

A tank system for studying benthic aquatic organisms at predictable levels of turbidity and sedimentation: Case study examining coral growth

Kenneth R. N. Anthony

James Cook University, School of Marine Biology and Aquaculture, Townsville Qld 4811, Australia;
CRC Reef Research Centre, James Cook University, Townsville Qld 4811, Australia

Abstract

A tank system is described for long-term exposure of sessile organisms to well-defined ranges of particle loads on a background of natural flowing seawater. Using low technology and a simple mathematical model, the concentration of suspended particulate matter (SPM) and the rate of sedimentation could be predicted and sustained with high precision. The system and operational procedures were tested in an 8-week experiment investigating the effect of SPM concentrations on the growth rates of two species of symbiotic scleractinian coral (*Goniastrea retiformis* and *Porites cylindrica*). To also evaluate the effect of shading by SPM on coral growth, two light levels corresponding to 3–4-m depth at the low and high particle concentrations were included in the design. The growth rates of corals in control tanks were not significantly different from those of conspecifics in situ. However, the patterns of growth rates vs. SPM and shading treatments differed between species. The growth rates of *G. retiformis* generally increased as a function of SPM concentration (range = ~1–16 mg L⁻¹), whereas the growth rates of *P. cylindrica* were unaffected by particle load. The shading effects corresponding to 16 mg SPM L⁻¹ at 3–4-m depth resulted in significantly reduced growth rates in both species. I hypothesize that the different growth patterns displayed by the two species are the results of different abilities to utilize SPM as a food source or different susceptibilities to SPM as a mechanical stress factor.

The high level of environmental control and the constancy of SPM treatment levels were reflected in the absence of tank effects on growth rates and provided sufficient statistical power to detect relatively small differences in growth rates between corals from different treatments.

SPM is a universal component of aquatic systems, and the ecological role of SPM for both pelagic and benthic communities has received increasing attention over the past three decades (for review, see Wotton [1994] and references therein). The perceived role of SPM, however, varies between ecosystems. In temperate benthic habitats, detrital SPM may constitute an important source of food for suspension feeders (Seiderer and Newell 1985; Barille et al. 1997), especially below the euphotic zone (Genin et al. 1992; Rosenberg 1995). On coral reefs, however, there is a general consensus that high loads of suspended and sedimenting particles represent a stress factor by smothering tissues and attenuating light for photosynthesis (reviewed by Rogers 1990). While a number of field studies have addressed the problems of turbidity and sedimentation on coral assemblages, their findings have been inconsistent. The reported effects of high turbidity levels and rates of sedimentation on corals range from high mortality (Dodge and Vaisnys 1977; Stafford-Smith 1992) to no discernible effect (Dollar and Grigg 1981; McClanahan and Obura 1997). Most studies have been conducted in environments with high spatial and temporal variability, potentially precluding the identification of tur-

bidity and sedimentation as the primary factors of stress or reduced growth in corals. Furthermore, increased particle fluxes are often associated with other factors that affect coral physiology (Brown and Howard 1985), such as freshwater runoff from land (e.g., Sakai and Nishihira 1991), wave action (Larcombe et al. 1995), reduced light (Dallmeyer et al. 1982; Te 1997), and high nutrient loads (Mitchell and Furnas 1997). Testing hypotheses of the effects of specific SPM levels on aspects of the biology of corals (and on benthic organisms in general) requires a higher degree of environmental control than can be obtained from field studies.

In this study, I describe and test a flow-through tank system that enables exposure of benthic organisms to highly predictable concentrations of SPM and rates of sedimentation. The development and design of this system was based on three requirements. Firstly, a background of ambient water from the reef was required to allow control groups to be established within the setup. Secondly, to enable interpretation of physiological responses (e.g., growth) with respect to particle loads, it was necessary to obtain stocks of natural SPM. The latter is especially important in experiments involving heterotrophic species in which growth may be strongly related to particle quality. Lastly, to allow hypothesis development on physiological responses to specific particle loads, a method was required for predicting and adjusting SPM concentrations within distinct, narrow ranges. I tested the operation and efficacy of the system in an 8-week experiment with two species of scleractinian coral. Specifically, I tested whether the growth rates of a coral with high SPM-feeding capacity were less severely affected by high turbidity and rates of sedimentation than a coral with low SPM-feeding ability.

Acknowledgments

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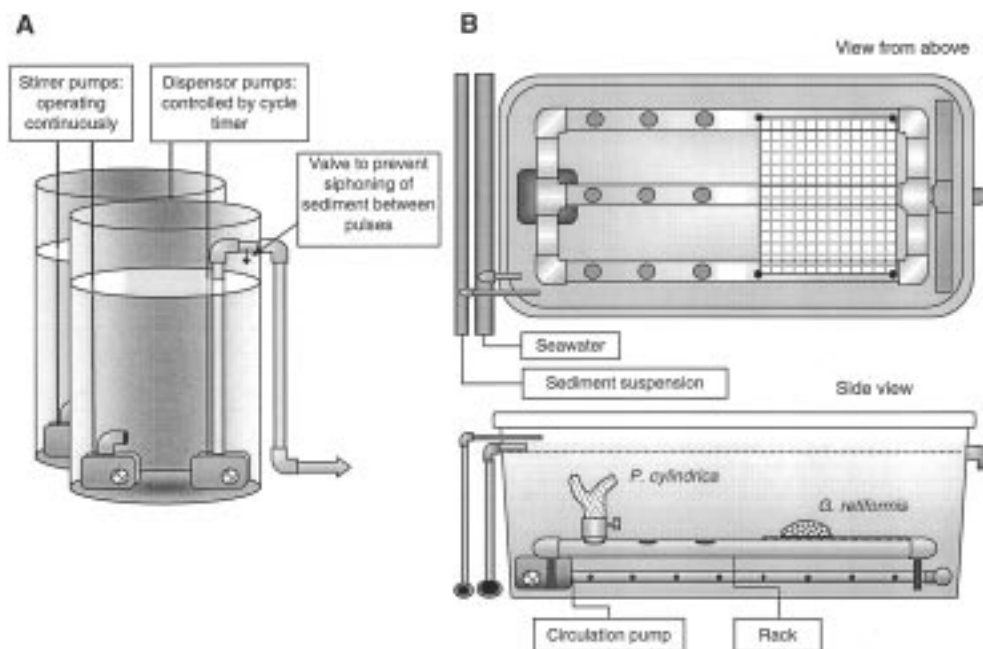


Fig. 1. Design and operation of (A) dispenser drums with sediment stock suspensions, and (B) coral treatment tanks. Corals were held in tanks with a flowthrough of natural seawater, and for two treatments, tanks received frequent pulses of sediment suspensions of known volume to establish two stable SPM treatment levels. Most of the added particulate matter was kept in suspension by a circulation pump under the coral rack in each tank.

Materials and methods

Description and design of the experimental setup—This study was conducted at Orpheus Island Research Station, located 15 km off the North Queensland coast, Australia (18°35'S, 146°20'E). The station is supplied with seawater pumped directly from the reef front of the adjacent Pioneer Bay. The system used in this study consisted of 32 white plastic bins (46 liters: 56 cm long, 37 cm wide, 22 cm deep) arranged in a 4.2-m-diameter shallow seawater pool. The water in the pool buffered spatial and temporal temperature variation, and the tarpaulin allowed ~40% penetration of natural sunlight. Half of the tanks (16) were covered with shade cloth (~25% light penetration) to mimic the shading effect of a high SPM concentration (16 mg dry weight [DW] L⁻¹) at 3–4-m depth on the reef (~2.8 Einsteins m⁻² d⁻¹), whereas the remaining tanks were left unshaded, receiving light levels corresponding to low to moderate SPM concentrations (4 mg DW L⁻¹) at 3–4-m depth (~11.3 Einsteins m⁻² d⁻¹, see Kirk 1994 and Te 1997 for the general relationship between particle concentration, depth, and light level). The ranges of experimental SPM levels targeted were typical of those recorded on nearshore reefs in the Great Barrier Reef lagoon (Larcombe et al. 1995).

Each of the 32 tanks received a constant supply of seawater (0.60 ± 0.03 L min⁻¹). For the purpose of establishing four different water qualities in the design (filtered, filtered + low SPM addition, filtered + high SPM addition, and control), three pipelines supplied seawater with different levels of filtration to different tanks. One line of water was rigorously filtered (~1 μm) to provide particle-depleted wa-

ter (eight tanks), the second was coarsely filtered (~15 μm) for use in treatments with particle addition (two levels, 16 tanks), and the third supplied unfiltered water directly from the reef to function as a control for particle depletion and addition (eight tanks). Two 50-liter drums functioned as sediment reservoirs and were connected to the two sets of tanks with particle addition. The spatial arrangement of tanks with different light levels, filtration levels, and levels of particle addition was randomized to control for the effect of tank position. To provide convection and near-bottom water flow, thereby reducing sedimentation of added particles, a circulation pump (AquaClear 401) fitted with spray bars was installed inside each tank (Fig. 1). The pumps generated an evenly distributed, but turbulent, flow of 10–15 cm s⁻¹ as determined by erosion of plaster blocks (Jokiel and Morrissey 1993).

Collection and quantification of particulate matter—Particulate matter similar to that found naturally was obtained by using the seston accumulated in a 500-liter sand filter connected to the main seawater intake of the station. The filter processed >400,000 liters of seawater per day. The particulate matter was retrieved by backwashing the sand filter daily into two 1,500-liter tanks, in which the particulates were allowed to settle over a 3–4-h period before transfer to a 25-liter carboy for further sedimentation. The period between collection of the sediment from the sand filter and its use in the experiment was 4–8 h. To enable instantaneous measurement and adjustment of the sediment concentration in the reservoirs, the relationship between light absorbance and SPM concentration was determined. Briefly, a subsam-

ple of sediment suspension was divided into two series of 20 aliquots diluted between 1 and 40 times. The first series was analyzed spectrophotometrically at a wavelength of 325 nm. The second series was filtered through GF/F filters (0.5- μm pore), rinsed with distilled water, and dried at 50°C for 24 h to obtain volume-specific DW. Within the range of sediment concentrations of 0.05–2 mg DW ml⁻¹, a second-order equation showed sediment concentration (C) to explain >99.9% of the variation in light absorbance (Abs = -0.20 C² + 1.47 C + 0.02).

Dispensation of SPM—The SPM was dispensed to the treatment tanks from two 50-liter drums holding stock suspensions of different concentrations (*see below*). The particulates were kept in constant suspension and circulation by a pump (Aquaclear 801) at the bottom of each drum (Fig. 1). Delivery of sediment to the coral tanks within each treatment was administered by a second pump connected to eight lines of 4-mm-diameter polypropylene tubing leading to the eight replicate tanks in each SPM treatment. A standard length of dispenser tubing ensured equal flow resistance and hence equal suspension flow rate to all tanks within a treatment level. Sediment was dispensed in discrete pulses of 15 s in duration at fixed time intervals (10 min in the growth study), controlled by an unequal-cycle timer (Rhombert Bräslert). Discrete pulses were preferred over continuous particle supply, because the former prevents sediment accumulation and anoxic residues inside the tubing. Each pulse delivered 80 \pm 2 ml of stock suspension to each of the eight tanks, resulting in an \sim 12-h lifetime for each 50-liter drum in the case of 10-min pulse intervals.

Modeling concentrations of SPM over time—The concentration of suspended particles in an experimental tank (C_t , mg DW L⁻¹) at time t (minutes) was a function of at least six parameters: (1) tank volume (V , liter), (2) particle concentration of the stock suspension (C_{st} , mg DW L⁻¹), (3) volume of stock suspension added per pulse (V_{st} , liter), (4) flow rate of seawater to each tank (FR , L min⁻¹), (5) sedimentation rate of particles escaping resuspension (SR , expressed as a clearance rate, L min⁻¹), and (6) time interval between pulses (T , min). For simplicity, particle delivery (PD) at each pulse will be expressed as $C_{st}V_{st}$ (mg DW).

After a sediment pulse, the depletion of particles over time (dC_t/dt , mg DW L⁻¹ min⁻¹) will be a function of particle concentration in the tank at time t (C_t) and the rates at which particles are removed from the water due to seawater flow-through (FR) and sedimentation (SR); hence,

$$dC_t/dt = -(FR + SR)C_t/V \quad (1)$$

Through separation of variables and subsequent integration, the SPM concentration in the tank is given by

$$C_t = C_0 e^{-(FR+SR)t/V} \quad (2)$$

where C_0 is the SPM concentration at the beginning of the pulse cycle. The model assumes complete mixing immediately after particle addition, which was verified in the experiment because sediment suspensions were generally homogenous within 10 s after each pulse. The particle

concentration immediately after the subsequent pulse ($C_{T+\delta}$) is then given by

$$C_{T+\delta} = C_0 e^{TK} + \Delta C_p \quad (3)$$

where $K = -(FR + SR)/V$, and ΔC_p is the increase in particle concentration due to the pulse (PD/V). Immediately prior to the next pulse (at $2T - \delta$), the particle concentration is then

$$C_{2T-\delta} = (C_0 e^{TK} + \Delta C_p) e^{TK} \quad (4)$$

Continuing this argument for a sequence of N pulse cycles at their start and end phases, respectively, the upper (C_U) and lower (C_L) limits of the concentration range are given by the following geometric series:

$$C_U = \Delta C_p (1 + e^{TK} + e^{2TK} + \dots + e^{NTK}) \quad (5.1)$$

$$= \Delta C_p (1 - e^{NTK}) / (1 - e^{TK}), \quad (5.2)$$

which at steady state (high N) approaches

$$\Delta C_p / (1 - e^{TK}) \quad (5.3)$$

Analogously,

$$C_L = \Delta C_p (e^{TK} + e^{2TK} + \dots + e^{NTK}) \quad (6.1)$$

$$= \Delta C_p e^{TK} (1 - e^{NTK}) / (1 - e^{TK}), \quad (6.2)$$

at steady state approaching

$$\Delta C_p e^{TK} / (1 - e^{TK}) \quad (6.3)$$

The difference between C_U and C_L at steady state is therefore given by ΔC_p ; i.e., the amount of sediment delivery per pulse relative to tank size governs the experimental range of particle concentrations. To maximize the precision of steady-state particle concentrations at a given tank volume, ΔC_p should be minimized—for example, by using low values for T and FR . Furthermore, the number of pulse cycles needed to reach 95% of C_U (an indication of system resilience) is predicted by

$$N_{0.95} = \ln(1 - 0.95) / TK \sim 3V / [T(FR + SR)] \quad (7)$$

Depending on the application, optimal system performance will be a compromise between high precision (e.g., short T , low FR) and high resilience (e.g., long T , high FR). An example with two different settings of parameters ΔC_p and T is depicted in Fig. 2.

Determination of SR and test of model predictions—Before the prediction of C_U (or C_L) by the model could be validated, SR was determined empirically. Sedimentation was measured indirectly by monitoring particle concentrations in two tanks without a flowthrough of seawater ($FR = 0$) but with water recirculation and racks identical to that of all other tanks in the system. After an initial addition of \sim 1.3 g sediment suspension per tank ($C_0 \sim 28$ mg DW L⁻¹), duplicate 50-ml samples were taken from each tank every 15 min for 1.5 h and filtered immediately through preweighed GF/F filters for gravimetric analyses. SR was hence calculated by fitting the model

$$C_t = C_0 e^{-tSR/V} \quad (8)$$

to the data sets using nonlinear estimation (STATISTICA

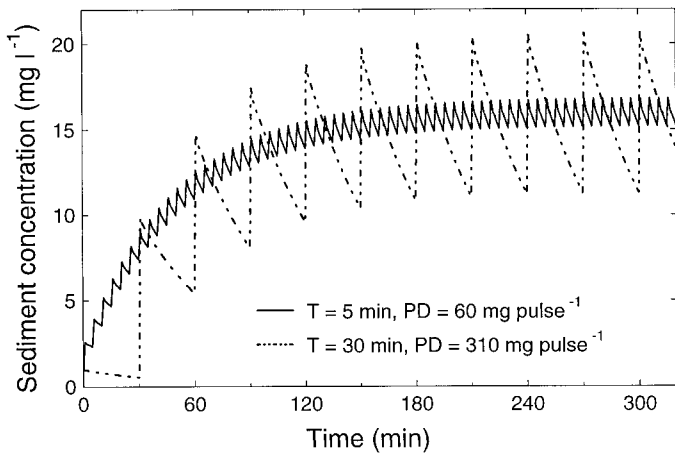


Fig. 2. Predicted concentration of suspended sediment in a coral growth tank as a function of time using two different combinations of PD and intervals between pulses (T). The graph shows that a narrow, stable range of particle concentrations is obtained by short pulse cycles. The two systems stabilize within the same time frame, independently of PD . V was 46 liters, FR was 0.6 L min^{-1} , and SR was assumed to be negligible.

1997). The prediction of an exponential decline in the particle concentration over time due to sedimentation is consistent with that of Reynolds et al. (1990).

To validate the prediction of C_U based on system parameters (including measured SR), C_U was monitored over a 16-h period in duplicate tanks identical to those above, except with an $FR = 0.60 \pm 0.03 \text{ L min}^{-1}$. Every 1–2 h, duplicate 50-ml water samples were taken from each tank ~ 20 s after a sediment pulse and filtered immediately. In both of the above tests, sampling volume was $< 2\%$ of tank volume and was replaced in the second test by a normal supply of seawater. The level of agreement between predicted and observed C_U was validated by fitting Eq. 5.2 to the data sets by nonlinear estimation. SR was entered as an unknown parameter in the model to compare predicted with measured sedimentation. The error range for predicted C_U was determined by varying the input variables FR , SR , and PD in Eq. 5.3 plus or minus the SE of their means.

Effects of particle processing on particle quality—To test the effect of the processing procedure on the quality of SPM, the organic C and N concentrations were compared between SPM from the tank system and from the field. Concurrent sampling from both tank system and field was carried out regularly over a 1-month period to account for temporal variability in water quality. Samples from the tank system were taken as duplicate 50-ml aliquots of the stock suspension. Water samples in the field were taken adjacent to the seawater intake in Pioneer Bay using a 2.5-liter Niskin bottle. All samples were filtered immediately through precombusted Whatman GF/F filters for gravimetric analysis of particulate DW. Organic C was determined with a Shimadzu 5000 C analyzer, and total N was determined with an Antek 720 C/N analyzer.

Coral growth study—A 2-month experiment was conducted in the tank system to examine the effects of turbidity on coral growth rates. The study involved four SPM levels as well as two light levels (shaded and unshaded, *see above*) to test whether two coral species with different feeding physiologies showed different growth rates in different turbidity regimes. One month prior to the tank experiment, ~ 300 specimens of each of two coral species (*G. retiformis* Lamarck and *P. cylindrica* Dana) were collected from the reef in Pioneer Bay. *G. retiformis* has a massive to dome-shaped growth form, whereas *P. cylindrica* has a digitate to branching form. Colonies of *G. retiformis* (5–7-cm diameter) were collected from the reef flat and placed onto nylon grids stretched across one-half of a rack (Fig. 1B). A tag with an identification code was fixed to the underside of each colony using epoxy putty. Branches of *P. cylindrica* (7–8-cm length) were broken off from their colonies and attached to numbered stands (polyvinyl chloride tubes, 15-mm inner diameter, 50 mm long) mounted onto racks (Fig. 1B). The base of each *P. cylindrica* branch was fixed inside one end of the tube by a nylon bolt. To allow the corals to recover from handling, they were left for 1 month at the site of collection. On the day prior to the growth experiment, all corals were transferred to the tank system and distributed haphazardly among treatments. Seven–eight corals of each species were assigned to each tank. After initial measurement of size (*see below*), eight caged racks with a total of ~ 60 colonies (or branches) of each species were transferred back to the reef (at 3–4-m depth) as field controls. Half of these were placed under shade screens to establish two light levels in the field analogous to those in the tanks. Because *G. retiformis* was collected on the reef flat, four shaded and four unshaded racks of this species were also deployed on the reef flat.

Coral growth was measured as the increase in buoyant weight during the 2-month experiment using the technique described by Spencer-Davies (1989). Corals were weighed in a constant-temperature room (25°C) using a digital balance (Sartorius, ± 1 mg) placed over a seawater bath. During weighings, the corals were suspended in the water bath by their stands (or tags) from a hook underneath the balance. Increments in buoyant weight were converted to increase in skeletal DW by multiplication with the correction factors 1.60 ± 0.05 (SE of $N = 20$) for *G. retiformis* and 1.71 ± 0.08 (SE of $N = 20$) for *P. cylindrica* (Anthony unpubl. data).

Tank system settings: For the growth study, system parameters T (10 min), FR ($0.60 \pm 0.03 \text{ L min}^{-1}$), and PD (high: $115 \pm 8 \text{ mg DW}$; low: $28 \pm 2 \text{ mg DW}$) were adjusted so that the range of particle concentrations at steady state ($C_{L,obs} - C_{U,obs}$) was $15.2\text{--}16.8 \text{ mg DW L}^{-1}$ for the high particle treatment and $3.6\text{--}4.4 \text{ mg DW L}^{-1}$ for the low treatment. These particle concentrations corresponded to the two experimental light conditions (*see above*) predicted to occur at 3–4-m depth under similar SPM regimes. The low FR was sufficient to maintain a high turnover rate of tank volume (more than once an hour) and yet allow an economical use of added particles. The system reached steady state, as governed by V , T , and FR , within ~ 3 h (Eq. 7; *see also Fig. 2*).

Table 1. Mean concentrations and quality of SPM \pm SE in four treatments of the experimental setup and respective concentrations in the field during the growth experiment (Jun–Aug 1997). The number of samples is given in parentheses. Ranges of SPM concentrations in tanks with particulates added (low and high) are predicted by the SPM concentration vs. time model (Eq. 5, 6).

| | Filtered | Raw | Field | Low | High | Field (reef slope) | | Tank system | |
|--|-----------------------|-----------------------|------------------------|---------|-----------|-----------------------|-------------------------|------------------------|-------------------------|
| | | | | | | Org. C | N | Org. C | N |
| Ranges of suspended particle concentrations (mg DW liter ⁻¹) | 0.7 \pm 0.1 (10) | 1.9 \pm 0.1 (12) | 1.4 \pm 0.12 (15) | 3.6–4.4 | 15.2–16.8 | | | | |
| Particle quality (% content of DW) | | | | | | 4.3 \pm 0.5 (10) | 0.41 \pm 0.05 (11) | 2.6 \pm 0.09 (10) | 0.42 \pm 0.01 (11) |

Data analysis of growth study—Effects of particle load and shading on growth rates were tested for each species separately using a three-way analysis of covariance (ANCOVA) with the factor *Tank* nested within both of the fixed factors. The initial colony weight was used as the covariate. Inclusion of both species in a single analysis resulted in slope heterogeneity (an interaction between the factors and the covariate), hence violating test assumptions. Field controls were excluded from the ANCOVA for the same reason. The factor *Tank* was important for the analysis because it enabled the assessment of environmental homogeneity in the tank system. Data were log-log transformed to provide variance homogeneity as well as slope equality, and Tukey's honest significant difference (HSD) test was used to identify which adjusted group means differed significantly.

Results and discussion

Effects of filtration procedure and storage on particle quality—The organic C content of the SPM in the stock suspensions was only half that of the seston filtered from

natural water (Table 1). This suggests that a significant proportion of the live material (e.g., microorganisms coating the particle surfaces) was removed during the filtration procedure and short-term storage and/or that organic contents were metabolized by nonattached bacteria. The low C content of the experimental relative to the ambient SPM may have reduced the heterotrophic contribution to the energy budgets, and hence the scope for growth, of both coral species in the tanks, especially in the shade, where phototrophic C fixation was likely to be low. However, the weight-specific N content of stock suspensions did not differ significantly from that in field samples, in agreement with the often higher N content of aged detrital material (Rice 1982). In high light conditions where photosynthesis is saturated, the nutrient content of ingested particles is likely to play a more important role for coral growth than organic C content (Dubinsky and Jokiel 1994; Muller et al. 1994).

Validation of sediment concentration model—The ranges of SPM and rates of sedimentation in the tanks were highly predictable over time. Measured SPM concentrations at steady state were well within the confidence band of the predicted C_V (Fig. 3). The latter was determined using a sedimentation rate of 0.12 (\pm 0.01, SE) L min⁻¹ estimated in tanks without flowthrough of seawater (Fig. 4). Conversely, fitting Eq. 5.2 to the observed C_V 's with unknown *SR* explained 94% of the

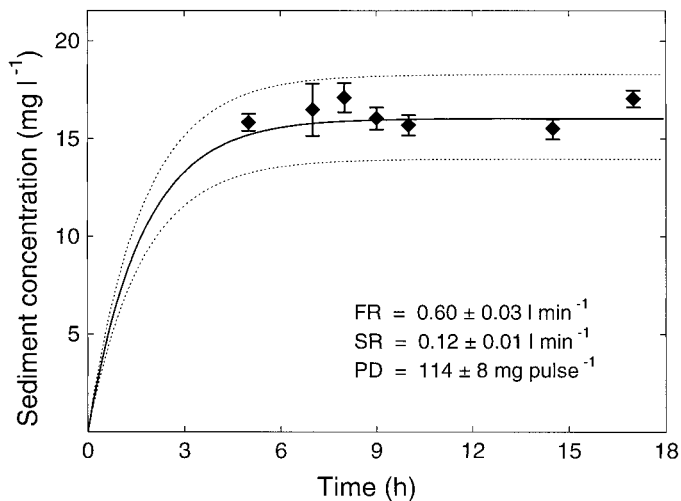


Fig. 3. Predicted and observed upper sediment concentration (C_V) at steady state. Observed sediment concentrations are means \pm SE of duplicate samples for two tanks. The solid line depicts mean predicted C_V (Eq. 5.2), and dashed lines represent the maximum error range for predicted C_V . Fitting Eq. 5.2 to the observed data with *SR* as a variable explained 94% of the variance, and *SR* was estimated to be 0.10 ± 0.01 (liters per minute) by this method, not significantly different from the *SR* measured (see Fig. 4).

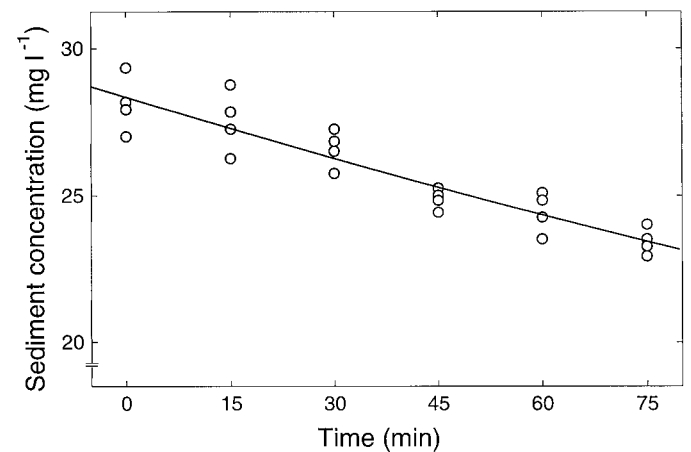


Fig. 4. Depletion of suspended particles due to sedimentation in two tanks without flowthrough of seawater. Data are duplicate samples from each of two tanks. The function $C_t = 28 e^{-SRt}$ provided a significant fit to the data ($P < 0.001$, $R^2 = 0.86$), and *SR* was estimated as 0.12 ± 0.01 (liters per minute).

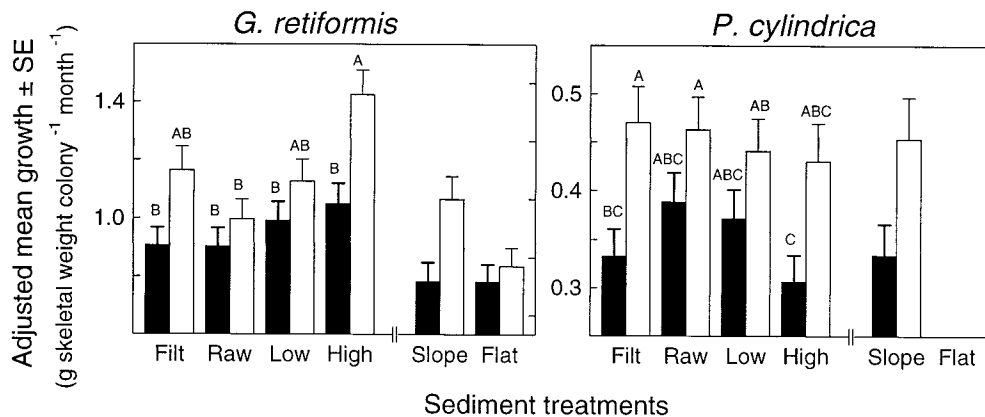


Fig. 5. Colony growth rate as a function of particle load and shading for two coral species. Data are adjusted means (g skeletal DW month⁻¹) ± SE of 27–31 coral colonies (*G. retiformis*) or branches (*P. cylindrica*). Mean initial skeletal weights were 28.9 g (±8.6, SE of $N = 293$) for *G. retiformis* and 6.5 g (±1.9, SE of $N = 276$) for *P. cylindrica*. Black and white bars represent shaded and unshaded treatments, respectively. Tukey's (HSD) groups (within species) are indicated by superscripts. *Slope* and *Flat* refer to field controls deployed on the reef slope (3–4-m depth) and the reef flat (0–1-m depth). *P. cylindrica* was not deployed on the reef flat because this species occurs subtidally only. Field controls were not included in the ANCOVA. Note different scales on y-axes.

variation in SPM concentration, and *SR* estimated by this model ($0.10 \pm 0.01 \text{ L min}^{-1}$) was almost identical to that determined in tanks without flowthrough. These rates of sedimentation corresponded to the deposition of 2.1–2.5 mg DW sediment $\text{cm}^{-2} \text{d}^{-1}$ (mean $C_t = 30 \text{ mg DW L}^{-1}$, area of tank floor = 2,072 cm^2), which are trivial compared to those rates measured in turbid, nearshore environments (Cortes and Risk 1985; Woolfe and Larcombe 1998). By minimizing sedimentation through high near-bottom convection, the system enabled examination of the effects of high particle concentrations without confounding effects of sedimentation. Conversely, regulating intensity of convection (resuspension) would enable testing effects and interactions of specific levels of sedimentation and particle concentration.

Elaborate artificial and natural flow-through systems have been used to examine organism and community responses to factors such as long-term nutrient enrichment (Larkum and Steven 1994; Stambler et al. 1994) and salinity variation (Cooper and Copeland 1973). However, the system and methods described here represent the first simple and inexpensive means of producing predictable levels of turbidity and sedimentation using natural SPM in long-term experiments. Optimal scaling of system parameters (e.g., V , T , and FR) produces high stability (resilience) of the steady-state particle concentration. This inherent stability is in part explained by the asymptotic way in which injected SPM reaches steady-state concentration in a flow-through tank (Fig. 2; Eq. 5, 6). The steady-state concentration is therefore relatively robust with respect to fluctuations in the system parameters, which reduces the need for continuous monitoring or computer control.

Effects of experimental sediment loading and shading on coral growth—Coral survivorship and general observations: The growth experiment indicated that the setup was ideal for

testing effects of water-quality treatments on corals. The survivorship of the tank population of *G. retiformis* was 100% compared to 75% on the field racks. The losses in the field were primarily due to the susceptibility of newly collected (stressed) colonies of this species to fish predators, which were not adequately excluded by caging. Conversely, *P. cylindrica* showed 78% survivorship in the tank setup and ~92% in the field. The mortality and partial mortality of *P. cylindrica* in the (mainly unshaded) tanks were in part due to its susceptibility to algal overgrowth around the branch bases, which originated from the stands. Colony peripheries of *G. retiformis* did not show any sign of stress despite contact with algae growing on the support mesh. Algal overgrowth was not observed for the field controls of *P. cylindrica* and was probably prevented by herbivory.

Coral growth rates: The growth rates of both species in control tanks (raw seawater) were not significantly lower than those in the field (Fig. 5), indicating that the tank environment satisfied the basic requirements for experimentation on the time scale of months. Growth rates of *G. retiformis* in the field were generally lower than those in the tanks, perhaps due to the impact from fish predation (see above). The patterns of growth responses to SPM concentrations and shading differed considerably between species (Fig. 5). The results of the ANCOVAs showed that the growth rates of both species were affected by shading, but only *G. retiformis* was affected by particle load (Table 2). The absence of tank effects on growth rates was an indication of the environmental homogeneity within the tank system, enabling interpretation of main effects. Interestingly, the growth rate of *G. retiformis* in the high SPM, unshaded treatment was significantly higher (>50%) than that of both tank and field controls in unshaded conditions (Fig. 5), indicating a nutritional advantage of high particle loads in this

Table 2. Summary results of a three-way nested ANCOVA for monthly colony growth at four particle treatments and two light regimes, with initial colony weight as covariate. Data (g skeletal DW month⁻¹) were log transformed. The tank factor was nested within particle and shading treatments. The two species were analyzed separately because of slope inequality (colony growth vs. initial weight) between species. See Fig. 5 for means and standard errors.

| Source of variation | <i>Goniastrea retiformis</i> | | | | <i>Porites cylindrica</i> | | | |
|---|------------------------------|-------------------------|------|--------|---------------------------|-------------------------|------|--------|
| | df | MS ($\times 10^{-3}$) | F | P | df | MS ($\times 10^{-3}$) | F | P |
| Particle concentration | 3 | 56.8 | 5.3 | 0.002 | 3 | 27.0 | 1.4 | 0.244 |
| Shading | 1 | 162.2 | 15.2 | <0.001 | 1 | 466.8 | 24.1 | <0.001 |
| Particle concentration \times shading | 3 | 14.4 | 1.4 | 0.259 | 3 | 16.1 | 0.8 | 0.477 |
| Tank effect | 24 | 13.4 | 1.3 | 0.202 | 24 | 23.4 | 1.2 | 0.236 |
| Error | 178 | 10.6 | | | 211 | 19.3 | | |

species. The growth rate of conspecifics in the filtered, unshaded treatment, however, was not significantly lower than that of the high SPM, unshaded treatment, suggesting that growth rate is not directly proportional to particle load in *G. retiformis*. The growth rates of shaded *P. cylindrica* were 13–24% lower than unshaded conspecifics (cf. 4–19% in *G. retiformis*) and did not differ significantly across particle treatments (Fig. 5). This pattern suggests that *P. cylindrica* does not supplement its nutrition with particle feeding at high SPM concentrations to the extent that *G. retiformis* does.

In preliminary feeding studies with ¹⁴C-labeled SPM, *G. retiformis* demonstrated a high heterotrophic capacity (>50 $\mu\text{g SPM DW cm}^{-2} \text{ h}^{-1}$, Anthony unpubl. data). Conversely, members of the genus *Porites* are assumed to depend mainly on autotrophy (Johannes and Tepley 1974; Edmunds and Spencer Davies 1986; Anthony 1999). The stronger adverse effect of shading on growth rate in *P. cylindrica* adds support to the latter hypothesis.

Relevance to studies of sediment effects on corals—Previous manipulative studies of sediment effects on coral assemblages have mainly involved spot loads in situ (e.g., Rogers 1983) or in aquaria (e.g., Stafford-Smith 1992) using coarse sedimented material. Riegel (1995) devised a method for continuous application of sand onto corals in a flow-through aquarium by recirculation of bottom sediments, although with limited control of dispensation over time. While treatments with discrete loads of sand mimic the resuspension and sedimentation resulting from discrete hydrodynamic events, they have no relevance to the often sustained concentrations of fine SPM characteristic of many inshore environments (Cortes and Risk 1985; Woolfe and Larcombe 1998). Fine SPM is the primary cause of reduced light penetration on inshore reefs (e.g., Te 1997), and, according to the results of this study, shading suppresses coral growth to a greater extent than particle loading per se. The large surface area of SPM for colonization by microorganisms (Almeida and Alcantara 1992; Crump et al. 1998) may enable a sufficiently high food value that SPM feeding by some coral species can offset the effects of reduced photosynthesis and sediment stress in turbid conditions.

Advantages and disadvantages of studying turbidity effects in tanks—The pros and cons of microcosms (e.g., tanks) in experimental ecology have been thoroughly debat-

ed (Carpenter 1996; Drake et al. 1996). While this debate has focused on the relevance of “bottle” experiments in community ecology (Peters 1991), the use of tank experiments in ecophysiological studies at the organism level has been less subject to reproach. However, some points of consideration may improve the relevance of tank experiments studying physiological responses to turbidity in the context of the natural environment. For instance, larger tanks with a flow regime mimicking that on the reef (e.g., waves and tides) would allow incorporation of hydrodynamics into models of particle–organism interactions, especially important for suspension (Shimeta and Jumars 1991) and deposit (Jumars and Nowell 1984) feeders. Also, a wider range of specimen sizes representing those of natural populations would reduce bias due to scaling. Although the advantages of such refinements are obvious, three important objectives for conducting long-term experimentation in tanks are likely to be sacrificed: high replicability at a reduced cost and effort.

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