

Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates

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ABSTRACT: A field experiment was used to examine the interactions among structurally complex, spatially shifting structure (macroalgae deposited by currents), less-complex stationary structure (seagrass), and mobile benthic invertebrates. I tested the effect of drift algal patches on underlying seagrass structure and fauna by establishing manipulated algal mats over seagrass for comparison with control seagrass plots. Control and experimental plots did not differ significantly for any variable prior to algal addition, but most seagrass structure was removed by this disturbance over a 6 mo period. In contrast, abundance of mobile fauna on experimental plots increased after 6 mo of algal cover relative to abundance on control plots. There was also greater evenness in the canopy fauna of the algal plots which contrasted with the high level of dominance apparent on control plots. Although the structurally complex mats formed by drifting algae provided short-term habitat enhancement for some fauna, long-term effects on fauna are probably negative due to mat ephemerality and degradation of seagrass.

KEY WORDS: Disturbance · Gap · Structural complexity · Macroalgae · Drift algae · Seagrass · *Laurencia* spp. · *Thalassia testudinum* · Caridea · Anomura · Brachyura · Mollusca · Ophiuroidea

INTRODUCTION

Work on the interaction of mobile animals with habitat structure (e.g. Wiens et al. 1985, Stamps et al. 1987, Wiens 1992, Ims 1995) emphasizes stationary, albeit slowly changing, mosaics. However, in some systems, portions of the mosaic are not spatially fixed (Forman 1995). I report on field manipulations used to examine the interactions among structurally complex, spatially shifting patches (drifting macroalgae), less-complex stationary structure (seagrass), and mobile benthic fauna.

Drift macroalgae do not comprise static, homogeneous structure. These algae often shift position in response to water motion (e.g. Williams Cowper 1978, Holmquist 1994, Bell et al. 1995). Although algae are typically viewed as inhabiting a 2-dimensional milieu

with space as a limiting resource (Dayton 1971, 1975, McRoy & Lloyd 1981), drift algae are an exception. Current-propelled clumps roll along the bottom (similar to tumbleweeds; Kilar & Norris 1988, Holmquist 1994) and frequently settle in large accumulations (Gore et al. 1981, Virnstein & Carbonara 1985, Olafsson 1988). The algae are patchily distributed (Virnstein & Carbonara 1985, Herrnkind & Butler 1986) and tend to occur in low-flow areas (Josselyn 1977, Kilar & Norris 1988, Bell & Hall 1997); accumulation in seagrass can be a function of seagrass patch size (Bell et al. 1995).

If a drifting algal patch is layered over the stationary seagrass structure, how is the latter affected? Dayton et al. (1984) described floating kelp plants creating gaps (canopy openings caused by mortality) in kelp-dominated assemblages. Several studies have suggested that increased macroalgal abundances associated with eutrophication are responsible for general seagrass declines (e.g. Guist & Humm 1976, Shepherd et al. 1989, Valiela et al. 1992, den Hartog 1994). Such

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degradation could occur via production of anoxic conditions (Williams Cowper 1978, Norkko & Bonsdorff 1996a), exploitation of dissolved gases or nutrient resources (Harlin & Thorne-Miller 1981), shading (Fitzpatrick & Kirkman 1995, Short et al. 1995), allelopathy (Fletcher 1975), or pH shifts (Wood 1972). However, seagrasses may have high resistance stability (*sensu* Dayton et al. 1984). The majority of seagrass biomass often lies within the substratum (Zieman 1982, Williams 1990). 'Root-biased' systems are relatively resistant to above-substratum disturbance (Pickett & White 1985), and clonal plants, such as seagrasses, are adapted to dynamic environments (Caraco & Kelly 1991). *Thalassia testudinum*, the dominant seagrass in the present study, has been shown to be resistant to natural disturbances (Burrell & Schubel 1977, Birch & Birch 1984), and it is primarily the above-ground biomass that is impacted by even severe hurricanes (Rogers et al. 1982).

Seasonally abundant drift algae tend to occur as mats in sheltered embayments, and these algae have been observed over unvegetated depressions (or 'blowouts'; Williams Cowper 1978, pers. obs.). Do drift algae simply accumulate over these blowouts because of hydrologic phenomena (Wood 1972, Williams Cowper 1978), or can the algae degrade the underlying seagrass structure and thus actually create gaps? My first objective in this investigation was to test whether shifting algae can modify configuration of stationary seagrass structure.

How is the assemblage of mobile fauna changed by vertical layering of macroalgal structure over that of seagrass? Sousa (1984) noted that the disturbance of sessile organisms is relatively well investigated but that effects on mobile animals are poorly understood. Restructuring of sessile communities may have severe indirect effects on mobile fauna (e.g. Onuf & Quammen 1983, Schowalter 1985), because sessile organisms often provide primary habitat and food resources for mobile animals. If algal masses do degrade underlying seagrasses, the primary habitat of the majority of seagrass-associated species (e.g. Holmquist et al. 1989a, Heck & Crowder 1991) would be removed. Further, the superimposed algae could produce anoxia (e.g. Valiela et al. 1992, Norkko & Bonsdorff 1996a), interfere with larval settlement (Olafsson 1988, Bonsdorff et al. 1995) or feeding activities (Raffaelli et al. 1991), and affect fauna via production of secondary metabolites (Anéer 1987, Hay & Fenical 1992). However, it is clear that algal structure, like that of seagrass, can harbor large assemblages of demersal fauna (Gore et al. 1981, Virnstein & Howard 1987, Holmquist 1994) and enhance both refuge quality (Leber 1985, Duffy & Hay 1991, Pohle et al. 1991) and food resources (Zimmerman et al. 1979, Hull 1987, Pohle et

al. 1991) in a variety of ways. Algal masses accumulating over seagrass are likely to import fauna (Gore et al. 1981) that are carried with the tumbling algae (Holmquist 1994). Mobile fauna may preferentially exploit sessile organisms damaged by disturbance (Sousa 1984): litter from terrestrial plant perturbations can enhance some arthropod communities (Santos & Whitford 1981, Seastedt & Crossley 1981), and seagrass litter is an important resource for some animals inhabiting seagrass (Fenchel 1970, Sogard et al. 1987). My second objective was to test whether superimposition of algal structure over seagrass structure results in shifts in the faunal assemblage.

White & Pickett (1985), drawing from Allen & Starr (1982), emphasize that in considering potential disturbance, one must bear in mind the dimensions of a given community. In the seagrass-drift algal assemblage, the ratio of algal patch size to the size of the seagrass ramets or mobile invertebrates is high. An algal accumulation with an area of only 1 m² is about 10⁴ times the basal area of a large seagrass shoot and about 10⁵ times the size of most associated animals. In this study, I test for effects of this scale of algal habitat addition on seagrasses and associated fauna.

METHODS

Study site. Field work was performed in shallow (2 to 3 m deep) seagrass beds in southwestern Florida Bay, Florida, USA. The seagrass meadows are composed of *Thalassia testudinum* (turtle grass), *Halodule wrightii* (shoal grass), and *Syringodium filiforme* (manatee grass) but are dominated by *T. testudinum* (area description in Holmquist et al. 1989b, Holmquist 1994). Sparse green algae, most commonly *Caulerpa* spp., *Halimeda* spp., *Penicillus* spp. (shaving brush), and *Udotea* spp. (mermaid's fan), are interspersed beneath the seagrass canopy. Red and brown macroalgae occur year-round; *Laurencia poiteaui* is the most common species. The algae are initially attached to solid substrata (rubble, mollusc fragments, etc.), but masses often break free after reaching a size of about 25 cm diameter (pers. obs.). Drifting *Laurencia* spp. is particularly abundant in the area between late fall and early spring (Josselyn 1977), and accumulations of individual clumps form mats that usually range from 0.4 to 1 m in thickness. Mats usually remain intact and in place for about 6 mo after which time they senesce and decompose or break up and disperse (Josselyn 1977, Virnstein & Carbonara 1985, Holmquist 1992).

Experimental protocol. I tested the null hypotheses of no effect of drift algal mats on underlying seagrass and no shifts in faunal assemblages by establishing (1) 12 manipulated algal mats over seagrass and (2) 12

control seagrass plots. I later compared the 2 sets of plots for both seagrass and fauna. In order to reproduce the degree of shading found under naturally occurring algal mats, I measured photosynthetic photon flux fluence rate under 50 natural mats with a Li-Cor LI-188B radiometer/photometer and a Li-Cor LI-192SB underwater cosine sensor. The sensor was mounted at a 90° angle to the main axis of a 3 m long PVC extension that was first used to position the sensor under the large mats without disturbing the algae, and then rotated 90° to bring the sensor to an upright position perpendicular to the substrate. Less than 1% of the incident light present just above the algae penetrated the mats.

Experimental and control plots were established contemporaneously with natural mat accumulation and were located randomly throughout the 'Atlantic' subenvironment (Zieman et al. 1989) of Florida Bay, in locations not subject to major algal deposition. Each experimental plot was covered with 1 m² of gathered *Laurencia poiteau*. Underwater transport of the algae to the experimental plots removed some associated fauna as do naturally tumbling algae prior to coming to rest (Holmquist 1994), so some animals were carried to the plots with the algae, but there were fewer of these organisms carried to the experimental plots than are typically associated with stationary algal masses. I accumulated the gathered algae on each plot, over a period of 1 wk, to a thickness of 0.4 m and to the levels of algal density and light penetration (as measured by the radiometer/photometer) observed in natural mats. Algal canopy height was thus about 40 cm versus 18 cm for seagrass on the study plots. The masses of algae were secured over each experimental plot with sections of large mesh (15 cm square) thin plastic netting. I maintained algal densities on the experimental plots for the next 6 mo, after which time I removed the drift algal cover. Little additional algae (occasional clumps <20 cm diameter) came to rest on the control and experimental plots.

Seagrass sampling. I sampled seagrass on control and experimental plots at the following times: (1) at the start of the experiment [immediately after initial faunal sampling (see below) and just before algal addition; n = 12 pairs of plots]; (2) after 6 mo of algal cover (immediately after faunal sampling and algal mat removal; n = 12); (3) 6 mo after algal removal (12 mo after the start of the experiment; n = 5); and (4) 18 mo after algal removal (24 mo after the start of the experiment; n = 5). The latter 2 sampling periods had a reduced number of replicates due to loss of marker buoys. I used a randomly placed quadrat with an area of 185 cm² for the initial sample from each plot. Short shoots (small, leaf-bearing shoots branching laterally from horizontal rhizomes; Zieman 1982) were pulled

by hand to avoid initial damage to the rhizome layer. Samples were transported on ice to the laboratory where seagrass shoots of each species and green algal holdfasts were counted. The green, photosynthetic portions of all seagrass blades collected within each quadrat were washed in dilute HCl with gentle scraping (similar to recommended protocol of Dauby & Poulicek 1995) to remove carbonate epiphytes and sediment and then dried at 95°C for 24 h to determine above-ground dry mass.

After the algal mats were removed from the experimental plots (6 mo), I sampled all plots with a corer (185 cm² sampling area). I used core samples, because I deemed the added information on below-ground biomass to outweigh damage to the plots at this stage of the experiment. I filled core holes with sediment. I discarded dead rhizomes and roots and washed living below-ground material with dilute HCl, to help remove sediment, and then dried these components as above to calculate below-ground dry mass. Above-ground material was processed as before.

Sampling within each plot at the final 2 junctures was also random, with the exception of avoidance of positions of previous core samples. The third series of samples was again taken with the corer. Because I was concerned about cumulative coring impact to the plots, the fourth series was collected with the quadrat and hand gathering of only above-ground components.

Faunal sampling. I sampled the demersal fauna of each control and experimental plot immediately before construction of algal mats and 6 mo later, just before algal mats were removed. The animals associated with both seagrass and algae were sampled with throw traps (drop traps; i.e. boxes lacking a solid top or bottom that are cleared of fauna with nets). Throw traps have been used in a number of studies (e.g. Kushlan 1981, Huh 1984, Erwin et al. 1985, Kushlan et al. 1986, Sogard et al. 1987, 1989, Holmquist et al. 1989a, c) and have been shown to be highly efficient, relative to other collecting devices, for quantitatively sampling demersal organisms in vegetated habitats (Kushlan 1981, Freeman et al. 1984, Jacobsen & Kushlan 1987, Rozas & Minello 1997). Throw trapping of well-separated stations is effectively sampling with replacement (Jacobsen & Kushlan 1987), and re-sampling seagrass-covered sites at 6 mo intervals over a period of 4 yr does not cause shifts in measures of seagrass cover or assemblages of mobile fauna (Holmquist unpubl.). However, throw trap sampling is highly disruptive to unvegetated mud bottoms (pers. obs. during work reported in Sogard et al. 1987, 1989, Holmquist et al. 1989a, c). Because throw trapping on the bare mud that remained on the plots after 6 mo of algal cover (see 'Results') would have greatly disrupted the seagrass recovery process, I opted not to

collect fauna after the algal mats were removed and during gap recovery.

I used a device and protocol derived from that of Sogard et al. (1987, 1989) and Holmquist et al. (1989a, c). The trap was a 0.5×0.5 m box without a top or bottom and was constructed of sheet aluminum with a 0.5 mm square mesh screen secured over the top of the trap. The clearing device was a 0.5 m wide framed and handled net (bar seine) with 0.5 mm square mesh. Although published work to date records the use of throw traps in shallow water, the devices can be used below the surface as well. My protocol was as follows: I swam the trap to the plot to be sampled, free-dove with the apparatus to the bottom, and pushed the trap into the seagrass or sediment. An assisting scuba-diver then removed a screen covering the trap aperture and steadied the trap, while I made 1 sweep of the canopy with the bar seine. The scuba-diver replaced the top screen, while I ascended with the sample-containing bar seine. The net downward force of the water against the ascending net was sufficient to prevent the escape of demersal organisms from the bar seine. I then emptied the bar seine of animals, detritus, and algae into a water-filled container on the support boat. Ten such sweeps were performed for each plot. These techniques sample the demersal fauna of the seagrass or algal canopy but do not attempt to sample the sediment surface or highly mobile fishes. All algae were removed from traps on experimental plots at the end of the 6 mo period of algal cover and retained. A relatively inclusive group of major taxa, i.e. molluscs, decapods, stomatopods, asteroids, and ophiuroids, were identified to species level for most taxa; some taxa, for instance peracarids, were not considered. Algal samples were washed in dilute HCl prior to drying at 95°C for 24 h for determination of dry mass (for relation to animal abundances).

Analysis. I converted vegetation parameters to per m^2 values to derive the corresponding dependent variables: seagrass standing crop (= g dry above-ground biomass m^{-2}), seagrass shoots m^{-2} (total and for each species), g dry below-ground biomass m^{-2} , and green algal holdfasts m^{-2} . Response variables for mobile fauna were total individuals m^{-2} , total individuals g^{-1} dry mass vegetation, and species richness. Cochran's tests (Underwood 1981, Kirk 1982, Day & Quinn 1989) indicated minor to moderate heteroscedasticity for several variables. This heterogeneity of variance was best mitigated by $\sqrt{y} + \sqrt{y+1}$ (Freeman & Tukey 1950, Kirk 1982) and \log_{10} transformations for vegetation and faunal data, respectively. After transformation, minor heteroscedasticity remained for 2 variables. Following significant repeated measures ANOVAs, I therefore made comparisons with the Welch-Aspin *t* test (Welch 1938, Aspin 1948) using Satterthwaite's degrees of

freedom (Satterthwaite 1946), because this test is robust to unequal variances (Day & Quinn 1989) with very little loss of power (Best & Rayner 1987). Although seagrass might be resistant to disturbance, it seemed improbable that algal mats would benefit seagrasses; I used 1-tailed tests for vegetation data. Directionality of effect for fauna was not predictable, so I used 2-tailed tests for these data. Although all tests were *a priori* orthogonal contrasts, I desired relatively tight control of type-1 error rate. I used the sequential Bonferroni adjustment (Holm 1979), which has greater power than the standard Bonferroni adjustment (Rice 1989), to correct probability values to familywise error rates. The families of contrasts were: all seagrass dependent variables, green algal density, and all dependent variables for mobile fauna. I provide both familywise and per contrast error rates.

RESULTS

Seagrass

Control and experimental plots did not differ significantly for any dependent variable prior to algal addition but were markedly different after algal addition. After 6 mo of algal cover, above-ground standing crop (Fig. 1A) and short shoot density (Fig. 1B) fell to about one-tenth of the levels of control plots and did not increase in the 6 mo following algal removal. After 18 mo of recovery, standing crop on the experimental plots was 29% of that on control plots but still differed significantly. Short shoots on experimental plots recovered to about half the density of the controls during this period. Below-ground biomass (Fig. 1C) on experimental plots was about one-half that of control plots after both 6 mo of algal cover and the ensuing 6 mo of recovery. Not a single green alga was quantified immediately after drift algal cover (Fig. 2). Green algae increased after 6 mo and reached 63% of control densities after 18 mo (not significant).

Most of the seagrass data are a function of *Thalassia testudinum*, because *Syringodium filiforme* and *Halodule wrightii* were comparatively sparse and patchily distributed. Although variance for the latter 2 species was high, there was some differential response among the 3 seagrasses. After 6 mo of algal cover, *T. testudinum*, *S. filiforme*, and *H. wrightii* fell to 12, 4, and 0% of their original densities, respectively (*T. testudinum*: 762 to 95; *S. filiforme*: 231 to 9; *H. wrightii*: 82 to 0 shoots m^{-2}). After 18 mo of recovery, *T. testudinum* and *S. filiforme* increased to about one-quarter of original densities. *H. wrightii*, however, increased to 261 shoots m^{-2} (SE = 130) which was over 3 times the original density of this species and equal to *T. testudinum* density after 18 mo.

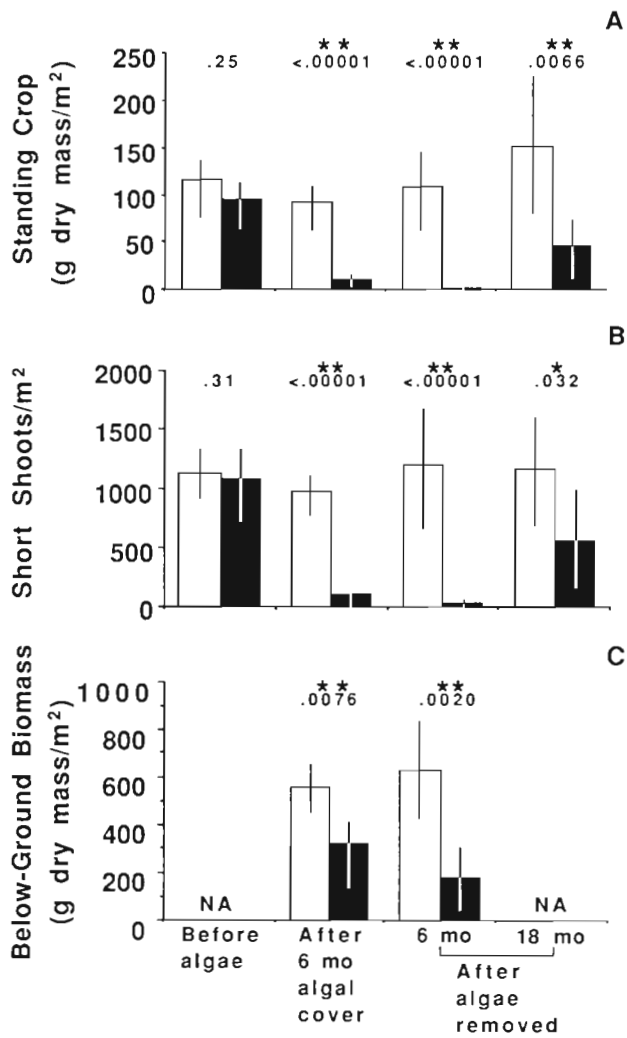


Fig. 1. Response of seagrass parameters to algal mat manipulations. (A) Standing crop, (B) shoot density, (C) below-ground biomass. Untransformed means on control (□) and experimental (■) plots are shown. NA: below-ground material was not collected during a given sampling series. Error bars are back-transformed 95% confidence intervals. *A difference between control and experimental plots which was significant at $p < 0.05$ following a 1-tailed Welch-Aspin t test. **A difference that was also significant at $p < 0.05$ following sequential Bonferroni correction to familywise error rate ($p = 0.033$)

Mobile fauna

Faunal abundance and species richness did not differ significantly between control and experimental plots before algal addition but diverged greatly during the experiment. Abundance of fauna on experimental plots increased after 6 mo of algal cover relative to abundance on control plots; this increase was by a factor of 6 when considered as a function of area (Fig. 3) or by a factor of 2 as a function of vegetation biomass (Fig. 4). Species richness was 4 times higher in the

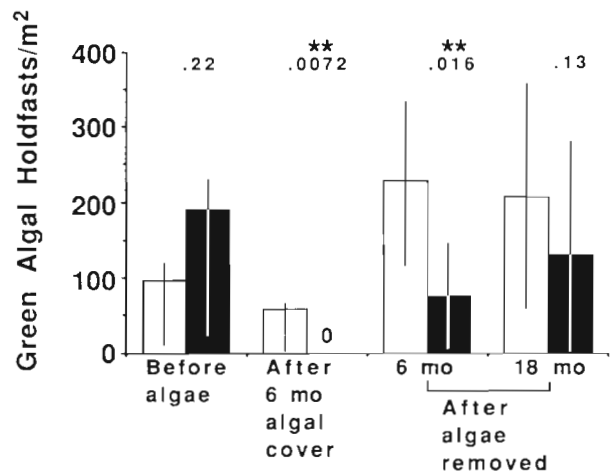


Fig. 2. Response of green algae (primarily *Caulerpa*, *Halimeda*, *Penicillus*, and *Udotea*) density to algal mat manipulations. Untransformed means on control (□) and experimental (■) plots are shown. Error bars as per Fig. 1. **A difference which was significant at $p < 0.05$ following sequential Bonferroni correction to familywise error rate ($p = 0.048$)

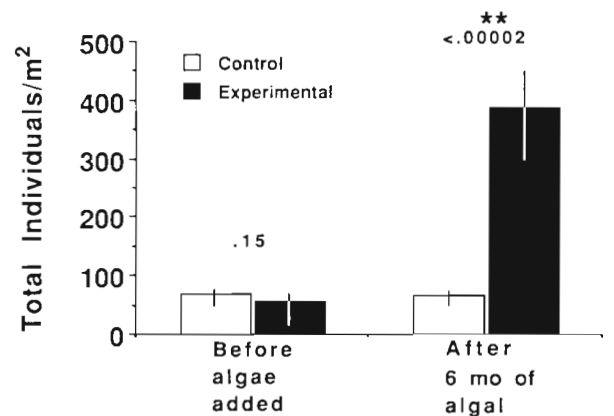


Fig. 3. Response of total individuals of canopy fauna m^{-2} to algal mat manipulations. Error bars as per Fig. 1; tests were 2-tailed. **A difference which was significant at $p < 0.05$ following sequential Bonferroni correction to familywise error rate ($p = 0.021$)

manipulated algal mats than in control seagrass plots (Fig. 5). My non-quantitative observations of plots in the months following algae removal revealed very few macrofauna on the denuded plots.

There was also greater evenness in the canopy fauna of the algal plots, which contrasted with the high level of dominance apparent on control plots (Table 1). The caridean shrimp *Thor floridanus* accounted for 72.1% of the total seagrass fauna; no other species represented >10% of the individuals quantified on control plots. In contrast, the dominant category for the algal

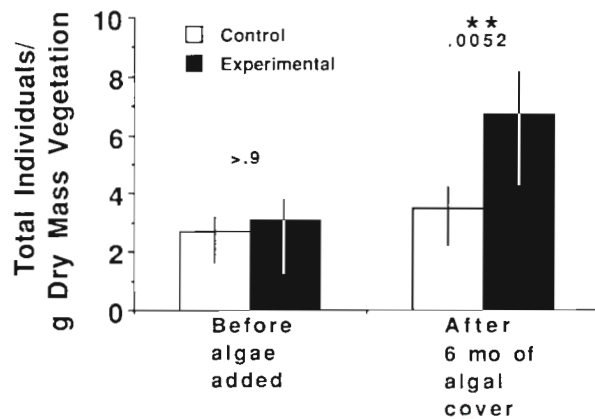


Fig. 4. Response of total individuals of canopy fauna g^{-1} dry mass of vegetation to algal mat manipulations. Error bars and ** as per Fig. 3

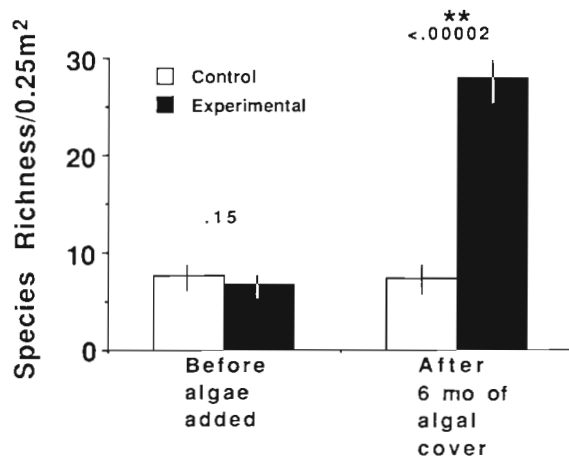


Fig. 5. Response of species richness of canopy fauna to algal mat manipulations. Error bars and ** as per Fig. 3

mats was Ophiuroidea, comprising 37.8% of the fauna; even this level of dominance was lessened, because this category was a composite grouping of 7 species of brittlestars. Several non-ophiroid species had relatively high abundance and less common species not presented in the table accounted for about 10% of the total individuals. Shrimps dominated the seagrass assemblage and comprised the 6 most common species and 93% of the total canopy fauna (Table 1). After algal cover, shrimps increased from 61 to 77 ind. m^{-2} but only represented 20% of the fauna. *Thor floridanus* and *Periclimenes americanus* increased in abundance, but *Hippolyte pleuracanthus* and *Periclimenes iridescens* were rare, and *Latreutes fucorum*, *Tozeuma carolinense*, and the commercial pink shrimp *Penaeus duorarum* were completely absent. Ophiuroids, crabs, gastropods, and bivalves were more common on the experimental, relative to the control, plots.

DISCUSSION

The superimposition of algal structure was a disturbance mechanism capable of opening sizable gaps in the seagrass canopy. Clarke & Kirkman (1989) described 3 levels of perturbations in seagrass meadows: Type 1—partial leaf damage; Type 2—total leaf destruction; and Type 3—leaf, rhizome, and root loss. The drift algal accumulations caused all 3 levels of damage to underlying seagrass over 6 mo (probably earlier; pers. obs.). This level of destruction occurred despite mitigation of stress via support of stressed by unstressed ramets (Tomasko & Dawes 1989) and reserves in the rhizome mat. Pickett & White (1985) suggest that root-biased systems are resistant to above-substratum disturbances, and seagrass meadows are decidedly root-biased. In south Florida, only 15 to 20% of total *Thalassia testudinum* biomass is comprised of seagrass blades (Zieman 1982), and roots and rhizomes accounted for about 84% of the total in

Table 1. Most common constituents of control seagrass plots and manipulated algal plots after 6 mo, given as number m^{-2} and percentage of total individuals collected for each treatment

	No. m^{-2}	%
Seagrass		
<i>Thor floridanus</i> Caridean shrimp	47.6	72.1
<i>Periclimenes americanus</i> Caridean shrimp	4.8	7.2
<i>Hippolyte pleuracanthus</i> Caridean shrimp ^a	3.2	4.9
<i>Latreutes fucorum</i> Caridean shrimp	2.3	3.5
<i>Periclimenes iridescens</i> Caridean shrimp	1.9	2.9
<i>Penaeus duorarum</i> Penaeid shrimp	0.9	1.4
<i>Mitrella argus</i> Gastropod	0.7	1.0
<i>Modulus modulus</i> Gastropod	0.7	1.0
<i>Astraea americana</i> Gastropod	0.5	0.8
<i>Tozeuma carolinense</i> Caridean shrimp	0.4	0.6
Other	3.1	4.7
Algal mats		
Ophiuroidea (> 7 spp.) Brittlestars ^b	147.0	37.8
<i>Thor floridanus</i> Caridean shrimp	65.5	16.8
<i>Paguristes tortugae</i> Hermit crab ^c	47.2	12.1
<i>Astraea americana</i> Gastropod	30.4	7.8
<i>Tegula fasciata</i> Gastropod	14.0	3.6
<i>Argopecten nucleus</i> Bivalve	11.7	3.0
<i>Mitrella argus</i> Gastropod	10.4	2.6
<i>Periclimenes americanus</i> Caridean shrimp	7.8	2.0
<i>Pagurus mclaughlinae</i> Hermit crab	7.4	1.9
<i>Neopanope packardii</i> Mud crab	7.0	1.8
Other	41.3	10.6

^aSee Gore et al. (1981) for discussion of *H. pleuracanthus-zostericola* complex

^b*Ophiopsila riisei* and *Ophionereis olivacea* were the most abundant brittlestars

^c*Paguristes tortugae* should be viewed as a species complex pending further systematic work (P. McLaughlin pers. comm.)

the meadows used in this study (Holmquist 1992). The below-ground component can reach 98% of total biomass in some systems (Williams 1990). Nevertheless, superimposed algae did cause extensive damage to this heavily root-biased meadow; the above-ground disturbance was sufficiently intense to damage the root-rhizome mat, a prerequisite for substantial alteration of such a system (Pickett & White 1985).

Although algal mats destroyed the primary structure utilized by seagrass-associated fauna on the experimental plots, the superimposed algae provided alternative structure that supported a highly abundant and species-rich assemblage of animals. Many of these species were present in seagrass as well (see also Virnstein & Howard 1987) but in lower numbers and with less regular occurrence. The high level of abundance and richness on the experimental plots was similar to that observed in naturally occurring algal mats and was maintained despite fairly low mean and minimum levels of dissolved oxygen (Holmquist 1992). In a study investigating effects of ice scour on the seagrass *Zostera marina* and associated fauna, Schneider & Mann (1991) found faunal abundances to rebound much more quickly than seagrass cover and attributed the rapid faunal recovery to growth of algae on the disturbed substrate. In my study, species that increased in abundance may have benefited from inherent characteristics of the algal mats such as provision of refuge from predation, enhanced food resources, or differential recruitment (e.g. Leber 1985, Eckman 1987, Duffy & Hay 1991, Pohle et al. 1991). Some animals were transported to the site with the accumulated algae, as is the case with naturally deposited algae (Holmquist 1994), and some of these fauna (or progeny thereof in the case of brooders) may have still been associated with the algal mats when they were sampled 6 mo after construction. Alternatively, other species may have benefited specifically from interaction of the algae with the seagrasses, particularly from increased production of seagrass detritus (an important resource for some seagrass fauna; Fenchel 1970, Sogard et al. 1987). Lastly, some species may have seemed to increase in abundance as a result of sampling in 2 different habitats. Sampling devices are rarely equally efficient on differing substrata, and some taxa, particularly molluscs, might be more easily captured in algae than in seagrass.

Some taxa, particularly shrimps, were conspicuously reduced in proportion in the algal mats. However, 2 common shrimps, *Thor floridanus* and *Periclimenes americanus*, increased in abundance, and Virnstein & Howard (1987) found crustaceans to be more abundant in clumps of algae than in seagrass. Positive responses of other taxa to algal mats, rather than negative responses by shrimps, may have led to the observed

proportional decrease in shrimp abundance. Nevertheless, several shrimp species present in the control seagrass were rare or absent in the macroalgal mats. Further, Holmquist (1994) found an average of 83 shrimps in small (25 cm diameter) algal clumps isolated in these seagrass beds. If abundance of shrimps increased linearly with additional volume of algal habitat, there should be well over 1000 shrimps m^{-2} algal mat rather than the observed 77 shrimps. This non-linearity in response to increased patch scale (see also Bell et al. 1995) suggests that shrimp could suffer disproportionately from the negative factors associated with algal mats (see 'Introduction'); for instance, these small natant species may be more susceptible to lower oxygen levels than more sedentary crabs, molluscs, and echinoderms.

Is an overlay of algal structure a source of disturbance for mobile fauna in grassbeds? With regard to the effect on fauna inhabiting seagrass structure that is newly covered by an algal mat, the answer is equivocal. Direct mortality is unlikely as algae accumulate a few clumps at a time; rather, small tumbling clumps harbor organisms (Holmquist 1994) and are likely to contribute animals to a local assemblage as the algae accumulate. Some species, including several shrimps, are probably reduced in proportion by slow emigration as the mat accumulates and the habitat changes. However, increased immigration of adults or recruitment of other taxa appear to more than compensate for the loss of overall abundance and biomass associated with reductions in some populations. The system does not appear to meet a commonly used criterion for disturbance effects: removal of biomass (Grime 1977). However, in a broader sense perturbation did occur: there was a deviation in a component of the ecological system (Rykiel 1985) and a disruption of community structure and change in resources (White & Pickett 1985). Although increased species richness of fauna was associated with a newly accumulated algal mat, it is unlikely that this increased diversity is a function of relaxation of pressure from competitive dominants as seen in other systems (e.g. Connell 1978, Sousa 1979). Drift algae provided a highly complex structure for fauna even as the mat destroyed the primary seagrass structure typically utilized by some of these animals. As Thistle (1981) and Van Blaricom (1982) suggested for other systems, it is probable that this provision of resources, rather than reduced competition, is responsible for the observed positive response of fauna.

Raffaelli et al. (1989) and Norkko & Bonsdorff (1996b) hypothesized that small mats of algae would have minimal negative, and possible positive, effects on underlying soft-substrate fauna but that contiguous mats would be detrimental. The same is probably true in the seagrass-macroalgal mosaic. Small algal patches

not coalesced into large mats do not kill underlying seagrass and are beneficial to fauna (Coen et al. 1981, Heck & Thoman 1981, Leber 1985). As an example, Holmquist (1992, 1994) found 25 cm diameter algal clumps to contain 2.3 and 7.5 times the number of epifauna as seagrass and sand, respectively, on a per unit area basis. The present study shows that larger mats can also support a high species richness and abundance of fauna, but the structural complexity provided by these larger *Laurencia* spp. mats is likely to be mitigated by ephemerality as Wilson et al. (1990) and Sogard & Able (1991) found for mats of the green alga *Ulva lactuca*. *Laurencia* spp. mats formed by drifting algae only persist for a period of months (Josselyn 1977, Virnstein & Carbonara 1985, Holmquist 1992); as the mats break up, structure for mobile fauna disappears. Even if a patch accumulates algal structure annually, the underlying gap exists in an unvegetated state during the balance of the year, during which time seagrass recovery progresses slowly (this study). Moreover, in addition to being ephemeral, the large algal patches degrade underlying seagrass structure. Although the high complexity of large mats formed by drifting algae augmented habitat for mobile fauna on a short temporal scale, longer-term effects on fauna are probably negative due to mat ephemerality and degradation of the less-complex, but consistently present, seagrass structure.

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