Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom.

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Abstract: Despite the acceptance of microzooplankton as significant consumers of phytoplankton production, surprisingly little is known about their role in the ecology of phytoplankton blooms. In conjunction with the southeastern Bering Sea Inner Front Project, we used the seawater dilution technique in late summer 1999 to quantify phytoplankton growth and microzooplankton herbivory, as well as microzooplankton abundance and biomass in the southeastern Bering Sea during a bloom of the coccolithophorid *Emiliania huxleyi*. Total chlorophyll *a* (Chl *a*) ranged from 0.40 to 4.45 μg C l^{-1}. Highest phytoplankton biomass was found within the bloom. Here, 75% of the phytoplankton biomass came from cells > 10 μm and was attributed to the increased abundance of the diatom *Nitzschia* spp. Nutrient enhanced total phytoplankton growth rates averaged 0.70 d^{-1} across all experimental stations. Average growth rates for > 10 μm and < 10 μm cells were nearly equal at 0.68 and 0.62 d^{-1}. Microzooplankton grazing varied among stations and size fractions. Grazing on phytoplankton cells > 10 μm ranged from 0.19 to 1.20 d^{-1}. Grazing on cells < 10 μm ranged from 0.02 to 1.06 d^{-1}, and was significantly higher at non-bloom (avg. 0.71 d^{-1}) than at bloom (avg. 0.14 d^{-1}) stations. Across all stations, grazing by microzooplankton accounted for 125% and 67% of phytoplankton growth for > 10 and < 10 μm cells, respectively. These findings contradict the paradigm that microzooplankton are constrained to diets of nanophytoplankton and strongly suggests their grazing behavior extends beyond boundaries set by size-based models. Heterotrophic dinoflagellates and oligotrich ciliates dominated the microzooplankton community. Estimates of abundance and biomass for microzooplankton > 10 μm were higher than previously reported for the region. Abundance and biomass ranged from 22,000 to 227,430 cells l^{-1} and 18 to 164 μg C l^{-1}, respectively. Highest abundance and biomass occurred in the bloom and corresponded with increased abundance of the large ciliate *Laboea*, and the heterotrophic dinoflagellates *Protoperidinium* and *Gyrodinium* spp. Significant positive correlation existed between phytoplankton biomass and heterotrophic dinoflagellate abundance (r^2 = 0.61) and biomass (r^2 = 0.51). Despite low grazing rates on phytoplankton < 10 μm within the bloom, the abundance and biomass of small microzooplankton (< 20 μm)

capable of grazing *E. huxleyi* was relatively high. This body of evidence, coupled with high grazing rates on large phytoplankton cells, suggests the phytoplankton community composition was in part regulated by herbivorous activity of microzooplankton. Because grazing behavior deviated from size-based model predictions and was not proportional to microzooplankton biomass, alternate mechanisms that structure phytoplankton communities were in effect in the southeastern Bering Sea. We hypothesize that these mechanisms included, but are not limited to, morphological or chemical signaling between phytoplankton and micrograzers, which led to selective grazing pressure. In addition to favorable chemical and physical parameters, these data suggest the genesis and temporal persistence of the *E. huxleyi* bloom is an effect of reduced microzooplankton grazing mortality.

Introduction

The southeastern Bering Sea is a biologically rich ecosystem whose high productivity is in part the result of the complex physical-chemical interactions occurring over the broad, shallow continental shelf (Springer *et al.*, 1996) that comprises ~50% of the total Bering Sea area. These interactions, which include water-column stratification from sea-ice melt (Alexander and Niebauer, 1981), eddies, and wind-driven vertical advection of nutrients into the upper mixed layer, provide the components necessary for high primary productivity.

Diatoms typically dominate phytoplankton biomass in the Bering Sea (Sukhanova *et al*., 1999). Classic food web models of the Bering Sea show diatom-produced biomass being transferred through crustacean zooplankton (Hood, 1999), ultimately supporting one of the world's largest fisheries (Loughlin *et al*., 1999). However, the classic model is in need of revision. Recent studies show some copepods preferentially feed on dinoflagellates and microzooplankton over diatoms (Stoecker and Capuzzo, 1990; Kleppel *et al*., 1991), which can be a sub-optimal food source. In one study, diatoms reduce fecundity (87% on average) compared to non-diatom prey (Ban *et al.*, 1997) and Miralto *et al*. (1999) found only 12% hatching success among copepods in a diatom-dominated bloom compared to 90% success in post-bloom conditions. Miralto *et al*. (1999) also isolated three antiproliferative aldehyde compounds from the diatoms *Thalassiosira rotula*, *Skeletonema costatum*, and *Pseudo-nitzschia delicatissima* that caused low hatching success.

If diatoms are a sub-optimal diet for copepods and other crustacean zooplankton, what supports the high crustacean biomass in the southeastern Bering Sea?

Microzooplankton, a component of the marine plankton consisting of protists and metazoa < 200 µm (Dussart, 1965) may be the answer. Microzooplankton display unique feeding mechanisms and behaviors that allow them to graze cells up to five times their volume (Jacobson and Anderson, 1986; Hanson and Calado, 1999). They are capable of grazing bacteria (Sherr and Sherr, 1994) and transporting bacterial biomass out of the microbial loop (Sherr and Sherr, 1988). They can grow at rates which equal or exceed prey growth (Sherr and Sherr, 1994) and can serve as a viable food source for metazoans (Gifford, 1991; Stoecker and Capuzzo, 1990).

Because microzooplankton are individually inconspicuous, recognition as significant consumers of oceanic primary production has come only in the last 20 years. Consequently, quantitative studies of microzooplankton herbivory are limited to a few regions of the world's oceans. These studies show that microzooplankton are the dominant consumers of phytoplankton production in both oligo- and eutrophic regions of the ocean (Lessard and Murrrell, 1998; Capriulo *et al*., 1991; Sherr and Sherr, 1992) and are capable of consuming > 100% of primary production (Gifford, 1988; Verity *et al*., 1996; Strom *et al.*, in press; Lessard and Murrell, 1998; Burkill *et al*., 1993). However, little is known of their feeding ecology in or around phytoplankton blooms.

Unusual climatic conditions in 1997 and 1998, including warmer than average sea temperatures (Hunt *et al*. 1999), were coincident with the first recorded bloom of the prymnesiophyte *Emiliania huxleyi* in the Bering Sea (Vance et al., 1998). The unexpected appearance of an *E. huxleyi* bloom in the Bering Sea is puzzling; however, the large spatial and temporal extent of the bloom is equally puzzling.

One explanation of the persistence of the bloom may lie in the functional morphology of *E. huxleyi*. *E. huxleyi*, like all coccolithophores, produces calcium carbonate plates (called coccoliths) that surround the cell. Besides altering the optical properties of the water (i.e. scattering light, thus reducing available PAR for phytoplankton deeper in the water column), these coccoliths may regulate the amount of light available to the cell; this capability allows *E. huxleyi* to live high in the water column (Young, 1994) where photoinhibition may limit growth of competing species of phytoplankton. This ability, coupled with the capacity to thrive at low nutrient concentrations, may give *E. huxleyi* a competitive advantage over larger phytoplankton species that typically dominate in the Bering Sea. However, this does not explain why microzooplankton herbivory does not reduce the standing crop of *E. huxleyi*. Because microzooplankton are capable of grazing 100% of phytoplankton production, the temporal persistence of the bloom suggests an uncoupling between grazing and primary productivity.

E. huxleyi is well within the size range of available prey for microzooplankton. Microzooplankton are capable of selectively choosing prey (Burkill *et al*., 1987; Buskey, 1997). The selection process may occur during detection, prey capture, handling, ingestion, or a combination of all four. The coccoliths surrounding *E. huxleyi* provide no physical protection from grazing, but are indigestible and may reduce their nutritional value, conceivably making coccolithophorids sub-optimal prey (Young, 1994).

An alternative explanation that would result in grazing selectivity is chemical defense by marine microbes. Recent studies have demonstrated that many algae are toxic to, or avoided by, micro- and metazooplankton (Admiraal *et al.*, 1986; Hansen, 1989;

Teegarden and Cembella, 1996). Wolfe *et al.* (1997) showed that certain laboratory strains of *E. huxleyi* have grazing-activated chemical defense mechanisms. However, grazing deterrence by means of chemical defense shows variability between grazer taxa, and its role in bloom ecology is poorly understood [Turner and Tester, 1997; see (Wolfe, 2000) for a complete review on algal chemical defense ecology].

Regardless of the specific interactions between *E. huxleyi* and their microzooplankton predators, interactions between microzooplankton and their prey significantly contribute to the structuring of marine plankton communities.
In order to make accurate predictions about the sustainability of the oceans, it is imperative that quantitative microzooplankton herbivory estimates are collected and incorporated into ocean food web models. We report here a study, conducted in collaboration with the 1999 Inner Front program, quantifying phytoplankton growth and mortality from microzooplankton grazing in the southeastern Bering Sea. To evaluate the availability of microzooplankton as food for crustacean zooplankton and larval fish, we also quantify microzooplankton abundance and biomass. This research also presents findings on microzooplankton herbivory, abundance, and activity within the *E. huxleyi* bloom that has proliferated in the southeastern Bering Sea for the past three years. Information gained from this research will help determine whether *E. huxleyi* can be implicated as a causative agent in restructured upper trophic level food web dynamics in the southeastern Bering Sea (Vance *et al*., 1998).

Methods

Methodological Considerations

Microzooplankton are often the same size as their phytoplankton prey; consequently, they can not be physically separated. For this reason, phytoplankton community growth rates in whole seawater samples are a measure of net growth

$$r = \mu - g \qquad (1)$$

where r is the net growth rate, μ is the intrinsic growth rate, and g is mortality due to grazing.

The dilution method (Landry and Hasset, 1982; Landry, 1993) simultaneously estimates the intrinsic rates of phytoplankton growth and grazing mortality of a microbial population. In principal, a seawater sample is diluted with particle-free seawater from the same source in sequential dilutions of whole seawater (WSW) with particle-free seawater (PFW). It is presumed that prey growth is density independent, whereas grazing mortality is density-dependent. Therefore, by minimizing encounter rates of prey with their predators, net growth rates will approximate intrinsic growth rates in the highly dilute treatments.

The dilution technique has four restrictive assumptions (Landry, 1993; Neuer and Cowles, 1994): phytoplankton growth rate is unaffected by dilution (i.e. growth must not be density-dependent); microzooplankton density does not change over the course of incubation; microzooplankton grazing rates are linear with respect to prey density; and phytoplankton growth is described by the exponential growth equation,

$$1/t \cdot \ln(P_t / P_0) = k - c \cdot g \qquad (2)$$

where P_t is the chlorophyll a (Chl *a*) concentration at time *t*; P_0 is the initial Chl *a* concentration; *k* and *g* are the instantaneous coefficients of population growth and grazing related mortality, respectively; and *c* is the dilution factor.

The disadvantages of the dilution method (Gallegos, 1989) are that the assumptions are difficult to test routinely, growth rates in dilute bottles may be affected by contaminants or enhancements in PFW, and threshold feeding responses at high dilutions may depress grazing rates in dilute samples more than dilution alone (Landry, 1993). In spite of the disadvantages, the dilution method was chosen because it provides simultaneous analysis of different components of a plankton community in a single experiment with minimal disruption to delicate organisms; furthermore, it is the only method that yields an estimate of community grazing rates.

Sampling

All samples were collected on board the RV *Alpha Helix* (cruise 222, 18 July – 23 Aug., 1999). Sampling stations selected (Table 1) represented three distinct biogeographical regions with respect to the *E. huxleyi* bloom: non-bloom (stations 1-4); bloom-fringe (stations 5-11); and bloom (stations 12-18) (Fig. 1). Bloom and bloom-fringe stations were identified based on the extent of visible discoloration of the water (for images of the 1999 bloom see http://rho.pmel.noaa.gov/vance/seawifs/bering.html). Blooms of *E. huxleyi* characteristically display high reflectance with only moderate levels of Chl *a* (Holligan *et al*., 1993; Garcia-Soto *et al*., 1995). Stations with high reflectance and chalky appearance were designated bloom, whereas stations with little and no reflectance (i.e. blue water) were designated bloom-fringe and non-bloom, respectively.

The biogeographic designations were confirmed by observation of *E. huxleyi* density using inverted microscopy. Seawater for dilution experiments, measurement of inorganic nutrients, and microzooplankton cell density was collected via a rosette of 5 l Niskin bottles attached to a CTD. Each bottle was equipped with an external spring-loaded closing system. Water was collected at depths corresponding to 50% surface irradiance (depth range 4 to 30 m; Table 1). Sampling times were subject to ship availability.

Dilution Experiments

Prior to use, all bottles, carboys, silicon tubing, and cartridge filters were soaked in 10% HCl for 24 h and subsequently rinsed with reverse osmosis H_2O and pre-rinsed with filtered seawater. Seawater for dilution experiments was prepared by gently draining the Niskin bottles through silicon tubing enclosed with 200 µm Nitex screen (to remove meso- and macrozooplankton) into two 20 l polycarbonate carboys. One carboy was kept in the dark at 6°C until experimental bottles were set up (no longer than 1 hour), while the second was allowed to gravity filter through a Gelman pleated capsule filter (0.2 µm pore size) to serve as the PFW.

Whole seawater (WSW) was gently siphoned (the end of the tube submerged) into 1 l polycarbonate bottles containing premeasured volumes of PFW to achieve target fractions (in duplicate) of whole seawater: 0.1, 0.2, 0.35, and 0.6, along with duplicate 1.0 WSW bottles for each dilution series. In order to satisfy the assumption that phytoplankton growth was unaffected by dilution, dissolved nutrients were added to all experimental bottles to reach target levels of 2 µM PO_4^- (added as KH_2PO_4) and 20 µM NO_3^- (added as KNO_3). Two additional bottles of 1.0 WSW were incubated without

added inorganic nutrients and served as controls for nutrient enrichment effects. Experimental bottles were enclosed in one layer of neutral density screen to simulate ambient irradiance and placed in on-deck incubators supplied with a continuous flow of surface seawater.

Initial chlorophyll samples (volumes ranged from 60 ml to 500 ml) were taken at each experimental location from 20 l WSW carboys. Quadruplicate samples for total Chl *a* were filtered through Poretics® GF-75 filters (0.7 µm effective pore size) at ~5 in. Hg vacuum pressure, while quadruplicate samples for > 10 µm Chl *a* were filtered through Poretics® polycarbonate filters (10 µm pore size). Filters were folded in tinfoil, placed in cryovials, and subsequently frozen in liquid nitrogen until processing. Two types of preserved samples were taken from the 20 l WSW carboy for cell enumeration and identification. Duplicate samples (250 ml) for microzooplankton enumeration were preserved in 10% (final concentration) acid Lugol's, while duplicate 15 ml samples for *E. huxleyi* enumeration were preserved in alkaline Lugol's (to prevent coccolith dissolution).

Size Fractionated Chlorophyll

GF-75 and 10 µm pore-size polycarbonate filters were placed in test tubes containing 6 ml of 90 % acetone (by volume). Extraction took place in the dark at –20 °C for 24 h. Chl *a* and phaeopigments were analyzed by a Turner Model 112 fluorometer following the methods of Parsons *et al.* (1984). Chl *a* concentrations were calculated according to Lorenzen (1966). Chl *a* in the < 10 µm size fraction was estimated from the difference between total (GF-75) and > 10 µm concentrations.

Nutrient analysis

Samples from the 20 l PFW carboy were taken to determine concentrations (µM) of PO_4^{3-}, $Si(OH)_4$, NO_2^-, NO_3^-, and NH_4^+. Samples were analyzed with an Alpkem autoanalyzer on board ship using the methods of Whitledge *et al*. (1981).

Phytoplankton specific growth and microzooplankton grazing

Each incubation bottle in the dilution series yields an independent estimate of the apparent growth rate (AGR) of the phytoplankton,

$$AGR(d^{-1}) = 1/t \ln(P_t/P_o) \qquad (3)$$

where t is the duration of the incubation in days, and P_o and P_t are the initial and final phytoplankton stocks (estimated from Chl *a*). The rate of phytoplankton growth and grazing mortality for phytoplankton cells in total, > 10 µm, and < 10 µm size fractions were estimated by Model I linear regression of AGR verses dilution factor (i.e. grazer density) (Landry, 1993). The ordinal intercept of the regression is the intrinsic rate of phytoplankton growth (µ, d^{-1}) in the absence of grazing, and the negative slope of the regression is the rate of mortality (g, d^{-1}) attributable to microzooplankton grazing. In regions of high phytoplankton biomass, prey availability may be saturating to grazers even in the dilute treatments. As a result, µand g are underestimated (Gallegos, 1989). Linear transformation of data is not possible for it violates the assumption that g is linearly related to dilution. At stations where grazing saturation occurred, µ was estimated with piecewise regression (Rivkin *et al*., 1999) by analyzing the three highest

dilutions (0.1, 0.2, and 0.35), whereas g was calculated by the rearrangement of equation (1) into

$$g = \mu - r \qquad (4)$$

where r is the net growth in nutrient enriched undiluted bottles. Phytoplankton growth rate in control bottles without the added inorganic nutrients was calculated as

$$\mu_{(-\text{nutrients})} = r_{(-\text{nutrients})} + g \qquad (5)$$

where r is the net growth in unenriched undiluted bottles (Strom and Strom, 1996) and g is the estimated grazing rate from the corresponding enriched dilution series.

Microzooplankton abundance and biomass

Whole seawater preserved samples were settled in inverted microscope counting chambers for 24 h. Settled volumes varied but were determined to allow for the enumeration and digitization of ≥ 200 cells. Acid Lugol's was chosen because it is fairly non-toxic to humans, and it preserves the greatest number of ciliates as compared with other fixatives (Stoecker *et al.*, 1995). Unfortunately, preservation in acid Lugol's does not allow phytoplankton autofluorescence to be maintained. Because it was not possible to unequivocally determine whether cells were autotrophic or heterotrophic, all ciliates and dinoflagellates > 10 µm were included in abundance, biomass, and volume estimates. However, strictly autotrophic species were rare, and many autotrophic dinoflagellates are capable of phagocytic activity (Steidinger and Tangen, 1996).

Cells in duplicate samples were enumerated and measured using a computer-aided digitizer (Roff and Hopcroft, 1986). Biovolume was converted to biomass using 0.19 pg C μm^{-3} for ciliates (Putt and Stoecker, 1989) and 0.14 pg C μm^{-3} for dinoflagellates

(Lessard, 1991). Metazoan larvae were encountered in a few samples, but were extremely rare. Thus, they were excluded from our estimates.

Statistical analysis

Differences among biogeographic regions for total, > 10 µm, and < 10 µm Chl *a*, rates of phytoplankton growth and grazing mortality (pooled regressions), as well as microzooplankton abundance and biomass were analyzed by one-way ANOVA (SPSS software). The assumption of homogenous variances was not met in all cases (> 10 µm Chl *a*, total phytoplankton growth, < 10 µm grazing, ciliate and heterotrophic dinoflagellate biomass). When this occurred, logarithmic transformations of data were performed. *A posteriori* multiple comparisons of ranked means were performed using Tukey's HSD test. Paired *t*-tests were used to test for differences between nutrient enriched and unenriched phytoplankton growth rates. Pearson correlations were used to test whether ambient nutrient concentrations correlated with phytoplankton biomass, and if phytoplankton biomass correlated with microzooplankton grazing rates.

Results

Size-fractionated Chl a

Total phytoplankton biomass, estimated from Chl *a*, significantly increased (F = 7.93, P = 0.004) from non-bloom and bloom-fringe stations (1-11) to the bloom stations (12-18) (Fig. 2). Values ranged from 0.36 to 4.45 µg Chl *a* l^{-1}. Surprisingly, despite the discoloration of the water from the increased presence of *E. huxleyi*, much of the increase

in phytoplankton biomass at bloom stations was associated with cells > 10 µm. Chl *a* in the > 10 µm size fraction was significantly lower ($F = 20.37$, $P < 0.000$) on average at non-bloom and bloom-fringe stations (avg. 0.20 µg l^{-1}, n = 11) than at bloom stations (avg. 1.60 µg l^{-1}, n = 7) (Fig. 2). Much of this difference appeared causative by increased abundance of the oceanic, bloom-forming diatom *Nitzschia* spp. at bloom stations

Phytoplankton biomass in cells < 10 µm did not differ significantly ($F = 0.56$, $P = 0.58$) (Fig. 2) between non-bloom and bloom stations. Average < 10 µm Chl *a* for the non-bloom, bloom-fringe, and bloom stations was 0.55 (n = 4), 0.77 (n = 7), and 0.87 (n = 7) µg Chl *a* l^{-1}, respectively. Although biomass did not differ significantly among regions, species composition in the < 10 µm community shifted from a mixed assemblage at the non-bloom stations to an assemblage dominated by *E. huxleyi* at the bloom-fringe and bloom stations (Table 2). This shift in species diversity was also evident in the visual discoloration of the water.

Nutrient concentrations

Inorganic nutrient concentrations showed extreme spatial heterogeneity (Table 3): NO_3^- ranged from 0.23 to 5.95 µM; PO_4^{3-} ranged from undetectable to 0.89 µM; SiO_2 ranged from 0.07 to 27.40 µM; and NH_4^+ ranged from 0.13 to 6.39 µM. Overall, near-surface nutrient levels were low during this study, and the highest values appear to represent isolated patches of nutrient enrichment. Only four stations (1, 2, 8, and 9) showed concentrations higher than 5 µM for $Si(OH)_4$ and only two locations (1, 9) registered concentrations greater than 1 µM NO_3^-. Conversely, only one station (3) registered a concentration less than 1 µM NH_4^+. No significant correlation existed

between phytoplankton biomass and surface nutrient concentrations (NO_3^-, PO_4^{3-}, $Si(OH)_4$, and NH_4^+; $P > 0.1$ in all cases).

Phytoplankton growth and microzooplankton herbivory

Nutrient-enhanced phytoplankton growth rates ranged widely across all experimental locations (Table 4). However, no significant differences existed in phytoplankton growth amongst the three biogeographical regions for total ($F = 3.54$, $P = 0.055$), > 10 µm ($F = 0.33$, $P = 0.72$), or < 10 µm Chl *a* ($F = 0.09$, $P = 0.92$).

Total phytoplankton growth rates ranged from 0.28 to 2.07 d^{-1}. The highest two values, 2.05 and 2.07 d^{-1}, were found at stations bordering the Pribilof Islands (stations 9, 10). This area is located on the seaward edge of the continental shelf and at the head of the Pribilof Canyon (Stabeno *et al.*, 1999). Consequently, deep, nutrient-rich water is introduced to biologically active stratified waters of the continental shelf.

Phytoplankton growth rates in the > 10 µm size fraction ranged from –0.29 to 2.05 d^{-1}. Growth rates for the < 10 µm size fraction showed a narrower range, from 0.29 to 1.12 d^{-1}.

In order to satisfy the assumption that dilution does not affect phytoplankton growth, inorganic nutrients were added to experimental bottles. Because addition of nutrients may promote phytoplankton growth and misrepresent *in situ* intrinsic growth rates, experimental bottles without added nutrients served as controls. Nutrient enrichment had no significant effect on phytoplankton growth for the three size classes indicating that, in general, phytoplankton growth rates in the Bering Sea during this study were not nutrient limited (Paired *t*-test, $P = 0.14$, 0.94, and 0.95 for total, > 10 µm, and <

10 µm Chl *a*, respectively). Interestingly, bottles with nutrient enrichment occasionally showed lower phytoplankton growth rates than unenriched bottles (Table 4).

Microzooplankton grazing rates varied among location and Chl *a* size fractions (Table 4). Microzooplankton grazing rates on total Chl *a* ranged from 0.08 to 1.02 d^{-1} (Table 4). Multiple comparison ranked means of pooled regressions showed significantly higher grazing on total Chl *a* at non-bloom versus bloom stations (F = 3.80, P = 0.047). Grazing rates exceeded phytoplankton growth rates at 3 of the 4 non-bloom stations (Fig. 3a). In contrast, at the bloom-fringe and bloom stations, growth equaled or exceeded grazing at 13 of the 14 stations.

Grazing on phytoplankton cells > 10 µm showed no significant difference amongst locations (F = 0.84, P = 0.449). Grazing rates ranged from 0.19 to 1.20 d^{-1} and were exceeded by phytoplankton growth at all 4 non-bloom stations, and at 4 of the 7 bloom-fringe stations (Fig. 3b). Unlike the pattern observed in the total phytoplankton assemblage, grazing on the large cells exceeded phytoplankton growth in 5 of the 7 bloom stations.

Phytoplankton growth and microzooplankton grazing showed the same pattern for the < 10 µm size fraction as for total Chl *a*. Grazing rates ranged from 0.02 to 1.06 d^{-1}. Grazing decreased relative to phytoplankton growth with increasing proximity to the bloom (Fig. 3c). Although no differences were observed in < 10 µm Chl *a* biomass among stations, grazing rates on < 10 µm Chl *a* were significantly lower at bloom than non-bloom locations (F = 3.95, P = 0.042).

Many studies have observed that a tight coupling exists between rates of microzooplankton grazing and small phytoplankton growth (summarized by Sherr and

Sherr, 1994). In our study, however, rates of phytoplankton growth and microzooplankton grazing were nearly equal in the > 10 µm size fraction (Fig. 3b). Conversely, most rates of phytoplankton growth for the total and < 10 µm size fractions were higher than the corresponding grazing rates. This suggests an uncoupling between grazing and growth which, in the absence of other loss processes, will result in an accumulation of phytoplankton standing stock, particularly for the smaller size fractions.

An obvious discrepancy exists in the grazing rates among the different locations for all size fractions. It could be argued that differences in grazing rates may be a functional response to prey availability; more chlorophyll in one size fraction may lead to higher grazing pressure for those cells encompassing that size range. Can this be the reason grazing rates were higher for > 10 µm Chl *a* than for < 10 µm Chl *a* within the bloom? To explore this possibility further, Chl *a* was plotted against grazing rates for the different biogeographical regions (Fig. 4). The non-bloom and bloom-fringe stations showed high and intermediate levels of grazing, respectively, at relatively low Chl *a* concentration (Fig. 4a-b). At non-bloom stations, the average Chl *a*/microzooplankton grazing ratio was 0.40 and 1.02 for > 10 and < 10 µm cells, respectively. At bloom fringe stations, the > 10 µm ratio was the same as non-bloom stations (0.41), whereas the < 10 µm ratio increased to 4.50. The bloom stations show low levels of grazing at high Chl *a* levels (Fig. 4c). This pattern is particularly evident for the small (< 10 µm) phytoplankton cells, where the Chl *a*/microzooplankton grazing ration was 9.50 for < 10 µm cells, compared to 3.22 for the > 10 µm cells. These results, in addition to the finding that, for < 10 µm Chl *a*, significant location-based differences existed in grazing rates but not Chl *a* concentrations, suggests that prey size and abundance are not the only

determinants of feeding rate. Given microzooplankton communities of equivalent size and composition, feeding behavior controlled by prey size and abundance would result in grazing rates proportional to Chl *a* levels. This was not seen in this study, for no significant positive correlations existed between Chl *a* concentrations and microzooplankton grazing rates. Instead, behaviors such as selective feeding may have been in effect.

Microzooplankton abundance and biomass

There were large differences among stations for microzooplankton abundance and biomass (Figs. 5 and 6). Overall, choreotrich ciliates and heterotrophic dinoflagellates dominated the microzooplankton community. Total microzooplankton abundance ranged from 22,000 to 227,430 cells l^{-1} and total biomass from 18.40 to 164.00 µg C l^{-1} (Fig. 5). Highest abundance occurred at stations 4, 14, 17 and 18. No significant differences were seen across stations for ciliate ($F = 3.33$, $P = 0.064$) or heterotrophic dinoflagellate abundance ($F = 1.64$, $P = 0.230$). Total microzooplankton ($F = 2.77$, $P = 0.095$), and ciliate ($F = 2.84$, $P = 0.090$) biomass showed no difference among regions whereas heterotrophic dinoflagellate biomass was significantly higher at bloom than at bloom-fringe stations ($F = 4.63$, $P = 0.027$)(Fig. 6). Highest total biomass occurred at stations 3, 12, 17 and 18. Ciliate abundance ($r^2 = -0.063$) and biomass ($r^2 = 0.111$) did not correlate with total phytoplankton biomass. In contrast, total microzooplankton abundance ($r^2 = 0.508$), as well as heterotrophic dinoflagellate abundance ($r^2 = 0.610$) and biomass ($r^2 = 0.511$) significantly correlated with total phytoplankton biomass. Because a large portion of phytoplankton biomass in the bloom was associated with large

diatoms, this suggests a tight coupling between microzooplankton community composition and phytoplankton community size structure.

With the exception of stations 1 and 3, abundance of heterotrophic dinoflagellates was higher than that of ciliates (Fig. 5). Fig. 7 shows the percent contribution to total abundance of different microzooplankton taxa at each location. Most stations were dominated in abundance by small round and miscellaneous cylindrical and thecated dinoflagellates. Stations 10, 12, 15, 16 and 18 had high abundance of *Gyrodinium* spp. and *Protoperidinium*-like dinoflagellates. These taxa are known to feed heavily, if not exclusively, on diatoms. Ciliate abundance was dominated by oligotrich ciliates between 5 and 40 µm in length. Station 3 had a high abundance of tintinnid ciliates. This is not surprising, for this station is just north of the Aleutian Island archipelago, and tintinnids are primarily a coastal microzooplankton group (Capriulo and Carpenter, 1983; Pierce and Turner, 1993).

Fig. 8 shows the percent contribution to total biomass by microzooplankton taxa at each experimental station. At most stations, total biomass was divided evenly between ciliates and dinoflagellates. Small round and miscellaneous cells again dominated heterotrophic dinoflagellate biomass. Aloricate choreotrich ciliates between 20 and 40 µm contributed most to ciliate biomass. Stations 8-12 and 15-17 saw a high biomass of ciliates > 40 µm. These cells were primarily the large chloroplast-retaining *Laboea* sp. Stations 2, 3, 8, and 15 had significant biomass contributions from tintinnids.

Discussion

The results of this study further implicate microzooplankton as the main consumers of phytoplankton production in highly productive marine ecosystems. Microzooplankton grazing rates averaged 114% (range 24-358%) and 79% (range 2-237%) of phytoplankton growth rates for > 10 µm and < 10 µm phytoplankton size fractions, respectively. These values fall within the range of grazing estimates from other coastal ecosystems (Burkill *et al*., 1987; Anderson *et al*., 1991; McManus and Ederington-Cantrell, 1992; Strom and Strom, 1996; Murrell and Hollibaugh, 1998).

As previously stated, the dilution method has restrictive assumptions that are difficult to test. If these assumptions are violated, they must be addressed before non-biased estimates of phytoplankton growth and microzooplankton grazing can be made. In this study, the assumption that grazing is linearly related to dilution was not met at all stations and is most likely a result of grazing saturation. Ambient Chl *a* concentrations were high enough that it is doubtful even the most dilute samples experienced concentrations below levels that would educe threshold feeding behavior. This is not uncommon in regions that experience moderate to high ambient Chl *a* concentrations (Gallegos, 1989). However, the violation of this assumption is easily rectified (see Methods) and non-biased estimates of phytoplankton growth can still be made with confidence.

A recent criticism of the dilution method is that differential numerical growth responses of grazers between dilutions throughout the incubation occur, and are not routinely tested (Dolan *et al*. 2000). Higher growth rates of microzooplankton in the less-dilute treatments results in higher grazing rates on the phytoplankton compared to highly

dilute treatments. This would increase the slope of the dilution regression, resulting in an artificially higher phytoplankton growth rate. Dolan *et al*. (2000) showed apparent growth rates of tintinnids and oligotrich ciliates decreased with increasing fraction of PFW at temperatures ranging from 16.1 to 18.6 ºC. Unfortunately, the potential response for microzooplankton growth to differentially respond according to dilution was not accounted for in this study, where temperatures ranged from 5 to 10 ºC. Contrary to the statement by Dolan *et al*. (2000) that oligotrich and tintinnid ciliates generally dominate microzooplankton communities, we found numerical dominance by heterotrophic dinoflagellates, and equal contributions to biomass from both major groups. As demonstrated by Strom and Morello (1998), heterotrophic dinoflagellates show lower growth rates (range 0.41-0.48 d^{-1}) than growth ciliate growth rates (range 0.77-1.01 d^{-1}) when fed identical diets at a constant temperature of 13 ºC. Consequently, the effects of variable grazer response between dilutions in our experiments can only be hypothesized until published data shows that high latitude microzooplankton communities (i.e. dominance by heterotrophic dinoflagellates) are affected by resource gradients on 24 hour time scales.

Despite low ambient nutrient concentrations, phytoplankton growth rates were surprisingly high. Total phytoplankton growth rates averaged 0.59, 1.04, and 0.42 d^{-1} for non-bloom, bloom-fringe, and bloom stations, respectively. These values correspond to 0.85, 1.50, and 0.61 doublings d^{-1}. Exceptionally high growth rates were experienced at stations 9 (2.05 d^{-1}) and 10 (2.07 d^{-1}) for total growth, and station 13 (2.05 d^{-1}) for growth in cells > 10 µm. Although these values are exceptionally high, they are similar to those reported by Boyd and Harrison (1999) from the northeast subarctic Pacific, whose values

were estimated from the turnover of algal carbon. An artifact of the dilution assay that may account for this elevated growth is changing irradiance intensity between *in situ* sample collection and experimental bottles, as well irradiance changes during the incubation. As noted in our methods, experimental bottles were layered with neutral density screen to simulate ambient irradiance [seawater was collected from depths corresponding to 50% surface irradiance levels (I_o)]. Phytoplankton conditioned to light levels above 50% I_o may respond by synthesizing more Chl *a* per cell to accommodate lower light levels. Unfortunately, this accumulation of Chl *a* on a cellular basis is construed as community growth in the dilution method. It is unlikely this response would cause much variation in our growth estimates, for all sampled were collected from the upper mixed layer. Physical conditions during the cruise favored an energetic, highly mixed and deep euphotic zone.

Phytoplankton growth was not nutrient limited throughout our study, suggesting the phytoplankton community was adapted to, and perhaps in part structured by, low ambient nutrient concentrations. This is not surprising given the phytoplankton community was numerically dominated by cells < 10 µm. The exception to this was the high abundance of large *Nitzschia* spp. diatoms, whose needle-like shape and high surface-volume ratio apparently allows it to flourish in nutrient depleted regions. The occurrence of a *Nitzschia* sp. diatom was also observed in a western English Channel *E. huxleyi* bloom (Garcia-Soto *et al*., 1995).

Surprisingly, we found that phytoplankton growth was occasionally adversely affected by nutrient addition. The target levels of 2 µM PO_4^- and 20 µM NO_3^- added to our dilution series are not above levels frequently encountered in the summer Bering Sea

(Shiomoto, 1999). However, because this study occurred during a period of low ambient nutrient concentrations, it is possible that the phytoplankton were conditioned to these low nutrient levels. The sudden increase in nutrients from our additions may have had sub-lethal negative effects on the phytoplankton growth. However, this explanation is only hypothetical. To our knowledge, no published data suggests this mechanism; consequently, a definitive explanation of our data is lacking.

Dilution experiments performed by Levasseur *et al*. (1996) during a bloom of *E. huxleyi* in the Raunefjorden fjord in Norway showed gross growth rates of *E. huxleyi* (1.08 to 1.23 d^{-1}) were approximately matched by microzooplankton grazing (1.02 to 1.32d^{-1}). This was not the case in the Bering Sea. In bloom waters, microzooplankton grazing rates were only 25% of phytoplankton growth, and grazing rates were significantly lower than at non-bloom stations. Also apparent was a shift in grazing pressure within the bloom from small to large phytoplankton. It could be argued that the shift in grazing pressure within the bloom to cells > 10 µm results from the substantial increase in biomass in that size fraction. Chl *a* associated with cells > 10 µm in bloom stations accounted for 63% of the total, whereas in the non-bloom stations it accounted for only 25% of the total. This explanation is unlikely; paralleling the increase in large phytoplankton was the increase in biomass of *Gyrodinium* spp. and *Protoperidinium*-like dinoflagellates and the large ciliate *Laboea* sp. These microzooplankton feed heavily on diatoms. *E. huxleyi*, which is approximately 5-8 µm, is most likely too small to efficiently be grazed by these large diatom-consuming microzooplankton. Phytoplankton < 10 µm are primarily grazed by protists ≤ 20 µm (Sherr and Sherr, 1994), which, in turn, are too small to graze on large diatoms. Surprisingly, despite a significant reduction in

grazing rates from non-bloom to bloom stations, small microzooplankton (10-20 µm) capable of grazing *E. huxleyi* and other small phytoplankton increased slightly in abundance (51,631 to 61,825 cells l^{-1}) and biomass (10.56 to 12.87 µg $C^{l-}1$) from non-bloom to bloom stations, respectively.

In light of the low grazing rates on phytoplankton < 10 µm, what then supports the high abundance and biomass of small microzooplankton? Although we did not measure heterotrophic bacterial biomass, it is possible bacterial biomass was high enough to support the nutritional demands of small microzooplankton. It is also possible high molecular weight polysaccharides, which can be assimilated at low concentrations (Sherr and Sherr, 1988) and suspended POM supported small microzooplankton biomass. However, it is unknown whether *E. huxleyi* leaks high molecular weight DOM, and if so, under what circumstances. Because of this and the fact we did not measure bacterial biomass, an unequivocal explanation as to what supports high microzooplankton biomass in the small size fractions within the bloom is lacking. A definitive answer would explain why *E. huxleyi* is accumulating (i.e. biomass is being removed from other resources), but would give no mechanistic information as to why grazing pressure was low on the *E. huxleyi* bloom.

One possibility is that the grazers are selectively choosing prey other than *E. huxleyi* . As previously suggested, coccoliths surrounding *E. huxleyi* may act as a morphological or chemical signal, indicating *E. huxleyi* is an unpalatable or indigestible prey. Signaling is defined as the transfer of information between two organisms by a biogenic stimulus that can be perceived by a sensory system and evoke an adaptive response (Dusenbery, 1992). If a micrograzer receives negative signals from contact with

inorganic coccoliths, reduced grazing pressure on *E. huxleyi* will result, thus leading to the possibility of bloom formation, as has been witnessed in the southeastern Bering Sea since 1997. This may be especially problematic if detached coccoliths accumulate in the water column once shed from a healthy cell. In a western English Channel *E. huxleyi* bloom, cells and detached coccoliths presented densities of > 2000 cells ml^{-1} and 350,000 coccoliths ml^{-1} (Garcia-Soto *et al.*, 1995).

A second possible signaling mechanism and alternative explanation for low grazing in the bloom would be the ability of *E. huxleyi* to chemically defend itself. Wolfe *et al.* (1997) showed that certain laboratory strains of *E. huxleyi* were grazed at lower rates than other morphologically identical strains. The proposed mechanism for reduced grazing pressure is the activated enzymatic cleavage of the compatible solute β-dimethylsulphoniopropionate (DMSP) to dimethyl sulphide, acrylate, and a proton (Wolfe *et al.*, 1996). Acrylate shows antimicrobial activity (Sieburth, 1960) and is presumed to accumulate in microzooplankton food vacuoles, thus reducing grazing pressure on DMSP producing algae. *E. huxleyi*, like many taxa from the Haptophyceae and Dinophyceae, is a notorious bloom forming species that produces concentrated intracellular DMSP (Wolfe, 2000). The mechanism for chemical feeding deterrence by DMSP cleavage is still poorly understood. However, Wolfe and Strom (unpubl. Data) showed the dinoflagellates *Amphidinium longum* and *Gymnodinium* sp. readily ingest *E. huxleyi* with low DMSP lyase activity (Wolfe, 2000), but grazing of high-lyase *E. huxleyi* is near zero. These prey strains were morphologically identical, with only slight variations in chemical composition (total C, N, protein, lipid, carbohydrate, mineral, and dry weight). Although other unknown mechanisms may contribute to feeding selectivity,

Wolfe (2000) states the only clear polymorphism that covaries with feeding selectivity is DMSP lyase activity and most likely results in feeding deterrence by microzooplankton. The application of this hypothesis to bloom dynamics remains purely conjectural until further research quantifying *in situ* DMSP lyase activity and DMS production rates are made.

A third mechanism that may account for low grazing rates on the *E. huxleyi* bloom would be top down control on microzooplankton. Perhaps grazing on small microzooplankton by large microzooplankton and metazoans are keeping small microzooplankton biomass low enough to allow blooms of small algae to form. These trophic cascades have been described in oceanic ecosystems (Shiomoto *et al*., 1997), but such top down control seems unlikely in this case; microzooplankton abundance and biomass estimates were higher than previously reported for this region, with highest values occurring in the bloom

In a study to determine whether protozoan biomass was sufficient to meet daily carbon requirements for first-feeding larval pollock, Howell-Kübler *et al.* (1996) measured abundance (300 to 6233 cells l^{-1}) and biomass (0.60 to 10.2 µg C l^{-1}) for microzooplankton > 20 µm in the southeastern Bering Sea in April of 1992. Because our measurements of biomass and abundance included all cells > 10 µm, we subsequently estimated abundance and biomass of microzooplankton > 20 µm only for comparison with their findings. We attained abundance values ranging from 9,112 to 70,834 cells l^{-1} and biomass values ranging from 9.51 to 132.5 µg C l^{-1}. These are still higher than those reported for an earlier season by Howell-Kübler *et al.* (1996), but more closely resemble their estimates from Shelikof Strait in May 1990, where abundance and biomass during

the onset of a diatom bloom ranged from 850 to 14,960 cells l^{-1} and 1.29 to 70.73 μg C l^{-1}, respectively.

Ciliate abundance and biomass showed little variation among stations. Conversely, heterotrophic dinoflagellate abundance and biomass significantly correlated with phytoplankton biomass. Because most of the biomass increase was from large phytoplankton, this suggests a tight coupling between dinoflagellates and diatoms. Thus, the physical-chemical environment that provides conditions conducive to diatom growth ultimately structures the microzooplankton community composition and biomass. If diatoms are sub-optimal diets for crustacean zooplankton as the literature suggests, this predictable increase in dinoflagellate abundance may provide the necessary carbon for metazoan and larval fish predators.

It is clear from our data that microzooplankton are significant, if not the primary, grazers of phytoplankton production in the Bering Sea summer. This finding is consistent with others from both oceanic and coastal ecosystems. Because algal blooms are seasonally predictive in shelf environments and provide satiating levels of biomass on short time scales, they are often associated with high biomass from higher order trophic levels. This is especially true in the southeastern Bering Sea, where primary production indirectly supports one of the world's largest fisheries, as well as sustaining large populations of migratory birds and marine mammals. Because of the ecological importance of this primary production, it is necessary to allocate the grazed production into the appropriate consumer category if we are to make predictions as to how this and other large ecosystems will adapt to climate variability.

In summation, despite low ambient nutrient levels and water temperatures, phytoplankton growth rates for both size fractions were high across all biogeographic regions. Microzooplankton grazing patterns varied between location, but in general seemed to shift from selective grazing on small phytoplankton cells outside the bloom to selectively grazing large cells within the bloom. This shift to grazing on large cells occurred despite an increase in abundance and biomass of small microzooplankton. The data presented here unequivocally implicate reduced microzooplankton grazing as contributing to the formation and temporal persistence of the *E. huxleyi* bloom. Unfortunately, the ultimate fate of the coccolithophore bloom remains unknown. Because microzooplankton grazing does not appear to a major loss process for the bloom, alternative explanations for its fate may include horizontal or vertical advection, viral lysis, or decreased production as ambient PAR decreases with progression of winter months.

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Table 1
Stations, biogeographic region, location, date, local time, sampling depth, and water temperature for dilution experiments conducted during the summer 1999 Inner Front cruise to the southeastern Bering Sea. BGR: biogeographic region. NB: non-bloom; BF: bloom-fringe; B: bloom.

Station	BGR	Latitude	Longitude	Date	Time (Local)	Depth (m)	Temp (…C)
1	NB	55… 17.38 N	164… 12.56 W	29 July 1999	1600	6	6.5
2	NB	55… 41.66 N	164… 33.10 W	27 July 1999	1240	8	6.0
3	NB	56… 52.48 N	159… 99.24 W	1 Aug 1999	1230	11	10.5
4	NB	56… 86.38 N	160… 52.89 W	31 July 1999	1320	9	6.8
5	BF	57… 13.20 N	164… 08.51 W	23 July 1999	0940	5	7.0
6	BF	56… 20.79 N	164… 33.78 W	21 July 1999	1800	30	1.5
7	BF	56… 81.54 N	164… 01.12 W	8 Aug 1999	1130	7	7.9
8	BF	57… 13.16 N	171… 21.88 W	16 Aug 1999	2114	10	8.4
9	BF	56… 46.12 N	169… 57.95 W	17 Aug 1999	0530	10	6.4
10	BF	57… 27.25 N	169… 39.45 W	16 Aug 1999	0029	6	8.3
11	BF	57… 77.16 N	163… 04.07 W	7 Aug 1999	1505	5	6.3
12	B	57… 45.78 N	163… 37.59 W	5 Aug 1999	2226	7	6.4
13	B	57… 30.29 N	163… 53.94 W	6 Aug 1999	1500	5	7.6
14	B	57… 18.83 N	163… 66.38 W	9 Aug 1999	0100	6	8.0
15	B	59… 38.38 N	167… 13.86 W	13 Aug 1999	0856	4	7.2
16	B	59… 10.35 N	167… 44.96 W	11 Aug 1999	1159	7	5.8
17	B	58… 44.73 N	168… 13.66 W	12 Aug 1999	1541	5	6.4
18	B	58… 21.67 N	168… 39.20 W	11 Aug 1999	2030	7	6.0

Table 2
Percent contribution (%) of > 10 μm and < 10 μm Chl *a* to total Chl *a* and dominant phytoplankton taxa for dilution experiment stations.

Station	% total Chl *a*		Phytoplankton assemblage
	> 10 μm	< 10 μm	
1	10	90	Many cryptomonads, chlorophytes, other small unidentified flagellates, small dinos (< 10 μm), no diatoms
2	7	93	Many cryptomonads, chlorophytes, other coccoid flagellates, no diatoms
3	37	63	Mixed assemblage of small flagellates (< 7 μm), few diatioms (*Nitzschia*, *Neurosigma*, *Chaetoceros*)
4	44	56	Few cryptomonads and chlorophytes, few diatoms (*Leptocylindrus*, *Nitzschia*)
5	12	88	*E. huxleyi*, cryptomonads, small round dinos (< 10 μm), no diatoms
6	22	78	Many cryptomonads, *Nitzschia*, few *E. huxleyi*
7	23	77	*E. huxleyi*, cryptomonads, cryptophytes, some *Nitzschia*
8	35	65	Small flagellates (≤ 5 μm), diatom fragments
9	21	79	Many cryptomonads, few *E. huxleyi*, *Rhizosolenia*, *Chaetoceros* fragments, other small coccoid flagellates
10	26	74	Large *Nitzschia* (> 50 μm), *Leptocylindrus*, few *E. huxleyi*, small dinos (< 10 μm)
11	34	66	Mixed diatoms (*Navicula*, *Coscinodiscus*, *Paralia*), few *E. huxleyi* and cryptomonads
12	65	35	Very many *Nitzschia* and *E. huxleyi*, few *Leptocylindrus,* few *Ceratium* (≅ 260 μm)
13	65	35	Numerical dominance by *E. huxleyi*, very few cryptomonads and *Leoptocylindrus*

(Continued next page)

Table 2. Continued from previous page.

Station	% total Chl *a*		Phytoplankton assemblage
	> 10 μm	< 10 μm	
14	61	39	Dominance by *E. huxleyi* and *Nitzschia*, very few cryptomonads
15	21	78	Very many *E. huxleyi*, mixed diatoms (*Nitzschia*, *Chaetoceros*, *Navicula*, *Pleurosigma*)
16	61	39	*E. huxleyi*, *Nitzschia*, small flagellates (≤ 5 μm), mixed assemblage of diatom fragments
17	78	22	Dominance by *E. huxleyi* and large *Nitzschia* (200 x 5 μm)
18	89	11	*E. huxleyi*, many *Nitzschia*, *Leptocylindrus*, *Thalassiosira*

Table 3
Initial surface inorganic nutrient concentrations (μM) for all dilution experiments. ND: not detectable.

Station	PO_4^{3-}	$Si(OH)_4$	NO_2^-	NH_4^+	NO_3^-
1	0.50	11.55	0.01	4.23	1.71
2	0.49	27.40	ND	3.77	0.42
3	0.46	3.90	ND	0.13	0.66
4	0.72	0.07	ND	4.59	0.83
5	ND	1.46	0.01	2.26	0.36
6	ND	1.40	ND	4.73	0.32
7	0.01	0.80	0.07	6.39	0.81
8	0.01	7.86	ND	1.75	0.40
9	0.89	14.82	ND	2.06	5.95
10	0.54	1.16	ND	3.04	0.65
11	0.55	1.24	0.07	2.10	0.81
12	0.51	0.31	ND	4.27	0.84
13	0.03	0.95	ND	5.97	0.23
14	0.54	1.36	0.07	3.74	0.87
15	0.45	0.92	ND	2.48	0.77
16	ND	0.68	ND	1.44	0.65
17	0.51	0.67	ND	2.34	0.77
18	0.42	0.62	ND	1.42	0.94

Table 4
Rates of phytoplankton growth (μ, d^{-1}) and grazing mortality (g, d^{-1}), and g:μ (%) for all dilution experiments. Growth rates followed by * denotes experiments in which grazing saturation occurred. Numbers in parenthesis are phytoplankton growth rates without added nutrients.

	Growth			Grazing			g:μ		
Station	Total	> 10 μm	< 10 μm	Total	> 10 μm	< 10 μm	Total	> 10 μm	< 10 μm
1	*0.72 ± 0.39 (0.56)	*0.97 ± 0.23 (0.95)	*0.68 ± 0.43 (0.48)	1.02 ± 0.14	0.67 ± 0.14	1.06 ± 0.19	141	69	155
2	0.42 ± 0.05 (0.77)	0.71 ± 0.07 (0.64)	0.40 ± 0.05 (0.83)	0.70 ± 0.09	0.19 ± 0.13	0.78 ± 0.10	166	27	195
3	0.38 ± 0.08 (0.37)	*0.61 ± 0.13 (0.52)	0.37 ± 0.08 (0.41)	0.60 ± 0.16	0.33 ± 0.01	0.88 ± 0.14	157	54	237
4	*0.84 ± 0.22 (0.71)	*1.13 ± 0.11 (1.04)	*0.63 ± 0.23 (0.45)	0.26 ± 0.08	0.48 ± 0.14	0.10 ± 0.04	31	42	16
5	0.44 ± 0.08 (0.24)	*0.88 ± 0.13 (0.68)	0.42 ± 0.09 (0.19)	0.25 ± 0.16	0.66 ± 0.14	0.21 ± 0.16	57	75	50
6	1.10 ± 0.13 (1.13)	0.55 ± 0.09 (0.56)	1.11 ± 0.24 (1.13)	0.22 ± 0.20	0.24 ± 0.16	0.10 ± 0.44	20	44	9
7	0.68 ± 0.08 (0.57)	0.80 ± 0.10 (0.49)	0.65 ± 0.09 (0.59)	0.35 ± 0.14	0.59 ± 0.18	0.28 ± 0.16	51	74	43
8	0.34 ± 0.07 (0.56)	0.13 ± 0.09 (0.08)	0.29 ± 0.08 (0.67)	0.53 ± 0.11	0.45 ± 0.16	0.58 ± 0.16	53	346	200
9	*2.05 ± 0.08 (1.99)	*0.74 ± 0.10 (0.71)	*0.58 ± 0.12 (0.55)	0.23 ± 0.01	1.20 ± 0.09	0.06 ± 0.08	11	162	10
10	*2.07 ± 0.09 (1.63)	*1.13 ± 0.08 (1.03)	*0.44 ± 0.12 (-0.22)	0.26 ± 0.02	0.44 ± 0.10	0.16 ± 0.02	13	39	36

(Continued next page)

Table 4. Continued from previous page.

Station	Growth			Grazing			g:μ		
	Total	> 10 μm	< 10 μm	Total	> 10 μm	< 10 μm	Total	> 10 μm	< 10 μm
11	*0.58 ± 0.21 (0.60)	*0.50 ± 0.21 (0.75)	*0.61 ± 0.35 (0.53)	0.53 ± 0.00	0.67 ± 0.03	0.49 ± 0.01	91	134	80
12	0.30 ± 0.07 (0.14)	0.32 ± 0.12 (0.20)	0.56 ± 0.16 (0.47)	0.08 ± 0.05	0.38 ± 0.20	0.04 ± 0.14	27	118	7
13	0.30 ± 0.19 (0.31)	2.05 ± 0.44 (2.64)	0.55 ± 0.51 (0.38)	0.33 ± 0.33	0.49 ± 0.16	0.25 ± 0.25	110	24	45
14	*0.61 ± 0.06 (0.37)	*0.57 ± 0.09 (0.44)	0.78 ± 0.15 (0.56)	0.41 ± 0.01	0.88 ± 0.07	0.16 ± 0.03	67	154	21
15	0.48 ± 0.09 (0.44)	*0.84 ± 0.28 (0.89)	0.45 ± 0.09 (0.38)	0.32 ± 0.16	0.73 ± 0.15	0.24 ± 0.16	67	87	53
16	*0.65 ± 0.32 (0.71)	0.42 ± 0.08 (0.25)	*0.46 ± 0.29 (0.65)	0.67 ± 0.04	0.67 ± 0.14	0.20 ± 0.18	103	160	43
17	0.28 ± 0.10 (0.18)	*-0.29 ± 0.23 (-0.48)	1.12 ± 0.20 (1.12)	0.22 ± 0.16	0.46 ± 0.06	0.05 ± 0.15	78	358	4
18	*0.31 ± 0.06 (-0.05)	0.15 ± 0.08 (-0.05)	1.09 ± 0.19 (1.06)	0.09 ± 0.03	0.44 ± 0.15	0.02 ± 0.30	29	293	2

Figure Legends

Figure 1. Map of the southeastern Bering Sea showing experimental station locations. (●) non-bloom; (❒) bloom-fringe; (▼) bloom.

Fig. 2 Chl *a* concentrations (µg l^{-1}) for (A) total, (B) > 10 µm, and (C) < 10 µm cells. Values are means (n = 4). Error bars represent upper 95% confidence intervals.

Fig. 3 Growth (µ, d^{-1}) and grazing (g, d^{-1}) rates for (A) total, (B) > 10 µm, and (C) < 10 µm Chl *a* for each biogeographical region. Line bisecting axis represents equal rates.

Fig. 4 Chl *a* (µg l^{-1}) and grazing (g, d^{-1}) rates for (A) non-bloom, (B) bloom-fringe, and (C) bloom stations.

Fig. 5 Microzooplankton abundance (cells l^{-1}). Values are means (n = 2). Error bars represent upper 95% confidence intervals.

Fig. 6 Microzooplankton biomass (µg C l^{-1}). Values are means (n = 2). Error bars represent upper 95% confidence intervals.

Fig. 7 Percent contribution of individual taxa to community abundance. Values are means (n = 2). hdinos: heterotrophic dinoflagellates; oligo: oligotrichs (aloricate choreotrich ciliates).

Fig. 8 Percent contribution of individual taxa to community biomass. Values are means (n = 2). hdinos: heterotrophic dinoflagellates; oligo: oligotrichs (aloricate choreotrich ciliates).

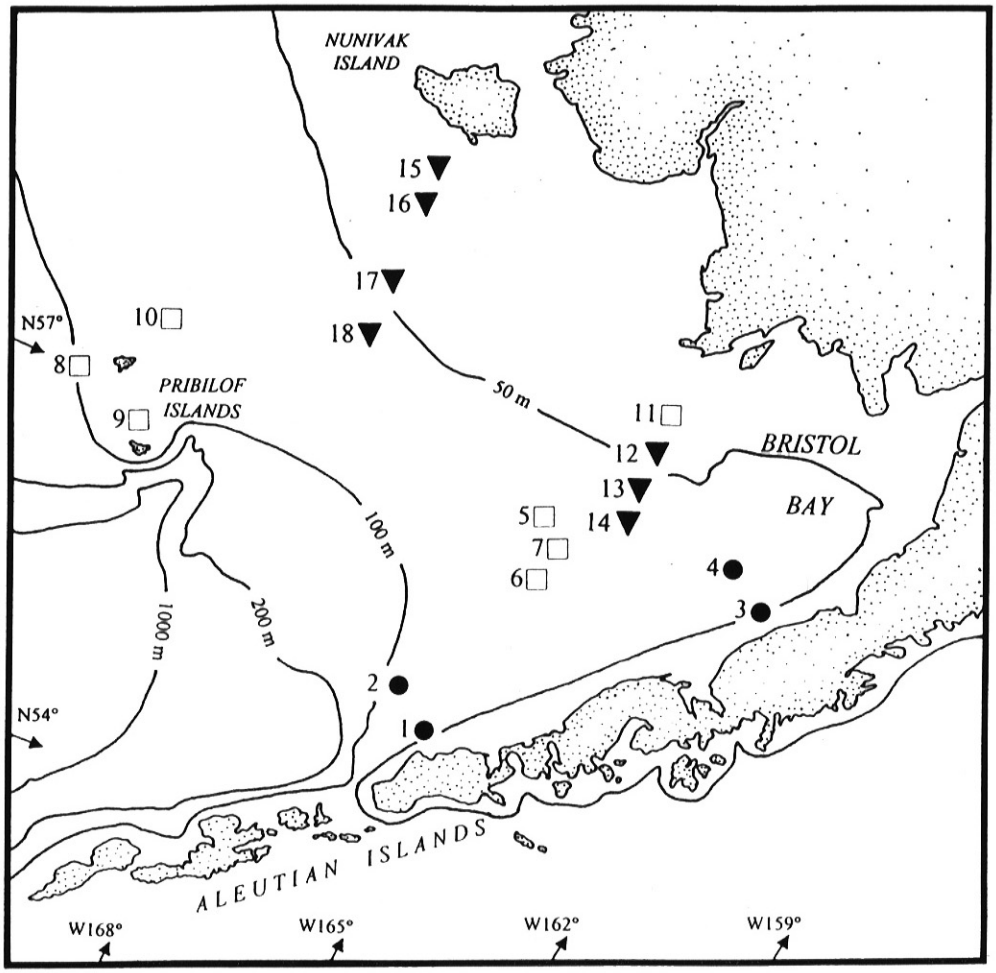
NUNIVAK
ISLAND
15
16
17
18
N57°
10
8
PRIBILOF
ISLANDS
9
50 m
11
12
BRISTOL
BAY
13
14
5
7
6
4
3
100 m
1000 m
200 m
2
1
N54°
ALEUTIAN ISLANDS
W168°
W165°
W162°
W159°

Figure 1

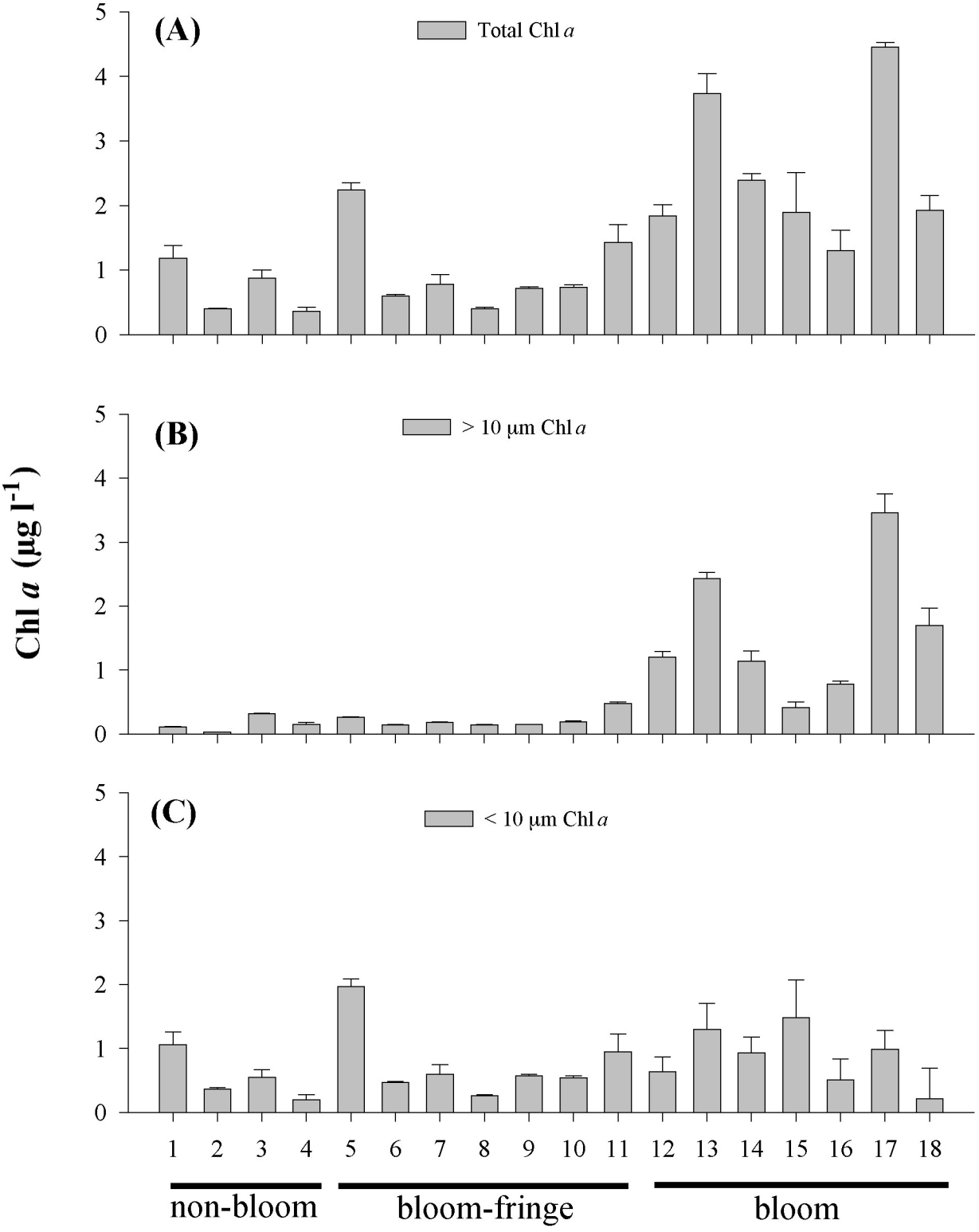
(A)
Total Chl a
(B)
> 10 μm Chl a
(C)
< 10 μm Chl a
Chl a (μg l-1)
0
1
2
3
4
5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
non-bloom
bloom-fringe
bloom
Station

Figure 2

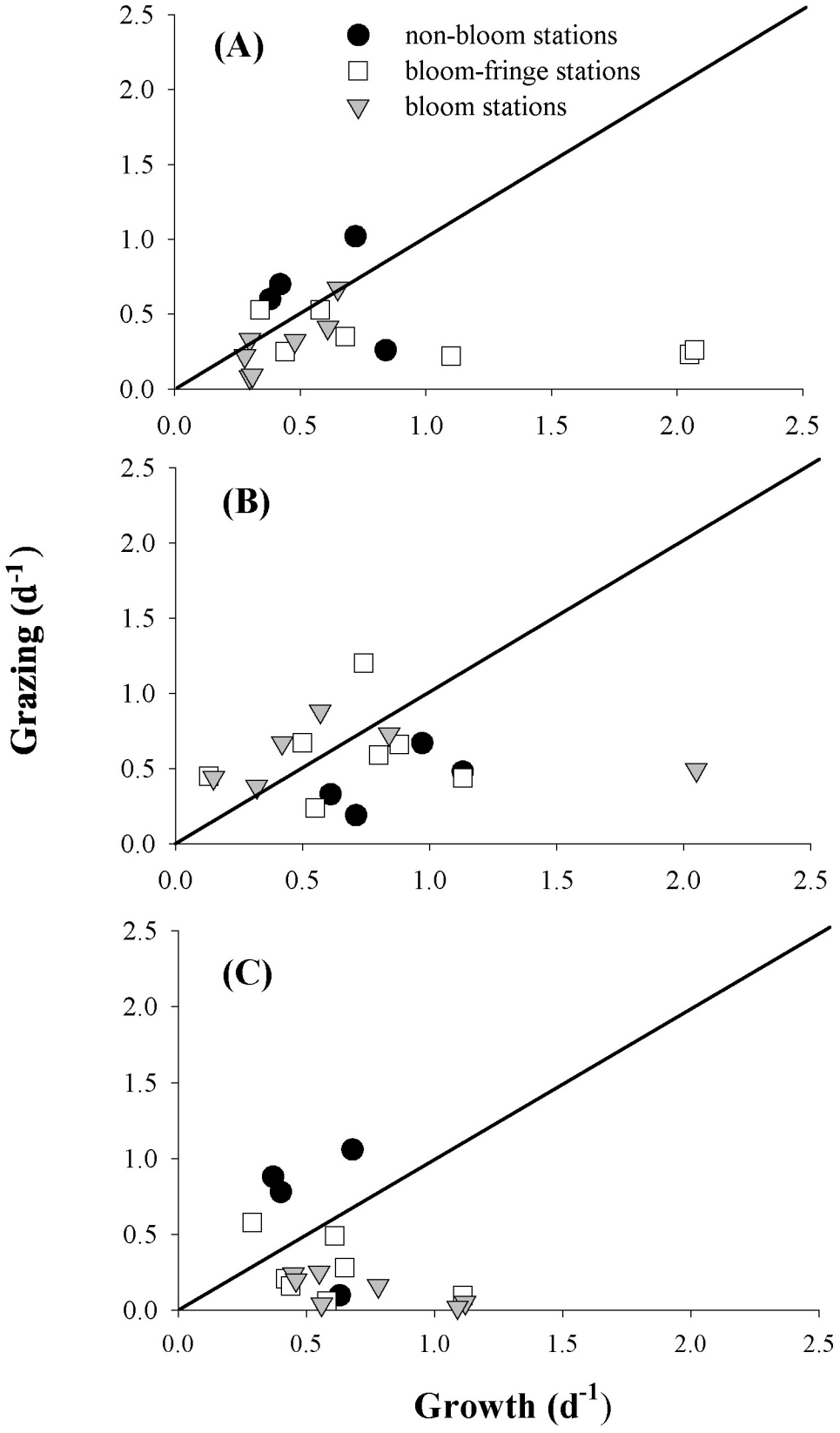
(A)
non-bloom stations
bloom-fringe stations
bloom stations
(B)
(C)
Grazing (d-1)
Growth (d-1)
0.0
0.5
1.0
1.5
2.0
2.5

Figure 3

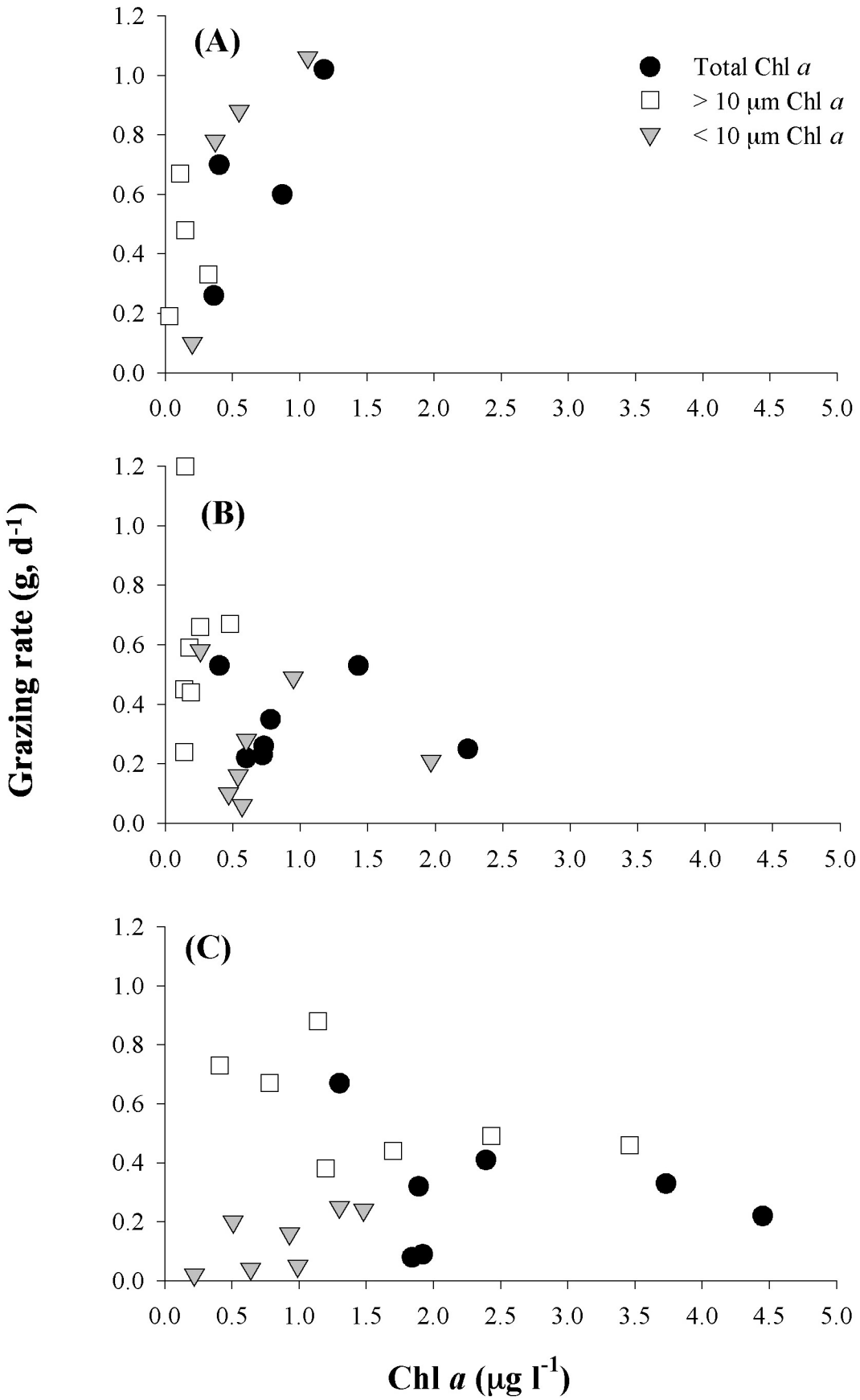
(A)
(B)
(C)
Total Chl a
> 10 µm Chl a
< 10 µm Chl a
Grazing rate (g, d-1)
Chl a (µg l-1)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0

Figure 4

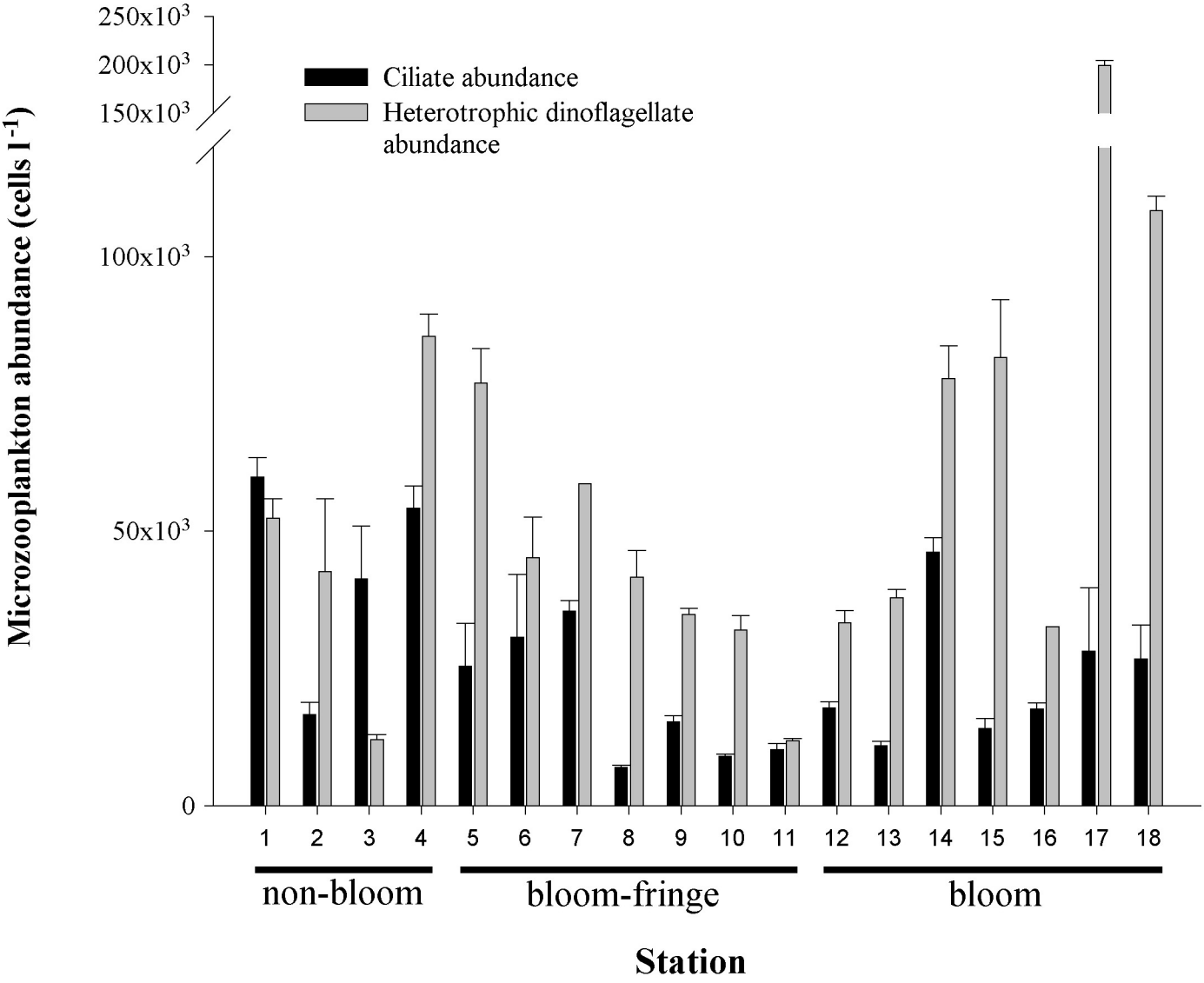
250x10³
200x10³
150x10³
100x10³
50x10³
0
Microzooplankton abundance (cells l⁻¹)
Ciliate abundance
Heterotrophic dinoflagellate abundance
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
non-bloom
bloom-fringe
bloom
Station

Figure 5

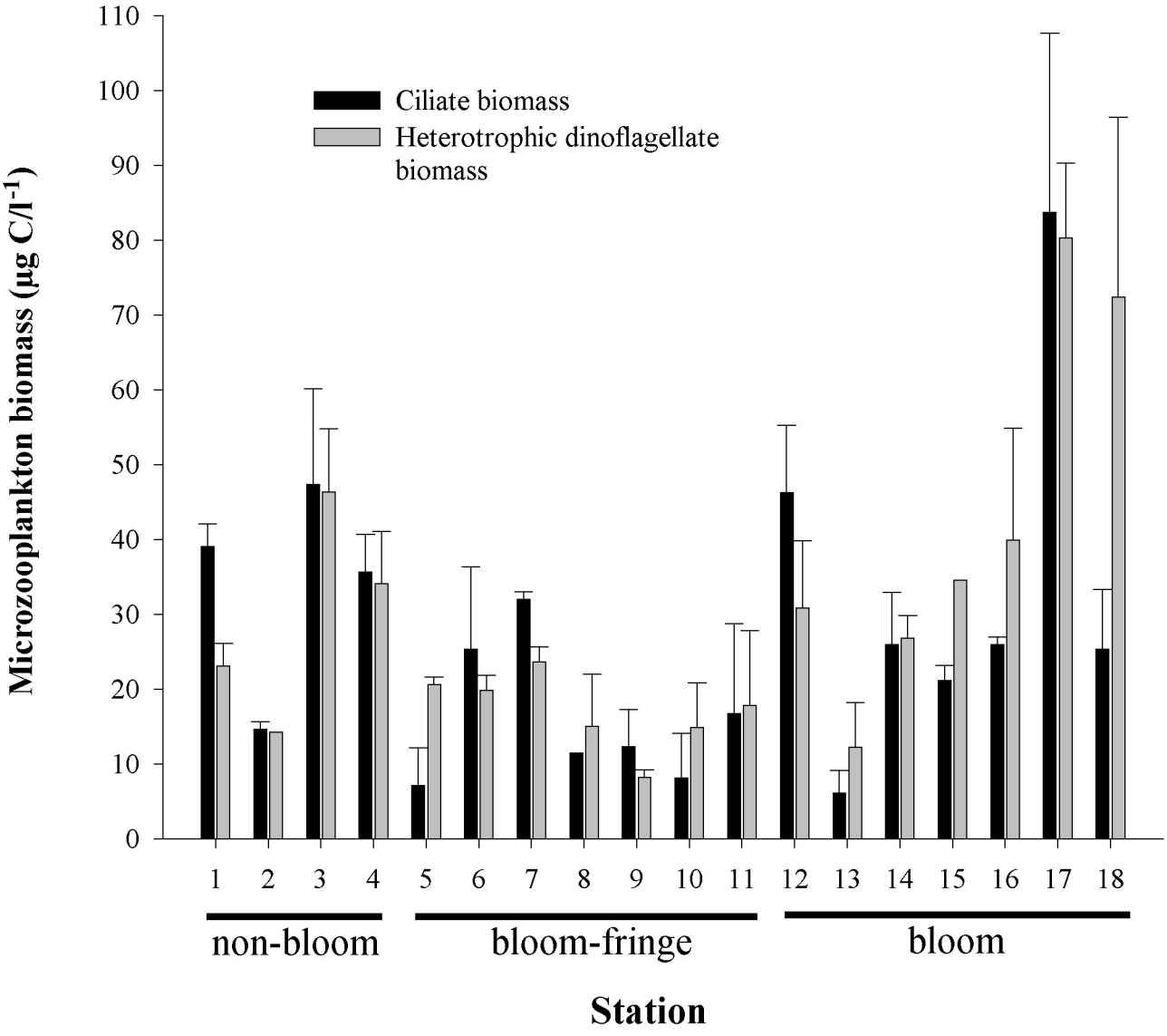
Microzooplankton biomass (µg C/l-1)
110
100
90
80
70
60
50
40
30
20
10
0
Ciliate biomass
Heterotrophic dinoflagellate biomass
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
non-bloom
bloom-fringe
bloom
Station

Figure 6

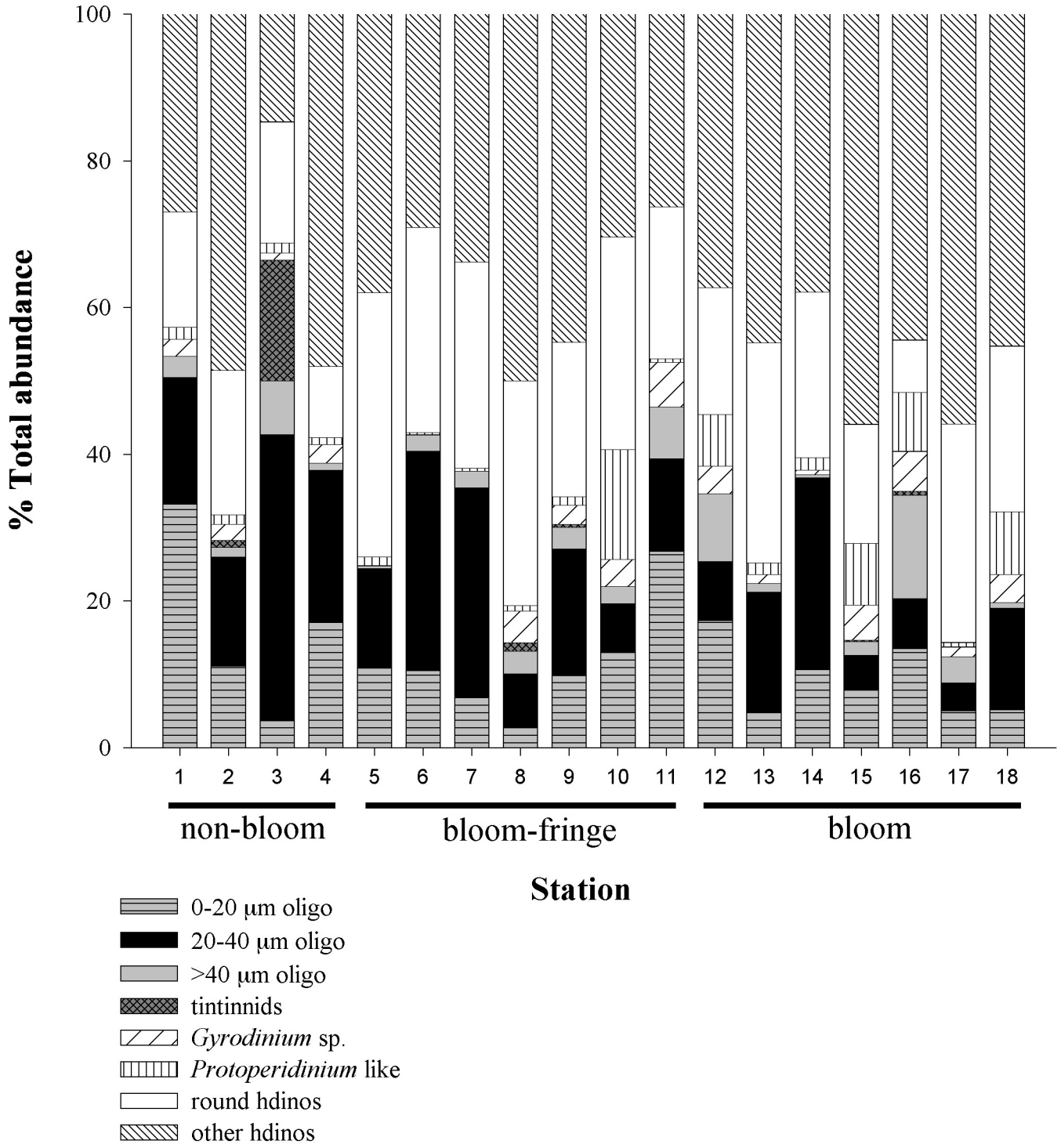
100
80
60
40
20
0
% Total abundance
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
non-bloom
bloom-fringe
bloom
Station
0-20 μm oligo
20-40 μm oligo
>40 μm oligo
tintinnids
Gyrodinium sp.
Protoperidinium like
round hdinos
other hdinos

Figure 7

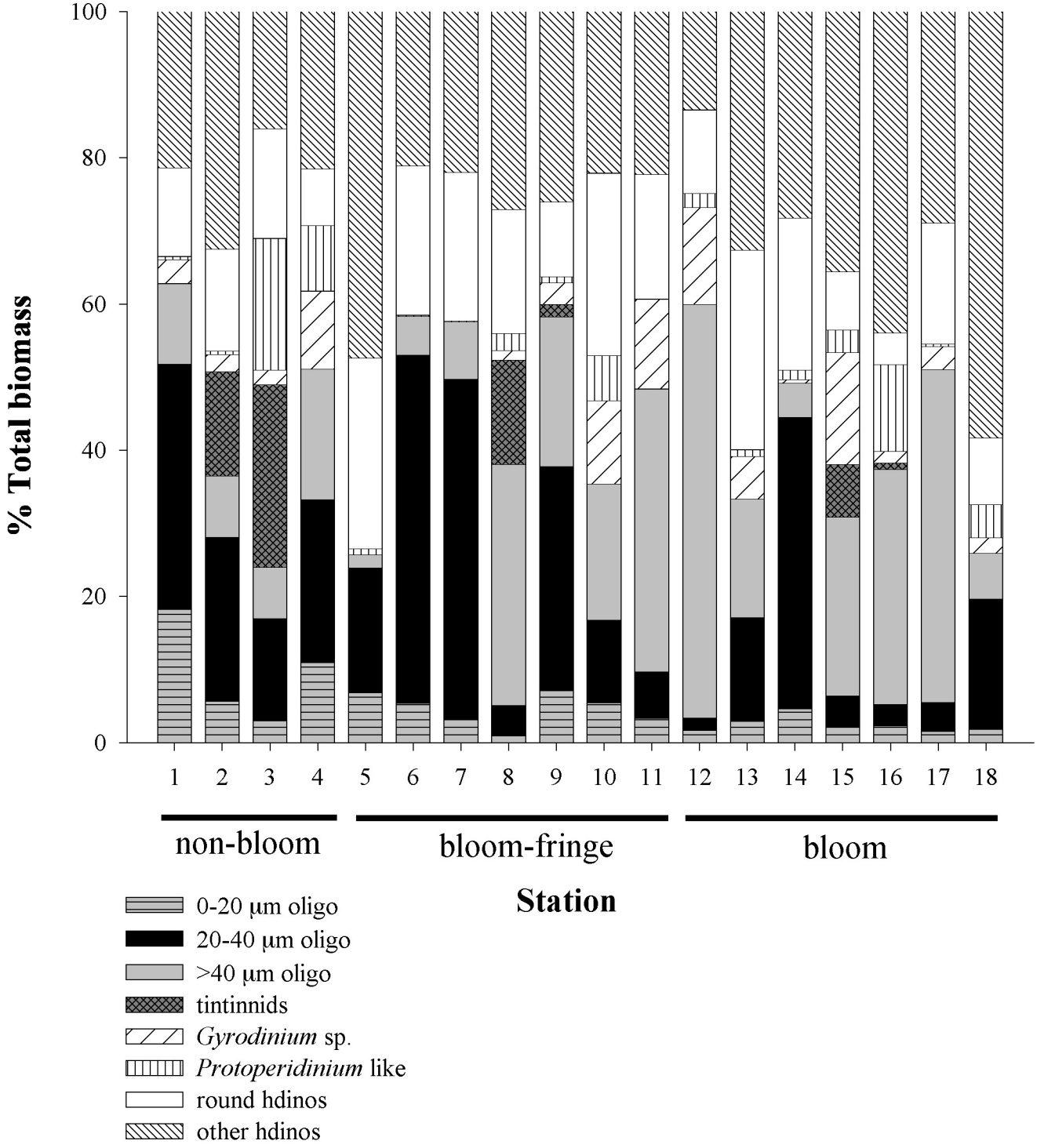
100
80
60
40
20
0
% Total biomass
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
non-bloom
bloom-fringe
bloom
Station
0-20 µm oligo
20-40 µm oligo
>40 µm oligo
tintinnids
Gyrodinium sp.
Protoperidinium like
round hdinos
other hdinos

Figure 8