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Journal of Experimental Marine Biology and Ecology 328 (2006) 22–34

**Journal of  
EXPERIMENTAL  
MARINE BIOLOGY  
AND ECOLOGY**

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# Effects of accumulations of sediments and drift algae on recruitment of sessile organisms associated with oyster reefs

M.S. Thomsen<sup>\*</sup>, K. McGlathery

Department of Environmental Science, P.O. Box 400123, University of Virginia, Charlottesville, VA 22904-4123, USA

Received 5 January 2005; received in revised form 7 June 2005; accepted 22 June 2005

## Abstract

Increases in sediment and drift algae accumulations have caused degradation of coastal lagoons worldwide. It is well known that these factors are stressors of seagrass beds, sediment fauna and coral reefs. However, little is known about the impacts on temperate hard-bottom assemblages within soft-bottom lagoons. To test if accumulations of sediment and drift algae (stress) affected recruitment of sessile oyster reef organisms, we constructed cages in Hog Island Bay, Virginia that trapped drifting macroalgae ( $\approx 2.7$  kg WW m<sup>2</sup>) and facilitated sedimentation ( $\approx 7$  mm per 2–3 month). The stress treatments and unstressed controls were placed in front, between, and behind reefs (position) to represent wave exposed ( $\approx 0.3$  m, windy conditions), current exposed ( $\approx 0.2$  m s<sup>-1</sup>, peak tide) and protected ( $\approx 0$  m, 0.0 m s<sup>-1</sup>) habitats. The percentage cover of recruited taxa onto bricks was mapped 4 times during a 1-year period. There were strong significant effects of stress on the total assemblage, plant (but not animal) richness, total plant and animal cover, and cover of the most common taxa. Unstressed bricks had high plant richness, high animal and plant cover, and high cover of the oyster *Crassostrea virginica*, the alien algae *Gracilaria vermiculophylla* and *Codium fragile*, the alga *Agardhiella subulata*, and high to medium cover of the opportunistic algae *Ulva curvata* and *Enteromorpha* spp. In comparison, sediment-stressed bricks had low plant richness, low animal and plant cover, and low cover of *C. virginica*, *G. vermiculophylla*, *C. fragile*, *A. subulata*, *U. curvata* and *Enteromorpha* spp. Similarly, algae-stressed bricks also had low cover of animals, *C. virginica*, *G. vermiculophylla*, *C. fragile*, and *A. subulata*, but intermediate plant richness and plant cover and high cover of *U. curvata* and *Enteromorpha* spp. Although reef position caused significant multivariate results, this factor was clearly less important than the stress factor. Our study shows that accumulations of sediments and drift algae have an adverse impact on sessile temperate reef organisms, reducing richness and abundance, but favoring a few small opportunistic taxa. As the reef-generating oysters themselves performed poorly under these stressors, the long-term impact of the causes of these stressors, eutrophication and urbanization, is likely to be diminished reefs with cascading adverse effects on sessile reef organisms.

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**Keywords:** Drift macroalgae; Oyster reefs; Recruitment; Sedimentation; Soft-bottom lagoons

<sup>\*</sup> Corresponding author. Present address: Department of Applied Sciences, Auckland University of Technology, Auckland, New Zealand. Tel.: +61 9 815 6035.

E-mail address: mads\_thomsen@mailcity.com (M.S. Thomsen).

## 1. Introduction

In soft-bottom lagoons and estuaries, oyster reefs provide three-dimensional habitats that contain rich and abundant floral and faunal assemblages (Galts-off, 1964; Barh and Lanier, 1981; Lenihan and Peterson, 1998). Oyster reefs alter local biogeochemical cycles by their water-filtering and sediment-binding capacities (Dame and Libes, 1993; Lenihan, 1999). They are similar to coral reefs, kelp forests, seagrass beds, and mussel beds in that they are composed of a few foundation species that facilitate the distribution and abundance of a range of associated species (Bruno et al., 2003). Oyster reefs also create topographic complexity and cause flow alterations (Barh and Lanier, 1981; Lenihan, 1999), thereby affecting processes that are influenced by hydrodynamics such as sedimentation (Lenihan, 1999; Airoldi, 2003) and drift algae accumulations (Raffaelli et al., 1998). Because of the ecological and economic benefits associated with oyster reefs, oysters are well studied from an autoecological perspective, but synecological field experiments on oyster reef assemblages are surprisingly few (Underwood and Anderson, 1994; Anderson and Underwood, 1997; Lenihan and Peterson, 1998; Anderson, 1999a; Lenihan et al., 2001).

The abundance of oysters are typically limited by diseases and predators (Barh and Lanier, 1981; Haven and Whitcomb, 1983; Mann, 2000) but agricultural runoff, urbanization and coastal development provide additional stresses that are increasingly threatening oyster reefs. Of particular importance in soft-bottom lagoons are the impacts of (1) enhanced sedimentation and sediment instability caused by urbanization, coastal development and decreased abundance of sediment-stabilizing habitat formers (e.g. salt marshes and seagrasses, Koch and Gust, 1999; Airoldi, 2003) and (2) enhanced drift algae accumulations caused by nutrient enrichment (Raffaelli et al., 1998). Sedimentation and drift algae accumulations severely reduce the distribution and productivity of rooted angiosperms (Hauxwell et al., 2001; McGlathery, 2001) and limit soft-bottom fauna by oxygen depletion, reduced larval recruitment, and interference with feeding (Hull, 1987; Raffaelli et al., 1998). How sedimentation and drift algae influence soft-bottom oyster reefs is not

known, however, it is likely that these stressors will be partly controlled by hydrodynamic conditions because strong currents can reduce sedimentation rates and flush out algal mats (Flindt et al., 1997; Salomonsen et al., 1997; Raffaelli et al., 1998). The effect of hydrodynamics will be controlled in part by the position in relation to the oyster reefs (Dame and Libes, 1993; Lenihan, 1999). Our objective was therefore to quantify relationships between hydrodynamics, spatial position (in relation to oyster reefs), and important stressors (sedimentation and drift algae accumulations) on sessile organisms. We first quantified the effects of spatial position on tidal currents, wave heights, sedimentation and drift algae accumulations, and then asked the following questions: (1) does spatial position affect assemblage composition, animal and plant richness and abundance, and abundance of key species of 'recruited' (settling, survival and growth, Keough and Downes, 1982) sessile reef organisms?, (2) does enhanced levels of sedimentation and drift algae (stress) affect recruitment?, and finally (3) does position and stress act independently or in combination, and which factor explains most of the recruitment variability?

## 2. Material and methods

### 2.1. Study site

Hog Island Bay is ca. 100 km<sup>2</sup> and is situated in the Virginia Coast Reserve. Hog Island Bay is characterized by soft substrata, high turbidity, high sedimentation and resuspension rates (Lawson, 2003), low water depth, and a tidal prism of ca. 1 m that creates large intertidal mudflats (Oertel, 2001). Nutrient loading to the lagoon is low relative to lagoons to the north along the Delmarva Peninsula (Boynton et al., 1996; Stanhope, 2003), but standing stock DON concentrations can be relatively high (McGlathery et al., 2001). There are numerous scattered oyster reefs (typically 10–1000 m<sup>2</sup> and 0.5–1 m high) that provide islands of hard substrata. Seagrasses are beginning to recolonize the lagoon, having been extinct since the 1930s, and unattached drift algae occur locally in high abundances (McGlathery et al., 2001).

## 2.2. Experimental design

Plots were allocated around mid-lagoon oyster reefs situated to the west of the Machipongo channel at 0.6–0.8 m below mean sea level (Fig. 1, Shoal site, McGlathery et al., 2001; Tyler et al., 2001). At these reefs, 12 sites were selected to represent ‘positions’ at the ‘front’, ‘between’ and ‘behind’ the oyster reefs ( $n=4$ ). To test for position effects, 6 of the 12 positions were randomly selected (letters, cf. Fig. 1). To test for stress effects,  $2 \times 3$  plots were allocated systematically to each of the randomly selected positions: unstressed control (U), sediment trap (S), algae trap (A). Each stress treatment was separated by ca. 1 m, and each set of 3 plots were separated by an additional 2–4 m. Sediment traps were constructed of  $50 \times 40 \times 40$  ( $l \times w \times h$ ) cm transparent plastic boxes with an open top. The boxes were fixed with 0.8 cm diameter rebar (inside in each corner through holes in the cage bottom), which also provided structural stabilization. Pilot experiments had shown that the boxes were efficient in triggering sediment deposition. To ensure normal tidal fluctuations in water level within each sediment trap, numerous small holes were drilled in the side walls and bottom. Five centimeters of adjacent sediments was added to each sediment trap. The traps were without roofs to allow for sedimentation and access for mobile grazers and predators and resulted in less than 5% light reduction accumulated over an entire day, an artifact considered ecologically insignificant (PAR, Apogee Quanta Meter, light reduction only occurring at low solar angles, Thom-

sen, 2004a). Drift algae traps were of the same dimensions as the sediment traps and were constructed of rebar positioned in the corners of a  $50 \times 40$  cm rectangle and connected by a string at 35 cm height above the sediment surface. Pilot experiments had shown that this construction efficiently trapped tumbling drift algae. The open structure had 0% PAR reduction and was considered unlikely to affect accessibility for mobile herbivores and predators. Note that cage controls were not included because within Hog Island Bay, nutrients, suspended solids, sedimentation, resuspension, light, drift algae transport, grazing and dislodgment are affected simultaneously by physical obstacles, making it difficult to construct specific cage controls (Tyler, 2002; Lawson, 2003; Rosinski, 2004). However, due to our open trap designs cage artifacts should be minimal.

## 2.3. Effects on hydrodynamics, sedimentation, and drift algae accumulation

To quantify trap artifacts and if position affected hydrodynamics, tidal currents were measured in the center of all plots (after removal of drift algae) with a Marsh–McBinney electromagnetic current meter on July 17 and June 25, 2002 when the water level was between 20 and 35 cm. Wave heights were estimated on several occasions under different weather conditions by recording wave heights using a 2-m ruler as a reference marker, but only in the unstressed control plots. To quantify cage artifacts, trap efficiency, and if position affected accumulated sediments and drift

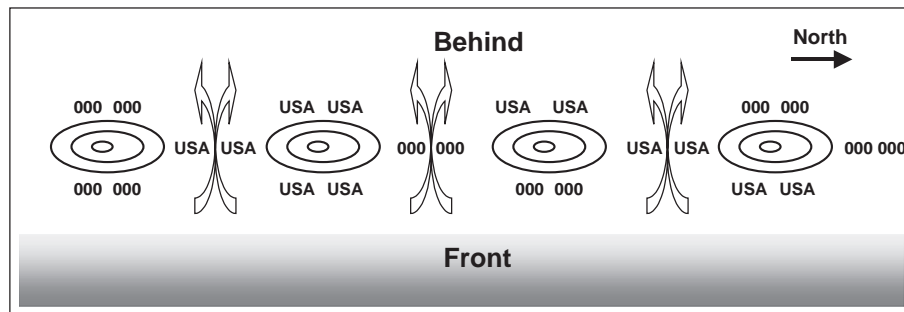


Fig. 1. Diagram of experimental design along a series of scattered oyster reefs (circles) facing towards a deeper channel (darker areas). Reefs are ca. 15–20 m long, 5–10 m wide and 0.8 m high (–0.8 to 0.0 m above MSL), although not completely elliptic. On incoming and outgoing tides, currents accelerate between reefs (arrows) and waves can be generated in fronts under windy conditions. Each plot is allocated a letter (U=unstressed, S=sediment stressed, A=algal stressed) and 0s correspond to unused locations. Individual plots are separated by ca. 1 m and sets (USA vs. USA) by ca. 2–4 m. Three bricks, separated by 1–4 cm, were placed within each of the 36 plots.

algae, we recorded sediment depth with a ruler to the nearest mm at 3 locations on each brick on March 7, June 11, and July 30, 2002 and collected drift algae in 50 × 40 cm sample frames on July 17, December 15 (2001), January 4, July 16, and August 5 (2002). All drift algae were brought to the lab, blotted with a towel and the wet weight was measured. Effect of position on hydrodynamics, sediment and algal accumulations, treatment efficiencies, and trap artifacts were evaluated graphically. Finally, we measured water temperature, oxygen level and salinity on July 24, 2001 with an Orion DO meter and a refractometer to ensure these variables did not differ between treatments: all plots were identical (28–29 °C, 5–6 mg O<sub>2</sub> L<sup>-1</sup>, and 34 ppt).

#### 2.4. Effects on recruitment

To test if position, stress or a combination of the two factors affected recruitment, 3 clay bricks (20 × 8 × 6 cm, separated by a few centimeters) were placed in each plot in July 2001. These 3 bricks were treated as sub-replicates, due to their position within an individual treatment, and data analysis was conducted on their combined mean cover. Preliminary experiments showed that sessile species found attached to oysters recruit onto bricks. Abundance was estimated on each brick by the visual percentage cover method instead of the pinpoint counting method (Dethier et al., 1993) because we focused on brick replication and species richness measurements. Before recording percentage cover, each brick was gently cleaned of sediments. A quadrat divided into 20 rectangles was used to facilitate cover estimations. Percentage cover could exceed 100% if organisms occupied different vertical layers or covered more than the area of the brick. For example, an organism could cover up to 1.5 × the size of the brick and would then be given 150% cover. Percentage cover was recorded in early March, mid-April, early June, and late July 2002 corresponding to a total of 432 sampled assemblages (3 stress × 3 position × 4 times × 4 replicates × 3 sub-replicates).

To statistically test for assemblage level effects species-sample data were analyzed with two-factorial NPMANOVAs for each of the 4 sampling times (Anderson, 2001). Effects on animal and plant richness and abundance, and abundance of key taxa were tested

with repeated-measures two-factorial ANOVAs. The key taxa were selected as the 6 most abundant recruiters in unstressed plots and included the oyster, *Crasostrea virginica* (Gmelin), the alien algae *Codium fragile* ssp. *tomentosoides* (van Goor) Silva and *Gracilaria vermiculophylla* (Ohmi) Papenfuss, and the algae *Agardhiella subulata* (C. Agardh) Kraft et Wynne, *Ulva curvata* (Kützinger) De Toni and *Enteromorpha* spp. (a mixture of *E. intestinalis* (L.) Link, *E. linza* (L.) J. Agardh and *E. prolifera* (Muller) J. Agardh). Note that *G. vermiculophylla* from Hog Island Bay previously was described as *G. verrucosa* Papenfuss (Humm, 1979; Thomsen, 2004a,b; Thomsen and McGlathery, 2005), but has changed taxonomic status based on recent *rbcL*-analysis (Gurgel, personal communication; Bellorin et al., 2004; Gurgel and Fredericq, 2004; Rueness, 2005). All data were Log( $x + 1$ ) transformed to reduce variance heterogeneity and the influence of outliers, and back-transformed for graphical display. Comparisons of Cochran's *C*-values showed that transformations generally worked, although some variables remained with heterogeneous variances. Because ANOVA is relatively robust to heterogeneity when sample sizes are large and the design balanced, these tests were still included (Underwood, 1997). Eta square ( $\eta^2$ ) was calculated to compare the relative contribution of each test factor to the total data variability (Levine and Hullet, 2002). Because the emphasis was on effects of position and stress, and not time, statistical analysis and discussions focused on the former. As the sample design was relatively large and with some variance heterogeneity, we were likely to detect trivial effects at standard significance levels ( $p < 0.05$ ). The repeated-measures ANOVA assume both an additive linear model that cannot test for interactions between time and the within-subject bricks, and sphericity of the variance-covariance matrix (i.e. variances of the differences between values of the response variable are the same for all pairs of treatments) (Underwood, 1997; Quinn and Keough, 2002). The data are not independent because the same bricks were sampled at successive times. This causes disturbance to the assemblages (Anderson and Underwood, 1994) and statistical problems. As a result, interpretations should be treated with caution. Also, since we focused on highly significant main effects, violation of the first assumption is of relatively little importance here. Violation of the

second assumption typically causes positive auto-correlation, with increased chance of type 1 error, simply because repeated measurements taken close together are more likely correlated than measurements separated by longer time intervals (Underwood, 1997; Quinn and Keough, 2002). We therefore analyzed data conservatively based on a combination of  $p < 0.01$  and  $\eta^2 > 5\%$  in order to prioritize factors of relevance, to simplify the analysis and to reduce the likelihood of type 1 error. Significant effects were followed by paired permutation  $t$ -tests on NPMA-NOVA and by Student–Neuman–Keuls tests on ANOVA (SNK tests on position and stress).

### 3. Results

#### 3.1. Effects of position on currents, sediment and algal accumulations, and trap efficiency

Position affected tidal currents (Fig. 2A) by accelerating velocities between reefs (unstressed plots,  $9 \text{ cm s}^{-1}$ ) compared to front and behind positions ( $< 2 \text{ cm s}^{-1}$ ). Current velocities were not affected by the algal traps but reduced velocities to less than  $1 \text{ cm s}^{-1}$  in all sediment traps. Wave heights were greatest in front (up to 30 cm), intermediate between (up to 10 cm), and least behind reefs (ripples). These wave heights are relevant for northern, northeastern, eastern, southeastern and southern windy conditions or when boat traffic in the channel to the east of the site was high; western winds only generated ripples at all locations. Position did not affect sediment accumulations in the unstressed plots (Fig. 2B), but caused lower algae accumulation in between reef plots compared to plots in front and behind reefs (Fig. 2C). However, these differences were minor compared to the high abundance of algae found in the algal traps (Fig. 2C). The traps generally worked according to their purpose; sediment depth (Fig. 2B, accumulated during 2–3 month) was greatest in the sediment traps (6.8 mm), intermediate in the unstressed plots (2.2 mm) and slightly lower in the algal traps (1.2 mm), whereas drift algae accumulations (Fig. 2C) were greatest in the algal traps ( $2.6 \text{ kg WW m}^{-2}$ ), medium in the sediment traps ( $1.2 \text{ kg WW m}^{-2}$ ) and the least in the unstressed plots ( $0.3 \text{ kg WW m}^{-2}$ ).

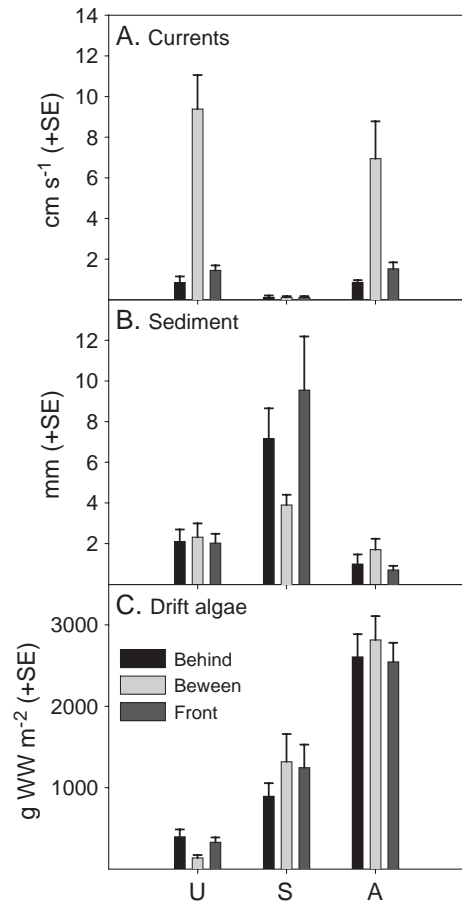


Fig. 2. Plots of current velocities (A,  $n=8$ ), accumulated sediments over a 2–4-month period (B,  $n=12$ ), and accumulated drift algae (C,  $n=20$ ). Time was pooled. U=unstressed, S=sediment stressed, A=algal stressed.

#### 3.2. Effects of position and stress on recruitment

The assemblage structure was strongly affected by stress, and to a lesser extent by position. The NPMA-NOVA showed significant effects of both factors for each sampling time, but no significant interaction effects (Table 1), where stress explained  $2\text{--}6 \times$  more of the data variability compared to position ( $\eta^2 = 41\text{--}68\%$  vs.  $11\text{--}19\%$ ). Of the pair-wise comparisons, all 12 were significant for stress but only 3 out of 12 for position (Behind vs. Front at Times 3 and 4, and Between vs. Front at Time 4). Animal richness was not affected by either stress or position (ca. 2 species per brick, Table 2A, Fig. 3A), whereas all remaining test variables (plant richness, animal and plant cover,

Table 1

NPMANOVA on  $\text{Log}(x+1)$  transformed percentage cover of sessile organisms for the assemblage data for each of four sampling times (Times 1–4)

| Factor                   | df |           |              |       |              |           |              |       |              |
|--------------------------|----|-----------|--------------|-------|--------------|-----------|--------------|-------|--------------|
|                          |    | SS        | $\eta^2$ (%) | F     | p            | SS        | $\eta^2$ (%) | F     | p            |
|                          |    | A. Time 1 |              |       |              | B. Time 2 |              |       |              |
| Stress                   | 2  | 23,154    | <b>55</b>    | 27.90 | <b>0.001</b> | 30,109    | <b>68</b>    | 52.13 | <b>0.001</b> |
| Position                 | 2  | 6368      | <b>15</b>    | 7.67  | <b>0.001</b> | 4878      | <b>11</b>    | 8.45  | <b>0.001</b> |
| Stress $\times$ Position | 4  | 1396      | 3            | 0.84  | 0.620        | 1456      | 3            | 1.26  | 0.251        |
| Error                    | 27 | 11,203    | 27           |       |              | 7798      | 18           |       |              |
|                          |    | C. Time 3 |              |       |              | D. Time 4 |              |       |              |
| Stress                   | 2  | 18,646    | <b>48</b>    | 18.76 | <b>0.001</b> | 16,074    | <b>41</b>    | 15.27 | <b>0.001</b> |
| Position                 | 2  | 6351      | <b>16</b>    | 6.39  | <b>0.001</b> | 7440      | <b>19</b>    | 7.07  | <b>0.001</b> |
| Stress $\times$ Position | 4  | 449       | 1            | 0.23  | 1.000        | 1773      | 4            | 0.84  | 0.640        |
| Error                    | 27 | 13,421    | 35           |       |              | 14,214    | 36           |       |              |

Significant values are in bold ( $p < 0.01$  and  $\eta^2 > 5\%$ ). All pair-wise comparisons for stress, but only 3 for position (Behind vs. Front Times 3 and 4, and Between vs. Front Time 4) were significant in post-hoc tests.

and cover of 6 key species) showed similar test statistics, only being significantly affected by stress (Tables 2 and 3, ignoring time). Plant richness (Fig. 3B) was greatest in unstressed plots (4.8 per brick), intermediate in algae plots (3.3 per brick) and least in sediment plots (2.1 per brick). Animal cover (Fig. 2C) was greatest in unstressed plots (6.2%) and least in sediment and algae

plots (2.2%) and plant cover (Fig. 2D) was also greatest in unstressed plots (28%), but intermediate in algal plots (10%), and least in sediment plots (1.6%). By adding animal and plant cover values, it can be noted that the total brick cover generally was below 50%, indicating that space was not a limiting resource during the 1-year study period and lessening the impacts of

Table 2

Repeated-measures ANOVA on  $\text{Log}(x+1)$  transformed animal richness (A), plant richness (B), cover of animals (C) and cover of algae (D)

| Factor                                 | df |                       |              |       |              |                      |              |        |               |
|----------------------------------------|----|-----------------------|--------------|-------|--------------|----------------------|--------------|--------|---------------|
|                                        |    | SS                    | $\eta^2$ (%) | F     | p            | SS                   | $\eta^2$ (%) | F      | p             |
|                                        |    | A. Animal Richness    |              |       |              | B. Plant Richness    |              |        |               |
| Stress                                 | 2  | 0.03                  | 1            | 0.57  | 0.570        | 1.85                 | <b>44</b>    | 3.53   | <b>0.000*</b> |
| Position                               | 2  | 0.03                  | 1            | 0.59  | 0.560        | 0.08                 | 2            | 2.85   | 0.076         |
| Stress $\times$ Position               | 4  | 0.36                  | 14           | 3.23  | 0.027        | 0.10                 | 2            | 1.69   | 0.180         |
| Error between                          | 27 | 0.75                  | 28           |       |              | 0.39                 | 9            |        |               |
| Time                                   | 3  | 0.34                  | 13           | 13.46 | 0.000        | 0.66                 | 16           | 29.07  | 0.000         |
| Stress $\times$ Time                   | 6  | 0.17                  | 7            | 3.48  | 0.004        | 0.29                 | 7            | 6.30   | 0.000         |
| Position $\times$ Time                 | 6  | 0.14                  | 5            | 2.85  | 0.015        | 0.09                 | 2            | 1.94   | 0.085         |
| Stress $\times$ Position $\times$ Time | 12 | 0.13                  | 5            | 1.34  | 0.216        | 0.12                 | 3            | 1.35   | 0.206         |
| Error within                           | 81 | 0.67                  | 26           |       |              | 0.61                 | 15           |        |               |
|                                        |    | C. Total Animal Cover |              |       |              | D. Total Plant Cover |              |        |               |
| Stress                                 | 2  | 3.15                  | <b>23</b>    | 13.82 | <b>0.000</b> | 22.83                | <b>65</b>    | 126.73 | <b>0.000</b>  |
| Position                               | 2  | 0.06                  | 0            | 0.27  | 0.767        | 1.15                 | 3            | 6.40   | 0.005         |
| Stress $\times$ Position               | 4  | 1.26                  | 9            | 2.77  | 0.048        | 0.31                 | 1            | 0.86   | 0.500         |
| Error between                          | 27 | 3.08                  | 22           |       |              | 2.43                 | 7            |        |               |
| Time                                   | 3  | 1.53                  | 11           | 15.38 | 0.000        | 3.54                 | 10           | 32.43  | 0.000         |
| Stress $\times$ Time                   | 6  | 0.34                  | 2            | 1.73  | 0.124        | 1.20                 | 3            | 5.48   | 0.000         |
| Position $\times$ Time                 | 6  | 0.74                  | 5            | 3.70  | 0.003        | 0.69                 | 2            | 3.17   | 0.008         |
| Stress $\times$ Position $\times$ Time | 12 | 1.00                  | 7            | 2.51  | 0.008        | 0.27                 | 1            | 0.62   | 0.823         |
| Error within                           | 81 | 2.68                  | 19           |       |              | 2.95                 | 8            |        |               |

Significant values are in bold ( $p < 0.01$  and  $\eta^2 > 5\%$ , time excluded). Asterisk after  $p$ -values indicate that Cochran's  $C$  was significant for that specific factor. Cf. Fig. 3 for SNK-test results.

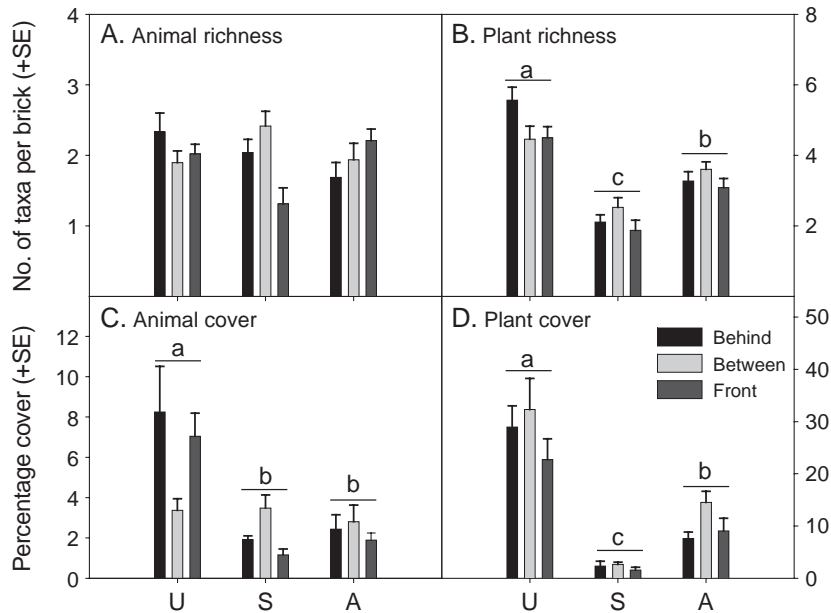


Fig. 3. Plots of animal (A) and plant (B) richness, and animal (C) and plant (D) cover. Time was pooled ( $n=16$ ). U=unstressed, S=sediment stressed, A=algal stressed. The same letters above bars denote values that were statistically similar (SNK-test on factors where  $p < 0.01$  and  $\eta^2 > 5\%$ , Table 2).

temporal autocorrelation (cf. Thomsen (2004a,b) for time-specific data). Four of the key species had identical treatment effects with greatest abundance in unstressed plots and least in sediment and algae plots: *C. virginica* (Fig. 4A)=4.5% vs. 0.7%, *C. fragile* (Fig. 4B)=3.4% vs. 0.0%, *G. vermiculophylla* (Fig. 4C)=14.1% vs. 1.0%, and *A. subulata* =7.8% vs. 0.0% (Fig. 4D). In contrast, *Enteromorpha* spp. (Fig. 4E) had greatest cover in algae plots (6.2%), intermediate in unstressed plots (1.4%) and least in sediment plots (0.4%). This was relatively similar to *U. curvata* (Fig. 4F) which had greatest cover in algae and unstressed plots (1.6%) and least in sediment plots (0.3%). It should be noted that, although statistically insignificant, *A. subulata* was completely absent in front of reefs and that *G. vermiculophylla* was particularly dominant between reefs. Finally, although not included in statistical tests, we observed subordinate species in unstressed plots to be the macroalgae *Ectocarpus* spp. (epiphytic on *G. vermiculophylla*) and *Punctaria latifolia* Greville, and the filter feeders *Membranipora* spp., *Amathia vidovici* Heller, *Bugula turrita* Alder (bryozoa), *Molgula* sp. (tunicate), and *Hydroides dianthus* Verrill (polychaete). Absolute

cover values of above filter feeders were low in all treatments but their relative abundance compared to the algae were much greater in the sediment-stressed plots.

#### 4. Discussion

Recruitment of sessile organisms are well documented in rocky systems (e.g. Connell, 1961; Hirata, 1987; Underwood and Skilleter, 1996). In comparison, few studies have considered recruitment of sessile organisms in soft-bottom systems, where oysters, mussels and man-made constructions provide patches of hard substratum (Underwood and Anderson, 1994; Anderson and Underwood, 1997; Anderson, 1999a,b; Connell and Glasby, 1999; Glasby, 1999a,b; Lenihan, 1999; Lenihan et al., 2001). We document that accumulations of sediments and drift algae negatively affect recruitment of sessile reef assemblages, including the reef-building *C. virginica*. If this species performance is reduced, reef generation and maintenance will deteriorate and reef assemblages will be further limited. Thus, eutrophication that enhances drift algae accumu-

Table 3

Repeated-measures ANOVA on the  $\text{Log}(x+1)$  transformed abundance of *C. virginica* (A), *C. fragile* (B), *G. vermiculophylla* (C), *A. subulata* (D), *Enteromorpha* spp. (E) and *U. curvata* (F)

| Factor                                 | df | SS    | $\eta^2$ (%) | F     | p                              | SS   | $\eta^2$ (%) | F     | p             |
|----------------------------------------|----|-------|--------------|-------|--------------------------------|------|--------------|-------|---------------|
| <i>A. Crassostrea virginica</i>        |    |       |              |       | <i>B. Codium fragile</i>       |      |              |       |               |
| Stress                                 | 2  | 6.25  | <b>38</b>    | 15.74 | <b>0.000*</b>                  | 7.15 | <b>53</b>    | 28.63 | <b>0.000*</b> |
| Position                               | 2  | 0.20  | 1            | 0.49  | 0.618                          | 0.15 | 1            | 0.59  | 0.561         |
| Stress $\times$ Position               | 4  | 1.06  | 6            | 1.34  | 0.281                          | 0.45 | 3            | 0.89  | 0.482         |
| Error between                          | 27 | 5.36  | 33           |       |                                | 3.37 | 25           |       |               |
| Time                                   | 3  | 0.21  | 1            | 2.35  | 0.079                          | 0.25 | 2            | 4.06  | 0.010         |
| Stress $\times$ Time                   | 6  | 0.17  | 1            | 0.94  | 0.474                          | 0.46 | 3            | 3.70  | 0.003         |
| Position $\times$ Time                 | 6  | 0.43  | 3            | 2.44  | 0.032                          | 0.03 | 0            | 0.27  | 0.950         |
| Stress $\times$ Position $\times$ Time | 12 | 0.38  | 2            | 1.08  | 0.391                          | 0.07 | 0            | 0.27  | 0.992         |
| Error within                           | 81 | 2.41  | 15           |       |                                | 1.67 | 12           |       |               |
| <i>C. Gracilaria vermiculophylla</i>   |    |       |              |       | <i>D. Agardhiella subulata</i> |      |              |       |               |
| Stress                                 | 2  | 20.05 | <b>63</b>    | 55.95 | <b>0.000</b>                   | 2.40 | <b>18</b>    | 5.63  | <b>0.009*</b> |
| Position                               | 2  | 1.60  | 5            | 4.47  | 0.021                          | 1.43 | 11           | 3.35  | 0.050*        |
| Stress $\times$ Position               | 4  | 0.48  | 2            | 0.67  | 0.616                          | 2.06 | 15           | 2.42  | 0.073         |
| Error between                          | 27 | 4.84  | 15           |       |                                | 5.75 | 42           |       |               |
| Time                                   | 3  | 0.61  | 2            | 7.07  | 0.000                          | 0.11 | 1            | 2.32  | 0.082         |
| Stress $\times$ Time                   | 6  | 1.43  | 4            | 8.27  | 0.000                          | 0.19 | 1            | 1.96  | 0.081         |
| Position $\times$ Time                 | 6  | 0.26  | 1            | 1.51  | 0.184                          | 0.14 | 1            | 1.44  | 0.210         |
| Stress $\times$ Position $\times$ Time | 12 | 0.39  | 1            | 1.12  | 0.355                          | 0.14 | 1            | 0.70  | 0.752         |
| Error within                           | 81 | 2.34  | 7            |       |                                | 1.31 | 10           |       |               |
| <i>E. Enteromorpha</i> spp.            |    |       |              |       | <i>F. Ulva curvata</i>         |      |              |       |               |
| Stress                                 | 2  | 6.36  | 31           | 82.71 | <b>0.000*</b>                  | 2.13 | 19           | 28.97 | <b>0.000*</b> |
| Position                               | 2  | 0.48  | 2            | 6.18  | 0.006                          | 0.14 | 1            | 1.95  | 0.163         |
| Stress $\times$ Position               | 4  | 0.17  | 1            | 1.11  | 0.371                          | 0.23 | 2            | 1.53  | 0.222         |
| Error between                          | 27 | 1.04  | 5            |       |                                | 0.99 | 9            |       |               |
| Time                                   | 3  | 7.14  | 35           | 97.45 | 0.000                          | 2.94 | 26           | 62.76 | 0.000         |
| Stress $\times$ Time                   | 6  | 2.60  | 13           | 17.73 | 0.000                          | 2.40 | 21           | 25.59 | 0.000         |
| Position $\times$ Time                 | 6  | 0.14  | 1            | 0.97  | 0.454                          | 0.60 | 5            | 6.41  | 0.000         |
| Stress $\times$ Position $\times$ Time | 12 | 0.46  | 2            | 1.57  | 0.118                          | 0.68 | 6            | 3.61  | 0.000         |
| Error within                           | 81 | 1.98  | 10           |       |                                | 1.27 | 11           |       |               |

Significant values are in bold ( $p < 0.01$  and  $\eta^2 > 5\%$ , time excluded). Asterisk after  $p$ -values indicate that Cochran's  $C$  was significant for that specific single factor. Cf. Fig. 4 for SNK-test results.

lation (Raffaelli et al., 1998), and urban development and changed land-use practices that enhance sedimentation (Airoldi, 2003), are likely to have large-scale negative effects on oyster reefs and associated biota.

#### 4.1. Unstressed recruitment

Macroalgae were more dominant recruiters in Hog Island Bay compared to other soft-bottom studies (Dean and Hurd, 1980; Barh and Lanier, 1981; Dame et al., 1992; Underwood and Anderson, 1994; Anderson and Underwood, 1997; Lenihan and Peterson, 1998; Anderson, 1999a; Lenihan, 1999), a dif-

ference partly attributed to recruitment panels from these other studies typically being incubated at lower elevations or facing downwards thereby receiving less light and algal propagules. The alien alga *G. vermiculophylla* was clearly the most abundant species, which adds a high recruitment ability to an array of successful adaptations to coastal lagoons, including high stress tolerance, high vegetative growth, and strong facilitation by the polychaete *Diopatra cuprea* (Bosch) (Wallentinus et al., 2004; Rueness, 2005; Thomsen and McGlathery, 2005). Another alien, *C. fragile*, was the fourth most abundant, demonstrating that *C. fragile* also is an efficient invader of barren



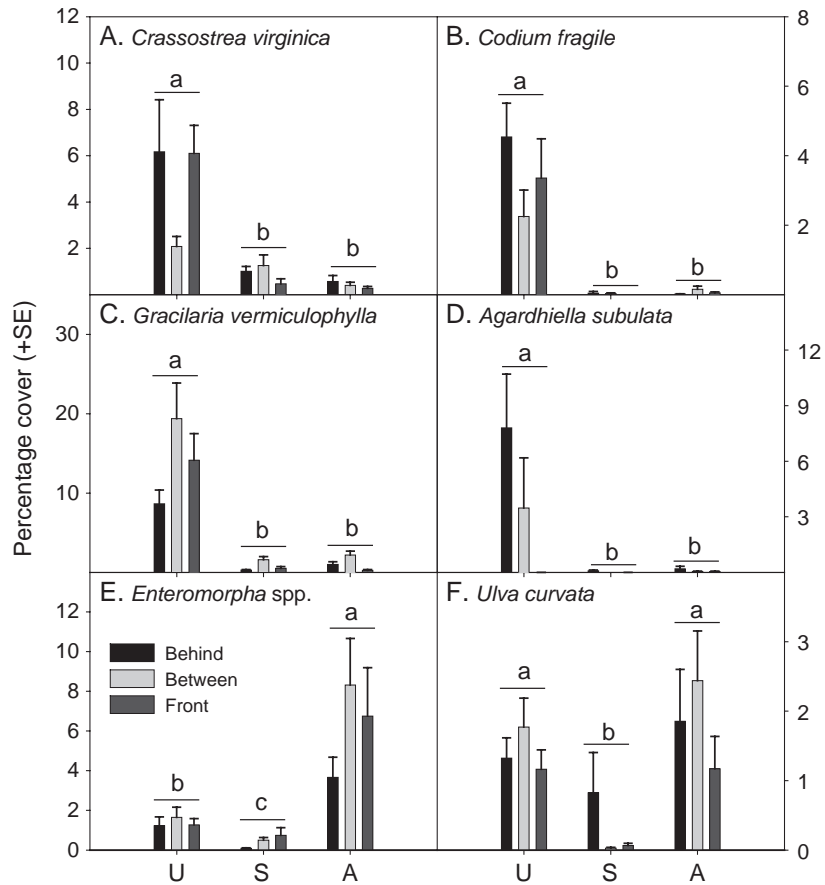


Fig. 4. Plots of cover of the six most abundant species. Time was pooled ( $n=16$ ). U=unstressed, S=sediment stressed, A=algal stressed. The same letters above bars denote values that were statistically similar (SNK-test on factors where  $p<0.01$  and  $\eta^2>5\%$ , Table 3).

hard substrata (Fralick and Mathieson, 1973; Malinowski and Ramus, 1973). In general, conspicuous algae (*U. curvata*, *A. subulata*, *C. fragile*, *G. vermiculophylla*) recruited in high densities. These species can in a few months grow into large thalli (Pedersen and Borum, 1996), but because large individuals are susceptible to dislodgment and pruning, currents and waves probably generate a continuous supply of fragments to the adjacent soft-bottom drift algae assemblages (Blanchette, 1997; Thomsen, 2004b). This spill-over effect likely minimizes the risk of local extinction of the soft-bottom drift algae. The most efficient animal recruiter was the oyster, similar to other soft-bottom studies (Underwood and Anderson, 1994; Anderson, 1999a; Lenihan, 1999). We noted that a large proportion died within a few months, possibly due to predation or disease (Barh and Lanier,

1981; O'Beirn et al., 1996; Lenihan, 1999). Despite a high mortality, the oyster shells increased topographic complexity, and may thereby have increased available space (Connor, 1980; Barh and Lanier, 1981). Other animals included filter-feeding subdominants that perform well in high depositional environments (Dean and Hurd, 1980). Oyster reefs have previously been suggested to affect hydrodynamics (Galtsoff, 1964; Barh and Lanier, 1981; Mann, 2000), and Lenihan (1999) showed that reef size and elevation influenced current velocities and hence oyster recruitment. We showed that currents accelerate between and waves break in front of intertidal reefs, potentially resulting in different rates of resuspension, light and nutrient conditions (Schoellhamer, 1996; Lawson, 2003), and to a smaller extent structuring the reef assemblage. These main effects were the absence of *A. subulata* in

front and high abundance of *G. vermiculophylla* between reefs. The absence of *A. subulata* was likely caused by wave-induced thallus breakage because it has a relatively low adhesion strength for its size (Thomsen, 2004b) and is easily fragmented. *G. vermiculophylla* may be particularly dominant between reefs because it seems to avoid entanglement by tumbling drift algae (Flindt et al., 1997; Holmquist, 1997), and withstand current forces well (Thomsen, 2004b).

#### 4.2. Sediment-stressed recruitment

Adverse effects of sedimentation have been documented on coral and rocky reef assemblages (e.g. Rogers, 1990; Fabricius and Wolanski, 1999; Airoldi, 2003; Eriksson and Johansson, 2003). Here we show that sessile organisms in soft-bottom lagoons also are affected negatively by high sedimentation. Enhanced sedimentation may be caused by decreased abundance of sediment stabilizers such as seagrasses or salt marsh plants or changed agricultural practices (Barh and Lanier, 1981; McManus, 1998; Airoldi, 2003). On the eastern shore of Virginia, these mechanisms, particularly the local absence of seagrasses, have likely caused enhanced sedimentation within the last decades (Haven and Whitcomb, 1983; Ralph and Short, 2002). Our experiment showed that sedimentation reduced the abundance of both plants and animals, and lowered plant richness substantially. However, animal richness was unaffected, demonstrating that many species did recruit onto the bricks, although with low survival and growth. In particular, filter feeders were less severely affected, compared to the algae, as expected due to their dependency on suspended organic particles (Dean and Hurd, 1980; Airoldi, 2003; Eriksson and Johansson, 2003). In contrast, the abundance of *C. virginica* was strongly reduced, probably because its ciliated gills are relatively sensitive to clogging (Ortega and Sutherland, 1992). Thus, although oysters occasionally recruited onto sediment-stressed bricks, they did not survive for long, suggesting that enhanced sedimentation will cause diminished reef structures and cascading stress on reef-dependent organisms. All the key algae were observed to recruit onto the sediment-stressed bricks, but with high mortality, and never grew into large individuals.

The opportunistic *U. curvata* and *Enteromorpha* sp. (Pedersen and Borum, 1996), and the stress-tolerant *G. vermiculophylla* (Rueness, 2005), were most common. In particular, many small *G. vermiculophylla* recruits were seen partly buried in the sediment layer, with blackened holdfasts and stipes, but nevertheless being stable over time, suggesting a high sediment tolerance. In comparison, the opportunistic algae utilized time windows with reduced sediment layers to temporarily occupy small amounts of space.

#### 4.3. Algae-stressed recruitment

Eutrophication typically causes increased drift algae abundance (Raffaelli et al., 1998), and we found that such accumulations ( $>2$  kg WW  $m^{-2}$ ) strongly inhibited oyster recruitment. Similar negative effects of algal accumulations have been observed on sediment fauna (Hull, 1987; Norkko and Bonsdorff, 1996; Osterling and Pihl, 2001). As densities of drift algae in eutrophied lagoons commonly exceed 1 kg WW  $m^{-2}$  (Raffaelli et al., 1998; Menezes and Comin, 2000), adverse effects on hard and soft substrata organisms are probably widespread and will likely increase as eutrophication proceeds. Algal stress affected the entire assemblage, manifested through low animal cover and medium plant cover and plant richness. Only few oysters and large perennial algae recruited and all had a high mortality. The effects of the drift algae cover were not related to the development of anoxia as observed in other studies (Raffaelli et al., 1998), as we did not observe algal decomposition or anoxia. Instead, the drift algae effects were likely due to reduced light penetration (Peckol and Rivers, 1996), smothering and filtering of propagules (Olafsson, 1988), reduced currents (Escartin and Aubrey, 1995), and interference with feeding apparatus (Norkko and Bonsdorff, 1996). *Enteromorpha* spp. and *U. curvata* were the most common space-occupying taxa, although only as mm-cm sized individuals. These taxa are ephemeral subdominants on primary substrates under intermediate disturbance regimes, but have high growth and reproductive capacities (Littler, 1980; Sousa, 1980; Poole and Raven, 1997). They probably dominated because of reduced grazing (Geertz-Hansen et al., 1993), reduced dislodgment (Hawes and Smith,

1995; Thomsen, 2004b) and reduced competition from canopy forming algae.

#### 4.4. Design considerations

Although temporal effects were of little interest compared to the effects of position and stress, our experiment still suffered from a repeated-measures design, which may cause temporal autocorrelation (Underwood, 1997). Such autocorrelation is likely to be positive because of an increased chance of finding a species if it was found on the same brick in a previous survey. This causes an increased likelihood of a type 1 error and significance was therefore evaluated conservatively at  $p < 0.01$ . However, it is also possible for autocorrelation to be negative. For example, a high cover of a single space-dominant canopy species (e.g. *G. vermiculophylla* or *C. fragile*) could decrease the chance of finding additional species the following survey, thereby causing an increased chance of a type 2 error for species richness. A solution to this lack of independence problem is to increase the number of incubated bricks and only sample each brick once (Underwood and Anderson, 1994; Anderson, 1999a,b). In addition, as in most experiments, our results are constrained temporally (initialized at a single time, in a single season, including a 1-year data series) and spatially (conducted at a single elevation level, at a single location), and extrapolation outside this domain should only be done with caution. Note, however, that most bricks had relatively low cover, providing substratum for recruitment throughout all seasons during the 1-year incubation period, even though the available area would shrink or expand depending on the cover of neighboring organisms. To provide more general recruitment data from soft-bottom systems, future studies should (a) include temporally independent sampling, (b) repeat experiments at several locations, elevation levels and seasons, and (c) include several life-history turnovers, i.e. typically longer than 1-year studies (Underwood and Anderson, 1994; Anderson et al., 1997; Anderson, 1999a,b).

#### 4.5. Conclusions

Sedimentation strongly reduced recruitment of most reef organisms, particularly the dominant conspicuous algae *G. vermiculophylla*, *A. subulata* and

*C. fragile*, two of which are alien to the system, and oyster *C. virginica*, leaving only a few inconspicuous stress tolerant taxa. Accumulations of drift algae also decreased abundance of space dominant taxa, whereas the opportunistic *Enteromorpha* spp. and *U. curvata* proliferated in these habitats as small individuals. The effects of position were less dramatic, but indicated that *G. vermiculophylla* dominates in habitats exposed to currents and that *A. subulata* cannot survive in wave exposed habitats. Our study shows that because the reef building oyster, *C. virginica*, performed poorly under sediments and drift algae stress, increased eutrophication and sedimentation may have wide-ranging adverse effects on reefs and on the diversity and abundance of associated biota.

#### Acknowledgements

The Virginia Coast Reserve of the Nature Conservancy provided access to study sites. This material is based upon work supported by the National Science Foundation under Grant nos. DEB-9411974 and DEB-0080381. M. Thomsen was also supported by the Danish Research Academy. [SS]

#### References

- Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 161–236.
- Anderson, M.J., 1999a. Distinguishing direct from indirect effects of grazers in intertidal estuarine assemblages. *J. Exp. Mar. Biol. Ecol.* 234, 199–218.
- Anderson, M.J., 1999b. Effects of patch size on colonisation in estuaries: revisiting the species–area relationship. *Oecologia* 118, 87–98.
- Anderson, M.J., 2001. A new non-parametric multivariate analysis of variance. *Aust. Ecol.* 26, 32–46.
- Anderson, M.J., Underwood, A.J., 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *J. Exp. Mar. Biol. Ecol.* 184, 217–236.
- Anderson, M.J., Underwood, A.J., 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage—a multivariate and univariate approach. *Oecologia* 109, 442–453.
- Anderson, R.J., Carrick, P., Levitt, G.J., Share, A., 1997. Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *Mar. Ecol. Prog. Ser.* 159, 265–273.
- Barh, L.M., Lanier, M.P., 1981. The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile. US

- Fish and Wildlife Service, Office of Biological Services, Washington, DC. 105 pp.
- Bellorin, A.M., Oliveira, M.C., Oliveira, E.C., 2004. *Gracilaria vermiculophylla*: a western Pacific species of Gracilariaceae (Rhodophyta) first recorded from the eastern Pacific. *Phycol. Res.* 52, 69–79.
- Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action—a case study with *Fucus gardneri*. *Ecology* 78, 1563–1578.
- Boynton, W.R., Hagy, J.D., Murray, L., Stokes, C., Kemp, W.M., 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries* 19, 408–421.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecol. Monogr.* 42, 710–723.
- Connell, S.D., Glasby, T.M., 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Mar. Environ. Res.* 47, 373–387.
- Connor, J.L., 1980. Distribution and seasonality of macroalgae on oyster communities of central Chesapeake Bay. *Bot. Mar.* 23, 711–717.
- Dame, R., Libes, S., 1993. Oyster reefs and nutrient retention in tidal creeks. *J. Exp. Mar. Biol. Ecol.* 171, 251–258.
- Dame, R.F., Spurrier, J.D., Zingmark, R.G., 1992. In situ metabolism of an oyster reef. *J. Exp. Mar. Biol. Ecol.* 164, 147–159.
- Dean, T.A., Hurd, L.E., 1980. Development in an estuarine fouling community: the influence of early colonist on later arrivals. *Oecologia* 46, 295–301.
- Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: ‘objective’ is not always better. *Mar. Ecol. Prog. Ser.* 96, 93–100.
- Eriksson, B.K., Johansson, G., 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Eur. J. Phycol.* 38, 217–222.
- Escartin, J., Aubrey, D.G., 1995. Flow structure and dispersion within algal mats. *Estuar. Coast. Shelf Sci.* 40, 451–472.
- Fabricius, K.E., Wolanski, E., 1999. Rapid smothering of coral reef organisms by muddy marine snow. *Estuar. Coast. Mar. Sci.* 50, 115–120.
- Flindt, M., Salomonsen, J., Carrer, M., Bocci, M., Kamp-Nielsen, L., 1997. Loss, growth and transport dynamics of *Chaetomorpha aerea* and *Ulva rigida* in the Lagoon of Venice during an early summer field campaign. *Ecol. Model.* 102, 133–141.
- Fralick, R.A., Mathieson, A.C., 1973. Ecological studies of *Codium fragile* in New England, USA. *Mar. Biol.* 19, 127–132.
- Galtsoff, P.S., 1964. The American oyster *Crassostrea virginica* (Gmelin). *Fish. Bull.*, vol. 64. U.S. Fishery and Wildlife Service, pp. 1–480.
- Geertz-Hansen, O., Sand-Jensen, K., Hansen, D.F., Christiansen, A., 1993. Growth and grazing control of abundance of the marine macroalgae, *Ulva lactuca* L. in a eutrophic Danish estuary. *Aquat. Bot.* 46, 101–109.
- Glasby, T.M., 1999a. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuar. Coast. Mar. Sci.* 48, 281–290.
- Glasby, T.M., 1999b. Effects of shading on subtidal epibiotic assemblages. *J. Exp. Mar. Biol. Ecol.* 234, 275–290.
- Gurgel, C.F.D., Fredericq, S., 2004. Systematics of the *Gracilariaceae* (Gracilariales, Rhodophyta): a critical assessment based on rbcL sequence analysis. *J. Phycol.* 40, 138–159.
- Hauxwell, J., Cebrian, J., Furlong, C., Valiela, I., 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology*, 1007–1022.
- Haven, D.S., Whitcomb, J.P., 1983. The origin and extent of oyster reefs in the James River, Virginia. *J. Shellfish Res.* 3, 141–151.
- Hawes, I., Smith, R., 1995. Effects of current velocity on the detachment of thalli of *Ulva lactuca* (Chlorophyta) in a New Zealand estuary. *J. Phycol.* 31, 875–880.
- Hirata, T., 1987. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan: II. Succession of invertebrates. *Mar. Ecol. Prog. Ser.* 38, 25–35.
- Holmquist, J.G., 1997. Disturbance and gap formation in a marine benthic mosaic—influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. *Mar. Ecol. Prog. Ser.* 158, 121–130.
- Hull, S.C., 1987. Macroalgal mats and species abundance: a field experiment. *Estuar. Coast. Shelf Sci.* 25, 519–532.
- Humm, H.J., 1979. *The Marine Algae of Virginia*. The University Press of Virginia, Virginia.
- Keough, M.J., Downes, B.J., 1982. Recruitment of marine invertebrates: the roles of active larval choices and early mortality. *Oecologia*, 348–352.
- Koch, E.W., Gust, G., 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* 184, 63–72.
- Lawson, S., 2003. Sediment suspension as a control of light availability in a coastal lagoon. Dissertation, University of Virginia, Charlottesville. 115 pp.
- Lenihan, H.S., 1999. Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecol. Monogr.* 69, 251–275.
- Lenihan, H.S., Peterson, C.H., 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol. Appl.* 8, 128–140.
- Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol. Appl.* 11, 764–782.
- Levine, T.R., Hullet, C.R., 2002. Eta squared, partial eta squared, and misreporting of effect size in communication research. *Human Commun. Res.* 28, 612–625.
- Littler, M.M., 1980. Morphological form and photosynthetic performance of marine macroalgae: tests of a functional/form hypothesis. *Bot. Mar.* 22, 161–165.
- Malinowski, K.C., Ramus, J., 1973. Growth of the green alga *Codium fragile* in a Connecticut estuary. *J. Phycol.* 9, 102–110.
- Mann, R., 2000. Restoring the oyster reef communities in the Chesapeake Bay: a commentary. *J. Shellfish Res.* 19, 335–339.

- McGlathery, K., 2001. Macroalgal blooms contribute to the decline in seagrasses in nutrient-enriched coastal waters. *J. Phycol.* 37, 453–456.
- McGlathery, K., Anderson, I., Tyler, C., 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Mar. Ecol. Prog. Ser.* 216, 1–15.
- McManus, J., 1998. Temporal and spatial variations in estuarine sedimentation. *Estuaries* 21, 622–634.
- Menedez, M., Comin, F., 2000. Spring and summer proliferation of floating macroalgae in a Mediterranean coastal lagoon (Tancad Lagoon, Ebro Delta, NE Spain). *Estuar. Coast. Mar. Sci.* 51, 215–226.
- Norkko, A., Bonsdorff, E., 1996. Altered benthic prey-availability due to episodic oxygen deficiency caused by drifting algal mats. *Mar. Ecol.* 17, 355–372.
- O’Beim, P.X., Walker, R.L., Heffernan, P.B., 1996. Enhancement of subtidal oyster, *Crassostrea virginica*, recruitment using mesh bag enclosures. *J. Shellfish Res.* 15, 313–318.
- Oertel, G.F., 2001. Hypsographic, hydro-hypsographic and hydrological analysis of coastal bay environments, Great Machipongo Bay, Virginia. *J. Coast. Res.* 17, 775–783.
- Olafsson, E.B., 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. *Mar. Biol.* 97, 571–574.
- Ortega, S., Sutherland, J.P., 1992. Recruitment and growth of the eastern oyster, *Crassostrea virginica*, in North Carolina. *Estuaries* 15, 158–170.
- Osterling, M., Pihl, L., 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. *J. Exp. Mar. Biol. Ecol.* 263, 159–183.
- Peckol, P., Rivers, J.S., 1996. Contribution by macroalgal mats to primary production of a shallow embayment under high and low nitrogen-loading rates. *Estuar. Coast. Shelf Sci.* 43, 311–325.
- Pedersen, M.F., Borum, J., 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Mar. Ecol. Prog. Ser.* 142, 261–272.
- Poole, L.J., Raven, J.A., 1997. The biology of *Enteromorpha*. *Prog. Phycol. Res.* 12, 1–148.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Raffaelli, D.G., Raven, J.A., Poole, L.J., 1998. Ecological impact of green macroalgal blooms. *Oceanogr. Mar. Biol. Annu. Rev.* 36, 97–125.
- Ralph, P.J., Short, C.A., 2002. Impact of the wasting disease pathogen *Labyrinthula zosterae*, on the photobiology of eelgrass *Zostera marina*. *Mar. Ecol. Prog. Ser.* 226, 265–271.
- Rogers, C.S., 1990. Responses of coral and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.* 62, 185–202.
- Rosinski, J.L., 2004. Controls on benthic biodiversity and trophic interactions in a temperate coastal lagoon. Dissertation, University of Virginia, Charlottesville. 397 pp.
- Rueness, J., 2005. Life history and molecular sequences of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta), a new introduction to European waters. *Phycologia* 44, 120–128.
- Salomonsen, J., Flindt, M.R., Geertz-Hansen, O., 1997. Significance of advective transport of *Ulva lactuca* for a biomass budget on a shallow water location. *Ecol. Model.* 102, 129–132.
- Schoellhamer, D.H., 1996. Anthropogenic sediment resuspension mechanisms in a shallow microtidal estuary. *Estuar. Coast. Shelf Sci.* 43, 533–548.
- Sousa, W.P., 1980. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49, 227–254.
- Stanhope, J.W., 2003. Relationships between watershed characteristics and baseflow nutrient discharges to eastern shore coastal lagoons, Virginia. Dissertation, College of William and Mary, Williamsburg. 135 pp.
- Thomsen, M.S., 2004a. Macroalgal distribution patterns and ecological performances in a tidal coastal lagoon, with emphasis on the non-indigenous *Codium fragile* ssp. *tomentosoides*. Dissertation, University of Virginia, Charlottesville. 315 pp.
- Thomsen, M.S., 2004b. Species, thallus size and substrate determine macroalgal break forces and break places in a low energy soft bottom lagoon. *Aquat. Bot.* 80, 153–161.
- Thomsen, M.S., McGlathery, K., 2005. Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. *Estuar. Coast. Shelf Sci.* 62, 63–73.
- Tyler, A.C., 2002. Impact of benthic algae on dissolved organic nitrogen in a temperate, coastal lagoon. Dissertation, University of Virginia, Charlottesville. 179 pp.
- Tyler, A.C., McGlathery, K.J., Anderson, I.C., 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuar. Coast. Shelf Sci.* 53, 155–168.
- Underwood, A.J., 1997. *Experiments in Ecology—Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- Underwood, A.J., Anderson, M.J., 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *J. Mar. Biol. Assoc. UK* 74, 563–584.
- Underwood, A.J., Skilleter, G.A., 1996. Effects of patch-size on the structure of assemblages in rock pools. *J. Exp. Mar. Biol. Ecol.* 197, 63–90.
- Wallentinus, I., Nyberg, C., Rueness, J., 2004. *Gracilaria vermiculophylla* in the Gotenborg archipelago. Programme and Abstracts, 13th International Seaweed Symposium, Bergen, Norway, p. 138.