

## Predicted impacts of elevated temperature on the magnitude of the winter-spring phytoplankton bloom in temperate coastal waters: A mesocosm study

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### Abstract

An experiment was conducted with six 13-m<sup>3</sup> land-based mesocosms (5 m deep) in December 1996/February 1997 to address the impact of increased temperature on the trophic structure of nutrient-rich coastal systems. All mesocosms were exposed to a high nutrient loading rate (2.31 mmol N m<sup>-3</sup> d<sup>-1</sup>:0.18 mmol P m<sup>-3</sup> d<sup>-1</sup>:0.165 mmol Si m<sup>-3</sup> d<sup>-1</sup>). Three treatment mesocosms were maintained at a temperature elevated ~1°C relative to the long-term (1977–1989) average, ambient temperature in the parent system, Narragansett Bay, Rhode Island, and elevated ~3°C from three control mesocosms. Warmer temperatures were hypothesized to result in lower phytoplankton biomass during the winter-spring bloom period as a result of increased grazing related to greater metabolic activity of both zooplankton and the benthos. Mean phytoplankton biomass and abundance were lower in the mesocosms with warmer temperatures. Well-developed phytoplankton blooms occurred in two of the three cool systems. The presence of high numbers of filter-feeding mussels (*Mytilus edulis*) prevented a bloom from occurring in the third cool system. Unlike most benthic organisms, mussels continue to filter at high rates even at very low temperatures. Analyses of variance (ANOVAs), after adjusting for mussel biomass, revealed significant ( $P < 0.05$ ) or near significant ( $P < 0.10$ ) differences in phytoplankton (abundance and biomass), zooplankton abundance, and sedimentation rates between warm and cool treatments. Experimental and literature data were combined to develop carbon budgets for the six systems. Budgets for the warm systems indicated that carbon produced by phytoplankton was lost primarily by grazing of zooplankton, mussels, or both (29–55%) and to a lesser degree, by sedimentation (29–43%). In the cool systems without mussels, losses via sedimentation (73–82%) predominated, with an average ninefold increase in the amount of material supplied to the benthos relative to warm systems.

The seasonal cycle of phytoplankton biomass in temperate regions is typically dominated by a winter-spring phytoplankton bloom and, to a lesser extent, one in the fall (Cushing 1959; Smayda 1973a). CO<sub>2</sub> production by our global industrial society has altered the earth's climate, with increased warming occurring in most regions of the northern hemisphere over the past century (Manabe and Stouffer 1994; Schuurmans 1995). Correlative evidence indicates that increased winter water temperature, resulting from climate warming, may affect the size of the winter-spring phytoplankton bloom in temperate coastal areas (Oviatt 1994). Since the fate of the photosynthetically produced organic matter can significantly influence the trophic structure of marine systems, it is important to understand the relationship

between temperature and bloom magnitude. In general, phytoplankton levels are controlled by a balance between “bottom-up” control through nutrient limitation and resource competition and “top-down” processes such as grazing (Ryther and Dunstan 1971; Schindler 1974; Carpenter et al. 1988; Durbin et al. 1992; Heiskanen et al. 1996). The interactions between these controlling factors regulate the biomass levels of the phytoplankton throughout the annual cycle and during bloom periods. Grazing by herbivores is a primary factor that reduces phytoplankton biomass in mesocosm experiments (Prins et al. 1995), field observations (Cloern 1982; Hily 1991; Mellina et al. 1995), and simulation models (Officer et al. 1982). Since temperature regulates grazing rate, predicted increases in temperature from global warming may consequently alter the balance of factors leading to bloom development. We hypothesize that increased grazing by the zooplankton and/or benthos could reduce the magnitude of winter-spring blooms despite the presence of abundant nutrients.

Processes controlling both the development of phytoplankton blooms and their fate have received increasing attention in recent years (Graf et al. 1982; Rudnick and Oviatt 1986; Laws et al. 1988). Factors recognized as important in controlling the onset of the winter-spring diatom bloom include light, temperature, nutrients, and grazing (Riley 1967; Smayda 1973b; Hitchcock and Smayda 1977; Townsend and Spinard 1986). Research has suggested that the annual winter-spring bloom in temperate areas is controlled by low temperatures that lead to a relaxation in grazing pressure (Pratt 1965; Martin 1970; Vargo 1976). Usually, zooplankton are considered to be the main grazers on phytoplankton, but benthic grazers and/or filter feeders may also be important in

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limiting phytoplankton biomass in well-mixed waters (Oviatt 1994). Low temperatures during the winter-spring bloom period have previously been correlated with low benthic grazing rates and small effect on phytoplankton levels (Rudnick and Oviatt 1986; Beatty 1991). The impact of increasing water temperatures due to global warming in systems where temperature-controlled grazing pressure regulates bloom development is potentially important.

Two fates generally considered for the diatom biomass are grazing by the zooplankton and direct sedimentation in the form of aggregates. The reported role of zooplankton grazing in removal of phytoplankton carbon during bloom periods is variable (Vargo 1976; Deason 1980; Laws et al. 1988). By contrast, numerous authors have suggested that sedimentation is a major loss process during phytoplankton blooms in estuarine and coastal areas (Smetacek et al. 1978; Peinert et al. 1982; Rudnick and Oviatt 1986; Keller and Riebesell 1989). Carbon input from the winter-spring bloom represents a significant portion of the annual input of fresh phytoplankton to the benthos (Durbin et al. 1975; Smetacek et al. 1978; McLaughlin et al. 1982; Sournia et al. 1987). The food-web structure of shallow coastal areas depends on the seasonal occurrence of the winter-spring diatom bloom.

In this paper, we examine the relationship between temperature and the flow of material between trophic levels in shallow coastal systems and specifically, test the hypothesized direct link between the magnitude of the winter-spring diatom bloom and warmer winter temperatures. Control systems were maintained at a temperature 2°C less than the long-term (1977–1989) average for the parent system, Narragansett Bay, Rhode Island. The study was conducted in six enclosed mesocosms of the Marine Ecosystem Research Laboratory (MERL) over a diatom-dominated winter-spring bloom. We examined the effects of altered temperature on the primary producers (photosynthetic algae), primary herbivores (zooplankton and their larvae), and the supply of organic matter to the benthos. Data collected in situ were combined with literature data to construct carbon budgets in the six systems. By successfully balancing the budgets, we demonstrate that the most important factors affecting bloom development in warm and cool systems have been identified.

## Methods

**Experimental design**—The experimental design consisted of two treatments using six outdoor mesocosms with three warm systems targeted for a temperature increase of +3°C relative to controls (referred to below as “cool”). A time series based on the average monthly temperature in lower Narragansett Bay from 1977 through 1989 was used to set the temperature differential between warm and cool mesocosms (Fig. 1). Weekly values were generated by linear interpolations between mean monthly measurements. Warm systems were heated 1°C relative to this temperature series, and the controls were cooled 2°C below the long-term (1977–1989) average Bay temperature. This approach was adopted to avoid unrealistic heating of the warm tanks relative to the ambient temperature of the source water (Narragansett Bay) in the event of a warm winter. Since the mod-

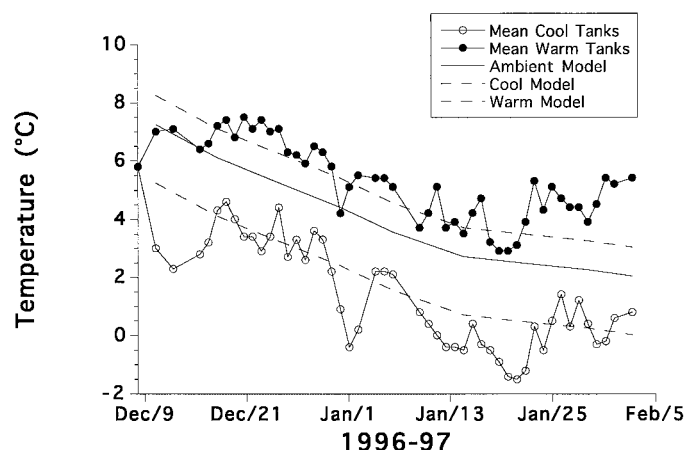


Fig. 1. The ambient temperature model used to set the weekly temperature values for the study and the observed mean temperatures for cool (open circles) and warm (closed circles) treatments over the experimental period. The ambient model was based on the mean monthly temperatures in Narragansett Bay in the lower West Passage from 1977 through 1989. The warm tanks were warmed 1°C above the ambient model, and the cool tanks were cooled 2°C below the model as shown in the figure.

el incorporates any warming that occurred over the 1977–1989 period, the control systems were cooled relative to it. Temperatures were controlled using polypropylene immersion-type heat exchangers hung 2 m below the surface in each mesocosm.

Inorganic nutrients ( $\text{NH}_4\text{Cl}$ ,  $\text{KH}_2\text{PO}_4$ , and  $\text{Na}_2\text{SiO}_3$ ) were added daily to the six mesocosms to ensure nutrient-rich conditions. A molar ratio of 12.80 N:1.00 P:0.91 Si was used to mimic the ratio of nutrients in sewage effluents discharged into the Providence River (Oviatt et al. 1986). The loading level for nitrogen ( $11.52 \text{ mmol m}^{-2} \text{ d}^{-1}$ ), phosphate ( $0.88 \text{ mmol m}^{-2} \text{ d}^{-1}$ ), and silicate ( $0.84 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) was four times the average annual loading (on an areal basis) to Narragansett Bay. The 4× loading is well within the range of loading expected or occurring in industrialized areas (Meybeck 1982). Triplicate treatments were established with natural plankton communities by filling the mesocosms with water from the adjacent Narragansett Bay. The experiment commenced on 9 December 1996 and ended on 3 February 1997.

**Mesocosms**—The mesocosms have been described in detail elsewhere (Oviatt et al. 1986). Each cylindrical enclosure consisted of a 5-m water column containing  $13 \text{ m}^3$  of water. For this experiment, the six mesocosms were established as well-mixed, flow-through systems. To induce natural levels of turbulence, mixing was applied via horizontal paddles located at 1-m depth intervals rotating with a rate of 4 rpm. The mixing schedule consisted of 2 h of mixing followed by 4 h of nonmixing, a scheme designed to simulate the semidiurnal tidal currents in the Bay. During the experimental period, mesocosms were operated with a daily input of 440 liters of water from the adjacent Narragansett Bay. Feeds occurred four times each day just prior to the begin-

ning of each mixing cycle, resulting in a 30-d turnover rate, which is similar to that of Narragansett Bay (Pilson 1985).

Each mesocosm contained a 37-cm-deep sediment tray that was filled with lower Narragansett Bay sediment containing an intact benthic community (as in Rudnick 1989). No attempt was made to manipulate the abundance of benthic organisms, which was intended to represent the range of natural variation seen at the sediment collection site.

*Water-column measurements*—From 9 December 1996 through 3 February 1997, incident light, light attenuation, temperature, dissolved inorganic nutrients ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{SiO}_4$ , and  $\text{PO}_4^{3-}$ ), chlorophyll *a* (Chl *a*), phytoplankton abundance, zooplankton abundance, sedimentation rate (dry weight), and a suite of other variables were periodically measured in each of the six mesocosms. Photosynthetically active radiation (PAR;  $\text{Einst. m}^{-2} \text{d}^{-1}$ , 400–700 nm) was measured using a LI-COR 1000 meter equipped with a LI 190SA quantum sensor. Light attenuation coefficients ( $k$ ,  $\text{m}^{-1}$ ) were derived from data collected using a cosine-corrected LI-COR LI-192S quantum sensor. The depth of the photic zone (depth of 1% light) was calculated as  $Z_p = 4.61/k$ .

Water temperature ( $^{\circ}\text{C}$ ) 10 cm below the surface of the well-mixed mesocosms was recorded daily. Dissolved inorganic nutrients (micromoles per liter) were measured weekly from samples collected in 2-liter amber polyethylene bottles from 1 m below the surface in each mesocosm during the morning mixing cycle. Samples were analyzed on a Technicon AutoAnalyzer with standard procedures (similar to those outlined in Strickland and Parsons 1972). Samples were analyzed immediately or frozen for future analysis. Primary and secondary standards (in seawater) were used to calculate concentrations (Oviatt and Hindle 1994). Standard deviations were  $<0.05 \mu\text{mol liter}^{-1}$  for all nutrients measured.

Replicate Chl *a* (micrograms per liter) was measured weekly from 10-ml aliquots of water subsampled from the amber bottles. Samples were filtered through 25-mm Whatman GF/F glass-fiber filters at 125 mm of Hg maximal vacuum. Two drops of 1% magnesium carbonate were added to each sample prior to filtration. Samples were extracted overnight in the freezer using 90% acetone and analyzed within 24 h on a field fluorometer (model 10, Turner Designs) (Yentsch and Menzel 1963; Lorenzen 1966).

Phytoplankton abundance (cells per milliliter) was measured weekly in each mesocosm from the amber bottles using standard techniques (Sournia 1978). Samples were preserved in Lugol's iodine solution and counted on an inverted microscope. Samples were either obtained by pouring 10 ml of well-mixed sample into a vial with two drops of Lugol's solution or concentrated (10:1) by pouring 100 ml of mixed sample into a 100-ml graduated cylinder, adding five drops of Lugol's solution, and letting settle for 1 week. The overlying 90 ml was then removed and the remaining 10 ml preserved with an additional drop of Lugol's solution. Depending on phytoplankton density, either unconcentrated or concentrated samples were counted by pipeting a 2-ml subsample into a 5-ml settling chamber and adding 3 ml of artificial seawater. Samples were settled for 20 h, and a known area of the chamber was counted (one to two diam-

eters, one-half chamber, or whole chamber) until at least 1,000 cells were counted.

Zooplankton samples were collected by pumping 50–100 liters of water at a constant rate from each of five depth intervals (0.1, 0.5, 1.0, 2.5, and 4.5 m). Pumped samples were integrated over each depth interval (e.g., 0.5 m represents 0.5–1 m) by raising the sample hose at a constant rate. Zooplankton  $>44 \mu\text{m}$  were filtered from the water samples, preserved in 10% formalin, staged, identified, and enumerated. Zooplankton were identified to species or genus level for adult and copepodite stages and to order or class for nauplii or other invertebrate larvae.

Sedimentation rates inside the enclosures were measured weekly during and just after the bloom event (6 January–3 February) with cylindrical sediment traps. Paired sediment traps (diameter = 4.5 cm, and height = 20 cm) were positioned on opposite sides of each mesocosm 20 cm above the bottom for 24–48 h. The resulting samples were filtered through precombusted and preweighed 2.5-cm Whatman GF/F filters and placed in a  $60^{\circ}\text{C}$  oven. Samples were reweighed after drying to a constant weight.

*Filtration rate models*—The abundance and biomass of mussels (*M. edulis*) were determined from diver-collected specimens at the end of the experiment. All mussels were enumerated and measured (millimeters) immediately after collection. A subsample of 25–30 mussels from each mesocosm was weighed (wet weight, grams) and subsequently oven dried at  $60^{\circ}\text{C}$  for 1 week to determine soft-tissue dry weight (grams). The relationship between dry weight and length was empirically determined using regression analysis and was subsequently used to estimate the dry weight for each mussel. Filtration rates (liter per hour) were then determined for individual mussels as a function of dry weight (and temperature) using filtration rate models developed by Thompson (1984).

Thompson's (1984) models were specific to *M. edulis* and were based on mussel biomass (dry weight of soft tissues, grams). Thompson's models were developed for temperatures from 0 to  $15^{\circ}\text{C}$ . We initially selected a model developed at  $1^{\circ}\text{C}$  for use in the cool (control) mesocosm (mean temperature =  $1.3^{\circ}\text{C}$ ) and a second model developed at  $5^{\circ}\text{C}$  for use in the warm systems (mean temperature =  $5.3^{\circ}\text{C}$ ). The model used for the controls was:

$$FR = 1.64DW^{0.413} \quad (1)$$

while the model used in the warm systems was:

$$FR = 1.95DW^{0.413} \quad (2)$$

with *FR* the filtration rate (liter per hour) and *DW* the dry weight of the soft tissue in grams. Filtration rates were calculated for individual mussels and summed to find the daily rate per system (liter per day). These rates were then converted to the number of days required to filter the entire water column (13,000 liters). The above approach is based on the mean temperatures observed in the cool vs. warm systems. To explore the impact of the observed variation in temperature (range =  $-1.7$  to  $4.0^{\circ}\text{C}$  in cool systems and  $2.5$  to  $7.2^{\circ}\text{C}$  in warm systems) (Fig. 1) on filtration rates, a series

Table 1. Filtration rates (liter h<sup>-1</sup>) for blue mussels in each mesocosm calculated from Thompson's (1984) filtration rate models at two temperatures and based on soft tissue dry weight of individual mussels. Filtration rates were converted to daily values (liter d<sup>-1</sup>) and used to calculate the period (days) required to filter an entire 13,000-liter mesocosm. Ranges for filtration rates (liter d<sup>-1</sup>) and period (days) were estimated by applying a series of models developed at the temperature ranges observed in the warm and cool systems.

Mesocosm	Treatment	Filtration rates		Period days (range)
		liter h <sup>-1</sup>	liter d <sup>-1</sup> (range)	
3	Warm	3.6	86 (72–91)	152.0 (142–180)
7	Warm	244.3	5,863 (4,932–6,194)	2.2 (2.1–2.6)
13	Warm	42.8	1,030 (866–1,090)	12.7 (11.9–15)
15	Cool	151.2	3,629 (3,386–4,781)	3.7 (2.7–3.8)

of Thompson's (1984) models developed at similar temperatures (cool: 1–4.5°C; warm: 2.5–7.5°C) were also applied.

**Statistical analysis**—We assessed the effect of elevated temperature on variables measured over time throughout the entire experimental period. To account for the variable numbers of mussels present in control and treatment mesocosms, we originally regressed each variable against mussel biomass (dry weight) and then analyzed the variance in the residuals of the regression analyses (similar to an analysis of covariance, ANCOVA). We used a nested ANOVA, which is equivalent to a repeated-measures analysis (Winer 1971). For this design, replicate mesocosms were nested within treatments and considered random. In testing for main effects (treatments controlled as part of experimental design), sample date was considered a repeated factor, and the degrees of freedom of error terms were not artificially inflated by frequent sampling. In those cases where there was a significant time-by-treatment interaction, we used a nested ANOVA on each sample date where replicate mesocosms were again considered random. Abundance data were transformed [ $\ln(x + 1)$ ] to reduce heterogeneity of variance prior to statistical analysis. Since mussel biomass was measured only once at the end of the experiment, it was considered constant per mesocosm throughout the experimental period.

**Carbon budgets**—Carbon budgets were developed to judge the relative importance of various source (phytoplankton production, P) and loss processes (zooplankton grazing, Z; mussel grazing, M; and sedimentation, S) over the bloom period in the warm vs. cool systems. Budgets were constructed for each system using a combination of experimental data and literature values. Phytoplankton production, daily productivity over the photic zone (P, milligrams C per square meter per day), was estimated as a function of phytoplankton biomass (milligrams Chl *a* per cubic meter),  $Z_p$ , the photic zone depth (m), and  $I_0$  surface irradiance (Einst. per square meter per day) (Keller 1988). Water-column phytoplankton carbon (B, milligrams C per square meter) was calculated by multiplying the standing crop of Chl *a* by 31, the slope of the regression of particulate organic carbon vs. Chl *a* for the mesocosms (Keller 1986). This value is within the range of values previously recorded for Narragansett Bay (Durbin et al. 1975). Standing crop biomass for copepods (milligrams C per square meter) was estimated by converting abundance of copepods (nauplii, copepodites, and adults) to body weight in carbon using temperature-dependent equa-

tions for *Acartia hudsonica*, the dominant copepod (Durbin and Durbin 1978; Durbin et al. 1992). Copepod grazing rates (based on percent body carbon ingested per day) were estimated as a function of the amount of phytoplankton carbon available using equations developed for *A. hudsonica* (adults and copepodites) at ~5°C (Deason 1980). The equation developed for adults was modified to reflect the higher metabolic rates of nauplii by multiplying by a factor of 2.5 (Pepitpa 1966). Grazing losses by mussels were calculated by multiplying the estimated filtration rates (Table 1) by phytoplankton biomass. The organic carbon content of sedimented material was calculated by multiplying dry weight by 2–3% during nonbloom conditions and by 5–6% during and just after the bloom (Oviatt and Nixon 1975). In all cases, units were converted to milligrams C per square meter prior to constructing carbon budgets for each system on a weekly time step.

## Results

**Light and light attenuation**—Incident PAR gradually increased over time. PAR ranged from a minimum of 1.1 Einst. m<sup>-2</sup> d<sup>-1</sup> near the beginning of the experimental period to a maximum of 18.7 Einst. m<sup>-2</sup> d<sup>-1</sup> near the end, with an average of 8.63 Einst. m<sup>-2</sup> d<sup>-1</sup> over the entire period. Light attenuation coefficients (k, m<sup>-1</sup>) were not significantly different between treatments and controls (ANOVA  $F = 1.37$ ,  $P = 0.31$ ). Attenuation coefficients varied with bloom development and ranged from 0.78 to 2.08, with a mean of 1.22 m<sup>-1</sup>. The mean depth of the photic zone ( $Z_p$ ) occurred at 3.93 m (range = 2.21 m to bottom).

**Temperature**—Water temperature in the warm mesocosms ranged from a high of 7.2°C in December to a low of 2.5°C in January, with an average of 5.27°C ( $\pm 0.14$  SE) over the experimental period (see Fig. 1). The cool systems decreased from 4.5°C to -1.7°C over the same period, with a mean temperature of 1.29°C ( $\pm 0.18$  SE). Since temperature did not vary significantly within treatments ( $P > 0.05$ ), daily means are shown by treatment (Fig. 1). These values are plotted relative to the weekly model temperatures: warm (+1°C), mean, and cool (-2°C). Although targeted for a temperature differential of 3°C, the actual difference between treatments was 3.98°C. The observed differences in temperature between the two treatments were significant ( $P < 0.05$ ). Water temperature in Narragansett Bay was relatively

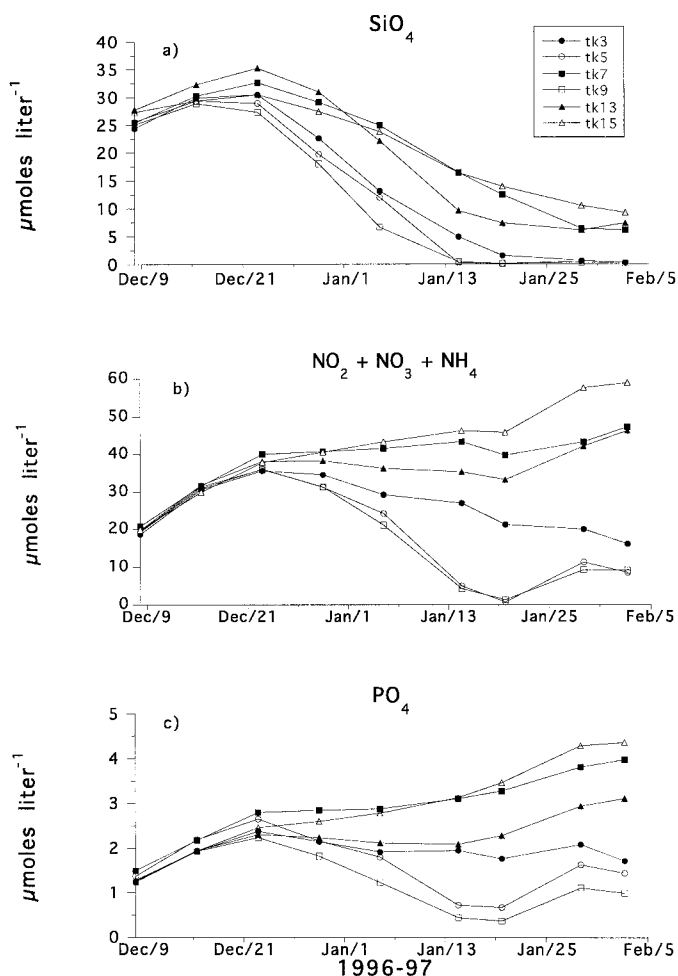


Fig. 2. Dissolved inorganic nutrient concentrations ( $\mu\text{moles liter}^{-1}$ ) as (a) silicate,  $\text{SiO}_4$ ; (b) total dissolved inorganic nitrogen ( $\text{NO}_2 + \text{NO}_3 + \text{NH}_4$ ); and (c) phosphate,  $\text{PO}_4$  in the warm (closed symbols) and cool (open symbols) mesocosms over the experimental period.

warm over the same period, with an average temperature of  $4.5^\circ\text{C}$ .

**Dissolved inorganic nutrients**—Nutrients increased in concentration gradually over the initial 3 weeks of the experiment then decreased (particularly silicate) with bloom development (Fig. 2). Data suggested that silicate, which decreased in all systems, was the limiting nutrient in three mesocosms (Fig. 2). Silicate declined to very low levels ( $<0.55 \mu\text{mol liter}^{-1}$ ) for 4 weeks at the end of the experiment in two controls. Similarly low levels ( $<1.53 \mu\text{mol liter}^{-1}$ ) were observed for the final 3 weeks in one warm system. Dissolved inorganic nitrogen ( $\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$ ) also reached very low values ( $<1.35 \mu\text{mol liter}^{-1}$ ) in the same two cool systems but for a shorter (1 week) period (Fig. 2). Nutrients did not appear to reach limiting values in the remaining control and warm mesocosms. Dissolved inorganic nutrient concentrations ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{SiO}_4$ , and  $\text{PO}_4^{3-}$ ) were not significantly different between treatments (ANOVA,  $P > 0.05$  in all cases).

**Phytoplankton**—On average, phytoplankton biomass (as Chl *a*) and abundance (total cells per milliliter) increased in cool systems relative to warm (Fig. 3). Chlorophyll increased from an average of  $\sim 1 \mu\text{g liter}^{-1}$  at the beginning of the experiment in all systems to  $\sim 92 \mu\text{g liter}^{-1}$  in cool systems and to only  $\sim 9 \mu\text{g liter}^{-1}$  in warm mesocosms. A similar trend was seen for mean numerical abundance of phytoplankton. Total numbers increased from values of  $\sim 160 \text{ cells ml}^{-1}$  to an average bloom peak of  $\sim 34,000 \text{ cells ml}^{-1}$  in controls and a peak of  $\sim 1,400 \text{ cells ml}^{-1}$  in warm systems. As demonstrated in Fig. 3, variability was high within treatments for both phytoplankton biomass and abundance. The source of the high variability within treatments was explained when phytoplankton biomass and abundance were plotted for individual mesocosms (Fig. 3). Dramatic increases in abundance and biomass occurred in two cool systems, with a moderate increase in one warm system. The remaining three systems (two warm mesocosms and one control) failed to bloom even though phytoplankton production was occurring, as implied by the previously noted decrease in silicate concentration.

In general, *Skeletonema costatum* was the dominant diatom in both warm and cool systems, followed by *Thalassiosira* spp., *Chaetoceros* spp., and *Detonula confervacea*. *Skeletonema* alone contributed  $>30\%$  to the total phytoplankton community (as cell counts) in both treatments. In mesocosms with blooms, the initial stage of the bloom was always dominated by *Skeletonema*, while the peak bloom period was dominated by either *Skeletonema* or *Thalassiosira*. *Chaetoceros* dominated the end of the bloom period (29 January–3 February) in the two cool systems with well-developed blooms. Flagellates were also an important component of the phytoplankton community over the experimental period. Flagellates dominated the postbloom period in the warm system with a moderate bloom.

The results for the repeated-measures ANOVAs after adjusting for the unequal numbers of mussels present in each mesocosm are presented in Table 2. Significant ( $P < 0.05$ ) and near significant ( $P < 0.10$ ) treatment effects were noted for biomass as Chl *a*, total phytoplankton abundance, and abundance of *S. costatum* over the experimental period. The levels of *Chaetoceros* spp., *Thalassiosira* spp., and *D. confervacea* were not significantly different throughout the experimental period but exhibited significant time-by-treatment interactions (Table 2). ANOVAs by sample date indicated significant differences between treatments for these species over the peak bloom period (30 December 1996–20 January 1997). In all cases, phytoplankton biomass and cell counts were elevated in the cool treatment relative to the warm.

**Zooplankton**—Mean abundance ( $\pm\text{SE}$ ) of total zooplankton (primarily copepods) for the triplicate control and treatment mesocosms over the experimental period is displayed in Fig. 4. Mean abundance was low at the start of the experiment ( $<2,000 \text{ m}^{-3}$ ) but increased substantially in warm systems ( $\sim 36,000 \text{ m}^{-3}$ ) relative to controls ( $\sim 10,000 \text{ m}^{-3}$ ) during the latter half of the experiment. Again, the variability between treatments is high, with the source of the variability revealed by examination of the data for the individual mesocosms (Fig. 4). Zooplankton abundance increased substan-

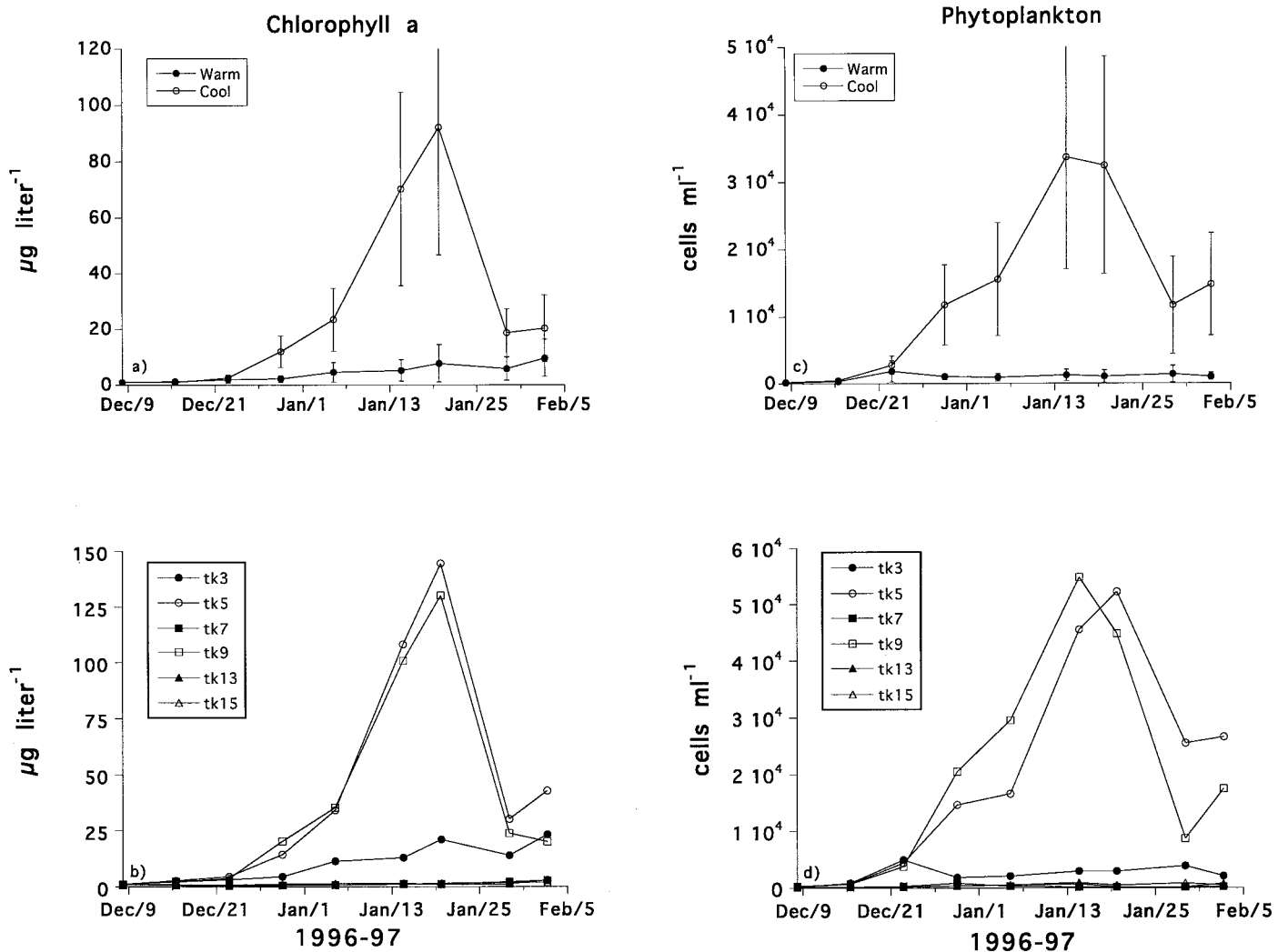


Fig. 3. Chl *a* ( $\mu\text{g liter}^{-1}$ ) and total phytoplankton cell counts ( $\text{cells ml}^{-1}$ ) shown both as the mean ( $\pm 1$  SE) by treatment and for the individual systems over the experimental period. Warm tanks are represented by closed symbols and cool tanks by open symbols.

tially in two of the three warm systems but very little in the cool systems. Abundance increased earlier (15 January) in tank 3 and reached a greater level ( $\sim 100,000 \text{ m}^{-3}$ ) compared with tank 13 ( $\sim 50,000 \text{ m}^{-3}$ ). The copepod community was dominated by *A. hudsonica* in all systems.

After accounting for variation in mussel biomass among treatments, nauplii, copepodites, adult copepods, and total zooplankton levels were significantly (ANOVA,  $P < 0.05$ ) or close to significantly (ANOVA,  $P < 0.10$ ) greater in the warm vs. the cool treatments over the experimental period (Table 2). When differences were not significant over the entire period, there were significant time-by-treatment interactions, which, when examined by sample date, indicated significant differences during the bloom and postbloom period (15 January–3 February 1997).

**Sedimentation rates**—Average ( $\pm$ SE) sedimentation rates (grams per square meter per day) for the warm vs. cool treatments over the bloom and postbloom period (9 January–3 February 1997) varied significantly between treatments (AN-

OVA,  $P = 0.05$ ) (Table 2). Sedimentation rates were higher and more variable in the cool systems (range =  $6.0\text{--}41.1 \text{ g m}^{-2} \text{ d}^{-1}$ ) relative to the warm systems (range =  $3.2\text{--}9.8 \text{ g m}^{-2} \text{ d}^{-1}$ ). Data were collected only after the initiation of the bloom period, and there were no significant time-by-treatment interactions.

**Mussels**—Mussel abundance, length, and total biomass varied considerably among the mesocosms (Table 3). Large numbers ( $\sim 60\text{--}100 \text{ m}^{-2}$ ) of mussels were present in two systems (tank 7, a warm system, and tank 15, a cool system), moderate numbers ( $\sim 10 \text{ m}^{-2}$ ) in an additional warm system (tank 13), and few or none in the remaining mesocosms. The mean lengths (Table 3) indicated a tendency for size to vary inversely with abundance. The total biomass per mesocosm (Table 3) was calculated using an empirical regression equation based on the 25–30 measurements for length (millimeters) and dry weight (grams, soft tissue) per system. Initially, a separate regression equation was developed for each mesocosm; however, analysis of covariance (ANCOVA) indi-

Table 2. Results of nested ANOVAs (equivalent to repeated-measures analyses) showing main effects and time-by-treatment (trt) interactions of experimental manipulations (warm vs. cool mesocosms) on phytoplankton, zooplankton, and sedimentation rates. Abundance data were natural logarithmically transformed prior to analysis ( $n = 42$ ).

Variable	Treatment effects		Trt × time interactions	
	F	P	F	P
Phytoplankton (cells ml <sup>-1</sup> ):				
<i>Skeletonema</i>	5.3	0.08	4.0	0.01
<i>Chaetoceros</i>	3.9	0.12	2.5	0.05
<i>Thalassiosira</i>	3.1	0.16	2.5	0.05
<i>Detonula</i>	3.2	0.15	2.5	0.05
Flagellates	5.1	0.08	0.9	NS
Total	8.9	0.04	4.0	0.01
Chl <i>a</i> (µg liter <sup>-1</sup> )	5.8	0.07	3.6	0.01
Zooplankton (number m <sup>-3</sup> ):				
Nauplii	6.4	0.06	2.9	0.03
Copepodites	16.3	0.02	0.5	NS
Adults	15.5	0.02	1.8	NS
Total	5.2	0.08	2.9	0.03
Sedimentation rate*				
(dry wt, g m <sup>-2</sup> d <sup>-1</sup> )	6.3	0.05	2.4	NS

\*  $n = 24$ .

cated no significant differences (ANCOVA,  $P > 0.05$ ) between the derived equations, and a single equation was therefore developed using the pooled data (dry weight =  $0.0126e^{0.0673(\text{length})}$ ). The fitted relationship explained 95% of the variation in the data and was used to calculate the dry weight from measurement of individual mussel length. These values were then summed to give the total mussel biomass in each mesocosm (Table 3). Despite the wide difference in abundance between the two systems with the most mussels (mesocosms 7 and 15), there is a close similarity in the total biomass because of the noted difference in size distribution (Table 3).

The estimated dry weight for each mussel was used to calculate filtration rates by applying Thompson's (1984) filtration rate models. The individual filtration rates for each mussel were summed to give the overall filtration rate per system (Table 1). These data were in turn used to calculate the period (days) required to filter the entire water column (13,000 liters). The results (Table 1) indicate that the entire water column in mesocosms 7 and 15, with abundant mussels, was filtered every 2–4 d. For mesocosm 13, with a moderate number of mussels, the filtration period was ~13 d. With few mussels present, the period to filter the entire water column (151 d) in mesocosm 3 was considerably greater than the turnover time for the system (30 d), and impacts were minimal. Additional models developed at temperatures close to the observed ranges in cool and warm systems were applied to provide estimates of variation around the above values (Table 1). The coefficients for Thompson's (1984) filtration rate models were relatively constant within a temperature range of 0–15°C. Based on Thompson's coefficients, a maximum increase in grazing of

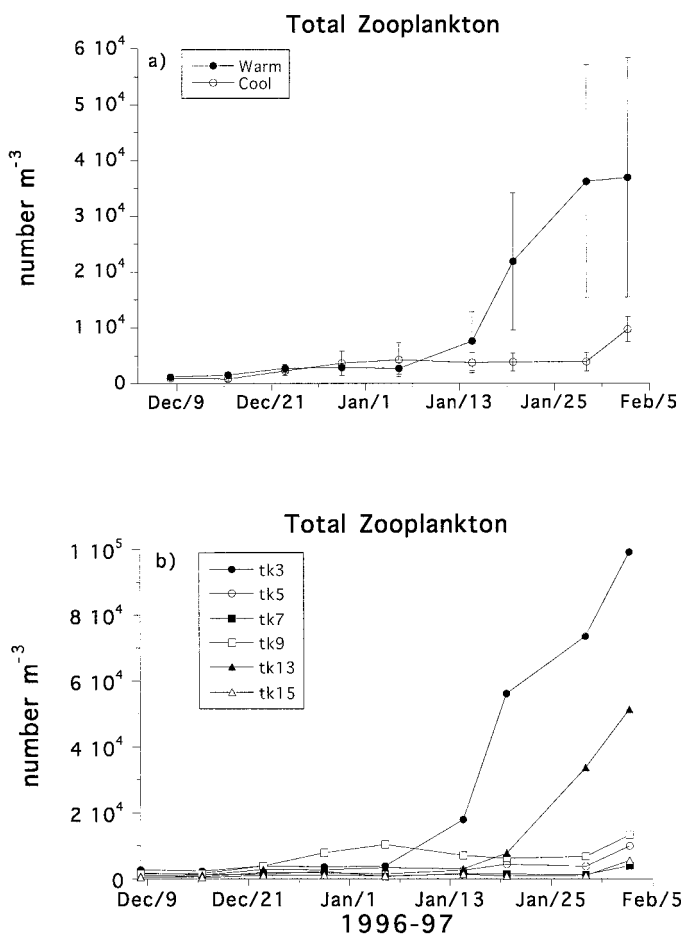


Fig. 4. Total zooplankton abundance (number m<sup>-3</sup>) shown both as the mean ( $\pm 1$  SE) by treatment and for the individual systems over the experimental period. Warm tanks are represented by closed symbols and cool tanks by open symbols.

18.9% would be expected at the range of temperatures occurring in our study. Since mussel biomass was variable among mesocosms and filtration rates are relatively unaffected by temperature (Thompson 1984), the impact of mussels on the experimental results was statistically removed, as previously described.

Table 3. Abundance, mean length (mm), and total dry weight of soft tissue (g) for blue mussels (*Mytilus edulis*) collected in each mesocosm at the end of the experiment. Total dry weight was calculated from an empirical regression equation ( $R^2 = 0.95$ ) developed from 25–30 measurements per system.

Meso-cosm	Treatment	Number	Length (Mean, mm)	Dry weight (Total, g)
3	Warm	2	52.5	2.17
5	Cool	0	—	—
7	Warm	251	39.8	47.47
9	Cool	0	—	—
13	Warm	25	59.4	18.61
15	Cool	154	46.5	42.27

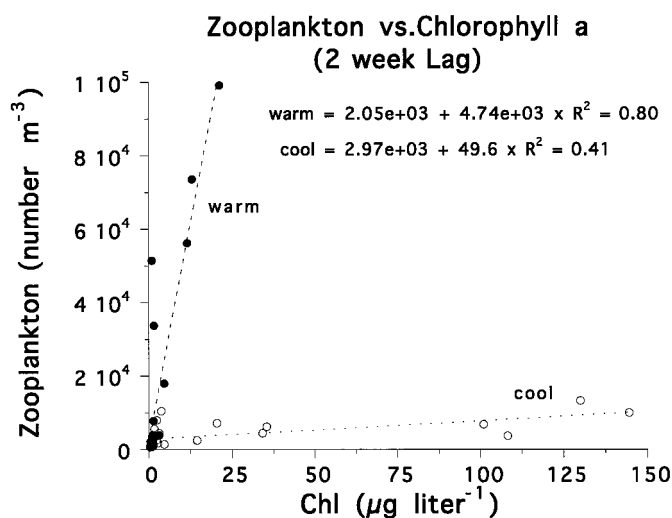


Fig. 5. Empirical relationships between zooplankton abundance (number  $m^{-3}$ ) and Chl  $a$  ( $\mu g$  liter $^{-1}$ ) lagged by 2 weeks in the warm (closed circles) and cool (open circles) treatments.

*Trophic interactions and temperature*—Temperature exerted a significant impact on the relationship between phytoplankton biomass and zooplankton abundance. Figure 5 illustrates just how different the two treatments were in their trophic response to the experimental increase in temperature. In warm systems, a moderate increase in Chl  $a$  was associated with a large increase in zooplankton abundance. In cool systems, large increases in phytoplankton biomass were associated with only slight increases in zooplankton levels. In both cases, the relationship was significant ( $P < 0.05$ ), with a lag time in zooplankton abundance of 2 weeks.

*Carbon budgets*—Based on the terms in the carbon budget, phytoplankton biomass (milligrams C per square meter) for each mesocosm was calculated weekly as:

$$B_{i+1} = B_i + P_i - Z_i - M_i - S_i \quad (3)$$

where biomass ( $B_i$ ) on 9 December ( $i = 1$ ) was initialized with the observed value, and  $P_i$  (production),  $Z_i$  (zooplankton grazing),  $M_i$  (mussel grazing), and  $S_i$  (sedimentation) were estimated as previously described. Predicted biomass values agree with our observations (Fig. 6). The close fit between observed and predicted biomass ( $R^2 = 0.98$ ,  $n = 48$ ) indicates that the major processes controlling phytoplankton biomass in the two treatments have been identified.

Carbon budgets (milligrams C per square meter) were calculated on a weekly time step and summed over the bloom period (6 January–3 February 1997) to compare the relative importance of source and loss processes between treatments (Fig. 7). In the absence of mussels, the cool systems are characterized by elevated production and high losses via sedimentation (Fig. 7). Compared with warm systems, they have reduced grazing and higher residual loss terms. In warm systems, production and sedimentation rates are reduced, and grazing by zooplankton and/or mussels is enhanced. In warm systems, zooplankton grazing and mussel grazing are inversely related ( $R^2 = 0.70$ ). The two systems with the high-

est abundance of mussels are remarkably similar in production and loss terms despite the temperature treatment.

## Discussion

In recent years, the annual bloom in Narragansett Bay has failed to materialize or has been of a much reduced magnitude relative to early years (Oviatt 1994). Research has indicated a significant ( $P = 0.0001$ ) increase in winter water temperature in Narragansett Bay over the past 35 yr ( $+0.075^\circ C$  yr $^{-1}$ ; Fig. 8) and a significant correlation between the magnitude of the winter-spring phytoplankton bloom (average biomass as Chl  $a$ ) and mean surface water temperature. Warm winters are correlated with decreased bloom size (Oviatt 1994). The mesocosm experiment was designed to test the hypothesis that experimentally increasing temperature would lead to a decreased bloom size in shallow coastal systems as a result of grazing by the benthos and/or zooplankton. Our results demonstrate that warmer winter water temperatures alter the allocation of material among the different components of the trophic structure. In the control (cool) systems, a high standing stock of phytoplankton was associated with low zooplankton abundance and the sedimentation of large amounts of fresh phytodetritus to the benthos. In warm systems, a relatively low standing stock of phytoplankton was associated with high zooplankton abundance and supplied little freshly sedimented material to the benthos (Fig. 7). The mean phytoplankton biomass and abundance in the cool systems over the bloom period (Fig. 3) were similar to the levels previously observed in the mesocosms at the same nutrient loading rate during an earlier nutrient addition experiment (Nixon et al. 1986). The corresponding values in the warm systems (Fig. 3) were significantly lower (Table 2). The dominant phytoplankton and zooplankton species present during the experiment are those typically observed during the winter-spring bloom period in the parent system, Narragansett Bay (Smayda 1973b; Durbin and Durbin 1981).

Three fates were observed for the diatom biomass present in the mesocosms: grazing by the zooplankton, grazing by the mussels, and direct sedimentation in the form of aggregates. These pathways process the organic matter in fundamentally different ways; therefore, the partitioning of organic matter among these pathways is an important influence on the trophic structure in coastal waters. Our results demonstrate that these pathways can be shifted or dramatically altered by variations in temperature such as those already occurring in response to global warming. It is important to note when interpreting the experimental results that although water temperature was increased  $3.98^\circ C$  relative to controls, the actual increase relative to Bay temperature over the same period was  $0.8^\circ C$ . In essence, the experiment is comparing current and future increases in winter temperatures resulting from global warming with temperatures more typical of cooler winters in the past (Fig. 8).

As previously noted, the role of zooplankton grazing in removal of phytoplankton carbon during bloom periods is reportedly variable (Vargo 1976; Deason 1980; Laws et al. 1988). Over the course of the spring bloom in Auke Bay,

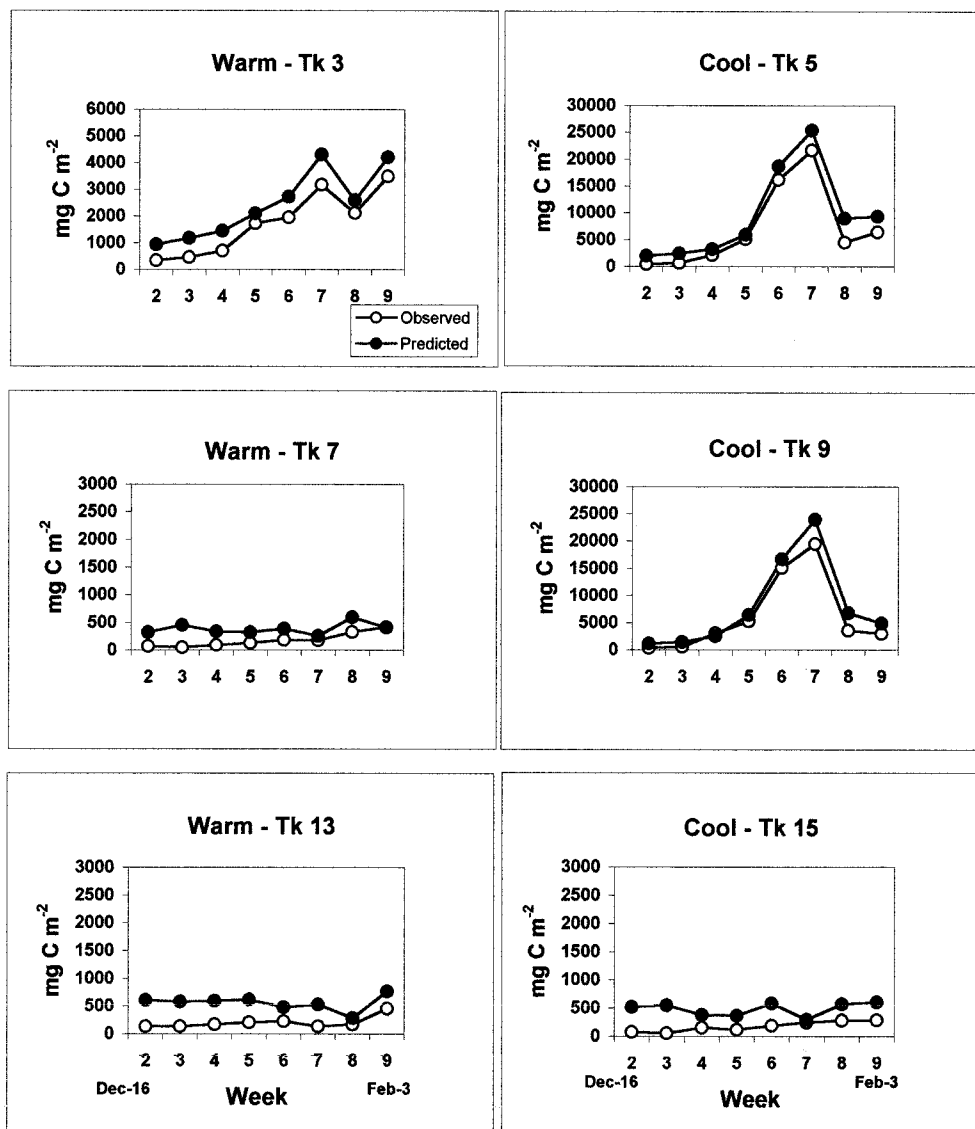


Fig. 6. Observed and predicted (Eq. 3) phytoplankton biomass ( $\text{mg C m}^{-2}$ ) based on carbon budgets developed from experimental data and literature sources. Values for successive weeks were predicted from information for the preceding week beginning with 16 December 1996 (week 2) and continuing through week 9 (3 February 1997).

Alaska, Laws et al. (1988) calculated that 58% of the biomass produced was lost through zooplankton grazing. Deason (1980) and Vargo (1976) concluded that zooplankton grazing removes little of the winter-spring bloom in Narragansett Bay, and Keller and Riebesell (1989) confirmed that losses due to zooplankton grazing during a winter-spring bloom in Narragansett Bay were 3–11% of the total losses. During our experiment, zooplankton abundance and calculated grazing rates were low in the cool systems and similar to levels previously reported for Narragansett Bay during the winter-spring bloom period. In warm systems, the higher grazing rates were more typical of values reported later in the spring-summer season (Deason 1980).

In general, the timing of events (the match or mismatch between periods of production and abundance of phyto-

plankton and their respective grazers) will greatly influence the magnitude of the bloom (Cushing 1982). In coastal areas and on temperate shelves, there has typically been a mismatch between the spring diatom bloom and peak zooplankton abundance. The phytoplankton are not efficiently cropped by the zooplankton but instead, sink to the seabed to supply the benthic food web (Walsh 1981; Smetacek et al. 1984). Frantz and Gieskes (1984) also presented evidence that most of the spring netplankton bloom in the North Sea was not grazed by copepods, and O'Reilly et al. (1987) suggested that this may be the case for Georges Bank. Our results indicate that the importance of zooplankton in controlling bloom dynamics via grazing is a function of temperature. Increasing temperature effectively enhances the match between the peak abundance of phytoplankton and

## Carbon Budget - Bloom Period

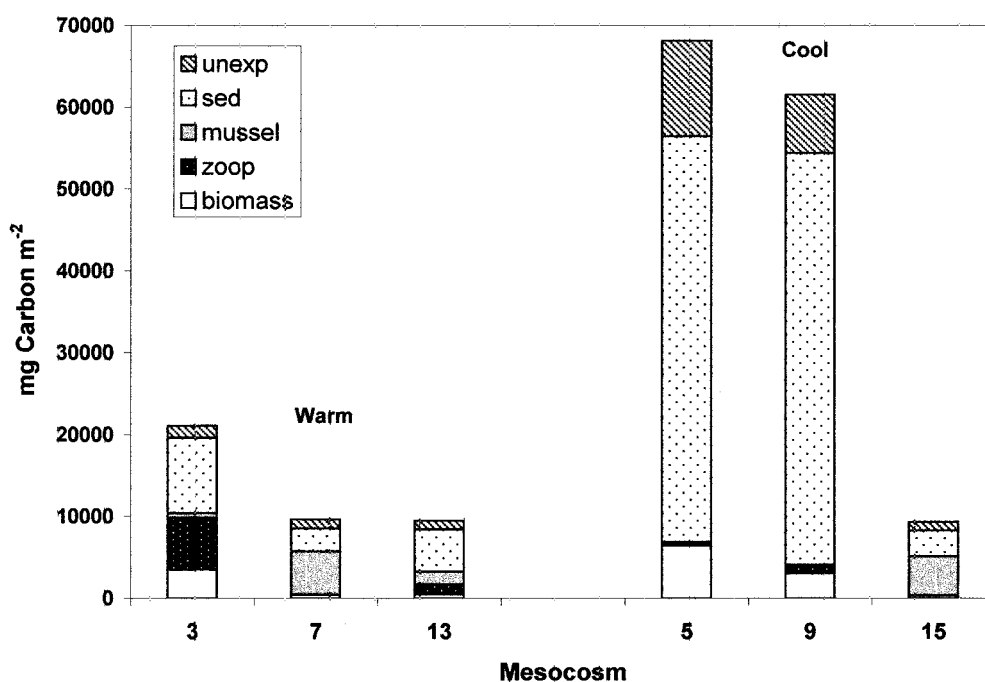


Fig. 7. Diagram showing the carbon budgets ( $\text{mg C m}^{-2}$ ) for the warm vs. cool mesocosms over the bloom period (6 January–3 February 1997). Bars represent the primary productivity summed over the bloom period, with subdivisions representing the various loss processes (unexp-residual loss; sed-sedimentation; mussel-grazing by mussels; zoop-grazing by zooplankton; biomass-standing crop at end).

zooplankton, resulting in a reduced bloom biomass and the funneling of carbon to the pelagic rather than the benthic system (Fig. 7).

The impact of temperature on zooplankton abundance was somewhat masked by the unequal presence of mussels within the experimental treatments. Zooplankton abundance was consistently low in the cool systems but highly variable in the warm systems (Fig. 4). Closer examination of the data indicates a significant inverse relationship between zooplankton abundance and mussel biomass in the warm systems (logarithmic regression analysis,  $R^2 = 0.98$ ), implying competition between zooplankton and mussels.

Application of Thompson's (1984) filtration rate models (Table 1) and development of the carbon budgets (Fig. 7) was particularly insightful. In systems with high mussel biomass (tank 7, a warm system, and tank 15, a cool system), the time to filter the entire water column was only 2–3 d. This period is approximately equal to the doubling time of phytoplankton at the experimental temperatures (Eppley 1972) and effectively explains why blooms failed to develop in these systems. In systems with high mussel biomass, grazing by mussels accounted for  $>50\%$  of the total losses (Fig. 7). In tank 3 (a warm system), the low number of mussels would require 152 d to filter the water column. Since this is greater than the 30-d turnover time of the mesocosm, the impact of mussels on the phytoplankton was slight (Fig. 7). Recall that tank 3 had both a moderate phytoplankton bloom

and a high number of zooplankton. Losses via zooplankton grazing accounted for 29% of the bloom biomass, a major increase relative to cool systems. And although 43% of the bloom material was lost via sedimentation, the actual supply of carbon to the benthos was considerably reduced relative to cool systems without mussels. A phytoplankton bloom failed to develop in tank 13 (a warm system with moderate mussel biomass), despite the fact that the time required for the mussels to filter the entire mesocosm (13,000 liters) was  $\sim 13$  d (Table 1) and considerably greater than the doubling time for phytoplankton at the experimental temperature (Eppley 1972). Zooplankton abundance increased in this system, although somewhat later and to a lesser degree, relative to tank 3, a warm system with few mussels. The carbon budget suggests that failure of a bloom to develop in tank 13 was due to the combined grazing by the zooplankton and mussels. In cool systems without mussels, well-developed phytoplankton blooms occurred, zooplankton abundance was low, and sedimentation was the major loss process, as also noted by Keller and Riebesell (1989) for the bloom period in Narragansett Bay. In general, the residual loss terms were positive, and predicted phytoplankton biomass was greater than observed (Fig. 6). Possible explanations for the residual losses include: nighttime phytoplankton respiration, excretion, and microzooplankton grazing—terms not included in the carbon budgets.

Since the presence of mussels in the mesocosms was not

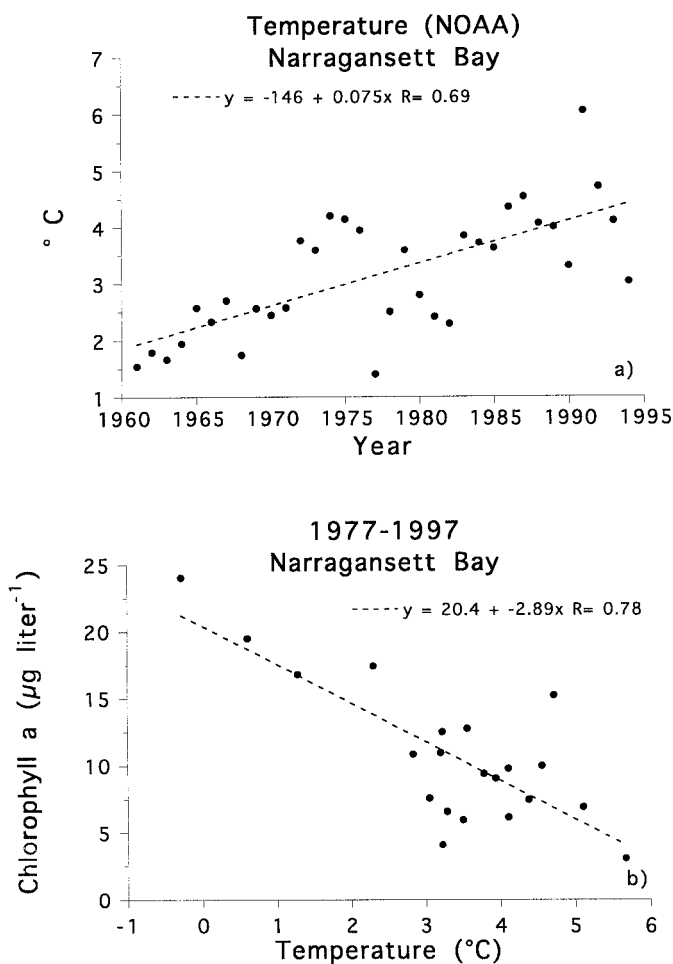


Fig. 8. (a) The increase in winter (JFM) temperature ( $^{\circ}\text{C}$ ) in Narragansett Bay, Rhode Island, from 1960 to 1995. Data were collected at 15-min intervals using a buoy moored in the East Passage of the Bay by the National Oceanographic and Atmospheric Administration. Winter temperature was calculated as the mean of the monthly temperatures for January, February, and March. The regression equation indicates an average increase of  $0.075^{\circ}\text{C yr}^{-1}$ , for a total increase of  $2.6^{\circ}\text{C}$  over the 35-yr period. (b) The relationship between mean Chl *a* concentration ( $\mu\text{g liter}^{-1}$ ) during the winter-spring phytoplankton bloom (bloom peak plus adjacent values) in Narragansett Bay vs. the average Bay temperature ( $^{\circ}\text{C}$ ) over the same period from 1977 through 1997. The data were collected in the lower West Passage of the Bay.

known at the start of the experiment, mussel biomass was measured only once at the end of the study. The statistical approach taken to separate the influence of mussels from temperature effects assumed that mussel biomass was constant throughout the experimental period. Physiological and ecological studies have frequently demonstrated that food supply is the single most important factor in determining mussel growth (Seed 1976; Widdows et al. 1979; Incze et al. 1981; Page and Riccard 1990). Phytoplankton biomass in mesocosms with mussels was low throughout the experimental period (average =  $0.17\text{--}0.20\text{ g C m}^{-2}$ ) and typical of periods with minimal growth rates (Campbell and Newell 1998). Authors have also indicated that growth of mussels

in temperate regions is typically low during winter (Bayne et al. 1976) and often accompanied by a lag of 4–6 weeks following an increase in phytoplankton availability (Page and Hubbard 1987).

The variable occurrence of mussels in the mesocosms combined with their unusual ability to filter at high rates at low temperatures was unanticipated at the start of the experiment. Although the mussels made the analysis of results more intricate, we view their presence as an example of the variability present in natural systems. Rather than confounding the experimental design, they added to the richness of the results and emphasize that local variability in bloom development under cool conditions is possible.

Below the euphotic zone, the production of benthic organisms ultimately relies on material produced in the surface waters (Smetacek 1984; Hargrave and Phillips 1986). During a relatively brief period (3–4 weeks), the winter-spring diatom bloom in many temperate coastal waters delivers as much as half of the total annual input of organic carbon to the benthos (Durbin et al. 1975; Smetacek et al. 1978; McLaughlin et al. 1982; Sournia et al. 1987). Carbon input from the winter-spring bloom thus represents a significant portion of the annual input of fresh phytoplankton to the benthos. Rudnick (1989) further suggested that benthic fauna thrived in the spring and early summer on detritus derived from the winter-spring diatom bloom and noted the importance of a time lag between the deposition and assimilation of phytodetritus. Generally, at higher temperatures, settling detritus is of lower quality, because primary production is dominated by slowly sinking nanoplankton that rapidly decomposes within the water column, and is of lower quantity because of high zooplankton grazing rates (Malone 1980; Durbin and Durbin 1981; Smetacek 1984; Hargrave and Phillips 1986; Pomeroy and Deibel 1986). The lower sedimentation rates observed in the warm vs. cool mesocosms represent a significant alteration in the flow of material through the trophic structure. Significantly less material is being supplied directly to the benthos in the form of freshly sedimented phytodetritus, and the quality of the material is most likely lower. Townsend and Cammen (1988) predicted that similar changes would be expected with variation in the timing of the spring phytoplankton bloom.

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