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SPECIES-SPECIFIC CHARACTERISTICS EXPLAIN THE PERSISTENCE OF *STIGEOCLONIUM TENUE* (CHLOROPHYTA) IN A WOODLAND STREAM[1]

Amy D. Rosemond[2] *and Susan H. Brawley*[3]

Department of Biology, Vanderbilt University, Nashville, Tennessee 37235

ABSTRACT

The heterotrichous alga Stigeoclonium tenue *Küetzing is dominant in many streams with high densities of herbivores. Previous* in situ *studies in Walker Branch (WB), a woodland stream in eastern Tennessee, indicated that dominance by* Stigeoclonium *basal cells was "grazer-dependent"; however,* Stigeoclonium *also appeared to have a lower biomass-specific productivity rate than other species that dominated when snails were experimentally removed. Here, an explicit test of the grazing dependence of* Stigeoclonium *was made with unialgal cultures established in the laboratory. Five different "assemblage types" were tested: 1 and 2) unialgal cultures of* Stigeoclonium *at low and high biomass, 3 and 4) a mixed assemblage of diatoms at low and high biomass, and 5) a natural stream community. Reduction in chlorophyll* a *after exposure to snail grazing was dependent on assemblage type (one-way ANOVA,* $P < 0.0001$*); low biomass* Stigeoclonium *tiles and tiles from the stream (on which basal cells of* Stigeoclonium *were dominant) were most grazer-resistant. In addition,* Stigeoclonium *had a lower biomass-specific productivity rate (measured as* $H^{14}CO_3^-$ *uptake) than a mixed assemblage of diatoms, regardless of biomass level, suggesting an underlying tradeoff between resistance to herbivory and competitive ability. Additional laboratory experiments were conducted to determine the response of* Stigeoclonium *to high (approx. 150* $\mu mol\ quanta \cdot m^{-2} \cdot s^{-1}$*) and low (approx. 25* $\mu mol\ quanta \cdot m^{-2} \cdot s^{-1}$*) irradiance when nutrients were at 1) ambient WB concentrations and 2) increased 1000× ambient concentrations. There was a positive response of growth to increased irradiance only under high nutrient conditions. This suggests that observed reductions in the abundance of* Stigeoclonium *under high irradiance/low nutrient conditions that occur on a seasonal basis in WB can be explained in part by autecological resource requirements of this alga. We use these results to model the response of algal communities dominated by basal-regenerating species (e.g.* Stigeoclonium*) to gradients in herbivory and productivity. The results of our culture studies, combined with an overview of factors affecting communities dominated by grazer-resistant species, illustrate how both broad-scale (e.g. functional form) and species-specific studies can be combined to achieve an understanding of community dynamics.*

Key index words: Chlorophyta; Elimia; *functional form theory; herbivory; irradiance; nutrients; snails; species-specific;* Stigeoclonium tenue

Herbivores can affect many characteristics of the autotrophic assemblages they graze (e.g. Huntly 1991, Brawley 1992, Steinman 1996). For example, when herbivores remove epiphytic or overstory species (= taxa), light and nutrient limitation to understory species may be relieved, but some shade-adapted species may disappear. In heavily grazed systems, herbivory can maximize biomass-specific productivity by creating communities low in biomass where all cells receive adequate light and nutrients. Alternatively, herbivores may reduce the biomass-specific productivity of plant or algal communities, possibly due to a tradeoff between species' resistance to herbivory and competitive ability (Lubchenco and Gaines 1981, Coley et al. 1985, Huntly 1987). Central to this hypothesis, which has been supported by several experimental studies (cf. Huntly 1991, but see Simms and Rausher 1987), is that a physiological cost is associated with herbivore resistance that nonresistant species do not incur. Because of this "peace dividend," nonresistant species have more energy to devote to growth or reproduction and are better resource competitors than grazer-resistant species as long as herbivores are absent. If this tradeoff plays an important role in determining community structure, species that are resistant to herbivory should persist under heavily grazed conditions. When a reduction in herbivory occurs, species that are less resistant should replace "defended" species due to their superior competitive ability.

Results from experiments conducted in a woodland stream support the tradeoff hypothesis; snail grazers reduced biomass, as well as biomass-specific growth rates of algae, compared to ungrazed controls (Rosemond 1993a, Rosemond et al. 1993). This suggests that competitive subordinates (species with lower growth rates) could dominate the community when herbivores were present. Community composition was very different between grazed and ungrazed treatments; basal cells of *Stigeoclonium tenue* Küetzing (hereafter referred to as *Stigeoclonium*) dominated grazed communities, and a mixed assemblage of diatoms dominated ungrazed communities.

Although *Stigeoclonium* was typically the dominant alga (contributing >45% of total algal biovolume at all times) in Walker Branch (WB) where the experimental work was conducted, seasonal variation in nutrients and irradiance affected its absolute and

[1] Received 11 July 1995. Accepted 25 October 1995.

[2] Present address and author for reprint requests: Institute of Ecology, University of Georgia, Athens, Georgia 30602.

[3] Present address: Department of Plant Biology and Pathology, University of Maine, Orono, Maine 04412.

relative abundance. In general, *Stigeoclonium* was less abundant at peak irradiances and minimal nutrient concentrations than under other conditions. In addition, we found a negative correlation between irradiance and the percentage abundance of *Stigeoclonium* on an annual basis (Rosemond 1994) and lower biovolume in the spring than in the summer months (Rosemond 1995) in WB.

In this study, we investigated some potential mechanisms to explain why *Stigeoclonium* persisted when snails were present at natural densities and why it was overgrown by other species of algae when snails were experimentally removed. We explicitly tested the resistance of algal species to herbivory by comparing the ability of the snails to reduce the biomass of *Stigeoclonium* versus the biomass of diatom assemblages. We also tested whether algal species that proliferated in the absence of snails (i.e. diatoms) had higher biomass-specific growth rates than *Stigeoclonium*. Using the tradeoff hypothesis, we predicted that diatoms would be more susceptible to herbivory than basal cells of *Stigeoclonium* and that diatom assemblages had higher growth rates (as an indicator of competitive ability) than *Stigeoclonium*, regardless of biomass level. We compared grazer resistance and growth rates of *Stigeoclonium* and diatom assemblages at both high and low biomass to separate the confounding effects of biomass level and species composition (both of which changed when grazers were removed in stream-side channels [Rosemond 1993a]). Our hypothesis was that changes we had observed in biomass-specific growth rates were due to changes in species dominance (based on tradeoffs between herbivore resistance and competitive ability), not changes in biomass.

In the second part of this study, we determined why *Stigeoclonium* was relatively less abundant under some conditions (high light and low nutrients) than others (low light or high nutrients) when grazers were present. To do this, we studied the growth of *Stigeoclonium* in unialgal culture under different light conditions in low-nutrient stream water and in stream water enriched with nitrogen (N) and phosphorus (P). These data would help explain, in part, how dominance of *Stigeoclonium* varied with seasonal changes in nutrient and light availability in a natural stream ecosystem.

MATERIALS AND METHODS

Walker Branch, a first-order stream located on the Department of Energy's Oak Ridge Reservation in Oak Ridge, Tennessee, flows through a forested watershed. Irradiance reaching the stream is reduced by the deciduous tree canopy from May to October to <1 mol quanta·m^{-2}·d^{-1}. Following leaf-fall, irradiance increases and reaches a peak (to approximately 4–6 mol quanta·m^{-2}·d^{-1}) in early April (Rosemond 1994). Nutrient concentrations in stream water exhibit a peak in the summer months and are lowest in the autumn and winter but, in general, are relatively low during all seasons (Mulholland 1992). The invertebrate community in WB is dominated by the grazing snail, *Elimia clavaeformis*, which occurs at densities >1000 individuals·m^{-2} year-round (Rosemond 1994).

Tests of herbivore resistance vs. competitive ability. We established growth of five different types of algal assemblages on unglazed, ceramic tiles (area = 5.3 cm^2) and compared them in terms of 1) resistance to snail grazing and 2) competitive ability, which was measured as biomass-specific productivity rate. The five assemblages were 1) *Stigeoclonium* (low biomass), (LOSTIG) 2) *Stigeoclonium* (high biomass) (HISTIG), 3) a mixed assemblage of diatoms (low biomass) (LODIAT), 4) a mixed assemblage of diatoms (high biomass) (HIDIAT), and 5) the ambient community in WB (STREAM).

Stigeoclonium was scraped from rocks in WB, cleaned of epiphytes and isolated from other species of algae (by dragging filaments through 2% agar), and grown in WC medium (Guillard 1975). To achieve a similar growth of *Stigeoclonium* on the standardized substrate, clumps of the alga were broken up using a tissue homogenizer and spread over tiles in Pyrex pans. *Stigeoclonium* is heterotrichous, having the ability to produce both upright and prostrate filaments (also referred to as basal cells), the later of which predominate under grazed conditions. Half of the *Stigeoclonium* assemblages were allowed to produce upright filaments and half of the assemblages were maintained in a simulated "grazed" state by scraping them every 1–2 d with a plastic comb (Idea Scientific, Inc., 14-well comb for gel electrophoresis). Biomass accrued on all tiles for approximately 3 weeks in an indoor culture chamber (Hotpak Inc.) with light levels at approximately 80 μmol quanta·m^{-2}·s^{-1} on a 10:14 h LD photoperiod (2.9 mol quanta·m^{-2}·d^{-1}) at 17° C.

Diatom assemblages were established over a 3-week period on ceramic tiles in the stream-side channels previously described in Rosemond (1993a). Results of previous experiments indicated that for a high biomass of diatoms to accrue in WB, snails had to be removed and nutrients (N and P) and light had to be increased over ambient levels. A solution of $NaNO_3$ and K_2PO_4 was continuously dripped into the channels to yield final concentrations of approximately 250 μg N·L^{-1} and 50 g P·L^{-1}. Light levels above the channels were elevated to 300 μmol quanta·m^{-2}·s^{-1} (approx. 10 mol quanta·m^{-2}·d^{-1}) as in Rosemond (1993a). Low-biomass diatom tiles were created by scraping off upper layers of cells with the same plastic comb used to "graze" the *Stigeoclonium* tiles.

On 28 March 1991, all algal assemblages were placed in the stream-side channels under ambient light and nutrient conditions. Tiles that had been placed in WB for >1 year (STREAM tiles) were also collected and placed in the channels. The study investigating short-term differential resistance to grazing was begun on the same day (28 March). Three tiles of each of the five assemblage types were placed in small (78-cm^2), flow-through chambers in a large plastic tray. Stream water was pumped from WB through the tray and overflowed back into the stream. Four replicate chambers were used for each assemblage, giving a total of 20 chambers each containing three tiles of one type of assemblage. Three snails of similar size were placed in each chamber and allowed to graze for 19 h. At the end of the experiment, tiles were collected from the chambers, and chlorophyll *a* was extracted in 10 mL dimethyl sulfoxide (DMSO) and determined spectrophotometrically (Palumbo et al. 1987). We then determined the reduction in chlorophyll *a* for each tile, based on an initial estimate of chlorophyll *a* from measurements made on 12 tiles of each assemblage type. Values that were used in statistical analyses were means of chlorophyll *a* reduction on the three tiles from replicate chambers. We used a one-way analysis of variance (ANOVA) (SAS 1988) to determine whether there were differences in chlorophyll reduction with assemblage type and a post-ANOVA multiple comparison test (Ryan's *Q*-test, Day and Quinn 1989) to determine differences between assemblages.

We then measured biomass-specific carbon fixation rates (as an indicator of competitive ability) of the five assemblage types on

29 March 1991. Tiles from the same pool of tiles used for the preceding grazing study were collected from the stream-side channels (where they had been for the previous 24 h under ambient stream conditions) and placed in recirculating chambers (approx. velocity = 30 $cm \cdot s^{-1}$, W. R. Hill, pers. commun.) in the laboratory containing 1 L of filtered (Gelman Type A/E filter) WB stream water. Three tiles of each type were placed in each of four chambers. Irradiance above the chambers was maintained at 220 μmole quanta $\cdot m^{-2} \cdot s^{-1}$, typical of springtime levels in WB. $NaH^{14}CO_3$ (specific activity 0.74 Mbq $\cdot mmol^{-1}$) was added to the water in each chamber, and $H^{14}CO_3^-$ uptake during a 3-h incubation was determined as described in Rosemond (1993a) following extraction of cells in DMSO. Phaeopigment-corrected chlorophyll *a* was determined spectrophotometrically (Strickland and Parsons 1972), and $H^{14}CO_3^-$ uptake was measured by liquid scintillation on subsamples of the extract (Palumbo et al. 1987). A one-way ANOVA, followed by Ryan's *Q*-test (Day and Quinn 1989), was used to determine differences in carbon fixation rates among assemblage types.

For determination and verification of species composition, an additional three tiles of each assemblage type were scraped with a toothbrush and the resultant slurry was preserved in 2% glutaraldehyde. Algal cells (>300/sample) were counted and identified at 400× using a Palmer-Maloney cell. Biovolumes were determined as in Rosemond (1993a).

Tests of irradiance and nutrient effects on Stigeoclonium. To determine effects of light and nutrients on *Stigeoclonium*, without the confounding effects of these factors on other algal species, we conducted two laboratory experiments using unialgal cultures. Each experiment lasted 12 days (26 April to 8 May 1991 and 9–21 September 1991). Prior to each experiment, we established growth of *Stigeoclonium* on unglazed ceramic tiles in an indoor culture chamber (as in the preceding study). We wanted to start the experiments with the prostrate growth form of *Stigeoclonium* being dominant, similar to what is found under field conditions in WB. Therefore, *Stigeoclonium* was established on the tiles, and after approximately 10 d snails were added to the Pyrex pans containing the tiles to graze the algae. We found that grazing by snails was much more effective in developing *Stigeoclonium* thalli that were dominated by basal cells than the artificial grazing technique previously used.

We used water collected from WB on 19 April 1991, which was filter-sterilized (with 0.22-μm Millipore Sterivex-GV filters), for media in the first experiment. For the second experiment, we used water collected from WB on 30 August 1991, which was filter-sterilized, and to which 1.55 mg $\cdot L^{-1}$ P as K_2HPO_4 and 14 mg $\cdot L^{-1}$ N as $NaNO_3$ were added. For each experiment, eight tiles were placed in the bottom of eight culture dishes (area = 71 cm^2), in 150 mL of media. During the first experiment 100 mL of the 150 mL of media were changed twice (after 3 and 5 d), and during the second experiment 100 mL of media were replaced every other day, to maintain high concentrations of nutrients. Initial and final aliquots of media were collected from each dish during each experiment. Media were filtered through a 0.22-μm filter and stored frozen in acid-washed plastic bottles until nutrient analyses were conducted. Concentrations of soluble reactive phosphorus (SRP), ammonium nitrogen (NH_4^+-N), and nitrate plus nitrite nitrogen ([NO_3^- + NO_2^-]-N) were measured in the media filtrate. Concentrations of SRP were measured using the ascorbic acid method (American Public Health Association 1985), NH_4^+-N by phenate colorimetry using an autoanalyzer (Technicon TRAACS 800) and [NO_3^- + NO_2^-]-N by Cu-Cd reduction followed by automated colorimetric analysis (U.S. Environmental Protection Agency 1983).

Under the two different nutrient conditions we established using the ambient and nutrient-enriched stream water as media, we tested for effects of irradiance and snail grazing on growth of *Stigeoclonium* using a factorial design. Treatments consisted of 1) grazed, high light (approx. 150 μmol quanta $\cdot m^{-2} \cdot s^{-1}$) (G/L), 2) ungrazed, high light (U/L), 3) grazed, shaded (approx. 25 μmol quanta $\cdot m^{-2} \cdot s^{-1}$) (G/S), and 4) ungrazed, shaded (U/S). All light treatments were on a 10:14 h LD photoperiod. Treatments were duplicated and randomly assigned among the culture dishes. Different irradiance treatments were achieved using a bank of cool-white fluorescent lights behind the culture dishes and a bank of lights suspended above the dishes. A "wall" of foil was placed in front of the dishes to equalize light levels between the front and back. Low light levels were created by surrounding each low light culture dish with three layers of neutral density netting (green mosquito netting). Grazed treatments received four snails per dish, simulating stream densities of 1000 snails $\cdot m^{-2}$ (Rosemond 1994). Because of observed snail inactivity in the high-light treatments in the high-nutrient experiment (see Results), snails were replaced during the high-nutrient experiment on 13 September and every 2 d thereafter.

At the end of each experiment, four tiles were collected from each culture dish, and each was placed in 3 or 6 mL of 90% acetone for extraction of pigments. Chlorophyll *a* was determined from the difference in absorbance at 663 nm before and after acidification of the pigment extract (Wetzel and Likens 1979). The remaining four tiles were collectively scraped using a razor blade and a stiff nylon brush, and the resultant slurry was preserved in 2% glutaraldehyde for cell counts. To estimate algal biovolume, >500 cells were counted per sample using a Palmer-Maloney cell. Dimensions of >50 cells were measured using an ocular micrometer, and average biovolumes of basal and erect cells were determined to convert cell density to biovolume. Two sets of four tiles were used for estimates of initial biovolume in both experiments. A new variable, Chl : biovolume (chlorophyll *a* concentration/biovolume), which normalized the amount of chlorophyll *a* to total algal biovolume, was calculated and compared among treatments. Effects of light and snail grazing on final *Stigeoclonium* biovolume (log transformed prior to analysis [Zar 1984]) and Chl : biovolume were determined by two-way ANOVA (SAS 1988).

RESULTS

Herbivore resistance vs. competitive ability. Algal assemblages on HISTIG tiles were comprised predominantly of upright filaments of *Stigeoclonium* (Table 1). Our grazing technique on LOSTIG tiles did not produce the intended predominance of basal cells of *Stigeoclonium*; however, biovolume of basal cells on LOSTIG tiles was greater than on the HISTIG tiles. Algal assemblages that colonized tiles in WB (STREAM) were dominated by basal cells of *Stigeoclonium*. Both HIDIAT and LODIAT tiles were dominated by *Peronia intermedium* (H. L. Sm.), with *Gomphonema olivaceoides* (Hust.), *Melosira varians* (Ag.), and *Nitzschia linearis* (W. Smith) contributing >5% of biovolume (Table 1).

Algal assemblages differed significantly in the quantity of chlorophyll *a* lost after 19 h of snail grazing (one-way ANOVA, $F = 42.97$, $P < 0.0001$, $df_{4,19}$). STREAM and LOSTIG assemblages lost the least chlorophyll, indicating that they were most resistant to grazing. The low and high biomass diatom assemblages (LODIAT, HIDIAT) lost >2.5 times more than the LOSTIG tiles, and the HISTIG tiles lost the greatest amount of chlorophyll *a* (Fig. 1).

Chlorophyll-specific carbon fixation rates also differed among algal assemblages (one-way ANOVA, $F = 45.39$, $P < 0.0001$, $df_{4,57}$). Diatom assemblages

TABLE 1. *Species composition (by biovolume) and biomass (chlorophyll a) of different "assemblage types" used in the grazing and productivity studies. LOSTIG = low biomass of* Stigeoclonium, *HISTIG = high biomass of* Stigeoclonium, *LODIAT = low biomass of mixed diatom assemblage, HIDIAT = high biomass of mixed diatom assemblage, STREAM = community growing on tiles in WB. Only species comprising ≥5% biovolume are listed. Chl a = chlorophyll a in μg·cm⁻² (basal) = basal cells, (erect) = erect cells.*

Assemblage type	Species	% Biovolume	Chl *a*
STREAM	*Stigeoclonium tenue* (basal)	79.9	2.97
	Cocconeis placentula	9.3	
	Audouinella sp.	5.3	
HISTIG	*Stigeoclonium tenue* (erect)	92.2	2.56
	Stigeoclonium tenue (basal)	4.9	
LOSTIG	*Stigeoclonium tenue* (erect)	64.6	0.66
	Stigeoclonium tenue (basal)	33.5	
HIDIAT	*Peronia intermedium*	74.4	4.71
	Melosira varians	8.8	
	Gomphonema olivaceoides	7.9	
LODIAT	*Peronia intermedium*	60.5	2.33
	Gomphonema olivaceoides	11.6	
	Nitzschia linearis	8.5	

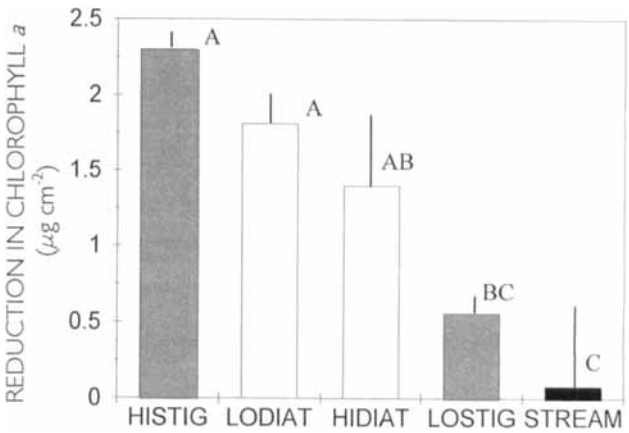

FIG. 1. Reduction in biomass (chlorophyll *a*) of different algal assemblage types after exposure to snail grazing. LOSTIG = low biomass of *Stigeoclonium*, HISTIG = high biomass of *Stigeoclonium*, LODIAT = low biomass of mixed diatom assemblage, HIDIAT = high biomass of mixed diatom assemblage, STREAM = community growing on tiles in Walker Branch. Means having the same letter are not significantly different by Ryan's *Q*-test. Bars = ±1 SE.

had greater chlorophyll-specific carbon fixation rates than *Stigeoclonium*, regardless of biomass level, and STREAM tiles had the lowest rates (Fig. 2).

Irradiance and nutrient effects on Stigeoclonium. Approximately 5-fold differences in light levels between high-light and low-light treatments were achieved in both laboratory experiments. Some variation in light existed among culture dishes, but irradiance ranged from 110 to 150 μmole quanta·m^{-2}·s^{-1} in high-light treatments (typical springtime light levels in WB) and from 20 to 30 μmole quanta·m^{-2}·s^{-1} in low-light treatments (typical summertime light levels in WB).

Nitrate and ammonia concentrations in the low-nutrient experiment (Table 2) were similar to streamwater concentrations at the time of the experiment in WB (NO_3^- = 17 g·L^{-1} and NH_4^+ = 0 g·L^{-1} on 8 April 1991, P. J. Mulholland, pers. commun.). Although SRP was not measured in this experiment, concentrations were assumed to be similar to those in WB, which were quite low (SRP = 1.7 g·L^{-1} on 8 April 1991, P. J. Mulholland, pers. commun.). There were no treatment effects on final nutrient concentrations in the low-nutrient experiment (Table 3); however, at the end of the experiment, the G/S treatment had the highest nitrate and ammonia concentrations (Table 2), suggesting that algal uptake was lower or remineralization of nitrogen was greater under shaded, grazed conditions than in other treatments.

Initial concentrations of N and P in the high-nutrient experiment were approximately 3 orders of magnitude higher than those used in the low-nutrient experiment (Table 2). Again, in media assayed at the end of the experiment, nutrient concentrations were generally highest in the G/S treatment, suggesting the lowest rates of net nutrient uptake or greatest remineralization (Table 2). Increased irradiance reduced final SRP and snail presence increased final SRP in the media (Table 3). Trends in NO_3^- and NH_4^+ were similar to SRP, but there were no significant treatment effects on their final concentrations.

In the low-nutrient experiment, increases in irradiance resulted in no significant increase in *Stigeoclonium* biovolume (Table 4, Fig. 3a). Chl:biovolume ratio was lowered at elevated light levels (Table 4, Fig. 3b), and thalli in both high-light treatments (G/L and U/L) were visibly "bleached" (i.e. pale yellow vs. green in color) compared to shaded treatments (Rosemond, pers. observ.). Grazers had a determining influence on both biovolume and quantity of chlorophyll *a* per biovolume. Snail grazing resulted in a net decrease in *Stigeoclonium* biovolume (Table 4, Fig. 3a) and an increase in Chl:biovolume ratio under both light conditions (Table 4, Fig. 3b).

In contrast to the lack of effects of irradiance under low-nutrient conditions, increased irradiance under high-nutrient conditions resulted in dramatic increases in *Stigeoclonium* biovolume (Table 4, Fig. 4a). For ungrazed treatments, *Stigeoclonium* growth was 64 times greater in the high-light treatments and 47 times greater in the shaded treatments when nutrients were at elevated levels (Fig. 4a), compared to growth in unamended stream water (low-nutrient experiment, Fig. 3a). Grazers were more effective at removing biomass under shaded than high-light conditions, where differences between grazed and ungrazed treatments were small (Fig. 4a). Snails became inactive after several hours in high-light treatments, in contrast to maintaining a high level of

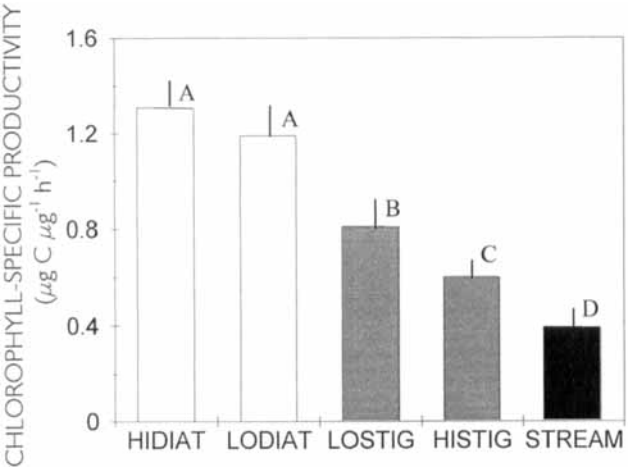

FIG. 2. Chlorophyll-specific productivity of different algal assemblage types. Assemblage types as in Figure 1. Means having the same letter are not significantly different by Ryan's *Q*-test. Bars = ±1 SE.

activity in shaded grazed treatments. When these snails were moved to dishes containing only stream water at similarly high light levels, they resumed "normal" behavior within hours, suggesting that they had become satiated on the high algal biomass in high-light treatments and were not otherwise affected. No effect of grazing on algal biovolume was found in the high-nutrient experiment, presumably due to the high variability in biovolume in the G/S treatment and the reduced effectiveness of snails in the G/L treatment. Trends in Chl : biovolume ratio were similar to those under low-nutrient conditions (highest in grazed, shaded treatments and lowest in high-light, ungrazed treatments), but high variability in the grazed, shaded replicates precluded any statistical effects (Table 4, Fig. 4b). The effect of high-light treatments on thallus color was remarkably less in this experiment than under low-nutrient conditions. All treatments were bright green in appearance (Rosemond, pers. observ.), although the G/L and U/L treatments were slightly more yellow-green than the shaded treatments.

DISCUSSION

Effects of herbivory. The characteristic algal community of WB exists primarily because of herbivory, coupled with species-specific characteristics of its dominant alga, *Stigeoclonium*. The results of this study show that unialgal cultures of *Stigeoclonium*, regardless of growth form (the predominance of erect vs. prostrate filaments), had low biomass-specific productivity compared to diatom assemblages and that the prostrate portion of this heterotrichous plant is the basis of its grazer resistance. Additional examples from terrestrial and marine systems (Lubchenco 1978, Hay 1981, Steneck 1982, McNaughton 1984, Huntly 1987, Lewis et al. 1987, Power et al. 1988, Steneck and Dethier 1994) indicate that grazer-dependent benthic floras often have a common characteristic: they typically have basal systems from which regeneration takes place.

In general, basal-regenerating species may have slower growth rates than other species that are grazer-susceptible, due to the underlying tradeoff between herbivore resistance and competitive ability. In this study, as well as others (J. Menge [= Lubchenco] 1975, Hay 1981, see references in Steinman 1996), lower biomass-specific productivity rates were found for grazer-resistant species or morphological types than for less resistant species. The lower productivity of grazer-resistant species has been attributed to the expenditure of energy for structural or chemical defenses that would otherwise go into growth or reproduction. This can occur on either an ecological (linked to phenotype or growth form) or evolutionary (linked to genotype) time scale. Our data suggest that this partitioning may be "fixed" genetically for *Stigeoclonium*, because both forms of *Stigeoclonium*, upright filaments and basal cells, had lower biomass-specific growth rates than the diatom assemblages that replaced them in the absence of grazers. Heteromorphic life histories of many marine (e.g. Paine et al. 1979, Lubchenco and Cubit 1980, Hay 1981, Dudgeon et al. 1995) and freshwater algae (see references in Steinman 1996) should be advantageous when there is pronounced temporal or spatial variation in disturbance. However, in aquatic systems like WB, in which a constant and high level of biological disturbance (i.e. herbivory) occurs, expression of heteromorphy (including heterotrichy) may be restricted to only basal, herbivore-resistant forms having inherently low rates of productivity. Apparently, both abiotic (scouring, other physical disturbances) and biotic (herbivory, bioturbation) disturbances can favor basal species.

The reduced productivity of the grazed communities cited above contrasts with results of other studies wherein grazing increased biomass-specific productivity rates (e.g. McNaughton 1976, 1979, Lamberti and Resh 1983, Ward et al. 1985, Stewart 1987, Gelwick and Matthews 1992). In these studies, there may have been more temporal or spatial escapes for plants from herbivory, allowing co-existence of a greater number of species with different growth forms than observed in WB and other studies where *Elimia* is the dominant herbivore. In a recent review of herbivore effects on freshwater algae, Steinman (1996) noted that all studies that reported reductions in biomass-specific productivity rate due to herbivory (in contrast to null or positive effects) involved grazing by *Elimia clavaeformis*. In addition, these communities were dominated by basal cells of *Stigeoclonium*. The plant/herbivore combination of *Elimia* and *Stigeoclonium* may represent a case that is on the extreme end of grazing intensity. A characteristic of *Elimia* may result in maintenance of high densities of these herbivores, despite typically low algal biomass: it can feed facultatively on both algae

TABLE 2. *Nutrient concentrations in low-and high-nutrient* Stigeoclonium *culture studies. Treatments: G/S = grazed, shaded, G/L = grazed, high light, U/S = ungrazed, shaded, U/L = ungrazed, high light. Values, in $\mu g/L^{-1}$, are means of two samples ± 1 SD, except where indicated. nm = not measured.*

Treatment	NO_3	NH_4	SRP
Low-nutrient experiment			
Initial (n = 1)	15.2	2.19	
G/S	44.1 (52.0)	27.1 (13.2)	nm
G/L	7.3 (3.5)	5.3 (2.2)	nm
U/S	11.1 (0.7)	4.6 (2.6)	nm
U/L	21.8 (10.8)	6.8 (1.2)	nm
High-nutrient experiment			
Initial	19,150 (70.7)	9.8 (2.8)	1110 (28.3)
G/S	13,540 (6279)	60.7 (38.9)	1233.5 (167.6)
G/L	9115 (417)	13.8 (5.66)	10.0 (7.1)
U/S	15,195 (983)	9.6 (7.1)	737.5 (139.3)
U/L	7605 (1379)	13.8 (4.5)	5.0 (0)

and leaf detritus. Snails allowed access to inputs of leaf litter in autumn (in *in situ* "corrals" in WB) grew >4 times more than snails that had access to periphyton but not leaf litter over a 42-d period (27 October to 7 December 1990) (Rosemond, unpubl. data). Leaf detritus, which is abundant in autumn in headwater streams where *Elimia* is abundant, may produce snail densities that are greater than those that could be supported by algae alone, resulting in "overgrazing" of algae at other times of the year.

Effects of resources. Whereas *Stigeoclonium*'s resistance to herbivory may explain its general dominance in the benthic algal community of WB, other characteristics of this alga may help explain seasonal changes in its abundance. Specifically, the high-nutrient requirement of *Stigeoclonium* may be important. In this study, there was a trend toward an acclimation response (i.e. a reduction in chlorophyll *a* content per unit biovolume) (Falkowski and LaRoche 1991) under both high- and low-nutrient concentrations when irradiance was increased (Richardson et al. 1983). However, increased irradiance at levels that mimicked natural levels of this resource in spring in WB resulted in an increase in *Stigeoclonium* biovolume only when concentrations of N and P were increased above natural streamwater concentrations, suggesting that the response of *Stigeoclonium* to irradiance is nutrient-dependent. *Stigeoclonium* has been used previously as an indicator of eutrophication, and many studies in addition to ours indicate that this alga requires high concentrations of N and P for rapid growth (e.g. McLean and Benson-Evans 1974, Francke and ten Cate 1980, De Vries et al. 1983, Chessman et al. 1992).

TABLE 3. *Irradiance and grazing effects on final nutrient concentrations in* Stigeoclonium *culture studies. Values shown are* F *values from two-way ANOVA.* ***P ≤ *0.001,* *P ≤ *0.05,* +P ≤ *0.10. nm = not measured. + = positive effect; − = negative effect.*

Treatment effect	NO_3	NH_4	SRP
Low-nutrient experiment			
Light	0.48	4.08	nm
Grazing	0.24	(+)4.69+	nm
Light × grazing	1.60	6.13+	nm
High-nutrient experiment			
Light	(−)6.80+	2.25	(−)160.96***
Grazing	0	3.24	(+)10.56*
Light × grazing	0.47	3.24	10.14*

TABLE 4. *Effects on total algal biovolume and the ratio between chlorophyll* a *and total algal biovolume (Chl : bio) determined by ANOVA.* F *values are listed.* *P ≤ *0.05,* +P ≤ *0.10. ns = not significant. + = positive effect; − = negative effect.*

Treatment effect	Biovolume	Chl : bio
Low-nutrient experiment		
Overall	5.26+	6.72*
Light	0.04 (ns)	(−)6.08+
Grazing	(−)15.73*	(+)8.87*
Light × grazing	0 (ns)	5.21+
High-nutrient experiment		
Overall	6.46*	1.49 (ns)
Light	(+)9.79*	1.87 (ns)
Grazing	(−)5.67+	1.30 (ns)
Light × grazing	3.93 (ns)	1.28 (ns)

The effects of *Stigeoclonium*'s high-nutrient demand are also evident from seasonal changes in its abundance in WB. When the stream is shaded (summer), concentrations of N and P are at their annual peak. Biovolume of *Stigeoclonium* is significantly higher in the summer than early spring in WB, when light levels are high and nutrient concentrations are low (Rosemond 1995). The lack of greater growth by *Stigeoclonium* and the yellowing that we observed when irradiance was increased in the low-nutrient experiment suggest that *Stigeoclonium* does not benefit from increases in light, even at relatively low levels (150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) when nutrient concentrations are low, as during spring in WB. In a stream nearby WB, algal communities dominated by *Stigeoclonium* had greater maximal photosynthetic rates per unit area (P_{MAX}) and greater initial slope (α) in photosynthesis–irradiance (P-I) curves at shaded sites (irradiance = 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) compared to open sites (irradiance = 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Hill et al. 1995). These data support our hypothesis that photosynthetic performance of *Stigeoclonium* is dependent on irradiance and is poor when light levels increase seasonally in headwater streams.

Presumably, other algal species can respond positively to increases in irradiance in low-nutrient streams like WB. Evidence from two previous studies in WB suggests that other species of algae have steeper positive responses to increases in irradiance and can outcompete *Stigeoclonium* for space under high-light and low-nutrient concentrations, thereby reducing its relative abundance. Rosemond (1994) found a negative correlation between the percentage abundance of *Stigeoclonium* and irradiance on an annual basis in WB, and Steinman (1992) found a reduction in the relative abundance of *Stigeoclonium*

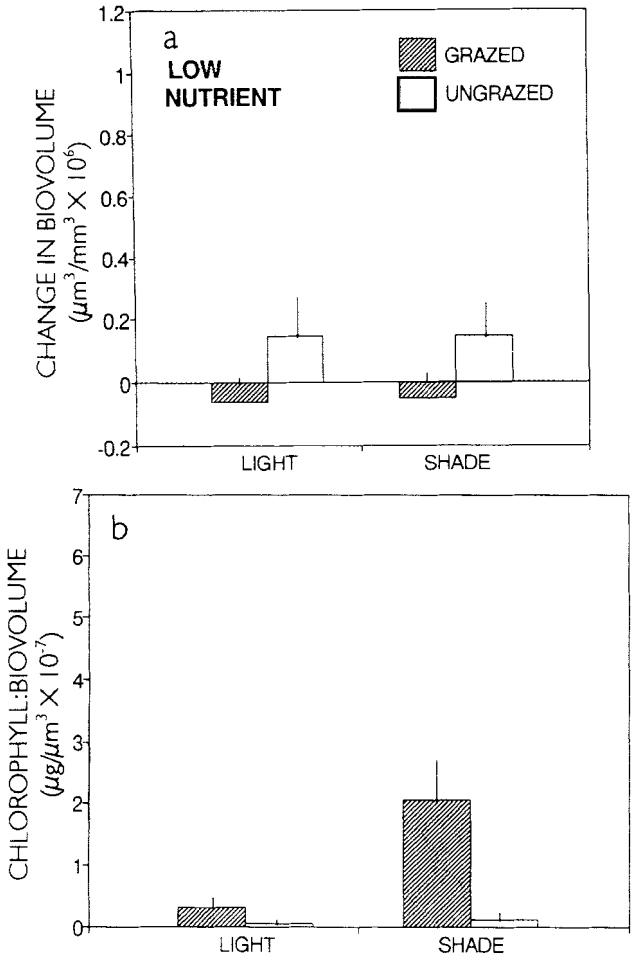

FIG. 3. Response of *Stigeoclonium* to two different light regimes (light = 150 μmol quanta·m^{-2}·s^{-1}, shade = 25 μmol quanta·m^{-2}·s^{-1}) under low-nutrient culture conditions in the presence (treatments = grazed) and absence (treatments = ungrazed) of snails. Experiment lasted 12 d. a) Change in *Stigeoclonium* biomass (as measured by biovolume) from the beginning to the end of the experiment. b) Ratio of chlorophyll *a* to biovolume (Chl : biovolume) measured at the end of the experiment. Bars = ±1 SE.

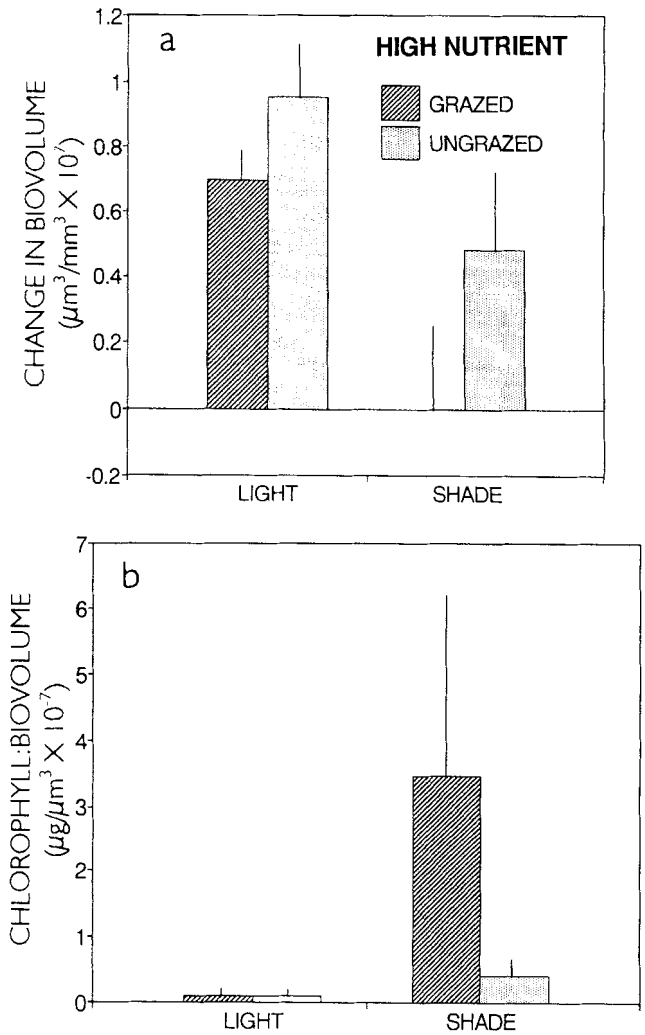

FIG. 4. Response of *Stigeoclonium* to two different light regimes (light = 150 μmol quanta·m^{-2}·s^{-1}, shade = 25 μmol quanta·m^{-2}·s^{-1}) under high-nutrient culture conditions in the presence (treatments = grazed) and absence (treatments = ungrazed) of snails. Experiment lasted 12 d. a) Change in *Stigeoclonium* biomass (as measured by biovolume) from the beginning to the end of the experiment. Note that y axes of Figures 3a and 4a differ by 1 order of magnitude. b) Ratio of chlorophyll *a* to biovolume (Chl : biovolume) measured at the end of the experiment. Bars = ±1 SE.

when light levels were experimentally increased in WB. However, other species, including a filamentous rhodophyte (*Audouinella* sp.) (Rosemond 1993a) and a diatom (*Cymbella minuta*) (Steinman 1992) were able to respond positively to increased irradiance when snails were present in WB. Additional studies also indicate that other species (particularly diatoms) have greater photosynthetic capacity at high irradiance than *Stigeoclonium*. In two studies in a stream nearby WB, P-I curves were developed for communities dominated by *Stigeoclonium* (Hill et al. 1995) and diatoms (Hill and Boston 1991). P_{MAX} and α were much greater for diatoms than for *Stigeoclonium*-dominated assemblages. For communities with similar development times (between 13 and 27 days *in situ*), P_{MAX} values were between 1.71 and 7.03 μg C·cm^{-2}·h^{-1} (diatoms) and between 0.512 and 0.670 μg C·cm^{-2}·h^{-1} (*Stigeoclonium*-dominated), and α values were between 0.014 and 0.041 (μg C·cm^{-2}·h^{-1})(μmol·m^{-2}·s^{-1})$^{-1}$ (diatoms) and between 0.004 and 0.010 (μg C·cm^{-2}·h^{-1})(μmol·m^{-2}·s^{-1})$^{-1}$ (*Stigeoclonium*-dominated). These data are consistent with our experiments indicating that *Stigeoclonium* is a poor competitor with other algal species (e.g. diatoms) at high irradiance levels.

In addition to the differences between *Stigeoclonium*'s and other species' physiological responses to high irradiance, *Stigeoclonium* may also become relatively more susceptible to herbivory when irradiance is increased. Increased light can result in an increased number of upright filaments (Francke 1982) and length of cells (Cox and Bold 1966) of *Stigeoclonium*, which may be easier for herbivores to consume than basal cells. The fact that both positive

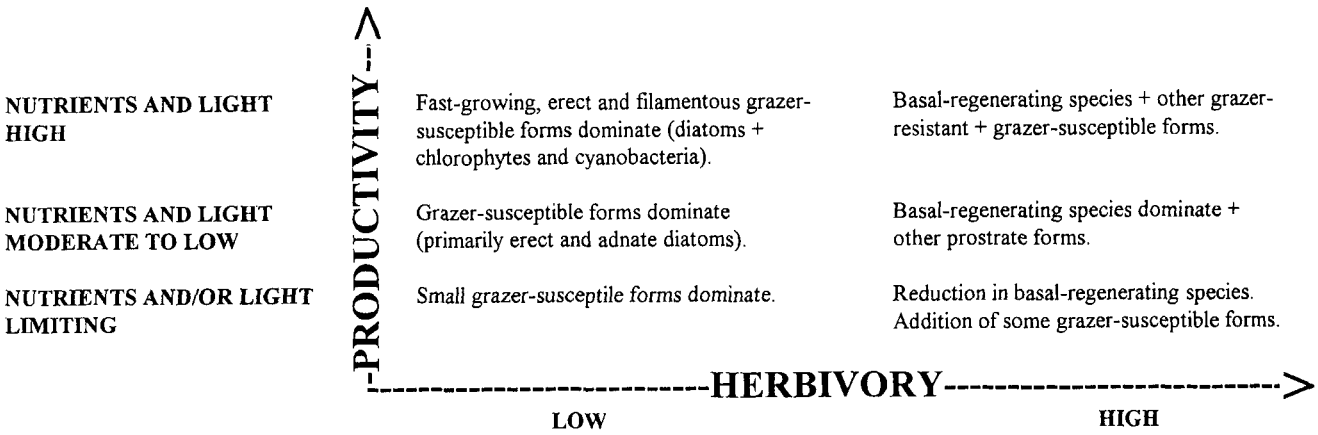

FIG. 5. Generalized response of basal-regenerating grazing systems to gradients in herbivory and productivity. Conditions are best for basal-regenerating species (e.g. *Stigeoclonium* basal cells, basal portions of *Calothrix* and *Rhizoclonium*) at high levels of herbivory (because susceptible forms are removed) and moderate levels of nutrients and light. These species tend to occur in association with a few other prostrate species (e.g. *Cocconeis*). When herbivory is high, increases in nutrients and light stimulate growth of basal-regenerating species, but other algal species, both grazer-resistant and grazer-susceptible forms, can also increase in abundance. When nutrients and light are severely limiting, grazer-resistant forms should be affected more than grazer-susceptible forms because of the hypothesized coupling between herbivore resistance and competitive ability. At high herbivory, this may result in a reduction in basal-regenerating species and a relative increase in grazer-susceptible forms (e.g. filamentous rhodophytes, small diatoms). In contrast to their dominance at high levels of herbivory, basal-regenerating species are outcompeted by overstory, grazer-susceptible forms at low levels of herbivory. At moderate levels of nutrients and light, diatoms (e.g. stalked *Gomphonema*) dominate the overstory, but as productivity increases, overgrowth is even more pronounced as growth rates of grazer-susceptible forms are greater than those of basal-regenerating species in response to increases in resources. Blooms of erect and filamentous diatoms (e.g. *Melosira*) as well as chlorophytes (e.g. *Spirogira*) and cyanobacteria (some of which may be basal-regenerating species) can take place. When nutrients and/or light are limiting at low levels of herbivory, grazer-susceptible forms with high surface : volume ratios that are consequently small in size (e.g. *Achnanthes* spp.) should dominate. This model is based in part from results of Stewart (1987), Power et al. (1988), McCormick and Stevenson (1989), Steinman et al. (1989), Mulholland et al. (1991), Gelwick and Matthews (1992), Hill et al. (1992), Steinman (1992), Rosemond et al. (1993a), and this study.

effects of light on snail growth rates (suggesting greater quantity or quality of ingested algae) (Rosemond 1993b, Hill et al. 1995) and negative effects of light on *Stigeoclonium* biomass (Rosemond 1993b) have been found supports this hypothesis.

The *Elimia/Stigeoclonium* grazing system can be used to illustrate the response of algal communities dominated by basal-regenerating species to changes in herbivory and resource availability. This system is similar to other systems in which basal portions of chlorophytes or cyanobacteria dominate under heavily grazed conditions and are overgrown by faster growing, grazer-susceptible forms (typically diatoms, e.g. *Melosira*, stalked *Gomphonema* [Power et al. 1988, Rosemond 1993a] and to some extent fast-growing chlorophytes, e.g. *Spirogira* [Gelwick and Matthews 1992]) when herbivores are experimentally excluded. These "basal-grazing assemblages" differ from other grazer/algal associations in streams in which grazed communities are dominated by adnate and prostrate diatoms ("diatom-grazing assemblages") and are replaced by filamentous chlorophytes and cyanobacteria when herbivores are removed (see references in Steinman 1996). Basal species that are truly heterotrichous (and are able to produce extensive basal thalli), such as *Stigeoclonium tenue*, may be particularly successful in heavily grazed systems. Patches of other basal species (e.g. *Rhizoclonium hieroglyphicum* (C. A. Ag.) Kuetzing) were found in WB but did not grow as extensively as *Stigeoclonium*. This could be due to a greater susceptibility to herbivores or other species-specific traits. For example, small blooms of *Rhizoclonium* filaments were observed in the spring in WB (Rosemond, pers. observ.), indicating that this species responds positively to high levels of irradiance (which only last 1–2 months in WB) and may not be as shade-tolerant as *Stigeoclonium* at other times of the year.

Figure 5 shows the generalized response of basal-regenerating algae to gradients in herbivory and productivity, which is similar to that constructed for marine algae by Steneck and Dethier (1994). Here, basal-regenerating species are the functional analogs to crustose algae in the marine systems, which dominate at high levels of herbivory and low productivity. Herbivores facilitate the persistence of the basal-regenerating species (sensu McNaughton 1984), but overgrowth of these species by grazer-susceptible forms occurs when herbivory is reduced and productivity is increased. However, in marine systems there is apparently a greater diversity of growth forms that flourish at low levels of herbivory than is found in freshwater systems (see Steneck and Dethier 1994).

Studies in lotic systems of the *Elimia/Stigeoclonium* grazing association indicate the factors that drive the dominance of this alga and perhaps other basal-regenerating species in heavily grazed streams.

There is a range of observational (Rosemond 1994, 1995) and experimental data for this species within the community (McCormick and Stevenson 1989, Mulholland et al. 1991, Hill et al. 1992, Steinman 1992, Rosemond 1993, Rosemond et al. 1993) and isolated in culture (this study) in which herbivores and/or nutrients and/or light have been manipulated, contributing to a complete picture of how it responds to these gradients. This and a recent study of marine algae (Dudgeon et al. 1995) are good examples of the importance of species-level studies in algal ecology; such studies do not represent "noise" (cf. Hay 1994). Rather, in order to understand existing community structure and predict effects of factors such as anthropogenic eutrophication on a community, both a broad (e.g. functional-form) and specific (e.g. autecological characteristics of species) understanding of the community is required.

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