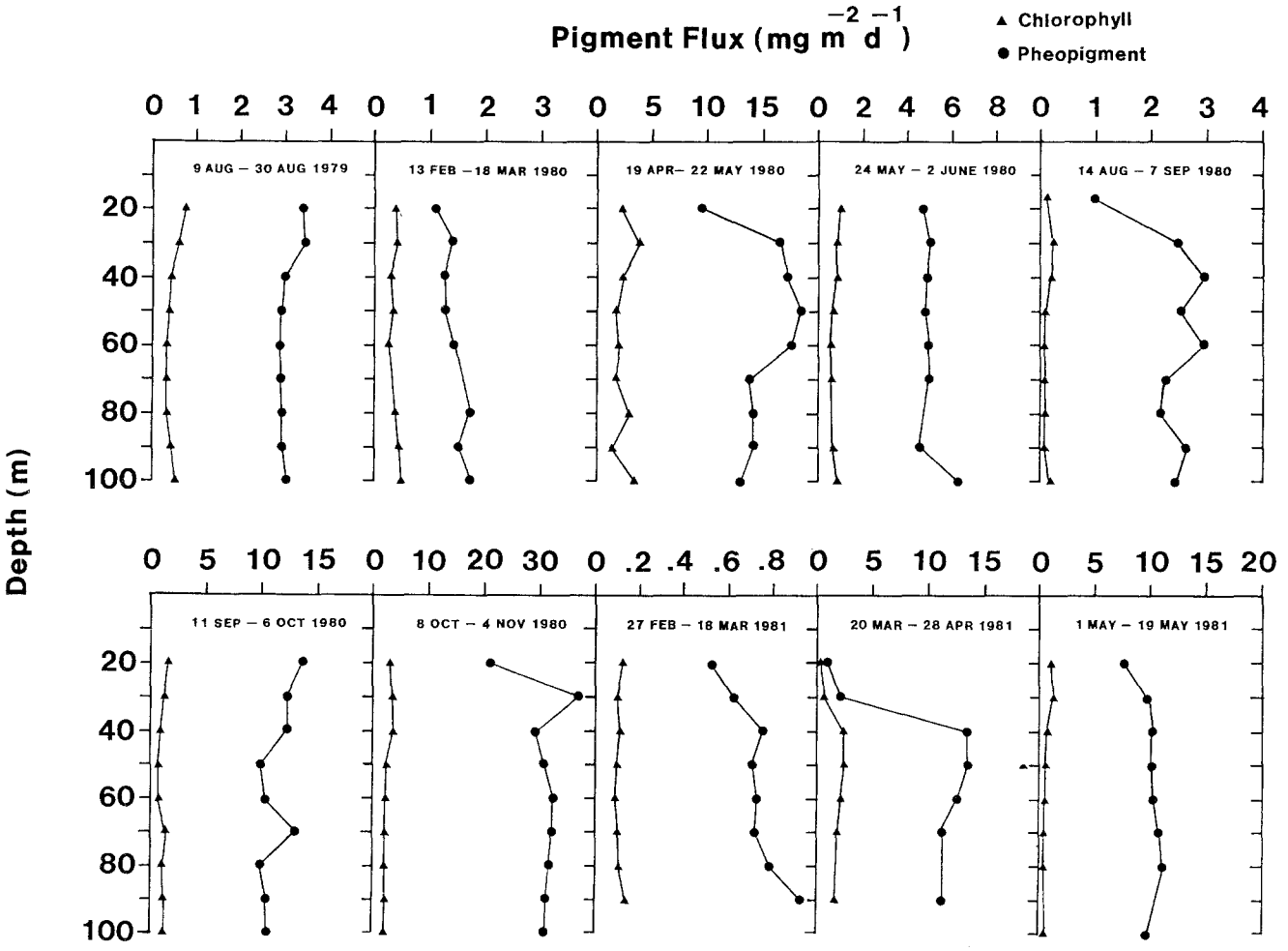

Fig. 1. Chlorophyll and pheopigment flux measured through the water column (20 to 100 m) in Dabob Bay, Washington, USA

90% acetone as an extractant (Lorenzen, 1966). Bottle casts for areal standing-crop measurements were always made at least to the 0.1% light depth (6 to 12 sampling depths). Primary production was measured using the conventional ^{14}C technique (24 h, dawn-dawn *in situ* incubations on tethered moorings, at least to the 0.1% light depth; 125 ml acid-washed Pyrex incubation bottles). On three occasions, chlorophyll ^{14}C-labeling experiments were made to estimate C:chl ratios in addition to primary production (Redalje and Laws, 1981; Welschmeyer and Lorenzen, 1984). Four-liter acid-washed Pyrex incubation bottles were used on those occasions. We detected no difference in the production rates measured in 125 ml or 4 000 ml bottles (cf. Gieskes *et al.*, 1979).

Dabob Bay was chosen as a site for budget experiments due to simplifications that could be made with respect to advective conditions. A map of the study area is given in Welschmeyer and Lorenzen (1985). A sill at the mouth of the bay and the lack of major freshwater tributaries result in minimal horizontal exchange in Dabob Bay. Tidal excursions at the study site are only ca. 100 to 200 m per cycle (Kollmeyer, 1965). Classic estuarine circulation is absent. Deep waters (> 120 m) show persistent oxygen minima (Ebbesmeyer *et al.*, 1975). Summer surface temperature is ca. 20 °C. In contrast, maximum summer surface-temperature in the adjoining well-mixed main basin of Puget Sound is only ca. 13 °C. The above conditions are indicative of the slow water movement in Dabob Bay. For the purpose of the budget to be described herein, we assume that Dabob Bay approximates a closed system, and advection is ignored.

Results

The fluxes of both chlorophyll and pheopigments measured at depths from 20 to 100 m are given in Fig. 1. The fluxes were sometimes reduced near the surface, but essentially uniform at depths in excess of the euphotic zone (> 35 m). This indicates that the bulk of the sinking pigments originated from within the euphotic zone and fecal pellet production was not significant at greater depths in the water column. The uniform profiles also show that the pigments (both chlorophyll and pheopigments) were not degraded during the vertical descent to the bottom (Lorenzen and Welschmeyer, 1983).

Table 1. Long-term pigment fluxes in Dabob Bay, Washington, USA

Trap depth (m)	Deployment		Trap exposure, Δt (d)	Pheopigment flux (mg m^{-2} d^{-1})	Chlorophyll flux (mg m^{-2} d^{-1})
	Time of day (hrs)	Date			
65	08.50	Dec. 2 1978	40.28	0.342	0.067
65	20.00	Jan. 11 1979	21.44	1.192	0.166
65	06.30	Feb. 1 1979	19.40	0.975	0.158
65	09.45	Feb. 22 1979	47.89	0.932	0.196
65	20.40	Apr. 11 1979	8.58	14.719	1.385
65	06.00	May 4 1979	8.52	18.091	2.899
65	18.30	May 12 1979	9.79	11.354	0.443
65	18.00	May 22 1979	27.52	7.904	0.610
70	03.00	June 22 1979	23.98	1.341	0.322
70	02.30	July 16 1979	24.17	0.782	0.128
70	12.00	Aug. 9 1979	20.96	2.833	0.343
70	15.45	Aug. 30 1979	40.68	4.607	0.457
55	19.00	Oct. 11 1979	18.54	3.000	0.322
65	10.00	Oct. 30 1979	20.92	4.403	0.604
65	10.50	Nov. 20 1979	23.91	11.421	1.481
65	12.00	Jan. 17 1980	26.25	5.595	0.984
65	19.30	Feb. 13 1980	33.54	1.437	0.264
90	23.30	Mar. 18 1980	30.40	12.490	2.854
75	20.30	Apr. 19 1980	32.50	18.376	1.509
60	13.05	May 24 1980	9.06	4.957	0.580
55	12.50	June 3 1980	22.90	4.083	0.510
65	10.30	June 26 1980	32.17	6.541	0.542
55	18.10	Aug. 12 1980	25.89	2.711	0.250
60	10.40	Sep. 11 1980	25.16	10.583	0.992
60	09.35	Oct. 8 1980	27.21	32.427	2.348
70	10.45	Jan. 7 1981	6.48	0.563	0.036
65	18.15	Jan. 26 1981	30.94	1.474	0.200
70	09.50	Feb. 27 1981	19.10	0.759	0.106
60	06.40	Mar. 20 1981	39.25	12.834	2.196
60	07.15	May 1 1981	20.38	10.185	0.581
80	17.45	May 20 1981	25.91	1.823	0.233

The fluxes of both chlorophyll and pheopigments from all sediment trap experiments are given in Table 1, together with sediment-trap depths and exposure times. The pigment fluxes are displayed in Fig. 2, showing the strong seasonal variations in the flux of both chlorophyll and pheopigments. Seasonal variations were conicident for both of the pigments; however, the absolute flux of pheopigments was much higher than that of chlorophyll. The average daily fluxes, obtained by integrating over the 2.5 yr period, were 0.76 mg m^{-2} d^{-1} and 6.53 mg m^{-2} d^{-1} for chlorophyll and pheopigments, respectively.

Primary production and pigment standing crops are listed in Table 2. The data are displayed in Fig. 2, revealing the characteristic spring and fall blooms, both in terms of production and algal standing crops. Since primary production estimates were missing between 19 June 1979 and 16 January 1980, this time period was omitted in the calculation of average daily primary production. The average daily rate of production was calculated by integrating the data between the two intervals: 28 November, 1978 – 19 June 1979 and 16 January 1980 – 19 June 1981. This represents a period of 720 d, during which 24 estimates of depth-integrated primary production were made. The average daily rate of primary production, calculated from the area under the curve in Fig. 2, was 531.4 mg C m^{-2} d^{-1}.

Welschmeyer and Lorenzen (1985) have presented estimates of the specific growth rates (d^{-1}) of the phytoplankton crops measured on 22 occasions in Dabob Bay during the same time period considered in the present work. Specific growth rates, μ (d^{-1}), combined with algal standing crops (as mg chl m^{-2}) can be used to calculate chlorophyll production rates, i.e., as the derivative of chl with respect to time, t:

$$\frac{\mathrm{dchl}}{\mathrm{d}t} = \mu \mathrm{chl}\,. \tag{1}$$

The data are included in Table 2 for the purpose of calculating chlorophyll production as in Eq. (1). A gap exists in the data set between 20 June 1979 and 23 May 1980. The average daily chlorophyll production, calculated over the intervals 28 November 1978 – 20 June 1979 and 23 May 1980 – 30 April 1981, was 16.1 mg chl m^{-2} d^{-1} ($\Delta t = 547$ d).

Table 2 also includes C:chl ratios estimated from growth rates, primary production and chlorophyll standing crops (Welschmeyer and Lorenzen, 1985). The average

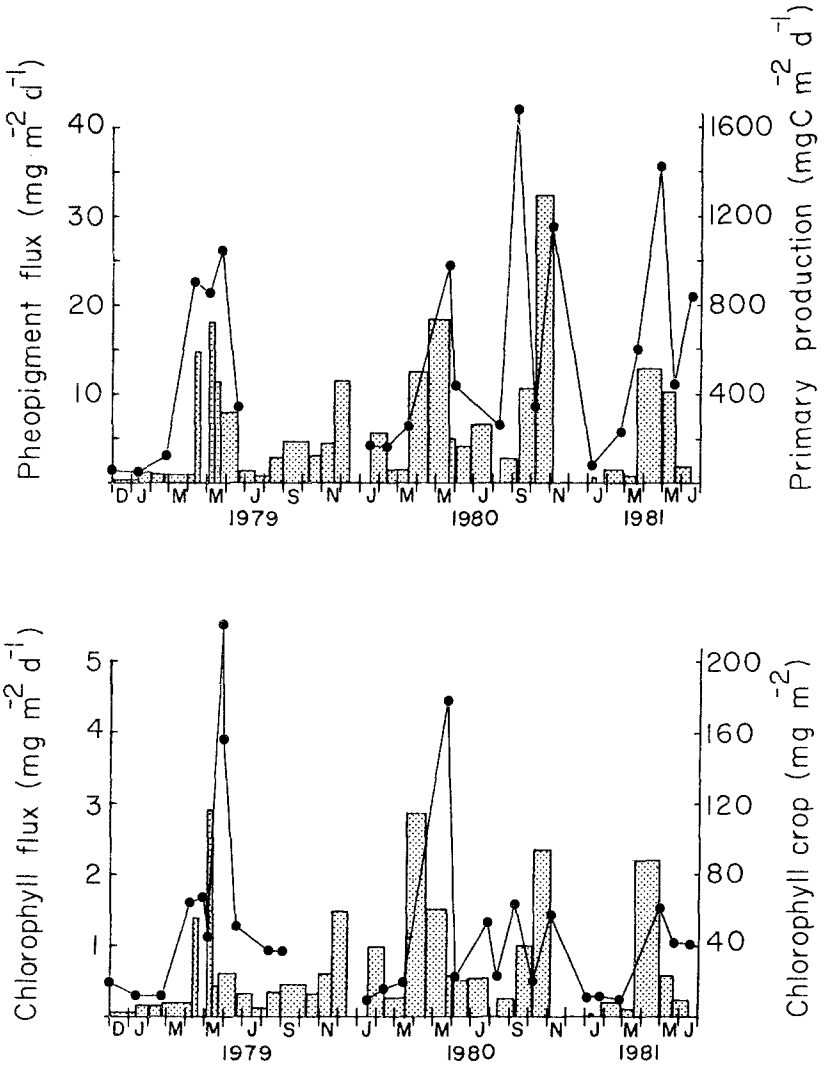

Fig. 2. Pigment fluxes (histogram) and primary production and chlorophyll crops (lines) in Dabob Bay

C:chl ratio of the 19 available estimates was 41.1. This value is not atypical of the range of C:chl values conventionally estimated for coastal phytoplankton assemblages (Lorenzen, 1968; Tett *et al.,* 1975; Banse, 1977; Malone and Chervin, 1979). The values also agree well with C:chl ratios estimated by the ^{14}C chlorophyll-labeling technique in Dabob Bay (Welschmeyer and Lorenzen, 1984, 1985). The average C:chl ratio of 41.1 combined with the average daily rate of primary production (531.4 mg C m^{-2} d^{-1}) yields an estimated average chlorophyll production rate of 12.9 mg chl m^{-2} d^{-1}.

Thus, we derive two similar estimates of average daily chlorophyll production (12.9 and 16.1 mg chl m^{-2} d^{-1}) using two sources of experimental data. One is based on combining the average photosynthetic carbon production with an appropriate estimate of C:chl, and the other is based on the product of specific growth rates and chlorophyll standing crops, integrated over time.

Table 3 compares estimates of chlorophyll production to the loss of pheopigment resulting from herbivorous grazing. Pheopigment flux was converted to its "chlorophyll-equivalent" by multiplying by 1.51. This assumes that (1) chlorophyll *a* is degraded to pheophorbide *a* with 100% molar efficiency (Shuman and Lorenzen, 1975); (2) pheophorbide *a* is the dominant pheopigment found in nature (Patterson and Parsons, 1963; Yentsch, 1967, Jeffrey, 1974; Shuman and Lorenzen, 1975; Vernet, 1983); and (3) pheopigments measured by fluorescent acidification techniques (in mg m^{-3}) are calculated as if they were pheophytin *a* (Holm-Hansen *et al.,* 1965; Lorenzen, 1967a). Thus, the factor 1.51 represents the ratio of the molecular weights of chlorophyll *a* (894) and pheophorbide *a* (593).

Discussion

Relative roles of herbivory and cell sinking

The pigment budget given in Table 3 shows that pheopigment flux, resulting from herbivorous macrozooplankton grazing, accounts for ca. 61 to 77% of the expected pro-

Table 2. Primary production and chlorophyll standing crop in Dabob Bay. Phytoplankton growth rates and microzooplankton grazing rates were taken from Welschmeyer and Lorenzen (1985). C:chl was calculated as C:chl = primary production ÷ [chlorophyll crop × $(e^{\mu t}-1)$], where $t = 1$ d. nd: no data

Date	Primary production (mg C m^{-2} d^{-1})	Chlorophyll crop (mg chl m^{-2})	Phytoplankton growth, μ (d^{-1})	Microzooplankton grazing, g (d^{-1})	C:chl (wt/wt)
28 Nov. 1978	24.99	23.58	0.053	0.009	19.47
30 Nov. 1978	61.47	18.98	0.065	0.014	48.22
10 Jan. 1979	57.67	11.00	0.121	0.009	40.76
21 Feb. 1979	117.80	11.62	0.264	0.092	33.55
9 Apr. 1979	898.64	64.20	0.141	0.030	92.44
11 Apr. 1979	918.29	69.68	0.085	0.037	148.55
1 May 1979	nd	65.92	0.212	0.048	nd
3 May 1979	858.39	45.72	0.251	0.079	65.81
22 May 1979	1 048.77	220.07	0.182	0.112	23.87
23 May 1979	nd	155.64	0.232	0.092	nd
19 June 1979	331.34	51.82	0.133	0.034	44.95
20 June 1979	nd	51.25	0.298	0.145	nd.
16 Jan. 1980	161.08	8.80	nd	nd	nd
12 Feb. 1980	163.87	15.31	nd	nd	nd
18 Mar. 1980	248.86	19.61	nd	nd	nd
23 May 1980	978.66	62.46	0.524	0.247	22.75
3 June 1980	445.15	21.90	0.426	0.180	38.27
13 Aug. 1980	262.69	21.50	0.431	0.122	22.68
10 Sep. 1980	1 672.30	64.37	0.805	0.107	21.01
7 Oct. 1980	323.70	19.57	0.481	0.099	26.78
5 Nov. 1980	1 160.18	55.87	0.924	0.053	13.67
6 Jan. 1981	70.92	9.94	0.380	0.098	15.43
27 Feb. 1981	242.55	8.86	0.511	0.270	41.05
19 Mar. 1981	605.95	24.64	0.445	0.186	43.88
30 Apr. 1981	1 417.14	60.72	0.815	0.458	18.54
21 May 1981	435.73	41.49	nd	nd	nd
16 June 1981	821.85	39.71	nd	nd	nd

Table 3. Pigment budget (%) for Dabob Bay (pigment flux compared to chlorophyll production). Chlorophyll (chl) production (prod.) was calculated by one of two methods (see footnote). Pheopigment flux is given as chlorophyll-equivalents (see "Results"). Chlorophyll flux represents the direct measurement of chlorophyll captured in sediment traps. All values are average daily rates obtained by integration over the 2.5 yr observational period

Chlorophyll production (mg chl m^{-2} d^{-1})		Pheopigment flux (as chl-equivalents) (mg chl-equiv. m^{-2} d^{-1})	Chlorophyll flux (mg chl m^{-2} d^{-1})	Budget (%)	
				Pheo flux:chl prod.	Chl flux:chl prod.
12.9[a]	16.1[b]	9.88	0.76	61.4–76.6	4.7–5.9

[a] Calculated from carbon production (^{14}C) and C:chl
[b] Calculated from depth-weighted specific growth rate (μ) and chlorophyll crop

duction of chlorophyll on an annual basis in Dabob Bay. The average daily flux of chlorophyll (0.76 mg chl m^{-2} d^{-1}), if added to the pheopigment flux, raises the percentages somewhat (66 to 83%). Thus, the loss of chlorophyll, resulting from the downward transport of sinking algal cells, does not comprise a major component of the pigment budget. Chlorophyll *a* flux was only ca. 7% of the total flux of chlorophyll-like pigments [0.76 ÷ (0.76 + 9.88)]. Similar results were also obtained when traps were deployed at the same depths in Dabob Bay but over shorter time scales, ranging from hours (Welschmeyer *et al.*, 1984) to days (Welschmeyer and Lorenzen, 1985).

Under some conditions, cell-sinking has been suggested to constitute a major source of loss to phytoplankton standing crops (Walsby and Reynolds, 1980), however, the results presented here suggest that cell-sinking is unimportant as a loss process on an overall annual basis in Dabob Bay. Moreover, there is reason to suspect that the cell-sinking losses estimated from downward chlorophyll flux may be high. Residual chlorophyll is typically found in zooplankton fecal pellets, presumably due to cells that resist digestion or are passed through the gut too rapidly to allow complete chlorophyll degradation. Thus, chlorophyll measured in sediment traps may represent, in part, chlorophyll which was lost in the form of rapidly sinking fecal pellets, not by cell-sinking. Residual chlorophyll typically constitutes 3 to 10% of the total weight of pigment in fecal material [chlorophyll + pheopigments (uncorrected for

molecular weight differences)] (Shuman and Lorenzen, 1975; Landry *et al.*, 1984; our own observation). The measured chlorophyll flux in Dabob Bay (0.76 mg chl m^{-2} d^{-1}) constituted ca. 10% of the total pigment flux (0.76 mg chl m^{-2} d^{-1} + 6.54 mg pheo m^{-2} d^{-1}). Thus, of the total average chlorophyll flux measured in this study, 30 to 95% of the sedimenting chlorophyll may have been lost as residual chlorophyll contained in rapidly sinking fecal pellets and not as direct cell-sinking.

In an earlier study in Dabob Bay, Shuman (1978) noted that counts of intact diatom cells were low in sediment traps compared to diatom crops in the overlying water column. Larger diatoms such as *Coscinodiscus* sp. (potentially fast-sinking) showed daily loss rates to the species standing crop that were typically < 1% d^{-1}. Shuman (1978) likewise concluded that cell-sinking losses were small in Dabob Bay.

It could be argued that high cell-sinking losses may be confined to relatively short periods of time, such as at the demise of blooms, resulting in the chance of underestimating the net impact of cell-sinking due to inadequate sample coverage. However, the sediment traps in our study were deployed for 82% of the observational period, including bloom periods, making it unlikely that time intervals of high chlorophyll flux were missed.

About 17 to 34% of the pigment budget remains unaccounted for. We suggest that small, herbivorous microzooplankton are responsible for consuming the remainder of the chlorophyll production. Due to its small size and low (or negligible) sinking rate, the pigmented fecal debris of microzooplankton herbivores is expected to contribute to the pool of suspended pheopigments and consequently would not be sampled by sediment traps (Shuman, 1978; SooHoo and Kiefer, 1982a; Welschmeyer and Lorenzen, 1985). Pheopigments suspended in the euphotic zone are indeed detectable all year round in Dabob Bay, and the areal crop of pheopigments (mg m^{-2}) averages 30% that of chlorophyll.

Rapid photodegradation of suspended pheopigments has been shown to prevent the accumulation of pheopigments over time (Lorenzen, 1967b; Shuman, 1978; SooHoo and Kiefer, 1982b; Welschmeyer, 1982). We have shown that up to 90% of the pheopigments may be photooxidized when exposed to a full day's sunlight at the surface (Welschmeyer and Lorenzen, 1985). Thus, the concentration of suspended pheopigments, at any given time, represents the net balance between pheopigment production (microzooplankton grazing) and pheopigment removal (photodegradation).

This concept, coupled with estimates of photodegradation rates, has been used to calculate microzooplankton grazing rates in Dabob Bay (Shuman, 1978; Welschmeyer and Lorenzen, 1985). During, 1975–1977, Shuman (1978) estimated that 23% of the total daily grazing rate was due to microzooplankton (seven experiments were made). On 22 occasions during the same time period considered in the present paper (1978–1981), Welschmeyer and Lorenzen (1985) estimated that 33% of the total grazing rate was due to microzooplankton. These percentages are close to the amount required to complete the pigment budget at hand.

Microzooplankton grazing rates from Welschmeyer and Lorenzen (1985) are included in Table 2 for the purpose of calculating the average daily consumption rate of chlorophyll by microzooplankton. The product of chlorophyll crops and microzooplankton grazing rates, integrated over the intervals, 28 November 1978 – 20 June 1979 and 23 May 1980 – 30 April 1981 ($\Delta t = 545$ d), yields an average chlorophyll consumption rate of 4.5 mg chl m^{-2} d^{-1} or 28 to 35% of the estimated chlorophyll production (Table 3). (Chl production was estimated to be 12.9 to 16.1 mg chl m^{-2} d^{-1}, Table 3.) Thus, given some uncertainties, the annual chlorophyll budget is essentially complete (94 to 118%).

Comparison to Bedford Basin

We are aware of only one previous study in which the flux of chlorophyll and pheopigments was measured over an annual cycle in a temperate marine environment [summarized in Hargrave (1980)]. The work of Hargrave and Taguchi (1978) in Bedford Basin, Nova Scotia, is of particular interest due to the physical and biological similarities to Dabob Bay. Table 4 summarizes the contrasts

Table 4. Comparison of physical and biological features of Dabob Bay, Washington and Bedford Basin, Nova Scotia. Standing crop, primary production and vertical fluxes in Bedford Basin are seasonally-integrated values obtained from Hargrave and Taguchi (1978); primary production from their Table 4, chlorophyll (chl) and pheopigments (pheo) standing crops from their Fig. 1 (integrated by planimetry, 0 to 30 m), and particulate fluxes from their Table 1. Values in parentheses represent seasonal range of chlorophyll and pheopigment concentrations. Carbon flux in Dabob Bay is from Copping (1982)

	Dabob Bay	Bedford Basin
Latitude	48°	42°
Depth (m)	110	70
Primary production (mg C m^{-2} d^{-1})	531	548
Chlorophyll (mg chl m^{-2})	44 (8.9–220)	52 (9.5–200)
Pheopigments (mg pheo m^{-2})	15 (3.1–38)	56 (12.1–103)
Carbon flux (mg C m^{-2} d^{-1})	290	207
Chlorophyll flux (mg chl m^{-2} d^{-1})	0.76	0.50
Pheopigment flux (mg pheo m^{-2} d^{-1})	6.54	0.56

between the two locations, showing that primary production, chlorophyll crops, seasonal amplitudes, and carbon and chlorophyll fluxes were remarkably similar. A major point of departure exists, however, in the comparison of pheopigment standing crops and the vertical flux of pheopigments. Pheopigment standing crops, on average, were about three times higher in Bedford Basin than in Dabob Bay, yet the downward flux of pheopigments was more than ten times lower. In Bedford Basin, chlorophyll flux and pheopigment flux (as chlorophyll-equivalents) accounted for only ca. 10% of the estimated chlorophyll production (assuming a C:chl ratio of ca. 40, as in Dabob Bay). It may initially be argued that particulate fluxes were underestimated in the Bedford Basin study, or overestimated in Dabob Bay. However, the similarity in carbon flux and chlorophyll flux in the two sites strongly opposes such a statement (Table 4). Further, the trapping efficiency of our sediment traps has been calibrated *in situ*, using ^{210}Pb as a standard (Lorenzen *et al.*, 1981), and the trap designs were similar in both studies (Hargrave and Burns, 1979).

From the preceding discussion, we offer the preliminary suggestion that differences in microzooplankton grazing activity account for most of the differences noted in pheopigment stocks and pheopigment fluxes in the two areas. A rough calculation follows. Since Dabob Bay and Bedford Basin are located at similar latitudes, we can assume that the potential for pheopigment photodegradation by solar radiation is similar. Welschmeyer and Lorenzen (1985) have shown that the calculated microzooplankton grazing rate is directly proportional to pheopigment standing crop and rate of photodegradation, but inversely proportional to the chlorophyll standing crop. That is,

$$g = (P k_l \bar{I})\, C^{-1}, \quad (2)$$

where g is the microzooplankton grazing rate (d^{-1}), P is the steady-state concentration of suspended pheopigments, in chlorophyll-equivalents (mg chl-equiv m^{-3}), k_l is the photodegradation constant for pheopigments ($m^2\ E^{-1}$), $\bar{I}$ is the average photosynthetically available radiation (PAR) over 1 d ($E\ m^{-2}\ d^{-1}$), and C is the steady-state concentration of chlorophyll (mg chl m^{-3}). The average grazing rate in the euphotic zone is obtained by integrating over depth.

Given the similar chlorophyll crops (Table 4) and similar photodegradation potential in the two areas, the higher pheopigment standing crops in Bedford Basin (Table 4) suggest that microzooplankton grazing rates were ca. three to four times greater than in Dabob Bay (Eq. 2). Based on calculations for microzooplankton grazing in Dabob Bay described previously (chlorophyll consumption = 4.5 mg chl $m^{-2}\ d^{-1}$), this suggests that the average chlorophyll consumption rate by microzooplankton could have been as high as 14 to 18 mg chl $m^{-2}\ d^{-1}$ in Bedford Basin, essentially accounting for all of the chlorophyll production (again, assuming a C:chl ratio of 41 for Bedford Basin). If the mass of pigments is to be conserved, this necessarily implies that the loss of pheopigments, sinking as large particles, must be greatly reduced in Bedford Basin. The data on pheopigment flux in Bedford Basin (Table 4) support this notion well.

Sources of error

Our calculations, based on simple fluorometric measurements of chlorophyll and pheopigments, lead to the conclusion that the impact of herbivory greatly outweighs that of cell-sinking as a phytoplankton loss process in Dabob Bay. The assumptions necessary for the calculations were outlined earlier. Below, we examine the possible effects on our conclusions if the necessary assumptions were violated. Specifically, we consider the effects of (1) grazer pigment conversions that are less than 100% efficient on a molar basis, (2) the interference of chlorophyll *b* on pheopigment estimates, and (3) the chance that pheophytin *a*, not pheophorbide *a*, is the dominant pheopigment produced by zooplankton.

The calculations used throughout our study assume that all grazers convert chlorophyll to pheophorbide with 100% molar efficiency. Some studies suggest that the conversion efficiency may be less for some organisms, i.e., the porphyrin ring is not entirely conserved as it passes through the herbivore gut (Daley, 1973; SooHoo and Kiefer, 1982 b). If such were the case in our present study, the calculated herbivore grazing-activity would be even greater than it now stands. That is, the measured pheopigment flux would be a remnant of higher chlorophyll losses than the present factor of 1.51 predicts. Landry *et al.* (1984) have used the assumption of 100% molar pigment conversion to calculate assimilation efficiencies of 69 to 85% for the copepod *Calanus pacificus*, quite reasonable values. Recent experiments with *C. pacificus*, similar to those of Shuman and Lorenzen (1975), have again shown 100% molar pigment conversion in the majority of cases (7 of 8 experiments; one experiment showed 50% efficiency) (P. Hassett, personal communication). Since the zooplankton of Dabob Bay are dominated by copepods (specifically *C. pacificus*), the assumption of 100% molar pigment conversion seems appropriate. However, the chance that some organisms may convert chlorophyll to pheophorbide with less efficiency implies that the estimates of herbivory given in our paper are probably conservative.

The possible overestimation of pheopigment concentration due to interference from chlorophyll *b* was not real (Lorenzen, 1981). In a later study in Dabob Bay, Vernet (1983) showed detectable chlorophyll *b* concentrations in only 4 of 21 trap samples which were analyzed by the high-performance liquid chromatography (HPLC) technique. Chlorophyll *b* was detectable in 59% of the water column samples ($n = 93$), but the average chlorophyll *a*:chlorophyll *b* ratio was 20, too high to cause significant overestimation of pheopigments (Gibbs, 1979; Lorenzen and Jeffrey, 1980; Lorenzen, 1981).

If grazers produce pheophytin *a* with 100% molar efficiency, rather than pheophorbide *a*, fluorometric measurements of "pheopigments" do not require a cor-

rection factor (i.e., 1.51) to give chlorophyll-equivalents. This follows, since fluorometric "pheopigments" are calculated as if they were pheophytin *a* (Holm-Hansen *et al.*, 1965; Lorenzen, 1967a). Thus, if pheophytin *a* constituted a significant portion of the total pheopigments in Dabob Bay, then our grazing rates will have been overestimated, potentially by a factor of 1.51. Pheophytin *a* has been found in higher concentrations than pheophorbide *a* in fecal material of some grazers, especially salps (Hallegraeff, 1981; Madin and Cetta, 1984; our own observation). This is not true in Dabob Bay, where copepods are the dominant zooplankton and salps are rare. Vernet (1983) found the average ratio of pheophorbide *a*:pheophytin *a* to be 25 (wt/wt) in sediment-trap material from Dabob Bay (HPLC technique). The molar ratio was 38. We have ignored the effect of pheophytin in the budget calculations given in Table 3 because of its presumed small effect. The average pheophorbide:pheophytin ratio of 25 obtained by Vernet (1983) suggests that our grazing rates may be high by a factor of 1%. Thus, our initial assumption, that "pheopigments" consists largely of pheophorbide *a*, seems valid and introduces an insignificant error to the budget calculations.

General considerations

The results obtained in Dabob Bay are consistent with the old cliché that most phytoplankton production is consumed by herbivores (Harvey, 1955). Moreover, in Dabob Bay the algae are consumed while suspended in the euphotic zone and little of the primary production is lost as a result of direct cell-sinking. The dominant grazers in Dabob Bay are macrozooplankton whose fecal material contributes directly to the downward flux of rapidly sinking organic matter.

An examination of the carbon:pheopigment ratio of the sediment-trap material (Table 4) clearly shows the large contribution that herbivore fecal material makes to the total flux of organic carbon in Dabob Bay. The C:pheopigment ratio of the trap material is 44.3 (calculated from data in Table 4). Expressed in chlorophyll equivalents (pheopigments $\times 1.51$) this gives a C:chl-equivalent ratio of 29.3. This is close to the average C:chl ratio of the phytoplankton (41), indicating that a significant portion of the downward carbon flux was of recent algal origin (cf. Lorenzen *et al.*, 1983). A rough estimate of the contribution that the fecal material of large herbivores makes to the total downward carbon flux can be made if the assimilation efficiency of the herbivores is known. When the C:chl ratio of food material is 41 and the herbivore assimilation efficiency is 70% (Landry *et al.*, 1984), the expected C:chl ratio of the herbivore fecal material is 12.3 [$41 \times (1 - 0.7)$, the resultant pheopigments being expressed as chlorophyll-equivalents]. Thus, of the total downward carbon flux in Dabob Bay, over 40% ($12.3 \div 29.4$) may have been due to the fecal material of larger herbivores; those herbivores that package egested material into fast-sinking particles.

A similar exercise shows clearly different results in open-ocean locations; carbon:pheopigment ratios in sediment-trap material from Ocean Station P fall in the range 150 to 300 (Lorenzen *et al.*, 1983); at oligotrophic sites, the ratio can exceed 1 000 (Central Pacific gyres, Western Caribbean, own unpublished data). These higher C:pheopigment ratios suggest a much lower grazing activity by large herbivores (macrozooplankton) in open-ocean areas than in Dabob Bay.

Our results based on pigment flux measurements are thus consistent with the general notion that the grazers of coastal marine systems are dominated by macrozooplankton (Beers and Stewart, 1967), although the analysis in Bedford Basin questions such generalities. The results also show that the macrozooplankton herbivores of Dabob Bay are efficient consumers of primary production, allowing little of the primary-produced algal material to be lost as a result of cell-sinking.

The low cell-sinking losses in Dabob Bay contrast sharply with high sinking losses reported in freshwater systems (Hutchinson, 1967; Walsby and Reynolds, 1980) and in some shallow coastal marine systems [see Smetacek (1984) for a review]. The low overall impact of cell-sinking on an annual basis in Dabob Bay has been outlined in Table 3. Further, examination of the seasonal data in Table 1 show that cell-sinking (chlorophyll flux) was never greater than 16% of the herbivorous loss (pheopigment flux) at any time of the year. The minimum and maximum ratios of pheopigment flux to chlorophyll flux were 4.2 and 25.6, respectively, corresponding to cell-sinking losses that were 15.8 and 2.6% of the herbivorous loss, respectively (pheopigments expressed as chlorophyll-equivalents). Thus, when seasonal variability is considered, we find no evidence that high cell-sinking losses occur, such as during post-bloom conditions.

Compared to freshwater systems, the lower cell-sinking losses in Dabob Bay are partially consistent with the tenet that deep planktonic systems cannot sustain extensive cell-sinking losses (Hutchinson, 1967; Smayda, 1970; Margalef, 1978); cells that are lost from the euphotic zone, or that sink to the bottom, either as vegetative cells or spores, will be re-entrained back to the euphotic zone with much greater likelihood in a shallow lake than in a deeper system such as Dabob Bay. In general, the absolute rate of sinking loss (d^{-1}) is also expected to be greater in lakes than in marine systems, simply due to the contrast in the depth of the euphotic zone. Maximum cell-sinking rates, typically 1 to 5 m d^{-1}, will result in much larger daily losses to the algal crop in a shallow lake where the euphotic zone depth may only extend to a few meters, than in the open ocean where 100 m is a more characteristic euphotic-zone depth. Maximum bottom depth in Dabob Bay is 195 m (110 m at our study site) and the maximum euphotic zone depth (1% light level) is ca. 35 m, certainly less than the open ocean, but apparently deep enough to contribute partially to the low observed cell-sinking losses. It is of some interest to

note that a recent freshwater example of low cell-sinking loss has been described in Lake Constance, a particularly deep lake (140 m; Sommer, 1984).

The low cell-sinking losses noted throughout the year in Dabob Bay are at odds with observations made in other coastal marine systems, where post-bloom sinking losses are high (Steele and Baird, 1972; Smetacek *et al.*, 1978; Malone and Chervin, 1979; Smetacek, 1980). The possibility that the phytoplankton of Dabob Bay are uniquely different from those of other coastal phytoplankton assemblages, and possibly adapted to minimize sinking rates, does not seem likely. For instance, the algae are not dominated by picoplankton ($< 1\,\mu$m) which, because of size, may be expected to sink slowly. A measurable crop of netplankton ($> 20\,\mu$m) exists at all times (5 to 50% of the algal crop), blooms are dominated by diatoms (often chain-forming) and cell-sinking rates estimated by short-term (1 to 3 d) sediment-trap experiments ranged from 0.08 to 2.94 m d^{-1} ($\bar{x} = 0.51$ m d^{-1}) (Welschmeyer and Lorenzen, 1985). These rates are quite similar to other direct measurements of algal sinking rates made in the field (Burns and Rosa, 1980; Bienfang, 1981, 1984).

That cell-sinking losses are always low, even though the phytoplankton show no evidence of extremely low sinking rates nor dominance by flagellates, implies that grazing pressure in Dabob Bay may be unusually high compared to other coastal systems, i.e., the cells are consumed before they are lost by sinking. Runge (1985) has provided evidence showing that *Calanus pacificus* females in Dabob Bay are more food-limited (lower egg-production rates) than the same species in the main basin of Puget Sound. Thus, food limitation may augment the food-capturing ability of zooplankton in Dabob Bay. However, it is clear that the zooplankton grazing capacity in Dabob Bay is not always great enough to keep pace with the phytoplankton production rates, i.e., phytoplankton blooms occur (Fig. 2). Thus, zooplankton graze at rates adequate to consume phytoplankton before a significant portion of the cells are lost by sinking, but not at rates adequate to prevent temporary buildup of phytoplankton biomass.

Compared to sediment-trap data we have collected elsewhere, we do not consider the higher impact of grazing versus sinking in Dabob Bay to be unusual. Table 5 summarizes the pigment composition of sediment-trap material from representative experiments made in all the marine areas we have examined. All trap material was collected by the same methods described in this paper. Pheopigments always outweighed chlorophyll (Table 5). This was true for both coastal and open-ocean regions. When pheopigments are expressed as chlorophyll-equivalents, the data in Table 5 (last column) suggest that herbivorous grazing losses are about an order of magnitude greater than cell-sinking losses in all the marine systems we have examined to date.

Conclusions

The conclusions derived from the pigment budget in Dabob Bay are as follows. On an annual basis, it appears that almost all the primary-produced chlorophyll is consumed by herbivores. About 61 to 77% is consumed by fecal-pellet-producing macrozooplankton and the remainder is consumed by microzooplankton, with only a small loss represented by algal cell-sinking. It necessarily

Table 5. Representative examples of sediment-trap pigment composition collected in various marine environments using same methods described in present paper. Last column gives chlorophyll (chl) as percent of total chlorophyll-like pigments, i.e., chl ÷ [chl + (pheo × 1.51)]

Location	Deployment time	Bottom depth (m)	Trap depth (m)	Pheo:chl of trap material	Chl as % of total chl-equiv.
Dabob Bay					
48°N; 123°W	1978–1981 (ave)	110	60	8.6	7.2
Washington Coast	20–23 Sep. 1976	120	70	7.6	8.0
	26–30 Sep. 1976	120	70	5.4	10.9
47°N; 124°W	17–26 July 1979	220	60	27.8	2.3
	28 July–1 Aug. 1979	230	60	6.4	9.4
S. California Bight					
33°N; 117°W	6–12 Nov. 1979	220	70	3.6	15.5
Ocean Station "P"	24–25 July 1978	~4 200	100	5.8	10.2
50°N; 145°W	16–19 June 1983	~4 200	60	4.4	13.1
N. Central Pacific Gyre					
28°N; 155°W	1–6 July 1980	~5 500	130	8.5	7.2
18°N; 157°W	9–13 Feb. 1981	~3 200	120	7.2	8.4
18°N; 157°W	14–19 Feb. 1981	~3 200	160	5.2	11.3
S. Central Pacific Gyre					
14°S; 151°W	6–8 Dec. 1980	~4 200	140	5.4	10.9
W. Caribbean					
13°N; 81°W	19–21 Oct. 1983	~1 800	125	5.1	11.5

follows that the loss of phytoplankton from the euphotic zone by mixing must be small. The tenet that herbivory is the dominant process controlling phytoplankton abundance is supported in this study. In Dabob Bay, the ultimate fate of most phytoplankton is to be consumed by herbivores.

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