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Succession of Microphytobenthos in a Restored Coastal Wetland

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ABSTRACT: Sediment microphytobenthos, such as diatoms and photosynthetic bacteria, are functionally important components of food webs and are key mediators of nutrient dynamics in marine wetlands. The medium to long-term recovery of benthic microproducers in restored habitats designed to improve degraded coastal wetland sites is largely unknown. Using taxon-specific photopigments, we describe the composition of microphytobenthic communities in a large restoration site in southern California and differences in the temporal recovery of biomass (chlorophyll *a*), composition, and taxonomic diversity between vegetated *Spartina foliosa* salt marsh and unvegetated mudflat. Visually distinct, spatially discreet, microphytobenthic patches appeared after no more than 7 mo within the restoration site and were distinguished by significant differences in biomass, taxonomic diversity, and the relative abundance of cyanobacteria versus diatoms. Sediment chlorophyll *a* concentrations within the restored site were similar to concentrations in nearby natural habitat 0.2–2.2 yr following marsh creation, suggesting rapid colonization by microproducers. Restored *Spartina* marsh very rapidly (between 0.2 and 1.2 yr) acquired microphytobenthic communities of similar composition and diversity to those in natural *Spartina* habitat, but restored mudflats took at least 1.6 to 2.2 yr to resemble natural mudflats. These results suggest relatively rapid recovery of microphytobenthic communities at the level of major taxonomic groups. Sediment features, such as pore water salinity and *Spartina* density, explained little variation in microphytobenthic taxonomic composition. The data imply that provision of structural heterogeneity in wetland construction (such as pools and vascular plants) might speed development of microproducer communities, but no direct seeding of sediment microfloras may be necessary.

Introduction

WETLAND MICROPHYTOBENTHOS

Sediment-dwelling algae and phototrophic bacteria, such as diatoms, cyanobacteria, green algae, and anoxygenic phototrophic bacteria, are of central importance to marine wetland food webs and to the functioning of coastal sedimentary habitats. Primary production by benthic algae and phototrophic bacteria (collectively called microphytobenthos) can rival the contribution made by vascular plants to total ecosystem production (Zedler 1980; Fejes et al. 2005) and often provides important trophic support to wetland consumers such as benthic macrofauna, meiofauna, and fishes (Currin et al. 1995; Kwak and Zedler 1997; Page 1997; Buffan-Dubau and Carman 2000). Wetland microproducers also function to stabilize sediments (Grant and Gust 1987; Austen et al. 1999) and to mediate fluxes of nitrogen and other nutrients through coastal habitats (Tyler et al. 2003).

Much of the research on the temporal variability of wetland microphytobenthic communities has focused on short-term or seasonal changes in assemblages. Work by Underwood and Paterson (1993a) showed seasonal differences in sediment chlorophyll *a* (chl *a*). Community composition may also change seasonally; Currin and Paerl (1998) found shifts in cyanobacterial taxa resident on dead *Spartina* shoots. Several researchers have found that winters tend to be characterized by higher diatom and green algal densities, whereas cyanobacteria and euglenoids are more common in summer floras (Carter 1933; Sage and Sullivan 1978; Zedler 1982). Using photopigment concentrations to track abundances of major taxonomic groups, Pinckney et al. (1995) noted shifts in the relative proportion of diatoms and cyanobacteria over a year's sampling in a North Carolina estuary, finding that cyanobacteria were more dominant during summer months.

Although it is fairly well understood that various benthic microalgae in marine wetlands (particularly diatoms and cyanobacteria) experience seasonal fluctuations in abundance, few studies have been conducted on longer-term changes in community abundance, composition, or diversity. Stal et al. (1985) noted a shift from an *Oscillatoria* (= *Lyngbya*?)-dominated to *Microcoleus*-dominated community over approximately 2 yr at an intertidal sand flat in the North Sea. Peletier (1996) examined

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changes in a mudflat diatom flora following reduced eutrophication and found a decadal-scale shift in the dominant *Navicula* species. Anecdotal evidence suggests a long-term rise in green algal blooms at Elkhorn Slough in central California, possibly a consequence of salt marsh recession (Zimmerman and Caffrey 2002). With a paucity of data on microphytobenthic succession, much more research needs to be conducted on longer-term temporal variation in benthic microproducer assemblages and the factors (human and otherwise) that regulate such dynamics.

Wetland Restoration

In many coastal regions worldwide, wetland restoration and rehabilitation attempts are underway to mitigate past and present destruction of intertidal habitats or to enhance stocks of selected taxa (Zedler 1996a). At three sites in San Diego County in southern California (these are among the larger of the coastal lagoons) approximately 85% of all tidal wetlands have been destroyed during the last 200 yr (Zedler 1996b). In the typical restoration projects in the region, former tidal land that was subsequently filled with soils, or upland areas adjacent to tidally-influenced marine habitat, are mechanically graded down to intertidal heights to expand aerial coverage of habitat. Various engineering experiments built into these restoration efforts (including the provision of intertidal channels and transplantation of native vegetation) are underway in the region to test mechanisms of colonization, tempo of recovery, and techniques for successful habitat rehabilitation (Zedler et al. 2001).

Only a few studies have addressed the question of microproducer succession in connection with restoration work. Underwood (1997) documented 3 yr of succession of wetland microproducer communities at a marsh in Britain and found compositional differences associated with different habitat types at the site. Several sites showed gradually declining chl *a* concentrations over several years (but no reference marsh comparison was conducted) and like Stal et al. (1985), Underwood found a transition from *Oscillatoria* to *Microcoleus* succession at one low intertidal location. Zheng et al. (2004) used replicate pairs of natural and restoration sites of variable age (1–25 yr) across North Carolina to examine temporal trajectories in salt marsh microproducer recovery. Sediment chl *a* in restored wetlands appeared to have recovered quickly and marsh age did not appear to influence the similarity between restored and natural functional groups, but diatom species composition was shown to gradually become more similar between restored and natural habitat as the age of sites increased.

Tijuana Estuary is one of the largest extant tidal wetlands along the southern California coast and has been home to at least two wetland restoration projects. In 1997, a small (< 1 hectare) wetland was constructed in the northeastern area of the estuary (Callaway et al. 2003). During 1999–2000, an additional site, the 8-hectare Model Marsh wetland, was constructed south south-east of the mouth of Tijuana Estuary.

We assessed the nature and tempo of microalgal and phototrophic bacterial succession at this latter restoration site by sampling one to three times annually for a period of 3 yr in unvegetated mudflat and *Spartina foliosa* salt marsh. Using a pigment-based approach to the study of microphytobenthic composition and taxonomic diversity, we addressed the following questions about succession in this sediment-based ecosystem. Which major taxonomic groups were present in the restoration site during early succession? What was the pigment composition of restored wetland sediment patches? How long did it take for microphytobenthic abundance and composition to recover (i.e., to match the levels of natural wetland) in mudflat versus *Spartina* marsh? How did plant densities, sediment salinity, and organic matter relate to microphytobenthic abundance, composition, and diversity? Were similar abiotic factors associated with variability in community structure in restored versus natural wetland?

Materials and Methods

Field Sampling

The Model Marsh was created by excavation of supralittoral sediment fill that covered former intertidal habitat. A single, approximately 3-m wide, channel was constructed to connect the restoration site to natural habitat hydrologically; the rest of the restored site is separated from surrounding habitat by an elevated soil berm (Wallace et al. 2005). The restored site contains 6 blocks with alternating presence and absence of excavated tidal creeks; each also supports mudflats (Wallace et al. 2005). A 30-m swath of *Spartina foliosa* (Poaceae) was planted at several densities in each of the 6 blocks (at tidal elevations between +1.00 and +1.75 m MLLW; Moseman et al. 2004), and additional halophyte species were planted in upper intertidal locations (King et al. 2001; Zedler et al. 2001). Tidal influence commenced at the restoration site in February 2000 (Moseman et al. 2004).

Several approaches were used to study macroalgal and microproducer floras in the restoration site during early succession. To study flotation of macroalgae into the restored wetland, algal traps consisting of 400-cm^2 wire mesh were suspended

TABLE 1. Sampling locations and dates in this study. NR = periodic natural versus restored wetland comparison. P = sampling of targeted patches. C = collection of marcroalgal rafts. REST = restored wetland; NAT = natural habitat; MUD = mudflat; SPAR = *Spartina foliosa* marsh.

Date	REST wetland age (yr)	Field sampling			
		REST MUD	REST SPAR	NAT MUD	NAT SPAR
March 2000	0.1	C			
April 2000	0.2	NR	NR	NR	NR
September 2000	0.6		P	NR	NR
April 2001	1.2	NR	NR	NR	NR
June–July 2000	1.4	P	P		
September 2001	1.6	NR	NR	NR	NR
April 2002	2.2	NR	NR	NR	NR
April 2003	3.2		NR		NR

about 10 cm above the sediment surface with bamboo stakes in lower elevation mudflat during February 2000. After approximately 2 wk, green macroalgae were identified (Abbott and Hollenberg 1976; nomenclature updated with Hayden and Waaland 2004).

During September 2000 (restored age = 0.6 yr) and June–July 2001 (restored age = 1.5 yr), sediment microproducers within the restored wetland were investigated by microscopy and collection of sediment for pigment analyses from replicate patches of distinct coloration and texture. In September 2000, collections of surface sediment (3 cores of 2 mm depth per replicate) were made from within *S. foliosa* habitat and consisted of the following target assemblages: yellowish, leathery patches (LTH), greenish sediments (GRN), and sediment from macroalgal (Chlorophyta)-dominated sediments (CHL1; about 4 replicates of each patch type sampled). In July 2001, sediment microphytobenthic assemblages from *Spartina* marsh and mudflats at tidal elevations above (mostly) and below the vegetated marsh were sampled in the restored wetland. Three cores of sediment material were taken from replicate patches of the following kinds of assemblages: yellowish sediment frequently found in upper littoral pools (YEL), deep-green-colored sediment in depressions and at edges of shallow pools (GRN), green macroalgae (Chlorophyta) and underlying sediment (CHL2), sediment underlying macroalgae (CHL1), pinkish or pinkish-white (usually dry) sediment (PNK), and sediment without distinct coloration (BRN; between 3–8 patches analyzed). There was no attempt to synchronize the kinds of assemblages sampled during September 2000 and July 2001 (common patches were chosen during each date), although GRN patches may have been roughly equivalent in both periods (all sampling is summarized in Table 1).

To study restored versus natural differences in community structure during the course of marsh maturation, benthic sediments were collected during April 2000 (age = 0.2 yr), April 2001 (1.2 yr), September 2001 (1.6 yr), April 2002 (2.2 yr), and April 2003 (3.2 yr) in restored and natural habitats (see Janousek 2005 for additional analyses of April 2002 communities). Sediment collection and field observations were made within haphazardly-placed 0.25-m^2 plots situated inside planted *Spartina* marsh and nearby mudflat within the restored site. Between 2 to 5 plots were sampled from each habitat in each of 6 blocks within the restoration site, but only a subset of plots are included here. Plots were also placed in replicate areas of natural *S. foliosa*-dominated marsh and nearby mudflat that were located along channels running from the restored site to near the mouth of the estuary (most of the southern arm). In each plot, densities of all *Spartina* plants (alive or otherwise) ≥ approximately 10 cm in height were recorded. One to three sediment cores for separation and analysis of pigments by high performance liquid chromatography (HPLC), with a surface area of 0.57 or 0.95 cm^2, were taken to 2–3 mm depth (April 2000), 5 mm depth (April 2002, 2003) or 10–20 mm depth (April 2001). Sediments were kept dark and later frozen (−20°C or −80°C) after field work was completed.

Sediment pore water salinities were determined in the field on a refractometer after pressing moist sediment against filters fit inside 10 ml plastic syringes. Organic content was determined by mass loss in surface sediment (0–1 cm depth) after 550°C combustion for several hours (Carver 1971).

Analyses of Sediment Pigments

Sediments were defrosted and treated with approximately 90% acetone and 10% seawater and kept chilled for about 24 h prior to separation via HPLC. For the April 2000 and 2001 work, estimates of sediment moisture for each habitat-site combination were made and used to determine the volume of acetone necessary to achieve extraction in 90% acetone. For the September 2001 to April 2003 samples, variation of sediment moisture in individual cores was determined by field collection of an

extra sediment core adjacent to pigment cores. Moisture content was determined in the lab after weighing, drying (at 60°C, ≥ 24 h), and reweighing sediment, and concentrations were then used to determine a per-core extraction volume of acetone. For the September 2000 samples, 3.0 ml of acetone was simply added to wet sediment regardless of initial water content.

Following extraction, sediment and supernatant were centrifuged and filtered through a cotton-fitted Pasteur pipette (Goericke 2002). Extracts were further diluted with water (5:12 water to solvent ratio) prior to analysis. Pigments were separated on one of two HPLC machines: a Shimadzu SCL-10A System controller, Waters 510 solvent pumps, and Waters 991 Photodiode Array (PDA; system 1) or a Waters 600E pump and system controller coupled to a SpectraSYSTEM AS3000 autosampler, a Spectra 100 variable wavelength detector, and a Waters 470 fluorescence detector (system 2). On system 1, pigment abundances were determined by PDA absorption at 440 nm. On system 2, pigments were detected by absorption at 450 nm and fluorescence detection (excitation at 430 nm, emission at 674 nm).

Several biphasic reverse-phase gradients were used for the separation of pigment extracts depending upon sampling period (see Janousek 2005). Extracts from all dates were separated to determine major carotenoids and chlorophylls; several extracts from April 2002 were reanalyzed on system 2 for determination of bacteriochlorophyll a concentrations using an alteration of the method of Goericke (2002) with absorbance detection at 700 nm (Janousek 2005).

HPLC systems were calibrated with pure pigment standards obtained from DHI Water and Environment (Hoersholm, Denmark) and provided by M. Vernet (chl *a*) or with PDA calibration factors (at 440 nm) provided by R. Goericke. Pigments were identified based on PDA-generated absorption spectra (350–800 nm) and intermittent analysis of monospecific plant and algal material (system 1) or by comparison of elution with plant and algal material (system 2). Extracts of *Thalassiosira weissflogii* and *Chaetoceros* (Bacillariophyceae), *Arthrospira platensis* (cyanobacteria), *Mentha* spp. (Lamiaceae, Anthophyta), *Dunaliella tertiolecta* (Chlorophyta), and *Lingulodinium polyedrum* (Dinophyta) served as standards.

Estimation of Community Composition and Diversity

The carotenoids fucoxanthin, zeaxanthin, and lutein were used to estimate the biomass of diatoms, cyanobacteria, and green algae/plant detritus, respectively (Pinckney et al. 1995; Janousek 2005). Bacteriochlorophyll *a* concentrations were used as an estimate of the biomass of anoxygenic phototrophic bacteria (mainly purple bacteria; Imhoff 1992), but were determined only for sediments collected in September 2000 and April 2002. Total microphytobenthic biomass was estimated by either chl *a* or as the total sediment concentration of diagnostic carotenoids (B = fuco + lute + zeax) where fuco = fucoxanthin, lute = lutein, and zeax = zeaxanthin concentrations (in $\mu g\ cm^{-2}$). Taxonomic composition was characterized by the ratio of zeaxanthin to fucoxanthin ($\mu g\ \mu g^{-1}$; Pinckney et al. 1995) or, for multivariate work, by determination of the individual dominance levels of each taxon (i.e., diatom dominance = fuco/B) to remove any variation in communities due to differences in total biomass. Taxonomic diversity was also determined for communities using Simpson's index ($1/D = [\Sigma p_p^2]^{-1}$, where p_p = fuco/B, lute/B, or zeax/B; Magurran 2004). Additional pigment concentrations (e.g., diatoxanthin, diadinoxanthin, chlorophylls b, $c_{1,2,3}$, and carotenes were determined via HPLC but inclusion of these into a diversity index or multivariate compositional analyses would add redundancy and inflate true community differences.

Statistical Analyses

To test for spatial differences in the community composition of microproducers between different communities in the restored wetland (September 2000 and July 2001), one factor analyses of variance (ANOVA) were performed on community biomass (chl *a*), the relative abundance of cyanobacteria versus diatoms (zeax/fuco), and taxonomic diversity (1/D). Tests were performed at $\alpha = 0.05$, but significance levels of $0.1 > p > 0.05$ were considered marginally significant for September 2000 data because of low replication; the results of a posteriori Tukey-Kramer comparisons (at $\alpha = 0.05$) are shown for ANOVA results where $p \leq 0.05$.

Analysis of natural and restored wetland differences (chl *a*, zeax/fuco, 1/D) was carried out for each successional time point (April 2000, April 2001, September 2001, April 2002, and April 2003) by one factor ANOVA conducted separately in *Spartina* salt marsh and unvegetated mudflat. Independence of samples across time was assumed because of the relatively long periods (5–7 mo) between sampling points and because of variation in exact sampling points from period to period.

Compositional differences between restored and natural wetlands were also investigated by nonmetric multidimensional scaling (nMDS) based on a Bray-Curtis similarity matrix (generated from 4th-root transformation of pigment dominances: fuco/B, lute/B, and zeax/B). Heterogeneity in assemblage composition between restored and natural

TABLE 2. Photosynthetic pigments found in wetland sediments at Tijuana Estuary (not exhaustive).

Pigment	Principal taxonomic affiliation(s)	Absorption maxima on HPLC system 1 (nm)
Chlorophyll *a*	All oxygenic phototrophs	431.0, 619.1, 665.1
Chlorophyll *b*	Green algae, plants, euglenoids	461.3, 647.2
Bacteriochlorophyll *a*	Purple anoxygenic photobacteria	363.1, 772.6
Fucoxanthin	Diatoms	451.2
Diatoxanthin	Diatoms, euglenoids	453.7, 484.1
Diadinoxanthin	Diatoms	448.7, 479.0
Myxoxanthophyll	Cyanobacteria	476.5, 509.5
Zeaxanthin	Cyanobacteria	453.7, 481.6
? Canthaxanthin	Cyanobacteria	484.1
Echinenone	Cyanobacteria	463.8
Lutein	Green algae, vascular plants	448.7, 474.0

mudflat and between restored and natural *Spartina* marsh was subsequently tested with ANOSIM (Primer 5 software, > 400 bootstraps). Within treatment homogeneity (e.g., similarity within restored *Spartina*) and between treatment heterogeneity (e.g., dissimilarity between restored and natural *Spartina*) were determined by SIMPER.

The influence of sediment pore water salinity, sediment organic content, and *Spartina* density on microphytobenthic abundance (chl *a*), composition (zeax/fuco), and diversity (1/D) were investigated via correlations. In each of these analyses, microphytobenthic assemblage data from April 2001, September 2001, April 2002, and April 2003 were pooled, but separate analyses were conducted for each habitat within the natural and restored wetland (4 analyses per pair of variables). The normality of all variables used in ANOVA and regressions were tested and data were transformed as needed (usually $\log_e$ or square root) prior to statistical tests. In a few rare cases, transformed distributions still showed substantial deviation from normality so Kruskall-Wallis or rank correlation (r_s) tests were used.

Results

Microproducer Composition within Restored Wetland

Rafted macroalgae collected in early March 2000 (restored age = 0.1 yr) were assigned to *Ulva* spp., including tentatively *U. prolifera* O.F. Müller and *U. clathrata* (Roth) C. Agardh. In September 2000 (restored age = 0.6 yr), various cyanobacteria (including *Oscillatoria* spp., *Microcoleus*, and a heterocyst-bearing filament) and diatoms (*Cylindrotheca, Gyrosigma*, and naviculoid pennate diatoms) were obtained from wetland sediments. Numerous algal and bacterial chlorophylls and carotenoids were extracted from both natural and restored wetland sediments at this time (Table 2).

By September 2000, microphytobenthic patches of distinct coloration and texture were also evident on the surface of sediments. In the three major assemblages sampled, sediment chl *a* differed between assemblages ($F_{2,9} = 14.8$, $p = 0.001$), with higher concentrations in LTH and GRN patches relative to sediment phototroph communities underlying macroalgae (CHL1; Fig. 1). Bacteriochlorophyll *a* abundances likewise differed among patches ($F_{2,9} = 5.0$, $p = 0.04$) and were significantly different between CHL1 and GRN communities (Tukey-Kramer a posteriori test at $\alpha = 0.05$). Microphytobenthic composition (zeax/fuco) and taxonomic diversity varied somewhat between sediment community type ($F_{2,10} = 3.5$, $p = 0.07$ and $F_{2,10} = 3.8$, $p = 0.06$, respectively), with lowest diversity and zeax/fuco ratios in LTH patches and higher diversity and relatively more cyanobacteria in GRN and CHL1 patches.

In July 2001 (restored age = 1.4 yr), restored wetland sediments also hosted a variety of visually-distinct communities; 6 distinct kinds of assemblages were targeted in field collections. Sediment pigment analyses revealed significant differences in chl *a* concentrations ($F_{5,27} = 12.8$, $p < 0.0001$; Fig. 2), zeax/fuco ratios ($F_{5,27} = 6.5$, $p = 0.0005$), and taxonomic diversity ($F_{5,27} = 2.7$, $p = 0.04$) between these communities. Phototroph biomass (chl *a*) was highest in YEL and GRN assemblages, intermediate in BRN communities, and lowest in PNK, CHL1, and CHL2 sediments. YEL and BRN assemblages possessed the highest abundance of cyanobacteria relative to diatoms. Cyanobacteria were relatively less prevalent in GRN, PNK, CHL1, and CHL2 communities. Although taxonomic diversity was significantly different across all assemblages considered together, a posteriori comparisons revealed no pairwise differences at $\alpha = 0.05$.

Long-term Changes in Biomass

Sediment chl *a* concentrations in restored mudflats and restored *Spartina* marsh rapidly matched or exceeded concentrations present in natural sediments. Two months following the opening of the restored site to tidal influence (April 2000), there was no difference in sediment chl *a* concentrations between restored and natural mudflats ($F_{1,10} < 0.1$,

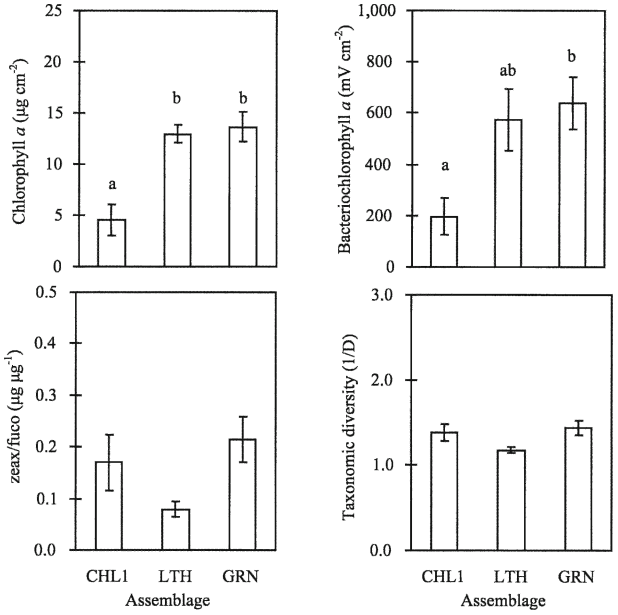

Fig. 1. Mean (± SE) concentrations of chlorophyll *a*, bacteriochlorophyll *a*, and variation in cyanobacteria to diatom abundance (zeax/fuco ratio) and taxonomic diversity, in visually distinct benthic assemblages collected from restored wetland habitat in September 2000. CHL1 = macroalgal dominated sediments; LTH = leathery, yellowish sediments; GRN = greenish sediments. Letters designate nonsignificant groups of means ($p > 0.05$).

$p > 0.9$), but natural *Spartina* salt marsh had chl *a* levels about four times higher than restored *Spartina* habitat ($F_{1,10} = 20.0$, $p = 0.0012$; Fig. 3). One year later (April 2001, age = 1.2 yr), restored and natural mudflats again supported similar chl *a* ($p = 0.20$). The natural-restored difference persisted in *Spartina* salt marsh ($p = 0.0006$), but at this time, restored *Spartina* sediment chl *a* exceeded natural sediment concentrations by almost a factor of three. At about 1.6 yr of marsh development (September 2001), mudflat chl *a* concentrations were similar ($F_{1,13} = 0.3$, $p > 0.5$), but *Spartina* chl *a* differed between restored and natural marsh ($F_{1,11} = 13.3$, $p = 0.0007$). By April 2002, sediment chl *a* concentrations were equivalent between restored and natural *Spartina* marsh ($F_{1,22} = 3.6$, $p = 0.07$) and restored and natural unvegetated mudflat ($F_{1,22} = 0.1$, $p > 0.7$). At the final sampling date in spring 2003 (restored age = 3.2 yr), chl *a* concentrations in natural and restored *Spartina* marsh were nearly identical ($F_{1,14} < 0.1$, $p > 0.9$).

Succession of Functional Composition and Diversity

Recovery of composition within the restored wetland was not as rapid as biomass evolution, but restored taxonomic composition was largely similar

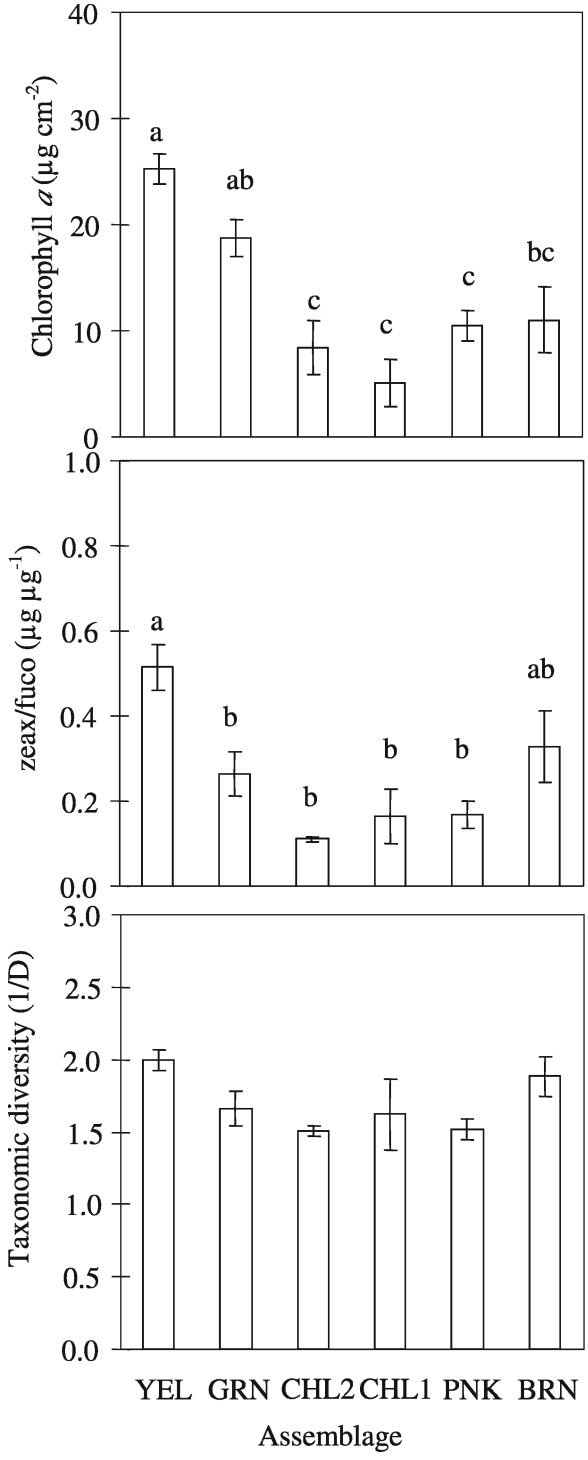

Fig. 2. Patch differences in mean (± SE) chlorophyll *a*, cyanobacteria to diatom pigment ratios (zeax/fuco), and diversity in restored wetland habitat in July 2001. There were no significant pairwise differences in diversity (all $p > 0.05$).

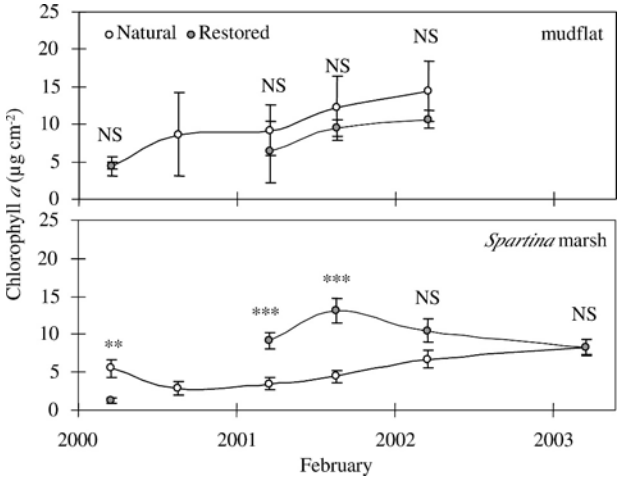

Fig. 3. Temporal variability in mean (± SE) sediment chlorophyll *a* concentrations in restored and natural mudflat and *Spartina foliosa* salt marsh. Tests of restored versus natural differences are indicated by: NS: not significant, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ****: $p \leq 0.0001$. The restored site was opened to tidal influence in February 2000.

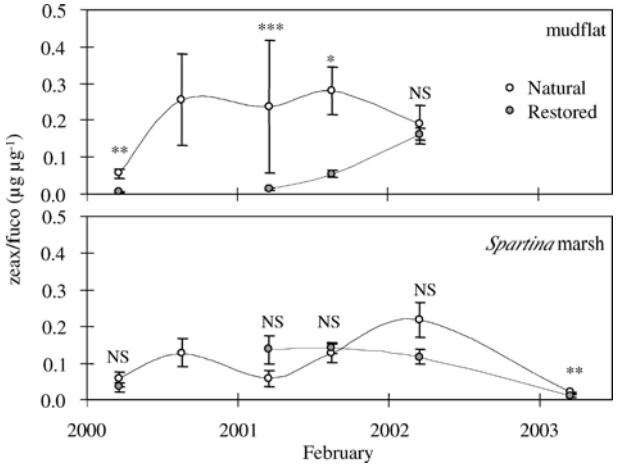

Fig. 4. Temporal changes in the mean (± SE) relative abundance of cyanobacteria and diatoms (zeax/fuco ratio) in natural and restored sediments in mudflat and *Spartina foliosa* salt marsh. Notation for tests of restored versus natural differences follow that of Fig. 3.

to that of natural sediment communities by 2.2 yr of development. Communities sampled early in the study (April 2000, restored wetland age = 0.2 yr) were characterized by relatively low zeax/fuco ratios (< 0.1) and low diversities, but there was a significantly higher zeax/fuco ratio ($F_{1,10} = 16.7$, $p = 0.002$) and significantly greater taxonomic diversity ($F_{1,10} = 12.7$, $p = 0.005$) in sediments from the natural mudflat than from the restored mudflat (Figs. 4 and 5). There was no difference between natural and restored *Spartina* salt marsh with respect to zeax/fuco ratios or diversity ($F_{1,10} = 1.3$, $p = 0.28$ and $F_{1,10} = 3.45$, $p = 0.09$, respectively). Multivariate community analyses based on the relative concentrations of fucoxanthin, lutein, and zeaxanthin were generally similar to the univariate results; restored sediments were distinctly different from natural sediments within mudflat habitat ($p \leq 0.002$, $R = 0.70$, ANOSIM), and there was a difference in composition, though weaker than in mudflat, between natural and restored *Spartina* marsh ($p = 0.04$, $R = 0.20$, ANOSIM; Fig. 6 and Table 3).

By April 2001 (restored wetland age = 1.2 yr), lower zeax/fuco ratios ($p = 0.0005$), and lower taxonomic diversity ($p = 0.0004$) in microproducer assemblages persisted within restored mudflat. A highly significant difference between restored and natural mudflat communities was also seen in the multivariate comparison of composition ($p < 0.0001$, $R = 0.54$, ANOSIM; Fig. 6 and Table 3). No difference in zeax/fuco ratios ($p = 0.15$), diversity ($p > 0.6$), or the multivariate analysis of composition ($p > 0.3$, $R = 0.01$, ANOSIM) was evident during April 2001 for *Spartina* salt marsh habitat. Differences in community composition and diversity between restored and natural mudflat continued into September 2001 (restored age = 1.7 yr). Restored mudflat communities hosted less cyanobacterial pigment relative to diatom pigment ($F_{1,21} = 7.6$, $p = 0.012$) and had lower taxonomic diversity ($F_{1,21} = 11.3$, $p = 0.003$) than natural sediments. Multivariate measures of composition confirmed mudflat differences ($p = 0.005$, $R =$

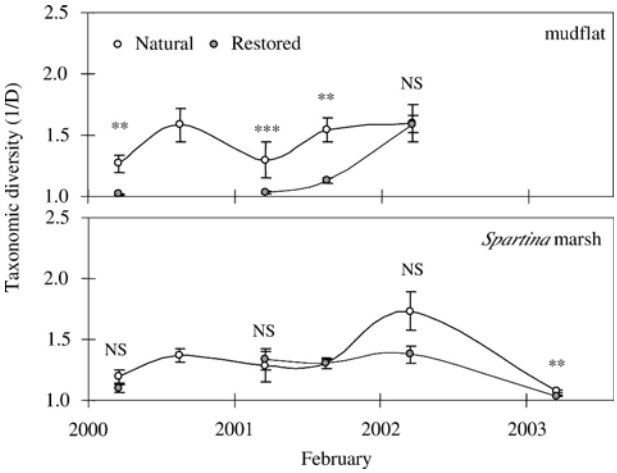

Fig. 5. Succession of microphytobenthic taxonomic diversity in mudflat and *Spartina* habitats from Tijuana Estuary. Mean (± SE) diversities are estimated by Simpson's index (1/D) incorporating lutein, zeaxanthin, and fucoxanthin concentrations. Notation for tests of restored versus natural differences follow that of Fig. 3.

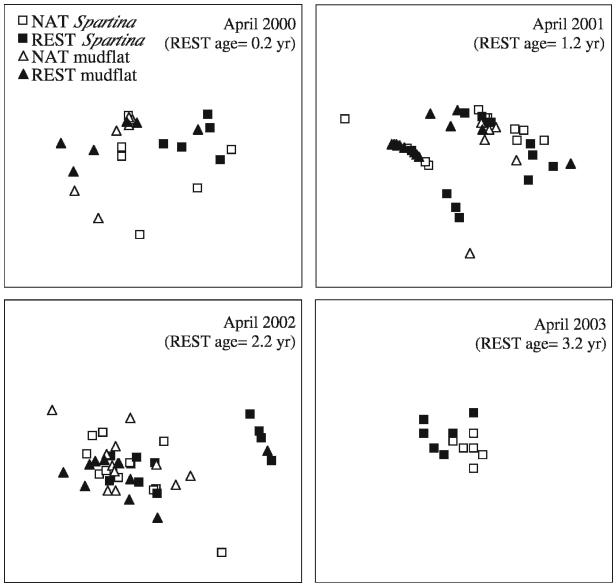

Fig. 6. nMDS representations of restored (REST) and natural (NAT) differences in sediment microproducer community composition in April 2000, April 2001, April 2002, and April 2003. nMDS analyses were based on relative pigment concentrations (fuco/B, lute/B, and zeax/B); distances between communities are proportional to differences in composition. April 2000 stress = 0.03, April 2001 stress = 0.05, April 2002 stress = 0.01, and April 2003 stress = 0.01. Some individual assemblages may not be visible due to overlap and one outlying assemblage from April 2003 is not shown.

0.28, ANOSIM). Like April 2001, there was no difference in zeax/fuco ratios ($F_{1,16} = 0.8$, $p > 0.3$), multivariate measures of composition ($p > 0.3$, $R = 0.06$, ANOSIM), or diversity ($F_{1,16} < 0.1$, $p > 0.9$) between restored and natural *Spartina* microproducer communities in September 2001.

By April 2002 (restored wetland age = 2.2 yr), zeax/fuco ratios and multivariate measures of composition were similar between restored and natural mudflat (for zeax/fuco $F_{1,21} < 0.1$, $p > 0.9$, and for ANOSIM $p > 0.2$, $R = 0.02$) and between restored and natural *Spartina* marsh (for zeax/fuco $F_{1,20} = 3.3$, $p = 0.08$, and for ANOSIM $p > 0.3$, $R = 0.02$; see also Fig. 5). Taxonomic diversity was also equivalent between sites ($F_{1,21} < 0.1$, $p > 0.9$ for mudflat and $F_{1,20} = 3.6$, $p = 0.07$ for *Spartina* habitat). During the final sampling period (April 2003, when the restored site was 3.2 yr old), *Spartina* sediment zeax/fuco ratios and diversities were substantially depressed relative to previous sampling dates. Minor but significantly elevated zeax/fuco ratios ($H_1 = 6.4$, $p = 0.01$, Kruskall-Wallis test) and diversities ($H_1 = 7.5$, $p = 0.006$, Kruskall-Wallis test) were observed in natural *Spartina* marsh relative to the restored site. Multivariate analyses of community composition at this time also suggested a significant restored versus natural wetland difference ($p = 0.0003$, $R = 0.52$, ANOSIM; Fig. 6 and Table 3).

Microphytobenthic Community Relationships with Environmental Variables

Pigment measures of microphytobenthic community structure (chl *a*, zeax/fuco, and 1/D) were compared with several environmental variables measured during the study (sediment pore water salinity, *Spartina* stem densities, and some data on sediment organic content). During April 2001, *Spartina* densities in natural marsh (mean ± SE: 191 ± 15) exceeded those of the sampled plots in the restored site (36 ± 11), but in April 2003, plots sampled from restored and natural habitat hosted similar densities (Janousek 2005). Mean (± SE) sediment pore water salinity in April 2001 was estimated as 41 ± 7 psu and 64 ± 5 psu in natural and restored *Spartina* marsh and 46 ± 4 psu and 47 ± 4 psu in natural and restored mudflat, respectively. Individual sampling locations in April 2001 and April 2002 occasionally reached salinities of at least 100 psu (the refractometer limit).

Most environmental measures showed no correlation with community structure. Chl *a* concentrations were not correlated with sediment pore water salinities in either restored *Spartina* marsh, natural marsh, restored mudflats, or natural mudflats (all $p > 0.05$). Zeax/fuco ratios and taxonomic diversity were both positively associated with pore water salinity in sediments from the restored mudflat (r

TABLE 3. Natural versus restored comparison of taxonomic composition with multivariate pigment analyses. Community composition was estimated using the relative abundance of fucoxanthin, lutein, and zeaxanthin in assemblages. Compositional homogeneity within treatments (SIM) and heterogeneity between treatments (DISSIM) was determined by SIMPER. Significance levels (p) of natural versus restored differences were generated with ANOSIM. Sample sizes (n_{rest}, n_{nat}) follow significance levels. NA = not measured.

		Spartina marsh				Mudflat			
	Age REST (yr)	Within REST SIM	Within NAT SIM	REST versus NAT DISSIM	ANOSIM p (n_{rest}, n_{nat})	Within REST SIM	Within NAT SIM	REST versus NAT DISSIM	ANOSIM p (n_{rest}, n_{nat})
April 2000	0.17	95.6%	92.3%	8.0%	0.039 (6, 6)	91.4%	94.9%	16.4%	0.002 (6,6)
April 2001	1.17	85.4%	85.1%	14.9%	0.32 (12, 11)	92.2%	88.7%	15.5%	< 0.0001 (16, 6)
September 2001	1.6	92.0%	92.2%	8.4%	0.30 (8, 10)	93.5%	87.0%	15.3%	0.005 (9, 14)
April 2002	2.2	91.9%	87.6%	10.5%	0.31 (10, 12)	95.7%	86.9%	9.2%	0.27 (11, 12)
April 2003	3.2	95.2%	98.1%	5.7%	< 0.001 (8, 8)	NA	NA	NA	NA

= 0.46, p = 0.005, n = 36 and r_s = 0.53, p = 0.008, n = 36, respectively), but no relationships existed between these variables and salinity within natural mudflats (both p > 0.2) or for either natural or restored *Spartina* habitat (all p > 0.1).

Spartina shoot densities were compared with microphytobenthic community composition for salt marsh plots. There was no relationship between shoot density and chl *a* in either natural or restored salt marsh (both p > 0.6). Shoot densities were not correlated with zeax/fuco or diversity in either kind of wetland (all p > 0.1). Like *Spartina* densities, sediment organic matter was not significantly correlated with sediment chl *a* or measures of composition and diversity within restored or natural *Spartina* marsh (all p > 0.1); no mudflat investigation was made.

Discussion

Biomass Recovery

The Model Marsh restoration site at Tijuana Estuary quickly acquired robust microphytobenthic populations. Chl *a* concentrations in both restored mudflat and salt marsh rapidly mirrored or exceeded concentrations in natural habitat. Pigment analyses suggested that colonization by diatoms and cyanobacteria had occurred at the restored site within < 2 mo of succession. Relatively low zeax/fuco ratios suggested that diatoms were particularly common members of the early flora at the restored site, so these microphototrophs probably accounted for the majority of chl *a* initially present in sediments.

Other studies that have examined microalgal colonization into new wetland habitats have also found rapid growth of microproducer populations (Underwood 1997). Zheng et al. (2004) found similar levels of sediment chl *a* between restored salt marshes of variable age and their paired reference systems, but epiphytic biomass (on vascular plants) recovered only after about a decade at their sites. In a study of two restored marshes in North Carolina, Piehler et al. (1998) found greater chl *a* concentrations at a 1 yr old site than at a 6 yr old marsh or in natural habitat. Other lines of evidence also confirm the high intrinsic capability of wetland microphytobenthic proliferation; Underwood and Paterson (1993b) noted rapid recovery of diatom biomass within days of herbicide application to sediment, and Williams (1964) documented very high population growth rates in benthic diatoms.

In any wetland restoration site initially free of resident consumer populations, rapid accumulation of microphytobenthic biomass might occur because of low densities of invertebrate consumers. At the present study site, Moseman et al. (2004) found that infaunal densities approached those of natural habitat after about 1 yr. It is possible that grazing pressure was low during the first year of succession at the restoration site. Other studies have found little or only moderate effects of invertebrate consumption on standing stocks of microproducers (Page et al. 1992; Posey et al. 1995), leaving open the possibility that early (within the first 1–2 yr of development) control of microproducer biomass could also have been more or less regulated by bottom-up processes, such as nutrient availability (e.g., Armitage and Fong 2004).

Distinct Microphytobenthic Patches

Within 7 mo (September 2000), restored marsh sediments acquired visually distinct microproducer communities that were characterized by different pigment signatures, with all communities probably containing cyanobacteria and anoxygenic photobacteria in addition to typical diatom populations. The following summer (July 2001, restored age = 1.4 yr), a variety of sediment communities were again present within the restored site. Such microphytobenthic patches of distinct character appear to be due largely to variability in the relative abundance of major taxonomic groups, not their presence or absence (Janousek 2005). Distinct communities may develop in wetland sediments in response to small-scale environmental features. At the Model Marsh the presence of shallow, high salinity pools appeared to be associated with microbial patches high in cyanobacterial populations. Pink mats were found almost exclusively at high intertidal elevations. Brotas and Plante-Cuny (1998) found higher microphytobenthic diversity in muddier sediments in a temperate European estuary. Microscale environmental variation, grazer patchiness, variation in disturbance history, and spatial differences in microalgal colonization or survival could contribute to small-scale horizontal patchiness. Comparison of salinity and zeax/fuco data suggested that community composition shifted to relatively greater cyanobacterial dominance in more saline sediments within restored mudflats, but this association was curiously absent from restored *Spartina* marsh and natural wetland of either habitat type.

As found in other wetland investigations (Zheng et al. 2004; Janousek 2005), diatoms appeared to be the dominant taxonomic group in most sediment communities analyzed in both natural wetland and the restored site. Zeaxanthin concentrations suggested that communities occasionally contained a substantial proportion of cyanobacteria (especially GRN and BRN communities sampled in July 2001 in the restored marsh), but in general, zeaxanthin was

much less abundant than the diatom carotenoid fucoxanthin. Green algae were relatively rare in this study, partly because the sampling scheme of our natural-restored comparisons generally avoided macroscopic Chlorophyta patches, but probably also because these macroalgae tend to occur in localized patches that do not cover a large fraction of the total sediment surface.

Temporal Evolution of Composition and Diversity

Despite the general rapidity of microproducer recovery found in this study, there were habitat-specific differences in the rate at which restored wetland communities resembled natural assemblages. According to the measures of composition and diversity investigated here (zeax/fuco ratios, multivariate analyses of community dominance, and taxonomic diversity), restored mudflat communities took at least 1.6 yr before closely resembling natural mudflat. During this early period, natural mudflat communities were consistently more enriched in cyanobacteria and had higher diversity. Recovery of composition and functional diversity appeared to be much more rapid (partially recovered by 0.2 yr) within restored *Spartina* marsh even though initial *Spartina* planting did not mimic natural habitat and plant densities took some time to match the natural system. Natural and restored *Spartina* marshes showed little evidence for meaningful differences until 2 yr later in wetland development (significantly higher bacteriochlorophyll *a* concentrations were observed in the restored wetland during April 2002; see Janousek 2005). At 3.2 yr of development (April 2003), there was significantly lower diversity and significantly less cyanobacteria relative to diatoms in restored *Spartina* marsh than in natural marsh, but this later-occurring disparity may have been related to substantial sedimentation that followed heavy rains in spring of that year. Zeax/fuco ratios and diversity in spring 2003 were depressed across both the restored site and natural habitat relative to spring 2002, and the restored-natural differences, though significant, were small in magnitude.

These habitat-level differences in succession may be accounted for by several factors. Natural mudflats in the southern arm of Tijuana Estuary are generally less extensive than mudflat within the restored site and are closer to either extensive regions of vegetated marsh or large channels. Our sampling scheme on most dates probably resulted in the selection of mudflat sediments closer to vegetated sediments in the natural marsh than in the restored marsh where mudflat communities were more influenced by the higher cyanobacterial content of vegetated salt marsh. Restored wetland epibenthic consumers (*Cerithidea*) may have been higher in restored mudflat than in natural habitat, preferentially consuming cyanobacteria (Armitage and Fong 2004). Since *Spartina* marsh was generally located at higher elevations than mudflat in the restored site (Wallace et al. 2005), differences in factors associated with the extent of tidal exposure (e.g., temperature) could have driven rates of recovery, with development of cyanobacterial populations occurring more rapidly at higher tidal elevations. Mudflat versus salt marsh differences in organic matter content may be related to habitat-level variation in cyanobacterial recovery; Janousek (2005) found some evidence for a positive association between zeax/fuco ratios and organic matter in nearby Mission Bay, California.

Restored Wetland Function

Observation of rapid recovery and the presence of distinct spatial heterogeneity in microphytobenthic communities in the restored site are positive indications of recovery of this wetland in Tijuana Estuary. The data presented here suggest that levels of microalgal biomass comparable to natural wetland habitat were present early in the restored site for support of invertebrate and vertebrate consumers that might use restored habitat, and the major taxonomic groups present in natural wetland (diatoms, cyanobacteria, and anoxygenic phototrophic bacteria) were present in the restored wetland flora during early succession. In particular, the presence of abundant cyanobacteria in at least some areas of the restored wetland suggests that the capacity for ecosystem processes supported by these organisms (such as nitrogen fixation and anoxygenic photosynthesis) would also be present. Since cyanobacteria in immature wetlands may play an important role in the supply of nitrogen to food webs (Piehler et al. 1998), tracking of prokaryotic producer populations as part of the evaluation of wetland mitigation may yield important insights. Currin et al. (1996) found nitrogen fixation rates an order of magnitude higher in a 1 yr old *Spartina* marsh in North Carolina than in natural marshland, but Langis et al. (1991) found that rates of nitrogen fixation were several times lower in a San Diego Bay restoration site compared with a nearby natural wetland. The present study suggests that data on microproducer community composition can provide more information on wetland recovery than could be gained from only routine measures of sediment chl *a*.

Management Implications

To rapidly promote robust microphytobenthic communities in marine restoration work, it may be important to provide ample variation in habitat structure via sediment topology and the distribution

of vascular plants. Microphytobenthos are believed to be very widely distributed throughout intertidal wetlands (Sage and Sullivan 1978), but because some taxa appear to have affinities for certain kinds of microhabitats (e.g., Zedler 1982), inclusion of habitat heterogeneity may promote greater variation in microphytobenthic composition in restoration work. Provision of shallow intertidal pools (this study), vascular plant canopies (Janousek 2005), or sandier areas of sediment (Currin et al. 1996) may provide more ideal microhabitats for cyanobacteria than flat, well-drained mudflats. Since restored wetlands are often depauperate in nutrients and organic matter long after their initial establishment (Craft 2000), it may be preferable to enhance the success of cyanobacteria and anoxygenic phototrophic bacteria by seeding sections of wetland habitat with detrital organic matter.

In addition to the assessment of plant, invertebrate, fish, and bird populations, future study of mitigation work in intertidal marine wetlands should track the recovery and temporal dynamics of benthic microalgal communities. Because they can be a major component of total ecosystem primary production in marine wetlands (Zedler 1980; Fejes et al. 2005), the status of microphytobenthic assemblages is likely to have effects on other trophic levels colonizing or transitioning a restoration site. Although generalist feeders may respond largely to changes in overall microalgal biomass, specialist feeders may be more sensitive to changes in the abundance of particular taxonomic groups. Variability in the taxonomic composition of wetland microalgal communities may alter food web support for grazers; several studies have shown that estuarine macroinvertebrates selectively injest size or taxon-specific components of the microflora (Whitlach and Obrebski 1980; Creach et al. 1997; Cognie et al. 2001). Shifts in microproducer composition may reveal changes in wetland nutrient concentrations or changes in the organic matter content or oxygenation of sediments. Compositional differences could also affect sediment stability.

In routine study of sediment microproducer succession, we note that a taxonomic approach (via techniques such as pigment diversity or rRNA analyses) provides several advantages. It can be completed more rapidly than intensive microscopic inventories of microfloras (where taxonomic difficulties, the likely need for time-consuming electron microscopy, and high spatial patchiness may hinder comprehensive study), yet will still reveal compositional differences that may correspond to important functional differences. Changes in the abundance of cyanobacteria may result in changes in sediment nitrogen fixation rates. A taxonomic approach provides enough resolution to be useful for tracking the temporal variation of particular groups that may be sensitive to differences in habitat characteristics or anthropogenic influences (although here species-level data would be even more desirable). Whichever techniques are employed, we suggest that study of microphytobenthic composition and diversity, in addition to simple measures of biomass, should be a frequent goal of wetland ecologists.

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