

Periphyton communities in experimental marine ecosystems: scaling the effects of removal from container walls

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ABSTRACT: Although it is widely held that growth of periphyton communities on walls of marine mesocosms creates artifacts which bias experimental results, there are surprisingly few studies that directly quantify such 'wall effects'. To test the hypotheses that the magnitude of wall effects is related to experimental system dimensions and that these effects can be controlled by routine periphyton removal, we conducted a series of studies using cylindrical mesocosms of 5 different sizes and shapes with treatments involving removal of wall periphyton. Results indicate that periphyton biomass and production were consistently and significantly reduced in containers receiving twice-weekly wall-cleaning treatment, but not in systems cleaned at weekly intervals. Whereas partitioning of ecosystem properties (total primary production and algal biomass) among wall, plankton, and sediment habitats revealed large and significant changes with wall-cleaning, treatment effects on the mean values of these and other ecosystem-level properties (e.g. nutrient concentrations) were small to negligible and generally inconsistent. Changes in biomass of wall periphyton and phytoplankton induced by wall-cleaning were significantly related to mesocosm radius. Reductions in wall periphyton with cleaning treatment were generally compensated by parallel increases in algal biomass in other habitats, with enhanced sediment microalgae only present in shallower systems. It appears that wall-cleaning also affected the abundance of benthic macrofauna and bacterioplankton, as well as phytoplankton taxonomic composition. Although periphyton dislodged through wall-cleaning were retained within the mesocosms in this study, we estimate that removal of this material from the experimental systems would have caused a severe nitrogen loss, equivalent to that required for supporting total ecosystem primary production.

KEY WORDS: Mesocosms · Experimental ecosystems · Scale · Wall-cleaning · Periphyton · Phytoplankton · Gross primary production · Sediment microalgae · Nutrients

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INTRODUCTION

Experimental ecosystems are basic and versatile tools commonly used in marine research (Giesy 1980, Grice & Reeve 1982, Lalli 1990, Beyers & Odum 1993). Although a wide range of sizes and shapes has been used, most of these experimental systems (referred to here as 'mesocosms') are relatively small ($\leq 1 \text{ m}^3$) in size (e.g. Petersen et al. 1999). Mesocosms have been used

to investigate diverse research topics including: trophic interactions (e.g. Threlkeld & Drenner 1987, Kuuppo-Leinikki et al. 1994); nutrient cycling and response to enrichment (e.g. Kelly et al. 1985, Oviatt et al. 1995, Chen et al. 2000); benthic-pelagic coupling (e.g. Threlkeld 1994); and contaminant effects (e.g. Kuiper 1981, Perez et al. 1991). Although container walls define experimental volume and help regulate material and energy exchange with external environ-

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ments, walls are also potential sites of inadvertent biological and chemical activities (Confer 1972, Eppley et al. 1978, Dudzik et al. 1979). Consequently, ecosystem dynamics and community interactions can be altered by periphytic growth on mesocosm walls (Harte et al. 1980, Chen et al. 1997).

Wall periphyton communities are analogous to assemblages growing on hard substrates in nature; however, their importance is exaggerated in experimental ecosystems due to a relatively higher ratio of surface area to water volume compared to most natural ecosystems (Dudzik et al. 1979). Wall periphyton can dominate algal biomass and gross primary production within short time periods (Rees 1979, Chen et al. 1997). Algal growth on mesocosm walls has been shown to significantly alter ambient light fields (Eppley et al. 1978), nutrient uptake and regeneration (Confer 1972, Chen et al. 2000) and trophic interactions (de Lafontaine & Leggett 1987) in experimental ecosystems. Recent studies have demonstrated that growth of wall periphyton and partitioning of primary production and nutrient uptake among wall, plankton and sediment habitats scale to the dimension of experimental containers (Chen et al. 1997, 2000).

Despite the widespread concern about experimental artifacts associated with wall periphyton (e.g. Dudzik et al. 1979), a surprisingly small proportion (<5%) of mesocosm studies indicate wall-cleaning in their experimental protocols (Petersen et al. 1999; our Table 1). Among the relatively few studies with routine wall-cleaning, a wide range of cleaning frequencies have been reported from daily to fortnightly intervals (Petersen et al. 1999; our Table 1). Although frequent cleaning may minimize 'wall effects,' the procedure is often logistically difficult and may alter nutrient and light regimes in experimental ecosystems (Eppley et al. 1978, Dudzik et al. 1979, Pilson et al. 1980).

In this study, we investigated how periphyton removal from container walls affects experimental ecosystem dynamics and how these effects vary with size and shape of experimental containers. Specific questions addressed here include the following: (1) Does wall-cleaning treatment significantly change ecological properties of specific assemblages and habitats (e.g. biomass, taxonomic composition and productivity of periphytic, planktonic and sediment algae, and abundances of bacterioplankton and benthic macrofauna) and of the integrated ecosystem (total nutrient content, algal biomass, and gross primary production)? (2) Are the responses of these ecological properties to routine wall-cleaning affected by the frequency of this treatment? (3) Do these responses to wall-cleaning vary with mesocosm dimensions?

Table 1. Periphyton removal from enclosure wall surfaces in a survey (364 studies) of aquatic mesocosms

Wall-cleaning frequency	No. of studies
Daily	5 ^a
Twice weekly	6 ^b
Weekly or less	6 ^c
No cleaning indicated	347 ^d
^a Edmondson (1955), Perez et al. (1977), Ringelberg & Kersting (1978), Heinle et al. (1979), Painting et al. (1989)	
^b Oviatt et al. (1984), Levin (1986), Oviatt et al. (1986), Rudnick & Oviatt (1986), Goldsborough & Kemp (1988), Sampou & Oviatt (1991)	
^c Raymont & Miller (1962), Gamble et al. (1977), Grice et al. (1980), Doering & Oviatt (1986), Burkholder et al. (1992), Neundorfer & Kemp (1993)	
^d Refer to Petersen et al. (1999) for complete list	

Table 2. Physical variables of experimental estuarine ecosystems. Mesocosms are designated as A, B, C, D, and E in order of increasing diameter

Physical variable	Mesocosm designation				
	A	B	C	D	E
Volume (m ³)	0.10	0.10	1.00	10.00	10.00
Depth (m)	1.00	0.46	1.00	2.15	1.00
Radius (m)	0.18	0.26	0.57	1.22	1.78
Wall area/volume (m ⁻¹)	11.25	7.68	3.54	1.64	1.12

MATERIALS AND METHODS

Experimental design. Studies were conducted using a series of replicate mesocosms of different size and shape. Mesocosms ranged in volume from 0.1 to 10.0 m³, with depth and radius ranging from approx. 0.5 to 2.2 m and 0.2 to 1.8 m, respectively; systems were designated A, B, C, D, and E in order of increasing radius (Table 2). Experimental treatment is defined as the regular removal of periphyton communities from container walls, with parallel mesocosms receiving no wall-cleaning designated as controls. Material removed from walls was left in the respective mesocosms to avoid altering mass balances of nutrients and organic matter (Neundorfer & Kemp 1993). Treatments were effected using an abrasive scrub cloth (3M Scotchbrite Scrubber Pads) fixed to wooden plates on poles which extended the whole depth of each mesocosm; the entire inner surfaces of the walls were scraped with each treatment.

The primary experiment involved a 6 wk study (31 January to 15 March 1996) using 6 replicate mesocosms of 3 different dimensions (A, B, C; 0.1 to 1.0 m³; Tables 2 & 3). For each size of mesocosm, replicate sys-

tems were randomly separated into 2 groups, one treated and one serving as a control. Material was removed from the wall surfaces of treated mesocosms at twice-weekly (3 to 4 d) intervals, while material was allowed to accumulate on the walls of control systems throughout the experiment. In addition, the effects of cleaning frequency (1 wk⁻¹ versus 2 wk⁻¹) were considered by comparing the results for the mid-radius mesocosms (B tanks) from this primary study with measurements from an earlier experiment in which these same systems were treated with weekly wall-cleaning (Table 3, Expt 2). Similarly, to broaden our interpretation of how effects of wall-cleaning might vary with mesocosm dimension, we also compared results from 2 earlier experiments—one with no wall-cleaning and one with weekly cleaning—involving mesocosms of 5 different dimension (Table 3, Expt 3).

Experimental systems. Cylindrical mesocosms were constructed of fiberglass-reinforced glazing material (Sun-Lite®) and housed in a temperature-controlled room. Water temperatures exhibited small diel variation, and mesocosms were illuminated by banks of fluorescent bulbs (supplemented with incandescent bulbs in the 1994 experiment) in a 12 h light:12 h dark cycle with mean surface light intensity of 155 $\mu\text{E m}^{-2} \text{s}^{-1}$ (range 147 to 160 $\mu\text{E m}^{-2} \text{s}^{-1}$, Table 4). An air conditioning system in the mesocosm facility, combined with insulation on the outer walls of each container, helped to maintain relatively constant water temperatures between experimental seasons and among different experimental systems, with mean values ranging from 19.7 to 22.7°C (Chen 1998). Mixing was accomplished by means of large, slow-moving PVC paddles, which produced relatively uniform turbulence typical of estuarine surface waters (Sanford 1997). All mesocosms were initiated with natural sediments and unfiltered estuarine water (salinity 8 to 12 psu) from the Chop-

Table 4. Mean photosynthetically available radiation (PAR; $\mu\text{E m}^{-2} \text{s}^{-1}$) at water surface and water temperature (Temp; °C) over the course of experiment. Temperature values are mean \pm diel range. PAR values are mean \pm SE of replicate (n = 3) mesocosms

Tank	Treatment	PAR	Temp
A	Control	157 \pm 4.1	18.6 \pm 1.5
	Cleaned	147 \pm 5.4	18.3 \pm 1.5
B	Control	150 \pm 1.9	21.0 \pm 2.4
	Cleaned	160 \pm 4.2	19.0 \pm 2.3
C	Control	158 \pm 5.6	19.6 \pm 1.6
	Cleaned	160 \pm 4.8	19.2 \pm 1.6

tank River estuary, a tributary of the Chesapeake Bay, USA. A portion (10%) of the water volume of each mesocosm was drained and replaced with filtered (0.5 μm) estuarine water daily. During a 10 d batch period (Days 25 to 35) of the primary experiment, water was not exchanged in order to allow depletion of nutrient levels. A nutrient pulse was administered in the primary experiment on Day 34 to bring concentrations of ammonium (NH_4^+), phosphate (PO_4^{3-}) and silica (dSi) up to 50, 3.1 and 50 μM , respectively. Similar nutrient pulse treatments were effected on Day 14 of the 1995, and Day 31 of the 1994 studies (Chen et al. 1997).

Sampling and analysis. Key properties and processes measured in this study include: light intensity, nutrient concentration, algal biomass and taxonomic composition (phytoplankton, wall periphyton, sediment microalgae), bacterioplankton abundance, benthic macrofaunal biomass and taxonomic composition, and primary productivity and respiration both for total ecosystem and for planktonic and periphytic components. The vertical distribution of photosynthetically available radiation (PAR) was measured weekly using hemispherical sensors (Li Cor, 2 π).

Dissolved inorganic nutrient concentrations (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-} , and dSi) were sampled twice-weekly and water column chlorophyll *a* (chl *a*) was sampled daily. Standard automated wet chemical methods were used to measure nutrient concentrations (Technicon AAI autoanalyzer) following filtration through precombusted GF/F filters (Parsons et al. 1984). *In vivo* water column chl *a* concentrations were determined fluorometrically (WET Labs Model 9602004), with measurements calibrated both by *in vitro* fluorometry (Turner Designs Model 10) following

Table 3. Experimental design

Expt no.	Cleaning frequency	Mesocosms involved ^a	Comments (timing)	Research question
1	2 wk ⁻¹	A, B, C	Primary Experiment (31 Jan–15 Mar 96)	Wall-cleaning effects
2	1 wk ⁻¹	B	Comparison of Expt 1 with earlier study (25 Jul–21 Aug 95)	Wall-cleaning frequency
3	1 wk ⁻¹	A, B, C, D, E	Comparison across wider range of container sizes and shapes with and without wall-cleaning (Expt 2, Jul–Aug 95; Expt 3, Jul–Aug 94)	Wall-cleaning effects across wider scales

^aSee Table 2 for mesocosm dimensions

extraction with 90 % acetone and by high performance liquid chromatography (HPLC; Van Heukelem et al. 1994).

Periphytic growth on mesocosm walls was measured by deploying and retrieving fiberglass strips fabricated from wall material. Replicate fiberglass strips were attached to mesocosm walls at the beginning of each experiment (Chen et al. 1997). Strips were removed periodically before wall-cleaning treatments, and used to estimate biomass and rates of periphyton primary production and respiration (see below). Occasionally, strips were retrieved both before and after cleaning treatments to assess cleaning efficiency. Scraped material was extracted in 90 % acetone and sonicated to aid pigment extraction (Whitney & Darley 1979, Chen et al. 1997). After centrifugation, extracted chl *a* was measured by fluorometry and calibrated with HPLC.

Biomass of sediment microalgae was estimated weekly in the primary experiment using chl *a* as an index. Sediment was collected using small (2.6 cm diam.) sediment cores. The top 1 cm of sediment samples was placed in a centrifuge tube and extracted in 100 % acetone, followed by a phase-separation spectrophotometric acidification technique (Whitney & Darley 1979). Chl *a* concentrations in hexane extracted samples were measured with a spectrophotometer (Milton Roy, Spectronic 301), calibrated by HPLC. Biomass values for both wall periphyton and sediment microalgae are reported as mg m^{-2} of sampled wall or sediment area, respectively. To compare with phytoplankton biomass (mg m^{-3}), these data were also converted to mg m^{-3} basis by multiplication by the respective ratios of wall area/water volume or sediment area/water volume (see Table 2).

Taxonomic compositions of planktonic, benthic, and periphytic algae were assessed using accessory pigment composition as an index. Samples were collected 1 to 4 d after nutrient addition and analyzed with HPLC (Van Heukelem et al. 1994). Multivariate regressions (Bidigare et al. 1986, Letelier et al. 1993, Barlow et al. 1995) were used to assess characteristic pigment ratios.

Abundance of bacterioplankton was measured weekly by acridine orange direct cell counts (Hobbie et al. 1977). Water samples were fixed with aqueous glutaraldehyde, stained with acridine orange, and filtered onto blackened 0.22 μm polycarbonate filters with 0.65 μm backing filters. Bacterioplankton cells were counted using a Zeiss Axiophot microscope at 1612 \times final magnification (Sanford et al. 2001).

Biomass and taxonomic composition of benthic macrofauna were measured at the beginning and end of experiment. Sediment cores (13.2 cm diam.) were sampled and sieved through 0.5 mm screens. Samples

were immediately stained with Rose Bengal and preserved in 10 % buffered formalin for subsequent species identification and weighing.

Rates of primary productivity and respiration for whole experimental ecosystems were continuously monitored by tracing changes in dissolved oxygen (O_2) concentration *in situ* using a series of galvanic O_2 sensors (OxyGuard Stationary probes) which were deployed in each mesocosm. These electrodes were calibrated twice-weekly with standard Winkler titration techniques (Carritt & Carpenter 1966). Net primary production (NPP) was taken as the net O_2 production during the light period. The decrease in O_2 concentration during daily 12 h dark periods was used to compute respiration (R). Gross primary production (GPP) was defined operationally as the sum of R (taken as a positive number) and NPP (Odum 1956, Oviatt et al. 1995, Chen et al. 1997). These metabolic rates were adjusted for air–water gas exchange with diffusion coefficients measured in a previous study (Petersen et al. 1997).

Rates of primary production and respiration for plankton and wall communities were determined periodically by measuring dawn-dusk-dawn changes in O_2 concentration in incubation chambers over 24 h periods (Petersen & Chen 1999). Chambers were constructed of clear acrylic tubes (7 cm diam.) which extended the whole depth of each mesocosm. Water in each chamber was stirred by an internally mounted stir-bar, and the top and bottom of each chamber were sealed with transparent acrylic caps to exclude sediments and eliminate gas exchange with the atmosphere (Petersen & Chen 1999). Two chambers were incubated concurrently in each mesocosm, one with ambient water only and the other with both water and a wall strip with periphyton growth. NPP, R and GPP values of plankton communities were estimated from the chambers with water only. These values were subtracted from those measured in chambers containing strips of wall material to estimate metabolic rates of the periphyton community.

Statistical analysis. Statistical analyses were performed using SYSTAT (1992) software. Repeated-measures analysis (Crowder & Hand 1990) was used to assess differences between treatments and controls in nutrient concentrations, autotrophic biomass, and GPP of whole ecosystems, as well as plankton and wall communities. In this case, significant differences were tested using p-values for treatment (p_1) and time \times treatment (p_2) effects. For most variables in the primary experiment (1996), effects of treatment were also analyzed by simple ANOVA on data pooled into 3 different time periods: initial (Days 1 to 24), batch (Days 25 to 35), and post-nutrient (Days 36 to 45). For the 2 secondary experiments (1994, 1995) comparing clean-

ing treatment versus control and weekly versus twice-weekly cleaning in separate time periods (Table 3), we tested for treatment effects using only ANOVA. Here, we assumed that the wall-cleaning treatment was the only difference between the separate experiments. Where appropriate, Fisher's least significant difference test (LSD) was used to identify differences between means.

Multivariate linear regressions of accessory pigments against chl *a* were used to determine the presence of major algal groups in each mesocosm habitat (plankton, sediments, periphyton) using the pigment biomarker method (Hooks et al. 1988, Millie et al. 1993). In this approach, it was assumed that alloxanthin is attributed exclusively to cryptophytes, that fucoxanthin is associated with diatoms, that lutein indicates chlorophytes, that peridinin indicates dinoflagellates, and that zeaxanthin is associated with cyanobacteria. We ignored the fact that a small fraction of fucoxanthin may be attributed to dinoflagellates when both diatom and dinoflagellate are present (Millie et al. 1993). This analysis may also underestimate contributions of dinoflagellates because some species do not contain peridinin (Bjørnland & Tangen 1979, Johnsen & Sakshaug 1993). Linear regression analysis was used to examine the relationships between mesocosm radius and differences in mean biomass between treated and control systems for both phytoplankton and wall periphyton.

RESULTS

Algal biomass

Wall-cleaning treatment at twice-weekly intervals effectively eliminated periphytic algae biomass from mesocosm walls over the course of experiment (Fig. 1a–c). On one occasion, direct evidence of the efficiency of periphyton removal was obtained by comparing periphytic biomass before and after wall-cleaning, where biomass values were reduced from 0.016 (± 0.011) to 0.005 (± 0.002) mg chl *a* m⁻² (mean \pm SE). Overall, periphytic biomass values were significantly higher ($p_1 < 0.05$ for treatment, $p_2 > 0.05$ for time \times treatment) in the control than in the cleaned systems for each of the 3 sizes of mesocosm (A, B, C), with overall mean values of 3.7 and 0.03 mg chl *a* m⁻², respectively. After the nutrient pulse treatment,

periphytic biomass increased rapidly in all control containers but not in the cleaned systems (Fig. 1a–c).

Significant differences in phytoplankton biomass (mg chl *a* m⁻³) between control and cleaned systems over the whole experiment were evident only in the narrow A tanks (p_1 and $p_2 < 0.05$). Significant treatment effects were, however, apparent in the post-nutrient period for all 3 sizes of experimental system (Fig. 1d–f). During this period, phytoplankton biomass was higher in cleaned than in control systems in A (p_1 and $p_2 < 0.01$) and B ($p_1 < 0.05$; $p_2 = 0.25$) tanks (Fig. 1d,e). The pattern was, however, inverse for the C tanks (p_1 and $p_2 < 0.01$), with the cleaned tanks having higher chl *a* during the batch mode and lower values following nutrient addition (Fig. 1f).

Sediment microalgal biomass (m⁻²) was similar for all tanks and treatments throughout the experiment

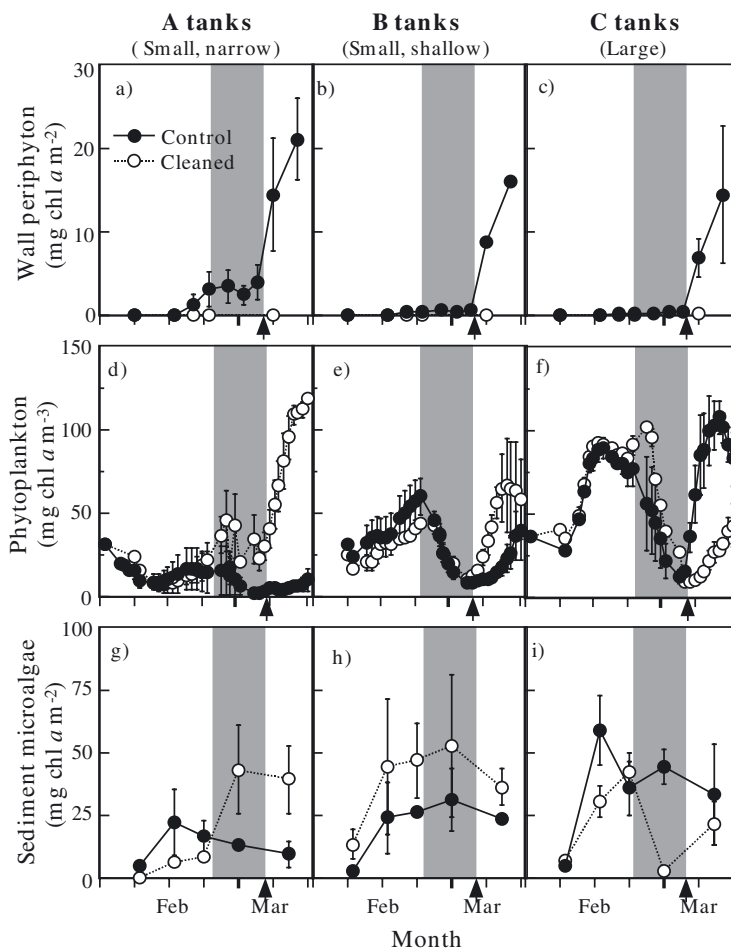


Fig. 1. Biomass time-course (mg chl *a*) of (a–c) wall periphyton (m⁻² wall area), (d–f) phytoplankton (m⁻³ water volume), and (g–i) sediment microalgae (m⁻² sediment area) of control (●) and twice-weekly cleaned (○) systems in A, B and C tanks. Values are mean \pm SE of replicate (n = 3) mesocosms. Batch mode is indicated by the shaded area, and the nutrient pulse is indicated by the arrow on the x-axis

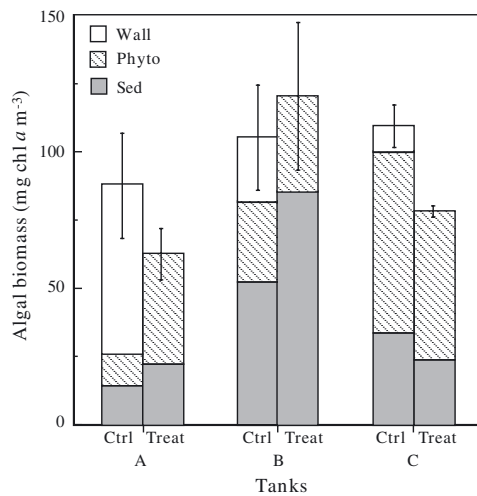


Fig. 2. Mean total algal biomass [phytoplankton (phyto) + sediment microalgae (sed) + wall periphyton (wall)] of controls and twice-weekly cleaned systems in A, B, and C tanks. Standard errors are shown for each treatment and mesocosm type

(Fig. 1g–i); however, different treatment effects were evident among different size systems. Wall-cleaning treatment resulted in significantly higher benthic microalgal biomass for both of the smaller (0.1 m³) mesocosm types, with differences in narrow (A) tanks being delayed and less pronounced (20.8 vs 13.6 mg chl a m⁻²) compared to those (38.7 vs 22.8 mg chl a m⁻²) in the shallower (B) tanks. In contrast, mean biomasses in the larger (1 m³) C tanks were variable but generally higher in the control systems, with values of 33.8 and 22.1 mg chl a m⁻², respectively.

Total algal biomass (TA = phytoplankton + sediment microalgae + wall periphyton) was not significantly affected by wall-cleaning treatment in A and B tanks. Small treatment effects on TA were evident ($p < 0.05$) in the larger C tanks, where wall-cleaning decreased biomass by 25% (Fig. 2). Relative contributions of the 3 algal components to TA varied with treatment and among experimental systems with different dimensions (Fig. 2). The untreated controls with highest TA values were found in C tanks, those with intermediate values in the B systems, and those with lowest values in the narrow A tanks. The contribution of phytoplankton to TA increased linearly with container radius in control systems ($r^2 = 0.88$, $p < 0.01$). The pattern was reversed for wall communities, where periphyton contributions decreased with container radius ($r^2 = 0.39$, $p = 0.07$). Biomass of sediment microalgae in untreated controls was highest in the shallow B tanks, intermediate in the larger C tanks, and lowest in the narrow A tanks. Similarly, in mesocosms receiving wall-cleaning treatment, TA followed the same rank order B > C > A (Fig. 2). Because wall periphyton were efficiently elim-

inated with cleaning, they contributed little to TA in treated systems. Phytoplankton comprised over 60% of total algal biomass in the treated A and C tanks. In contrast, more than 70% of algal biomass was comprised of sediment microalgae in the shallow B tanks (Fig. 2). When all data are pooled, sediment microalgae biomass is linearly related to bottom light intensity ($r^2 = 0.60$, $p < 0.01$).

Algal taxonomic composition

The results of multiple regression models of 5 key accessory pigments (alloxanthin [allo], fucoxanthin [fuco], lutein, peridinin [perid], zeaxanthin [zeax]) against chl *a* were highly significant for each of the 3 algal habitat assemblages ($r^2 = 0.99$, $p < 0.01$). Equations were as follows: phytoplanktonic chl *a* = 2.19 [fuco] + 6.04 [lutein] + 2.22 [perid] + 1.19 [zeax]; sediment microalgal chl *a* = 2.07 [fuco] + 3.45 [lutein] + 0.32

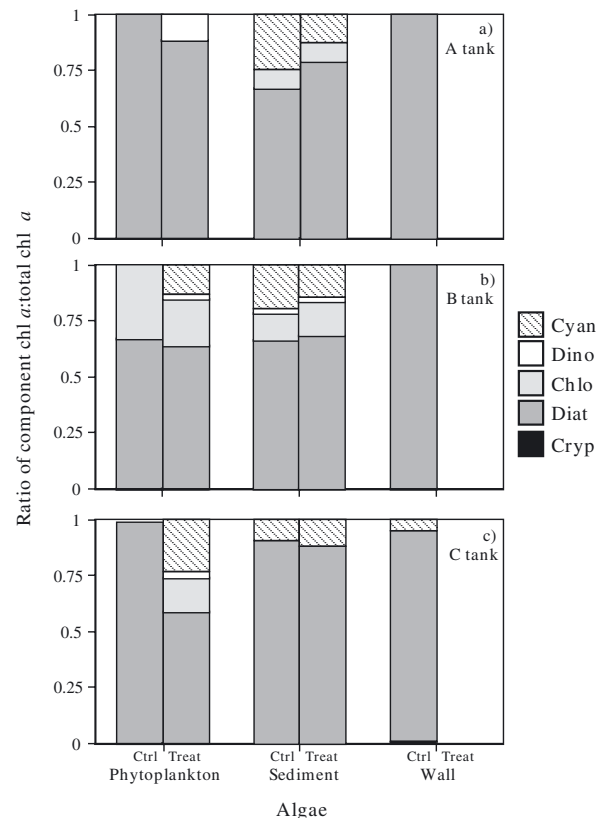


Fig. 3. Ratio of accessory pigments to total chl *a* in plankton, wall, and benthic habitats in controls and twice-weekly cleaned systems in A, B, and C tanks. Samples were collected 1 to 4 d after nutrient addition, and no wall periphyton samples were taken from the treated systems. Chlo = Chlorophytes; Cryp = Cryptophytes; Cyan = Cyanobacteria; Diat = Diatoms; Dino = Dinoflagellates

[perid] + 1.59 [zeax]; wall periphytic chl *a* = 2.17 [fuco] + 9.23 [zeax] + 0.78 [allo]. These regression coefficients were multiplied by observed accessory pigment concentrations to estimate the contribution of cells bearing these pigments to total algal biomass for each system.

Overall, the strongest effects of treatment on algal taxonomic composition were evident for phytoplankton, with little effect apparent for either sediment microalgae or wall periphyton. All mesocosm algal communities were dominated by diatoms (fucoxanthin) (Fig. 3). Dinoflagellates (peridinin) were also relatively abundant in phytoplankton in treated A tanks, but not in controls (Fig. 3a). Diatoms and chlorophytes (lutein) occurred in all the B tanks, with dinoflagellates and cyanobacteria (zeaxanthin) also evident in treated B tanks (Fig. 3b). Phytoplankton composition in treated C tanks was similar to that in treated B tanks, with diatoms dominant and relatively few cyanobacteria in controls (Fig. 3c).

Very few effects of treatment on taxonomic composition were apparent for sediment microalgae in any mesocosm size (Fig. 3). Sediment microalgae were also dominated by diatoms, with cyanobacteria, chlorophytes (A and B tanks) and dinoflagellates (B tanks) also present. Wall periphyton was entirely composed of diatoms in A and B tanks (Fig. 3a,b), with small proportions of cyanobacteria and cryptophytes in the control C tanks (Fig. 3c).

Gross primary production (GPP)

Dynamics of total ecosystem GPP were similar among mesocosms of different dimensions, with rates (m^{-3}) slightly higher in B and C compared to A systems. The effects of treatment on whole system GPP were generally negligible over the course of the experiments (Fig. 4a–c). In the period following nutrient addition, however, rates in C tanks were significantly decreased with treatment (Fig. 4c; $p_1 < 0.05$; $p_2 < 0.01$). In contrast, GPP rates for planktonic components were significantly enhanced with wall-cleaning treatment ($p_1 < 0.01$; $p_2 < 0.05$) in the narrow A tanks (Fig. 4d). Although similar effects on B tank plankton were evident during the post-nutrient period, there were no significant effects of treatment for either B or C tanks (Fig. 4e,f). Mean values of wall community GPP appeared to decrease with wall-cleaning; however, variance was high and differences were not significant (Fig. 4g–i).

Nutrient concentrations

Temporal variations in nutrient (dissolved inorganic nitrogen [DIN], phosphate [PO_4^{3-}], and silica [dSi]) concentrations were similar in treated and control systems throughout the experiment in mesocosms of all 3 dimensions (Fig. 5). Even though mean nutrient concentrations were consistently higher in treated systems following nutrient input, these differences were not significant for most nutrients. The only significant treatment effect (p_1 and $p_2 < 0.01$) was for dSi concentrations in C tanks (Fig. 5i).

Bacterioplankton

Bacterioplankton abundances were similar in treated and control mesocosms during initial and batch

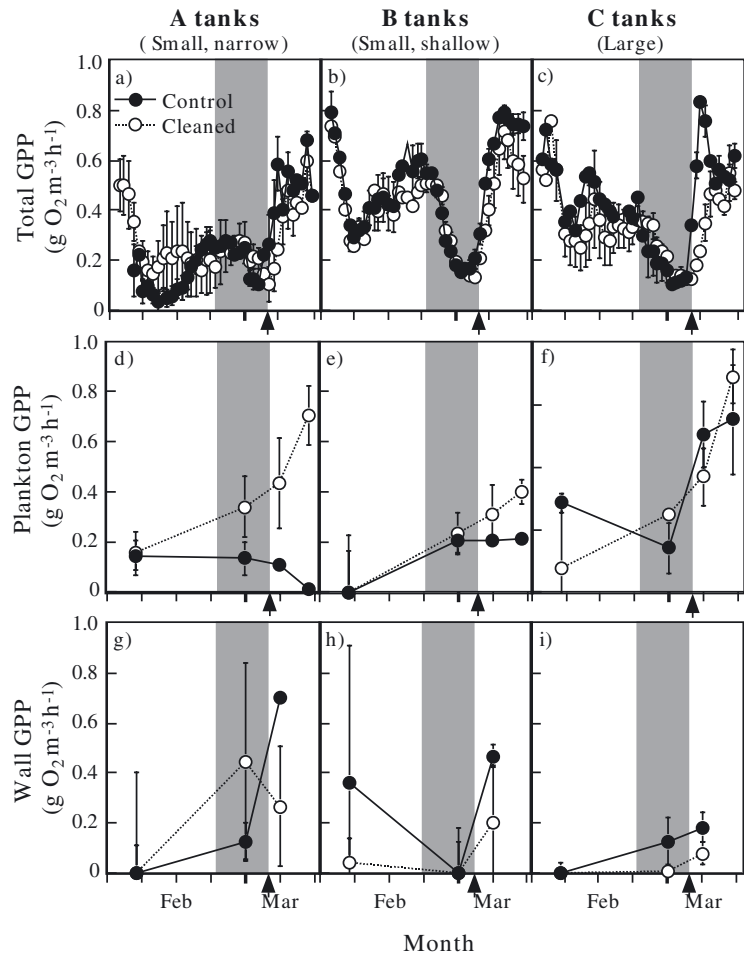


Fig. 4. Gross primary production (GPP) time-course of (a–c) total ecosystem, (d–f) planktonic and (g–i) wall communities in control (●) and twice-weekly cleaned (○) systems in A, B and C tanks. Values are mean \pm SE of replicate ($n = 3$) mesocosms. Batch mode is indicated by the shaded area, and the nutrient pulse is indicated by the arrow on the x-axis

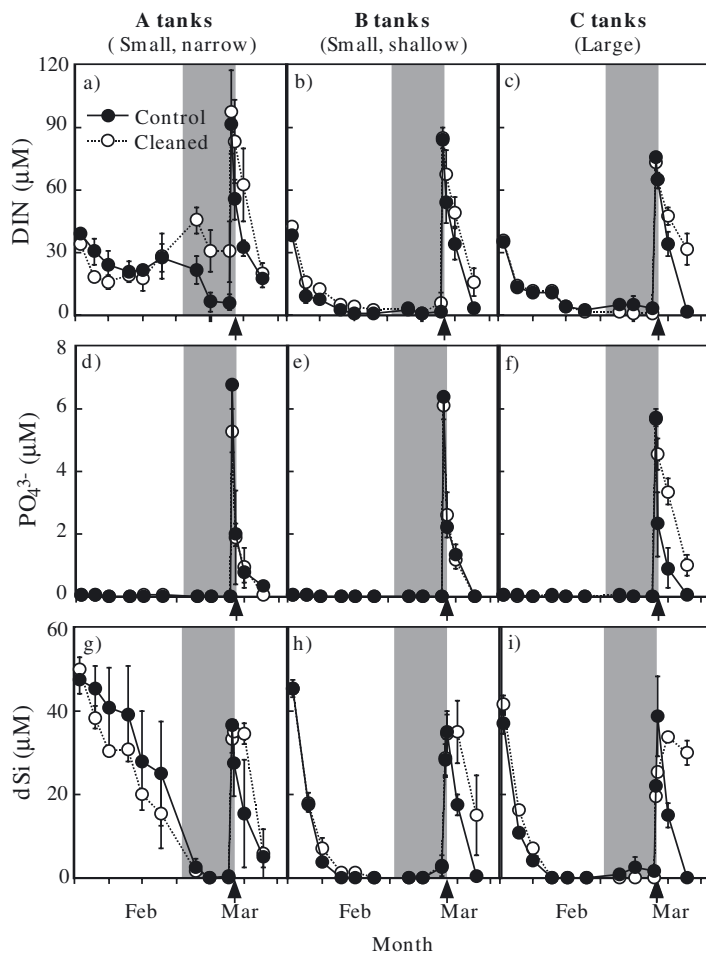


Fig. 5. Time-course of (a–c) dissolved inorganic nitrogen (DIN), (d–f) phosphate (PO_4^{3-}), and (g–i) silica (dSi) concentration in control (●) and twice-weekly cleaned (○) systems in A, B and C tanks. Values are mean \pm SE of replicate ($n = 3$) mesocosms. Batch mode is indicated by the shaded area, and the nutrient pulse is indicated by the arrow on the x-axis

periods in all 3 systems (Table 5). In the post-nutrient period, bacterioplankton abundances were significantly higher in treated systems in B ($p < 0.01$) and C ($p < 0.05$) tanks, but not in the A tanks. Bacterioplankton abundances over the whole experimental duration were significantly elevated in treated B and C (both $p \leq 0.01$) tanks; however, this trend is clearly driven by the large differences during the post-nutrient period (Table 5).

Benthic macrofauna

Sediment samples collected near the beginning of the experiment revealed that the benthic macrofauna were dominated by 3 phyla (i.e. Annelida, Arthropoda, and Insecta) with mean

total biomass (\pm SE) of $4.3 (\pm 1.4)$ g wet weight m^{-2} for all experimental systems. By the end of the experiment total benthic biomass ranged from about 8 to 30 g wet weight m^{-2} , and communities were dominated by both annelids (i.e. polychaetes and oligochaetes) and arthropods (i.e. amphipods and isopods) in all mesocosms (Table 6). Insects were also found in the A and C tanks, and cnidarians (anemone) were observed in the B tanks. Mean macrofaunal biomass values were consistently 30 to 250% higher in treated mesocosms (Table 6). Variability was generally high, however, and wall-cleaning effects were significant only for the biomass of insects and the total benthic macrofaunal community in C tanks.

Wall-cleaning frequency

Comparison of ecosystem properties in B tanks cleaned twice-weekly during the 1996 experiment with those measured in an earlier (1995) experiment employing once-weekly wall-cleaning (see Table 3) provided a tentative test for the effects of varying wall-cleaning frequency. Periphyton communities were not efficiently removed from B tanks subjected to weekly wall-cleaning treatment (Table 7). Whereas twice-weekly cleaning resulted in significant (100-fold) periphyton reductions, weekly cleaning resulted in a decrease in mean periphytic biomass of only 40% (from 1.6 to 1.0 mg chl a m^{-2}). This effect was not statistically significant (Table 7).

Although wall-cleaning at either frequency (1 wk^{-1} or 2 wk^{-1}) resulted in generally higher mean biomass values for phytoplankton (18 to 35%) and sediment microalgae (84%), differences were not significant (Table 7). Similarly, although

Table 5. Mean bacterioplankton abundance ($\times 10^9$ cells l^{-1}). Values are average abundances of initial (Days 1 to 24), batch (Days 25 to 35), post-nutrient periods (Days 36 to 45), and over the whole experiment period of replicate ($n = 3$) mesocosms expressed as mean \pm SE. * $p < 0.05$, ** $p \leq 0.01$

Tank	Treatment	Initial	Batch	Post	Whole
A	Control	3.2 ± 0.6	1.9 ± 0.1	3.3 ± 0.8	2.9 ± 0.3
	Cleaned	3.1 ± 0.4	2.2 ± 0.5	5.4 ± 0.8	3.4 ± 0.4
B	Control	2.8 ± 0.2	2.9 ± 0.3	$2.0 \pm 0.3^{**}$	$2.6 \pm 0.2^{**}$
	Cleaned	3.2 ± 0.2	3.6 ± 0.5	$7.4 \pm 1.0^{**}$	$4.3 \pm 0.5^{**}$
C	Control	2.9 ± 0.2	2.7 ± 0.5	$4.3 \pm 0.8^*$	$3.2 \pm 0.3^{**}$
	Cleaned	2.5 ± 0.2	2.3 ± 0.1	$7.9 \pm 1.3^*$	$3.8 \pm 0.6^{**}$

Table 6. Biomass (g wet weight m⁻²) and taxonomic composition of benthic macrofauna at the end of experiment. Values are mean ± SE of replicate (n = 3) mesocosms. *p < 0.05, -: no animals recorded

Macrofauna	Treatment	Mesocosm designation		
		A	B	C
Annelida	Control	18.1 ± 16.6	6.6 ± 2.8	9.4 ± 1.1
	Cleaned	26.0 ± 21.8	20.4 ± 14.6	16.9 ± 5.6
Arthropoda	Control	1.2 ± 0.6	1.2 ± 0.7	2.1 ± 0.8
	Cleaned	0.6 ± 0.3	7.2 ± 2.1	1.7 ± 1.2
Cnidaria	Control	-	0.1 ± 0.1	-
	Cleaned	-	0.8 ± 0.8	-
Insecta	Control	0.7 ± 0.7	-	0.6 ± 0.4*
	Cleaned	0.1 ± 0.1	-	3.7 ± 0.7*
Total	Control	20.1 ± 15.6	7.9 ± 3.0	12.1 ± 2.0*
	Cleaned	26.6 ± 21.5	28.4 ± 17.3	22.2 ± 6.6*

small consistent differences were observed for other variables (e.g. GPP, DIN, PO₄³⁻, dSi) with treatment, these were not statistically significant in either weekly or twice-weekly treatments (Table 7).

The coefficients of variability (variance/mean) for algal biomass and nutrient concentrations tended to be slightly higher for systems receiving wall-cleaning compared to controls, particularly at the twice-weekly frequency (Table 7). For GPP, however, there was no consistent change in relative variance with wall-cleaning at either frequency.

Effects over a broader range of container dimensions

Differences in wall-cleaning effects were also considered for all 5 container types (volume range 0.1 to 10 m³,

see Table 2) by comparing results from experiments conducted in the summers of successive years (see Table 3). To facilitate comparison of changes in periphyton and phytoplankton biomasses, both are expressed in units of mg chl a m⁻³ of water volume. Periphytic algal biomass (Table 8) was significantly higher on uncleaned mesocosm walls compared to those with weekly cleaning for mesocosms of all 5 dimensions. Mean phytoplankton biomass values were higher or similar in cleaned compared to control systems (Table 8). In spite of large (6- to 25-fold) and significant differences in periphytic biomass between treated and control meso-

cosms, treatment had much smaller and inconsistent effects on ecosystem GPP, with rates ranging from 30% higher to 50% lower. Relative variance (variance/mean) in GPP rates measured for replicate tanks were remarkably low, being less than 0.06 for 8 of 10 treatment replicates. Consequently, small (mean of 22%) decreases in GPP with treatment in A, C, and D systems were detectable (Table 8).

Although periphytic biomass was significantly decreased by wall-cleaning treatment in all container types, there were significant negative correlations between periphyton chl a and system radius for both control and treated systems, with r² values of 0.57 (p < 0.01) and 0.35 (p < 0.05), respectively. In contrast, phytoplankton biomass tended to increase linearly with container radius for treated systems (r² = 0.35, p < 0.05), but not controls (Table 8).

Table 7. Effects of weekly and twice-weekly cleaning frequency on ecological properties of small mesocosms^a. Data given are average values of biomass of wall periphyton, sediment microalgae (mg chl a m⁻²) and phytoplankton (mg chl a m⁻³); gross primary production (GPP; g O₂ m⁻³ h⁻¹) of whole ecosystem, plankton and wall communities; and concentrations (μM) of dissolved inorganic nitrogen (DIN), phosphate (PO₄³⁻), and silica (dSi) sampled 1 to 2 wk⁻¹ over the experiment. Values are mean ± SE of replicate (n = 3) mesocosms. nd: not done, *p < 0.01

Variable	Component	Weekly	Cleaned	Twice-weekly	Cleaned
		Control		Control	
Biomass	Wall periphyton	1.6 ± 0.5	1.0 ± 0.1	3.0 ± 0.2*	0.0 ± 0.0*
	Phytoplankton	4.4 ± 0.7	6.1 ± 1.7	29.9 ± 2.5	35.2 ± 5.5
	Sediment algae	nd	nd	51.9 ± 8.8	85.1 ± 28.1
GPP	Wall periphyton	0.27 ± 0.13	0.19 ± 0.12	0.24 ± 0.24	0.02 ± 0.07
	Plankton	0.11 ± 0.07	0.05 ± 0.02	0.14 ± 0.06	0.22 ± 0.05
	Whole ecosystem	0.33 ± 0.05	0.32 ± 0.04	0.48 ± 0.02	0.42 ± 0.02
Nutrient	DIN	1.68 ± 0.36	2.63 ± 0.38	17.98 ± 0.88	23.41 ± 2.48
	PO ₄ ³⁻	0.05 ± 0.01	0.09 ± 0.04	0.78 ± 0.03	0.77 ± 0.09
	dSi	25.4 ± 3.0	31.1 ± 8.6	11.52 ± 0.87	14.54 ± 2.61

^aExperiments with B tanks (0.46 m depth, 0.1 m³ volume) at weekly intervals were conducted in 1995; those with twice-weekly were done in 1996 (see Table 3)

Table 8. Ecological properties of mesocosms of different size and shape (A to E, see Table 2) without and with wall-cleaning treatment (weekly) during successive summer experiments in 1994^a and 1995, respectively. Data given are for average biomass of phytoplankton (sampled daily) and wall periphyton (sampled weekly), and for ecosystem gross primary production (GPP; sampled daily) over the course of experiments. Values are mean \pm SE of replicate (n = 3) mesocosms. *p < 0.05, **p < 0.01

Tank	Treatment	Algal biomass, mg chl <i>a</i> m ⁻³		Whole GPP (g O ₂ m ⁻³ h ⁻¹)
		Wall periphyton	Phytoplankton	
A	Control	109.2 \pm 16.9**	5.5 \pm 0.3	0.32 \pm 0.01**
	Cleaned	14.8 \pm 7.0**	4.4 \pm 0.4	0.17 \pm 0.01**
B	Control	73.5 \pm 11.3**	6.5 \pm 1.0	0.28 \pm 0.00
	Cleaned	7.6 \pm 0.9**	6.1 \pm 1.7	0.32 \pm 0.04
C	Control	43.0 \pm 2.7**	4.7 \pm 0.4**	0.26 \pm 0.00*
	Cleaned	7.7 \pm 2.0**	10.7 \pm 0.8**	0.24 \pm 0.01*
D	Control	51.4 \pm 5.1**	4.8 \pm 0.2*	0.17 \pm 0.01**
	Cleaned	2.1 \pm 0.4**	9.6 \pm 1.7*	0.13 \pm 0.00**
E	Control	20.6 \pm 3.1**	5.9 \pm 0.5**	0.22 \pm 0.01
	Cleaned	2.5 \pm 0.9**	10.2 \pm 0.5**	0.29 \pm 0.06

^aValues for 1994 experiment ('control') are from Chen et al. (1997)

To consider further how mesocosm dimension may influence responses to wall-cleaning treatment, differences in algal biomass between treated systems and controls were calculated for each experimental ecosystem. In general, the decrease in periphytic biomass (control minus cleaned) was inversely related to container radius for both weekly and twice-weekly treatments (Fig. 6). These relationships were highly significant for weekly cleaning ($r^2 = 0.52$, $p < 0.01$, Fig. 6a) and marginally significant for twice-weekly treatment systems ($r^2 = 0.39$, $p = 0.07$, Fig. 6b). In addition, an inverse pattern was observed for phytoplankton biomass responses to treatment, where treatment induced an enhancement of phytoplankton that increased linearly from narrower to wider mesocosms ($r^2 = 0.67$, $p < 0.01$, Fig. 6b). Note that the absolute values for slopes of the respective increases in phytoplankton and decreases in periphyton biomass versus container radius were similar (≈ 100), suggesting a direct connection between the 2 trends. Differences in sediment microalgal biomass in response to treatment were more closely related to mesocosm depth, with the largest differences in the shallow B tanks, followed by the A and then the C tanks.

DISCUSSION

Treatment effects on periphyton growth

Although mesocosms are valuable research tools for ecology studies (e.g. Beyers & Odum 1993), periphytic growth on container walls may seriously reduce exper-

imental realism and confound extrapolation of results to natural ecosystems (e.g. Dudzik et al. 1979, Harte et al. 1980). Whereas it is likely impossible to eliminate wall growth completely, several approaches have been suggested for minimizing the effects. These include: reducing duration of experiments (Harte et al. 1980), increasing container radius (Chen et al. 1997, 2000), periodic wall replacement (Dudzik et al. 1979, Lundgren 1985), and routine wall cleaning (e.g. Gamble et al. 1977, Kuiper 1984).

Physical cleaning of container walls, which is the most common approach employed for control of periphyton growth (e.g. Petersen et al. 1999), can be effective when done at a relatively high-frequency (Pilson et al. 1980). In the present study, we found that peri-

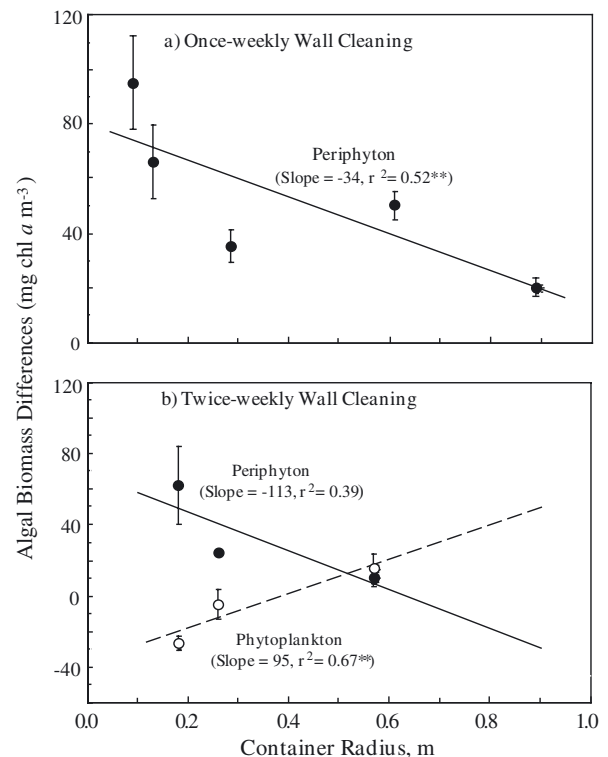


Fig. 6. Relationship between container radius and wall-cleaning induced differences in algal biomass (control–cleaned) for (a) wall periphyton with once-weekly wall-cleaning treatment, and (b) periphyton (filled symbols and solid lines) and phytoplankton (open symbols and dashed lines) with twice-weekly treatment. Slopes and r^2 values are given for linear regressions of radius and biomass differences for phytoplankton and wall periphyton. **p < 0.01

phytic algae was effectively removed with twice-weekly treatment, but much less so with weekly wall-cleaning (Table 7). Algal and bacterial cells, which tend to remain tightly bound to container walls and be resistant to physical removal (Dudzik et al. 1979), have high intrinsic growth rates that enable the periphyton community to rapidly re-establish biomass within days after scraping. In our mesocosms, periphyton dominated total algal biomass within a few days after weekly wall-cleaning, especially under nutrient-rich conditions with warm temperatures (Chen et al. 1997).

Treatment effects on other algal assemblages

Previous studies have demonstrated significant uptake of water column nutrients by periphyton growing either on hard substrates in nature (Cattaneo 1987, Hansson 1990) or on mesocosm walls (Chen et al. 2000). The commonly observed decline of phytoplankton coinciding with rapid periphyton accumulation in aquatic mesocosms (Jassby et al. 1977, Rees 1979, Chen et al. 1997) may also reflect competition for nutrients. In this study, wall-cleaning generally resulted in increased phytoplankton biomass in the smaller A and B containers, particularly during the post-nutrient period when wall periphyton dominated (Fig. 1d,e). Nutrient concentrations in these experiments tended to be slightly higher in containers receiving wall-cleaning treatments compared to untreated controls (Fig. 5), and this may have contributed to the increased abundance of planktonic algae. In addition, diatoms dislodged (with cleaning) from container walls may represent 'recruits' to the planktonic assemblages, which were also dominated by diatoms (Fig. 3).

For the larger C tanks, a surprising inverse pattern was observed, where wall-cleaning treatment resulted in lower phytoplankton biomass (Fig. 1f). We can only speculate on the explanation for this counter-intuitive observation. Evidence from previous studies using these experimental systems (Chen et al. 1997) suggests that herbivorous zooplankton (copepods) tend to congregate near container walls and feed on periphyton biomass. The impact of this grazing was generally more pronounced for narrower systems (Chen et al. 2000), being inversely related to container radius (ranging from 0.2 to 1.8 m). In intermediate width containers (e.g. our 0.6 m radius C tanks), it is likely that zooplankton tend to redirect their grazing pressure to phytoplankton when wall periphyton are dislodged from walls. This might explain the reduced phytoplankton abundance observed with wall-cleaning in C tanks (Fig. 1f).

The mean biomass of sediment microalgae was significantly higher in the cleaned systems than in the

controls for smaller (A and B) containers, although differences were confined to the batch and post-nutrient periods for the A tanks (Fig. 1g,h). Rates of sediment GPP were, however, not significantly enhanced with wall-cleaning suggesting this response may be attributable more to recruitment of dislodged periphytic diatoms to the sediment habitat rather than to nutrient-enhanced algal growth. Indeed, sediment microalgae do not always respond to nutrient addition to overlying waters (Blumenshine et al. 1997), because cell growth depends more on nutrients diffusing from underlying sediment (e.g. Granéli & Sundbäck 1985). The mean values for both biomass and GPP for sediment microalgae in the larger C tanks declined markedly (although not significantly) with wall-cleaning treatment. A possible mechanism, analogous to that suggested for phytoplankton responses in the C systems, would involve increased abundance of insects and other motile epibenthic herbivores (Table 6) shifting their predominant food source from periphyton to sediment microalgae. Overall, however, sediment microalgal growth in these mesocosms appears to have been more directly related to light availability. The significant linear relationship evident between mean sediment microalgal biomass and bottom light intensity is consistent with numerous field observations (e.g. Pinckney & Zingmark 1993a).

Taxonomic composition of phytoplankton was also affected by wall-cleaning in the post-nutrient period (Fig. 3). Although phytoplankton was dominated by diatoms in both control and treated systems, a greater taxonomic richness was found in the cleaned systems (Fig. 3). Previous studies in these systems indicate that wall periphyton tend to regulate both nutrient concentrations and the N/P ratio in the water column (Chen et al. 2000). Since the composition of algal assemblages tends to vary with the N/P ratio (Tilman et al. 1982), this suggests a mechanism by which wall periphyton regulate phytoplankton community competition.

Other community responses to treatment

Not only did wall-cleaning affect biomass and taxonomic composition of planktonic algal assemblages, but it apparently also enhanced growth of bacterioplankton under nutrient rich conditions following the nutrient pulse (Table 5). Although abundances of planktonic bacteria tend to be regulated by grazing activity and/or substrate availability (e.g. Sanders et al. 1992), frequent reports of significant correlations between bacterioplankton and phytoplankton abundances (e.g. Azam et al. 1983, Cole et al. 1988, Shiah & Ducklow 1995) underscore the tendency for substrate limitation to dominate. The relatively high abundances

of bacterioplankton in our experimental systems compared to those observed in the Chesapeake Bay (Shiah 1993, Sanford et al. 2001) indicate that predation rates may be relatively low in these mesocosms. In the present study, bacterioplankton abundances generally followed phytoplankton chl *a* trends. Both were relatively constant and unaffected by wall-cleaning during initial periods of the experiment; however, both exhibited marked increases in response to nutrient additions, particularly in systems with wall-cleaning (Fig. 1d–f, Table 5).

Among the numerous factors typically cited as regulating growth of benthic macrofauna, food availability is of primary importance (Smetacek 1984, Rasmussen & Kalff 1987, Widbom & Elmgren 1988). Phytoplankton deposition from the overlying water column and related pelagic-benthic interactions represent the major food sources for deposit-feeding benthos in coastal environments (Grassle et al. 1985, Rasmussen & Kalff 1987). Animals dominating the experimental macrofauna in this study were all deposit-feeders (Table 6; Day et al. 1989). Indeed, in the present experiment sediment chl *a* levels were significantly increased with wall-cleaning (Figs. 1g–i & 2), indicating elevated food supplies for benthic deposit-feeding macrofauna (e.g. Reise 1992). Whereas significantly higher phytoplankton biomass was evident in wall-cleaning systems, increases occurred several days after nutrient additions (Fig. 1d–f). Increased sediment chl *a* levels associated with wall-cleaning may be attributable more to dislodged periphytic algal cells than to sinking phytoplankton or to *in situ* growth. Mean macrofaunal biomass levels were consistently higher (by 30 to 260%) in the cleaned systems than in the controls for all 3 mesocosm types. Due to high variability among replicate systems, however, differences were significant only in the larger C systems (Table 6).

Periphyton effects on ecosystem-level properties

Even though control experimental ecosystems were dominated by their periphytic communities, values for total algal biomass and ecosystem GPP were relatively independent of wall-cleaning treatment and mesocosm dimension (Figs. 1, 2 & 4). Evidently, a compensatory balance between periphyton and other algal assemblages (viz. phytoplankton and sediment microalgae) exists through their competition for limited supplies of light and nutrients (e.g. Lewis & Platt 1982). Conversely, however, these counteracting shifts in algal abundance suggest that the development of phytoplankton and sediment microalgae may be inhibited by the growth of wall periphyton. This was the case in our experiments, where relative contributions of the 3 dom-

inant habitats (planktonic, periphytic, benthic) to ecosystem primary production and total algal biomass varied significantly between the control and cleaned systems (Figs. 1, 2 & 4). These results indicate that wall-cleaning may be less important for experiments in which total ecosystem properties are of primary interest than for studies focusing on the dynamics of organisms or processes within a particular habitat.

Whereas previous studies have found that aspects of nutrient cycling are significantly altered by growth of periphytic communities in experimental ecosystems (Confer 1972, Eppley et al. 1978, Harte et al. 1980, Blumenshine et al. 1997, Chen et al. 2000), the results of the present study suggest that effects tend to be muted at the ecosystem level. We found that nutrient concentrations were slightly lower (by 0 to 20%) in some control systems; however, differences between control and treated mesocosms were generally not significant (Fig. 5, Table 7). Significant increases in nutrient concentrations with wall-cleaning were evident only in C tanks following the nutrient pulse (Fig. 5). Apparently, demand for nutrients remained relatively unaffected by wall-cleaning because of compensatory increases in phytoplankton and sediment microalgae accompanying removal of wall periphyton (Chen et al. 2000). As a consequence, wall-cleaning did not substantially disrupt the overall nutrient balance in these experimental systems.

Although we chose to retain scraped periphyton within treated experimental ecosystems in this study, we can compute the potential impact that periphyton removal from containers would have had on system nitrogen budgets. The difference between periphytic chl *a* levels in treated and control systems ranged from approximately 10 to 60 mg chl *a* m⁻³ and 20 to 100 mg chl *a* m⁻³ for twice-weekly and once-weekly treatments, respectively (Fig. 6). Assuming an average carbon/chl-*a* ratio of 75 (J. E. Petersen et al. unpubl. data) and Redfield stoichiometry, the equivalent N removed from walls ranged from approximately 10 to 100 μmol l⁻¹, which would be equivalent to N removal rates of 3 to 30 μmol l⁻¹ d⁻¹. These rates can be compared to the equivalent N uptake associated with the GPP of the experimental ecosystems (Fig. 4). Assuming a photosynthetic quotient of 1.25 and Redfield stoichiometry, we estimated a GPP N-demand of 10 to 30 μmol l⁻¹ d⁻¹, suggesting that removal of periphyton from the containers would have had an enormous impact on the productivity of these experimental ecosystems.

Scaling responses to container dimensions

As observed in previous studies (Chen et al. 1997), the relative contribution of wall periphyton to total

algal biomass was inversely related to mesocosm radius (Fig. 2). Hence, effects of wall periphyton on processes such as nutrient cycling would have also tended to decrease with container radius. On the other hand, biomass of sediment microalgae in these experimental systems was significantly related to bottom light intensity, which in turn is generally related to water depth (e.g. Kirk 1994). Similar positive relationships between microphytobenthic biomass and light at the sediment surface have been reported for many natural coastal systems (e.g. Sundbäck & Granéli 1988, Pinckney & Zingmark 1993b). In experimental ecosystems such as those in this study, however, light at the sediment-water interface may also depend on container radius, because of the attenuation associated with container walls (e.g. Chen et al. 2000). Similarly, phytoplankton biomass was also directly related to container radius in control mesocosms (Fig. 2), and this relationship may derive, in part, from indirect effects of competition between phytoplankton and wall periphyton for limited nutrient pools (Chen et al. 2000).

As a consequence of the strong effects of container radius on periphyton growth in this study, responses to wall-cleaning treatment also varied with the radius of the experimental systems. In fact, the difference in periphytic algal biomass between the cleaned and control systems (control minus treated) decreased linearly with mesocosm radius (Fig. 6), where larger differences indicate more periphyton removed. The slope of this relationship was greater (i.e. stronger scaling effect) for systems receiving twice-weekly treatment. We found a positive linear relationship between container radius and biomass differences for phytoplankton (Fig. 6b). This trend is consistent with the idea of competitive balance among algal groups vying for the same limited resources, where increased phytoplankton growth 'compensates' for periphyton loss due to cleaning. The similarity in the absolute values for slopes of periphyton decrease and phytoplankton increase with radius (Fig. 6b) suggests that much of the reduction in periphyton biomass with wall-cleaning could be explained by a comparable increase in phytoplankton. Sediment microalgae showed no such relationship between container radius and the biomass differences with cleaning treatment. Differences in sediment microalgal biomass between treatments and controls were, however, substantially larger in the shallower (0.5 m depth) B tanks compared to the deeper (1 m depth) A and C systems, suggesting a stronger scaling response to system depth.

In summary, our observations reveal that routine removal of periphyton from the walls of experimental systems results in significant changes in the structure and partitioning of biomass among wall, plankton, and sediment habitats. Ecosystem-level properties, includ-

ing primary production, total algal biomass and nutrient concentrations are, however, generally unaffected by wall-cleaning. Whereas twice-weekly removal of materials from container walls efficiently controlled periphyton growth, weekly cleaning was much less effective. The relative impact of wall-cleaning on periphyton and phytoplankton biomass scaled consistently to the radius of experimental containers. Although periphyton scraped from container walls was not removed from the experimental systems in this study, simple calculations indicate that doing so would have resulted in disruption of system nutrient balances. Thus, we conclude that while growth of periphyton on walls is an artifact inherent to experimental ecosystems, effects are generally confined to properties related to specific habitats (e.g. planktonic, benthic) rather than those pertaining to the integrated ecosystem. These effects can be minimized with frequent ($>2 \text{ wk}^{-1}$) routine cleaning, as well as retention of periphytic material within the experimental system and use of relatively wide ($> 1 \text{ m diam.}$) containers.

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