

CONFLICTING MANAGEMENT GOALS: MANATEES AND INVASIVE COMPETITORS INHIBIT RESTORATION OF A NATIVE MACROPHYTE

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Abstract. *Vallisneria americana* is a native macrophyte in freshwater and oligohaline ecosystems, often forming meadows that significantly affect ecosystem carbon and nutrient cycling and provide structural habitat. *Vallisneria* has declined in abundance in several Florida lakes, rivers, and estuaries. We conducted an 11-month field experiment in Kings Bay, Florida, USA, to determine factors that might affect successful transplantation of *Vallisneria* and to guide potential future restoration efforts by water resource management agencies. To determine the effects of herbivores and other primary producers on *Vallisneria* production, we conducted a 2 × 2 factorial experiment at three sites in which we allowed or denied: (1) relatively large herbivores (>3 cm) and (2) other primary producers (e.g., *Myriophyllum spicatum*, *Hydrilla verticillata*, *Lyngbya* sp.) access to 1.5 × 1.5-m transplanted plots of *Vallisneria*. Within one month, *Vallisneria* disappeared from 80% of herbivore-access plots due primarily to consumption by manatees. *Vallisneria* density was reduced a variable amount (0–50%) in response to competitors, due to site-specific variation in natural abundance of other primary producers (at two sites, we observed extensive colonization by other primary producers and a strong treatment effect). Most of this competitive effect was attributable to Eurasian watermilfoil (*Myriophyllum spicatum*); after pooling *Vallisneria* density data across sites, we observed a negative exponential relationship between shoot density of *Vallisneria* and stem density of *Myriophyllum* for every sampling date. We observed variable recruitment of *Vallisneria* transplants into larger size classes among sites, but not between treatments, and large, established plants grew at similar rates whether in monospecific or mixed stands, with evidence for reduced mass-specific growth in dense stands. Hence, a probable mechanism by which *Myriophyllum* reduces *Vallisneria* occurs via space limitation, and reduction in *Vallisneria* densities and/or recruitment and growth of new shoots. We conclude that two different management goals (restoration of *Vallisneria* and protection of manatees) are in conflict and must be simultaneously considered to devise effective and sustainable ecosystem management scenarios. Due to the highly managed nature of freshwater systems worldwide, the limitations of extrapolating experimental results and the importance of site-specific pilot experiments should also be recognized.

Key words: aquatic restoration; herbivory; *Hydrilla verticillata*; *Lyngbya*; manatee; milfoil; *Myriophyllum spicatum*; nutrient; seagrass; transplant; *Vallisneria americana*; wild celery.

INTRODUCTION

Over the past several decades, loss of native submersed aquatic vegetation (SAV) has been a reoccurring phenomenon in shallow freshwater, estuarine, and marine systems worldwide (Bayley et al. 1978, Rybicki and Carter 1986, Schloesser and Manny 1990, Kimber et al. 1995, Short and Wyllie-Echeverria 1996, Rogers et al. 1997, Valiela et al. 1997, Duffy and Baltz 1998, Hauxwell et al. 2001), and can often be attributed to a relatively limited number of factors. Repeatedly, human-induced alterations to chemical, physical, and/or

biological features of landscapes or adjoining waters have caused declines in SAV. Anthropogenic nutrient loading from watersheds to aquatic systems is one of the most pervasive human effects on aquatic systems (GESAMP [Joint Group of Experts on the Scientific Aspects of Marine Pollution] 1990, National Research Council 1994, U.S. Geological Survey 1999, Chambers et al. 2001) and has led to extensive loss of light-limited SAV via competitive exclusion by fast-growing, nutrient-limited algae (Kemp et al. 1983, Short et al. 1993, Carter et al. 1996, Short and Wyllie-Echeverria 1996, Valiela et al. 1997, Hauxwell et al. 2001). Sediment transport as a result of development and agricultural activities in adjoining land parcels may also result in declines in SAV (Kemp et al. 1983). Particularly in inland systems, the introduction of an exotic plant (Lind and Cottam 1969, Van et al. 1976, 1999, Titus and Adams 1979, McFarland and Rogers 1998) or her-

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bivore (Hestand and Carter 1978, Roberts et al. 1995, Wilson 2002) also may significantly reduce areal coverage by native macrophytes.

Because identification of the various factors that may cause declines in SAV has occurred relatively recently (in the past 10–30 years), the daunting task of restoration is a relatively new challenge for ecologists and water resource managers. To achieve long-term success, restoration of SAV habitat must involve at least three phases: (1) understanding the mechanisms by which initial loss of SAV habitat occurred, (2) restoring the original ecological setting, so that physical, chemical, and biological conditions are again hospitable to the target species, and (3) identifying a successful planting protocol that results in the persistence and dispersal of the population. Considerable effort has been expended in estuarine and marine environments, where, for example, (1) identification of the relationship between nutrient loading from watersheds and decline in areal coverage of seagrasses has been established (Valiela and Cole 2002, Hauxwell et al. 2003a), (2) reductions in nutrient loads have been achieved so that seagrasses have returned to systems in which they had been lost (e.g., Tampa Bay [Johansson and Greening 2000]), (3) planting protocols for several species have been established (*Zostera marina* [Davis and Short 1997, Orth et al. 1999], *Thalassia testudinum* [Tomasko et al. 1991], and *Halodule wrightii* [Sheridan et al. 1998]), and (4) experimental work on transplant success has been conducted around the world (Chesapeake Bay region, USA [Orth et al. 1999], Florida, USA [Tomasko et al. 1991], North Carolina, USA [Kenworthy and Fonseca 1992], California, USA [Zimmerman et al. 1995], New Hampshire, USA [Davis et al. 1998], Texas, USA [Sheridan et al. 1998], British Columbia, Canada [Harrison 1990], and Australia [West et al. 1990]).

In contrast to the availability of numerous published reports focused on seagrass restoration, there is a paucity of published information on restoration of native macrophytes in primarily freshwater environments (Smart et al. 1998). In this study, we were interested in identifying the factors that were likely to affect restoration of *Vallisneria americana* Michx. in a spring-fed system in Florida. *Vallisneria americana* is a native macrophyte in freshwater and oligohaline ecosystems, ranging from Central America to Canada (Korschgen and Green 1988), and like many seagrass species, often forms meadows that significantly affect ecosystem carbon and nutrient cycling, bind sediments, fuel significant secondary productivity, and provide structural habitat to a myriad of aquatic organisms. *Vallisneria* also has declined in abundance in many freshwater and estuarine systems (Bayley et al. 1978, Rybicki and Carter 1986, Schloesser and Manny 1990, Kimber et al. 1995, Rogers et al. 1997, Duffy and Baltz 1998). Restoration efforts aimed at revegetating shallow freshwater systems with *Vallisneria* have been initiated in

several systems in Florida, but at considerable cost and with variable success (B. Hujik [Florida Fish and Wildlife Conservation Commission], *personal communication*; see also Jagers 1994).

Despite the relative similarity of causes for decline in SAV, the factors that affect its re-establishment may be much more diverse and may include “natural” as well as anthropogenic causes. As with other native species of submersed aquatic vegetation, several factors may affect successful restoration of *Vallisneria*. Increases in anthropogenic nutrient supply or sediment loads to inland waters, accompanied by degraded water clarity, has resulted in loss of light-limited rooted macrophytes in freshwater environments (Chambers and Kalff 1985, Barko et al. 1986) and may limit potential for restoration. Infestations of nonnative macrophytes, including Eurasian watermilfoil (*Myriophyllum spicatum* L.) and hydrilla (*Hydrilla verticillata* (L.f.) Royle) may also competitively exclude native freshwater macrophytes, including *Vallisneria* (Lind and Cottam 1969, Van et al. 1976, 1999, Titus and Adams 1979, McFarland and Rogers 1998), and inhibit restoration efforts. Nonnative herbivores (e.g., grass carp (*Ctenopharyngodon idella* Val.) or the rusty crayfish (*Orconectes rusticus*) may severely affect native SAV (Hestand and Carter 1978, Roberts et al. 1995, Wilson 2002), and along with native herbivores (e.g., turtles, manatees, muskrats, waterfowl; Carter and Rybicki 1985), may also inhibit restoration efforts. Given the range of potential anthropogenic and natural processes that may affect restoration, small-scale pilot experiments are a potentially powerful way to understand the importance of different factors in controlling macrophyte dynamics and, thus, the feasibility of alternative management strategies, before large-scale transplantation is undertaken.

Study site

We conducted an experiment in Kings Bay, Florida, USA, designed to assess the feasibility of large-scale restoration of *Vallisneria americana* and to identify factors that might affect successful restoration. Kings Bay (Citrus County, Florida; Fig. 1) is a spring-fed, tidally influenced oligohaline/freshwater system (see Frazer et al. 2001b, Hoyer et al. 2001) which connects to the Gulf of Mexico via the 11-km long Crystal River (Frazer et al. 2001a). Water-based recreational use of Kings Bay is extensive (Southwest Florida Water Management District [SWFWMD] 2001), with ~70 000 annual visitors, and includes boating, fishing, scuba diving, and snorkeling. Many of these visitors travel to Kings Bay, specifically, to observe the hundreds of manatees (*Trichechus manatus* Linnaeus) that seek the relatively warm, 25°C, spring waters as refuge during winter.

Long-time visitors and residents of Kings Bay have noted both degrading water clarity and alterations in populations of submersed aquatic vegetation over the

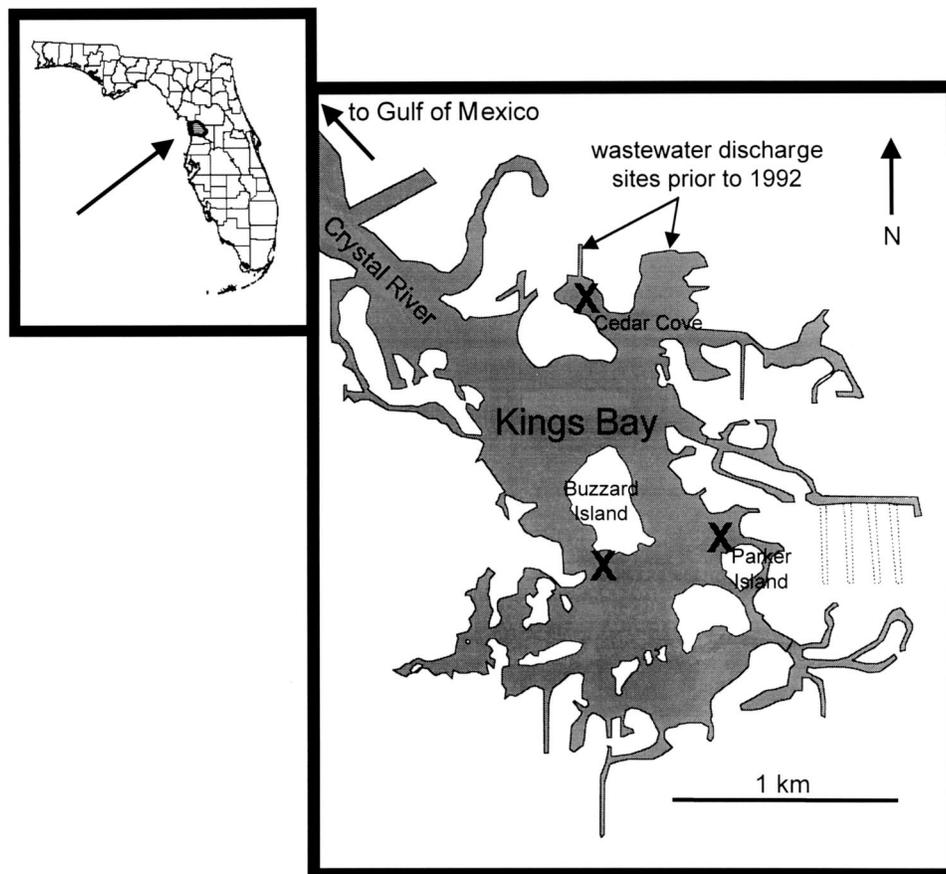


FIG. 1. Map of the Kings Bay/Crystal River estuarine/spring system. Site locations of transplanted plots of *Vallisneria americana* are indicated with X's. The inset shows the study location in Citrus County, Florida, USA.

past several decades, including an overall decline in areal coverage of *Vallisneria* and a concomitant increase in coverage by both exotic macrophytes and nutrient-limited algal taxa (Romie 1990). Although there are anecdotal accounts that *Vallisneria* once dominated the benthic vegetation of Kings Bay, this native macrophyte is now restricted to limited patch meadows (Frazer and Hale 2001). Exotic macrophytes, including *Hydrilla verticillata* (introduced to Kings Bay in the 1960s; Langeland 1990) and Eurasian watermilfoil (*Myriophyllum spicatum*, also introduced in the 1960s; Blackburn and Weldon 1967) are now prominent components of the community of SAV in Kings Bay (Frazer and Hale 2001, Hoyer et al. 2001), and have been shown to displace *Vallisneria* in other systems (Lind and Cottam 1969, Van et al. 1976, 1999, Titus and Adams 1979, McFarland and Rogers 1998). *Lyngbya* sp., a native, filamentous cyanobacteria, has also bloomed in areas of Kings Bay (mid-1980s; Romie 1990), and altered habitat, impaired recreational activities, and caused odor problems. *Lyngbya* forms dense mats on the bottom of lakes and rivers, and as trapped gases within canopies of *Lyngbya* increase throughout the day, these mats often float to the surface. These

floating mats clog waterways, shade other vegetation, and transport *Lyngbya*, and other attached incidental macrophytes, to other areas of the bay. Dense canopies of filamentous macroalgae, similar in form and function to *Lyngbya*, have also been shown to displace aquatic plants (Hauxwell et al. 2001).

In 1992, in response to complaints of degraded water clarity and shifts in macrophyte community structure, the City of Crystal River (Florida) diverted treated wastewater effluent that had been directly discharged into Kings Bay by employing an upland spray disposal method. Nutrient concentrations were subsequently reduced in a large portion of the Bay (Terrell and Canfield 1996). Presumably, it is possible that the growth of nutrient-limited competitors of *Vallisneria*, including *Lyngbya* and phytoplankton, may have also been reduced (see, however, Terrell and Canfield 1996), making Kings Bay a potential site for future large-scale restoration. This is possible, of course, only if: (1) initial decline of *Vallisneria* had been a result of degraded water clarity and/or increased competition from nutrient-limited taxa, (2) improvement in water quality was sufficient to ameliorate these historical effects, and (3)

TABLE 1. Summary of environmental data in Kings Bay, Florida.

Site	Total			Temperature (°C)	Salinity (‰)	Sediment characteristics	
	Phosphorus (µg/L)	Nitrogen (µg/L)	Chlorophyll (µg/L)			Organic matter (%)	Silt/clay (%)
Cedar Cove	28 ± 4	244 ± 17	7 ± 3	23 ± 2	0.3 ± 0.1	3.7	2.9
Parker Island	28 ± 5	236 ± 44	9 ± 6	25 ± 4	1.4 ± 0.3	0.8	5.0
Buzzard Island	28 ± 3	254 ± 51	9 ± 5	25 ± 3	1.6 ± 0.3	1.6	2.9
Baywide mean	28 ± 4	239 ± 16	9 ± 6	24 ± 3	1.5 ± 0.2		

Notes: Values given are annual means ± 1 SD and are for water quality data for sites sampled monthly in 2000 in the vicinity of Cedar Cove, Parker Island, and Buzzard Island (Florida LAKEWATCH, University of Florida, Gainesville, Florida, USA; methods described in Hoyer et al. [1997]). Sediment characteristics are taken from Belanger et al. (1993).

other factors do not prevent *Vallisneria* from responding to improved water quality.

This study was designed to facilitate the successful management and restoration of Kings Bay and other similarly affected spring-fed systems. Our general goals were threefold: (1) to ascertain whether Kings Bay may be a suitable site for future successful restoration of *Vallisneria*, (2) to determine whether transplant success might vary among sites within Kings Bay, and (3) to determine what factors might affect successful restoration. In this paper, we specifically describe results of a field experiment designed to assess the effects of: (1) large herbivores (especially manatees), and (2) other native or exotic primary producers, on a suite of demographic features of transplanted *Vallisneria*.

MATERIALS AND METHODS

Experimental design and transplanting protocol

To determine the effect of both herbivores and other primary producers (as well as interactive effects) on success of transplants of *Vallisneria*, we conducted a 2 × 2 factorial field experiment in which we allowed or denied: (1) relatively large herbivores (>3 cm; e.g., manatees, turtles, waterfowl, certain fishes) and (2) other primary producers (i.e., *Myriophyllum*, *Hydrilla*, *Lyngbya*) access to transplanted plots of *Vallisneria*. Comparisons between plots with allowed or denied access to herbivores and/or fast-growing opportunistic producers allowed us to assess their effects on *Vallisneria* density and other demographic parameters, and whether active exclusion of herbivores and other primary producers might be necessary for the successful long-term restoration of *Vallisneria*.

In January 2001, a team of scuba divers transplanted individual *Vallisneria* rosettes (purchased from Aquatic Plants of Florida, Sarasota, Florida, USA) within 1.5 × 1.5-m plots (naturally void of dense vegetation) at three sites. Within a given site, plots were situated ~2 m apart in depths of ~0.8–1.2 m at mean low water. Shoot planting density was ~200 m⁻², and 15–25-cm tall plants were used. Within a given site, there were three replicates of each of the following treatments. In treatment 1, herbivores were allowed and other primary producers were allowed. In treatment 2, herbivores

were allowed and other primary producers were excluded. In treatment 3, herbivores were excluded and other primary producers were allowed. In treatment 4, herbivores were excluded and other primary producers were excluded.

To exclude herbivores (treatments 3 and 4), we placed plastic fencing (2.5-cm mesh) around the sides of plots (leaving the top open). This fencing was tall enough (~2 m) to extend above the water surface at high tide (the typical tidal range in Kings Bay is ~1 m). The mesh fence excluded herbivores >3 cm, while minimally affecting water circulation and light (see Hauxwell et al. 2001). Plots in treatments 1 and 2 were left open to herbivores. To exclude other primary producers (treatments 2 and 4), plots were routinely monitored, and producers other than *Vallisneria* were hand-removed by snorkelers every two weeks. We were able to effectively remove macrophytes and loose clumps of filamentous algae, but did not attempt to remove attached epiphytes. In treatments 1 and 3, we allowed (but did not facilitate) colonization by other primary producers over the 11-month study period.

To incorporate spatial heterogeneity in response parameters, we conducted this experiment at three sites: (1) within the northwest inlet of Cedar Cove, (2) along the northern shore of Parker Island, and (3) along the southern shore of Buzzard Island (Fig. 1). The experimental design resulted in 36 total plots, requiring ~17 000 transplanted shoots. In the days immediately following the initiation of the experiment, sites were visited to qualitatively assess transplant success and identify potential herbivores.

Environmental data for the study sites are provided in Table 1, and indicate little differences among sites for total phosphorus, total nitrogen, or chlorophyll concentrations. Physical variables like temperature and salinity were also similar among sites. Sediments at all sites were dominated by fine and very fine sands, with some variation in the percentage of organic matter among sites (Table 1).

Measurements of response variables

Response variables monitored within plots over time (January to November 2001) included: *Vallisneria* shoot density (monthly), aboveground growth rates (bi-

monthly), shoot size distributions (quarterly), and density of other primary producers (stem density and percent cover, both measured monthly). Measurements were made within the centermost 1 m² of plots to allow some buffering (~25 cm) of potential edge effects. To compare transplant performance to that of naturally occurring *Vallisneria*, we simultaneously collected density and growth measurements (using the same methods as those described for experimental plots) from a meadow located adjacent to the plots at Buzzards Island.

To quantify densities of *Vallisneria*, *Myriophyllum*, and *Hydrilla* within each plot, scuba divers counted total numbers of shoots or stems enclosed within three haphazardly placed 30 × 30-cm quadrats. Within the same quadrats, divers also quantified the percent coverage of *Lyngbya* sp. and less common plants (including *Stuckenia pectinata*, *Najas guadalupensis*, and *Ceratophyllum demersum*).

Measurements of in situ aboveground growth by relatively large, established plants (≥4 leaves per shoot and ≥30 cm tall) were made on a bimonthly basis throughout the course of the experiment, after an initial acclimatization period following planting. We modified the hole-punching technique commonly used for seagrasses (Zieman and Wetzel 1980), and appropriate for many wide-bladed aquatic plants exhibiting a basal meristem (Hauxwell et al. 2003b). Scuba divers tagged seven relatively large, established plants in each plot, and punched two needle holes (18 gauge) at the base of each leaf per shoot. Tagged plants were retrieved one month after punching. Shoots were transported to the laboratory and frozen until total length, width, and leaf elongation for each leaf of each shoot could be measured. Because growth may also vary with shoot size, we simultaneously collected shoot mass data (total leaf surface area) on plants selected for growth measurements.

To convert aboveground shoot characteristics and leaf growth from units of surface area to shoot mass, we calculated a mean leaf specific density from ~120 shoots set aside prior to transplantation. We determined leaf specific density, by first removing epiphytic material from each leaf of each shoot (using a glass slide), measuring leaf surface area, and then drying leaves at 70°C to a constant weight, and weighing. A conversion factor (0.0034 g/cm², $r^2 = 0.92$, $P < 0.0001$) was calculated and applied to length and width data of transplanted shoots to estimate final aboveground mass (mg/shoot) and the mass of new tissue produced for the interval between punching and retrieval. Daily growth (mg·shoot⁻¹·d⁻¹) was estimated by dividing the production of new tissue by the time elapsed since punching, and mass-specific leaf growth rates (%/d) were determined by dividing daily growth rates by final aboveground shoot mass × 100 (Dennison 1987).

Changes in size distributions of plants within treatment plots can yield information regarding the effect

of other primary producers on: (1) recruitment of new shoots and (2) recruitment of transplanted shoots into larger size classes. To obtain nondestructive estimates of *Vallisneria* individual shoot mass and size distributions within plots, we developed a relationship between mass and morphological parameters of *Vallisneria* that could be easily and repeatedly obtained by scuba divers without harvesting plants. Using 300 plants that we had set aside prior to the transplantation experiments, shoot mass was determined and detailed morphological characteristics of shoots were measured. Leaf area proved a reliable predictor of plant mass: Aboveground shoot mass (in g) = 0.0030((leaves per shoot × length of longest leaf (in cm) × width of longest leaf (in cm))^{0.915}). This equation correlated well with our data ($P < 0.0001$, $r^2 = 0.93$). To assess size distributions in situ, scuba divers counted the number of leaves and measured the length and width of the longest leaf from 10 plants within a defined area of each plot three and five months after the initial planting. Together with the previously fitted regression equation, this yielded estimates of *Vallisneria* shoot mass and size distributions within plots over time.

RESULTS

Effect of herbivores and other primary producers on Vallisneria shoot densities

The density of *Vallisneria* in plots exposed to herbivores declined rapidly, and within one month, plants were absent from 80% of the open plots (Fig. 2). *Vallisneria*, however, was still present and relatively abundant in all of the fenced plots (Fig. 2). At Cedar Cove and Parker Island, the effect of herbivory was most pronounced; within one week of initiating the experiment, we observed a near total loss of transplants in all open plots. The effects of herbivory at Buzzard Island were dramatic, but less pronounced (~50% of open plots had some plants remaining), possibly because plots at this site were in slightly shallower depths, which may have reduced access by large herbivores during low tides. These results greatly contrast with those observed for naturally occurring *Vallisneria* (Fig. 2, bottom, dashed line), suggesting either that transplanted plants were selectively targeted by herbivores or that in the absence of herbivores natural meadows would exhibit dramatic increases in density.

Manatees were the most likely herbivore causing these large effects, and we observed manatees grazing in our plots soon after initiating the experiment. A daily mean of >200 manatees were counted within the 1.8-km² Kings Bay during the initial stages of the experiment (aerial surveys by Joyce Kleen, U.S. Fish and Wildlife Service), and manatees consumed plants directly from the hands of divers as they attempted to plant *Vallisneria* in two independent, yet similar in design, experiments (D. Tomasko, D. Bristol, and G. Sheehy, *personal communication*; Hauxwell et al., *in*

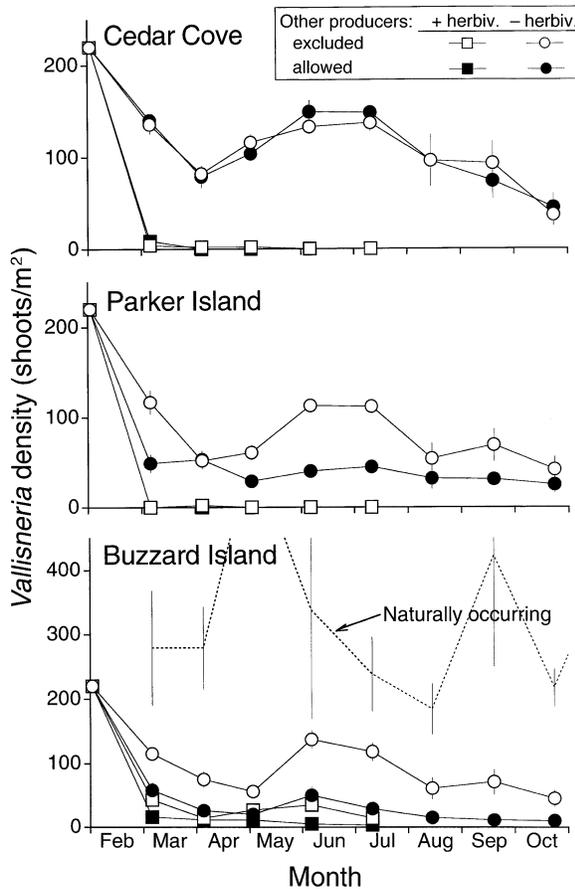


FIG. 2. Density of transplanted shoots of *Vallisneria americana* in plots in which herbivores or other primary producers were either allowed or excluded during 2001 at the Cedar Cove (top), Parker Island (middle), and Buzzard Island (bottom) sites in Kings Bay, Florida (means \pm 1 SE). The dashed line in the bottom panel indicates density of naturally occurring *Vallisneria* in a patchy meadow adjacent to the transplanted plots at Buzzard Island.

press). Additionally, we observed very limited effects of other grazers (e.g., assessed by observation of activity in the area and by grazing scars imprinted on leaves), and based upon the rapid removal of plants during this experiment, conclude that manatees are the most significant grazer in the system with regard to *Vallisneria* restoration.

After the initial mortality, plants did not return to any of the plots that were initially affected by manatees. Since manatees consumed almost all of the plants in exposed plots, and these plots remained void of *Vallisneria*, we ceased monitoring the open plots in July 2001. Given the obvious detrimental effect of herbivores on transplants, the remaining results (and accompanying statistical analyses) focus only on the effect of other primary producers (i.e., using herbivore exclusion plots).

Even in plots that excluded large herbivores, density declined by \sim 50% in the first month, probably due to

mortality induced by handling and transplantation (Fig. 2). After the first month, shoots in these plots appeared healthy and were actively growing; after three months density increased. Overall, long term fluctuations in the caged plots were similar to the pattern observed in an adjacent natural meadow, with early summer peaks in shoot density followed by decreases in density at the end of the growing season.

Response of *Vallisneria* densities to the presence or absence of other primary producers varied among sites (Fig. 2, Table 2), due to site-specific differences in the density or coverage of other primary producers that colonized plots (Fig. 3). At Cedar Cove, where colonization of other primary producers was minimal in all plots (Fig. 3, top panels), we observed no effect of other primary producers on *Vallisneria* densities (Table 2), and *Vallisneria* coverage extended beyond the perimeter of the original plots (J. Hauxwell, *personal observation*). There were, however, significant effects of other primary producers on *Vallisneria* densities at the other sites (Fig. 2, Table 2), where colonization by other primary producers was extensive relative to plots in which other primary producers were actively excluded (Fig. 3, middle and bottom panels). At both the Buzzard Island (strong significant effect, Table 2) and Parker Island (marginally significant effect, Table 2) sites, *Vallisneria* density in plots where colonization by other primary producers was allowed was \sim 50% the density in plots in which other primary producers were actively excluded.

Primary producers that colonized plots included Eurasian watermilfoil (*Myriophyllum spicatum*), hydrilla (*Hydrilla verticillata*), sago pondweed (*Stuckenia pectinata*), southern naiad (*Najas guadalupensis*), coontail (*Ceratophyllum demersum*), and filamentous cyanobacteria (*Lyngbya* sp.) (Fig. 3). Routine hand removal of weeds by snorkelers was effective in maintaining very low biomass of other primary producers in exclusion plots (Fig. 3, compare left and right panels). Where allowed, colonization by other primary producers at the Cedar Cove site was minimal (Fig. 3). However, at Parker Island and Buzzard Island, *Myriophyllum* became a dominant feature of the vegetation in plots in which we allowed colonization, extending into the water column over one meter and reaching densities greater than twice that of *Vallisneria* in those plots. At both of these sites, *Myriophyllum* densities peaked in late June. Based on data simultaneously obtained from benthic cores, these high densities correspond to dried biomass values greater than 400 g/m². *Hydrilla* and other species were generally rare and exhibited, at most, only minor peaks at both sites.

Because *Myriophyllum spicatum* was the most abundant competitor, we assessed the effect of *Myriophyllum* on *Vallisneria* density with regression analyses using monthly stem and shoot density data for both taxa in all of the herbivore-exclusion plots at all sites. Though our experimental design did not include ma-

TABLE 2. Results of three-factor (treatment, site, and time) and two-factor (treatment and time, within each site) repeated-measures ANOVAs used to test for differences in densities of transplanted *Vallisneria americana* over time in plots that either excluded or allowed colonization by other primary producers at the three study sites in Kings Bay, Florida (depicted in Fig. 2).

Site and factor	df	MS	F	P
All				
Treatment	1	33 642	13.18	0.0035
Site	2	31 602	12.38	0.0012
Treatment \times site	2	9358	3.67	0.0572
Plots within treatments	12	2553		
Time	7	8301	15.01	<0.0001
Time \times treatment	7	387	0.70	0.6720
Time \times site	14	2308	4.17	<0.0001
Time \times treatment \times site	14	1079	1.95	0.0320
Time \times plots within treatments	84	553		
Cedar Cove				
Treatment	1	6	0.01	0.9491
Plots within treatments	4	1304		
Time	7	7735	16.40	<0.0001
Time \times treatment	7	208	0.44	0.8677
Time \times plots within treatments	28	472		
Parker Island				
Treatment	1	18 644	5.57	0.0777
Plots within treatments	4	3347		
Time	7	2128	2.65	0.0311
Time \times treatment	7	1138	1.42	0.0238
Time \times plots within treatments	28	803		
Buzzard Island				
Treatment	1	33 708	11.20	0.0287
Plots within treatments	4	3010		
Time	7	3055	7.95	<0.0001
Time \times treatment	7	1199	3.12	0.0145
Time \times plots within treatments	28	384		

nipulating stem densities of *Myriophyllum*, differential colonization of the various treatment plots provided sufficient variation in *Myriophyllum* densities to be useful in a regression approach. We found a significant negative exponential relationship between shoot density of *Vallisneria* and stem density *Myriophyllum* for each sampling date (Fig. 4).

Effect of other primary producers on Vallisneria shoot growth rates

Although we targeted relatively large, established plants for measuring growth, and specifically avoided small newly recruiting plants, shoots that were sampled spanned a range of size classes. We were, however, successful in targeting the larger plants; in 80% of the cases, plants were >1 g, falling within the upper 75% of the size distribution.

Because growth increased with plant size (Fig. 5; regression analyses for pooled treatments, $P < 0.05$ in all cases), we included size as a covariate in a mixed effects model to test for differences in growth rates of *Vallisneria* over time in plots that either excluded or allowed colonization by other primary producers at the three study sites (Table 3; Littell et al. 1996, SAS PROC MIXED with fixed factors of treatment, site, and time and plot as a random factor). While we observed sig-

nificant differences in shoot growth rates among sites and dates, absolute growth rates of plants responded marginally, if at all, to treatment effects of other primary producers (including inconsistent responses, given the significant treatment \times site \times time interaction; Table 3). This effect of competitors, if real, was generally in the opposite direction from what we anticipated; plants grew similarly or worse when competitors were removed (Figs. 5 and 6).

To better visualize the growth responses, we estimated absolute and mass-specific growth rates. In situ growth of transplanted shoots varied among sites and over time (Table 4), ranging from 7 to 32 mg·shoot⁻¹·d⁻¹ (Fig. 6, top panels), representing turnover rates ranging from 0.7 to 1.6% per d (Fig. 6, bottom panels). Absolute and mass-specific growth rates generally decreased over the sampling period (Fig. 6). Absolute growth of plants at Cedar Cove and Parker Island was generally greater than that at Buzzards Island, largely because plants at Buzzard Island were smaller (Fig. 5 and see also Fig. 8). As expected, absolute growth of transplants was somewhat lower than that of naturally occurring *Vallisneria* for much of the study period (Fig. 6, upper right panel, dashed line). The results for specific growth (Fig. 6, bottom panels) are approximately comparable to our statistical analyses described above

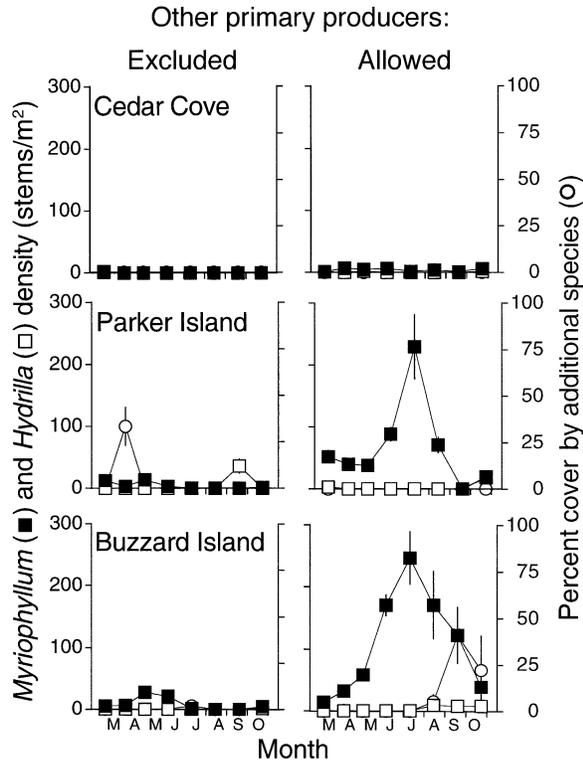


FIG. 3. Stem density of Eurasian watermilfoil (*Myriophyllum spicatum*) and hydrilla (*Hydrilla verticillata*) and percent cover of additional primary producers over time at the Cedar Cove (top), Parker Island (middle), and Buzzard Island sites (bottom) in Kings Bay, Florida, in transplanted plots of *Vallisneria americana* in which colonization of other primary producers was excluded (left) or allowed (right; means \pm 1 SE). Additional primary producers that colonized experimental plots included a filamentous cyanobacterium (*Lyngbya* sp.), sago pondweed (*Stuckenia pectinata*), southern naiad (*Najas guadalupensis*), and coontail (*Ceratophyllum demersum*).

(Table 3; Fig. 5): i.e., the slope of the relationship between $\log(\text{growth})$ and $\log(\text{mass})$ was 1.18 (fairly close to, albeit slightly greater than a slope of 1, which would be expected if specific growth did not vary with plant size). Indeed, Fig. 6 (bottom panels) shows (1) the detected interaction between site, time, and treatment, and (2) the slightly reduced growth of *Vallisneria* in weeded plots, as well as (3) lower specific growth rates of plants at Cedar Cove, where *Vallisneria* densities in all plots were relatively high (Fig. 2). After factoring out the effect of plant size, both the magnitude and seasonal pattern of mass-specific growth of transplants was similar to that of naturally occurring *Vallisneria* (Fig. 6, lower right panel, dashed line).

Because weeding reduced the density of competitors, but increased the density of *Vallisneria*, it is possible that the reduced (or lack of increased) growth in weeded plots was related to increased *Vallisneria* density. In fact, when pooled across all sites and treatments,

there was a negative linear relationship between mean *Vallisneria* mass-specific growth rate and *Vallisneria* shoot density on each date (Fig. 7; although this was statistically significant on only one of the four dates). Repeatedly, points from the Cedar Cove site clustered in a manner indicating low specific growth rates at high shoot densities.

Effect of other primary producers on *Vallisneria* shoot size distributions

Using the relationship between morphometric variables and shoot size (described in the *Materials and Methods: Measurement of response variables*) and in situ field measurements of the necessary variables within transplanted plots over time, we were able to assess whether there were shifts in size distributions of plants (1) within sites over time, (2) between treatments, and (3) among sites. Results, including initial shoot mass

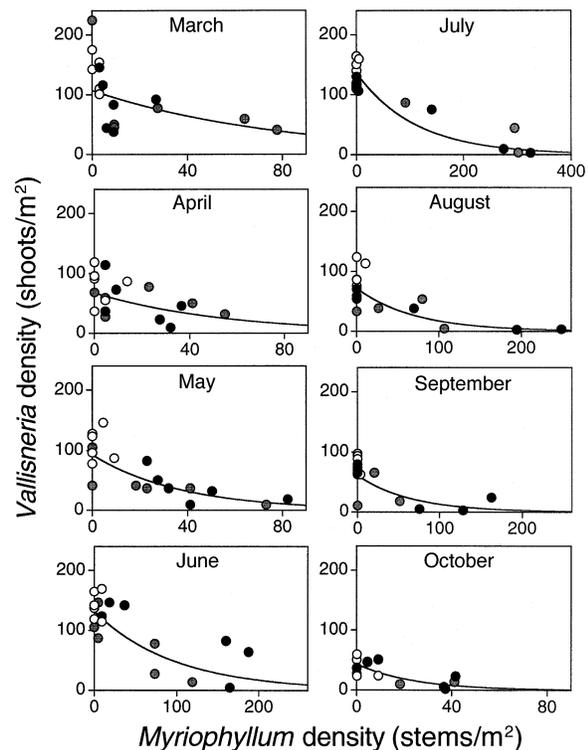


FIG. 4. Stem density of Eurasian watermilfoil (*Myriophyllum spicatum*) vs. shoot density of *Vallisneria americana* (raw data of means in Figs. 2 and 3) in plots in which we excluded or allowed colonization by other primary producers for each date over the sampling period in 2011 at the three experimental sites (symbols represent means within plots, treatments not distinguished; open circles = Cedar Cove, gray circles = Parker Island, black circles = Buzzard Island) in Kings Bay, Florida. Each regression was significant at $P < 0.001$: March, $y = 107(e^{-0.013x})$, $r^2 = 0.27$; April, $y = 68(e^{-0.018x})$, $r^2 = 0.23$; May, $y = 93(e^{-0.027x})$, $r^2 = 0.68$; June, $y = 131(e^{-0.010x})$, $r^2 = 0.49$; July, $y = 136(e^{-0.009x})$, $r^2 = 0.82$; August, $y = 72(e^{-0.014x})$, $r^2 = 0.81$; September, $y = 66(e^{-0.016x})$, $r^2 = 0.50$; October, $y = 44(e^{-0.042x})$, $r^2 = 0.57$.

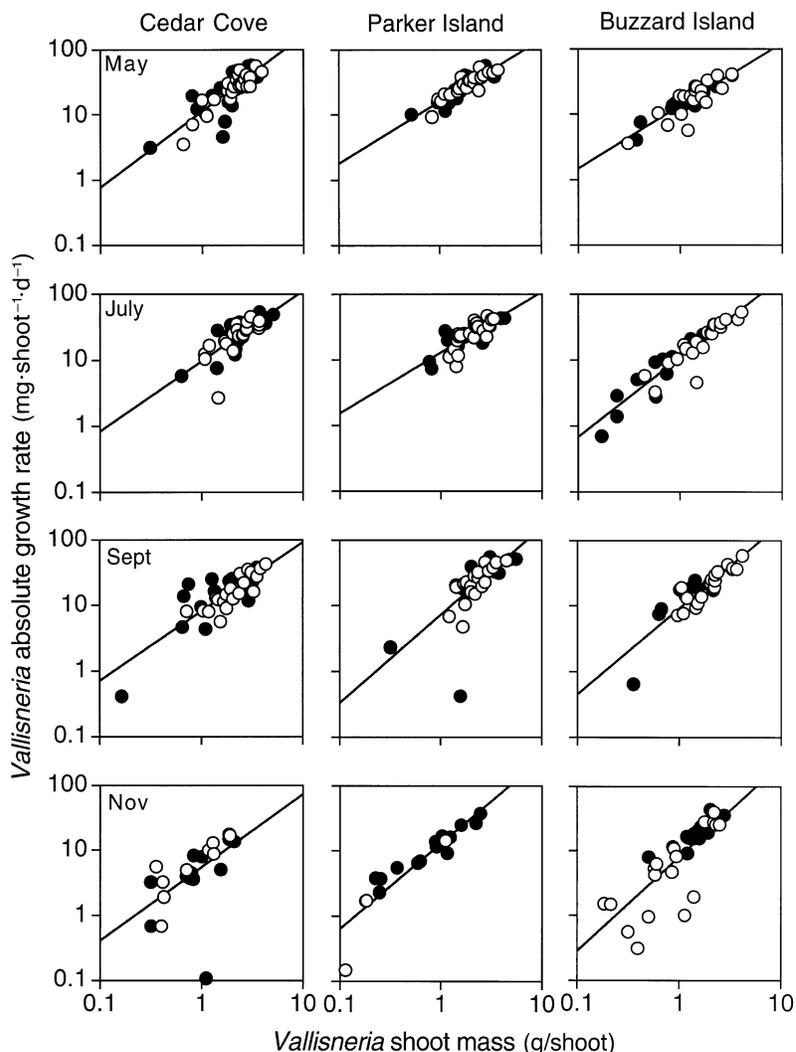


FIG. 5. Growth rates of individual *Vallisneria americana* shoots vs. aboveground shoot mass in plots in which we excluded (open circles) or allowed (black circles) colonization by other primary producers for each date over the sampling period in 2001 at the three experimental sites in Kings Bay, Florida (all as dry mass). Because there were no differences in slopes of regressions between treatments in any individual case ($P > 0.05$; comparison of multiple slopes, Sokal and Rohlf 1995), regression lines and statistics correspond to regression data pooled between treatments (Cedar Cove: May, $y = 11.4(x^{1.17})$, $r^2 = 0.69$; July, $y = 9.7(x^{1.07})$, $r^2 = 0.58$; September, $y = 8.2(x^{1.06})$, $r^2 = 0.66$; November, $y = 5.5(x^{1.13})$, $r^2 = 0.33$. Parker Island: May, $y = 15.9(x^{0.95})$, $r^2 = 0.79$; July, $y = 13.1(x^{0.92})$, $r^2 = 0.64$; September, $y = 7.2(x^{1.34})$, $r^2 = 0.48$; November, $y = 13.0(x^{1.31})$, $r^2 = 0.88$. Buzzard Island: May, $y = 13.6(x^{0.96})$, $r^2 = 0.77$; July, $y = 11.1(x^{1.21})$, $r^2 = 0.87$; September, $y = 9.1(x^{1.30})$, $r^2 = 0.77$; November, $y = 8.0(x^{1.45})$, $r^2 = 0.74$).

from laboratory measurements and subsequent (after five months) field measurements of shoot mass, are shown in Fig. 8, and provide before and after snapshots of *Vallisneria* in plots at the three sites.

At planting, the frequency distribution of shoot mass was skewed toward smaller plants (<0.5 g, 15–25 cm tall). After three months (*data not shown*), size frequency distributions shifted toward larger plants, indicating active growth of transplants. After five months, size frequency distributions of plants were significantly different than the initial distribution (Fig. 8).

At five months, there were also significant differences in plant sizes among sites with smaller plants at the Buzzard site and larger plants at the Cedar Cove site (Table 5). Plants at Cedar Cove, in fact, extended to the surface at low tide (up to 1.5 m tall). The presence of very small plants at all sites indicated recruitment of small, new plants. Though there was a significant effect of other primary producers on *Vallisneria* densities, removal of competitors had no demonstrable effect on the mean size of *Vallisneria* at any of the sites (Table 5).

TABLE 3. Results of a mixed effects model (Littell et al. 1996, SAS PROC MIXED) used to test for differences in growth rates of *Vallisneria americana* over time in plots that either excluded or allowed colonization by other primary producers at the three study sites in Kings Bay, Florida, and that incorporated shoot mass as a covariate with shoot growth (fixed factors = treatment, site, and time; random factor = plot; data were log transformed and are depicted in Fig. 5; see also Fig. 6, bottom panels).

Factor	df	F	P
Treatment	1, 12	3.59	0.082
Site	2, 12	8.11	0.006
Time	3, 32	16.83	<0.0001
Shoot mass	1, 386	711.13	<0.0001
Treatment × site	2, 12	2.18	0.156
Treatment × time	3, 32	0.93	0.438
Site × time	6, 32	1.04	0.416
Treatment × site × time	6, 32	2.80	0.027

DISCUSSION

Productivity of naturally occurring and transplanted Vallisneria

Despite the many ecological values inherent in preserving *Vallisneria* habitat and the widespread efforts to restore *Vallisneria* in areas in which it has declined, there remains a paucity of information on even the most basic demographic parameters in *Vallisneria* populations, including annual dynamics of density and growth, let alone ecosystem effects on carbon fixation

or nutrient cycling, i.e., *what* are we restoring? Baseline ecological data are crucial for assessing successful restoration of *Vallisneria*, as well as the ecological implications of restoration (including the likely effects of restoration on system productivity). To our knowledge, this study provides the only information on transplant and natural stand productivity to date. Notably, *minimum* rates of *Vallisneria* production ($\sim 4.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, Figs. 2 and 6; Hauxwell et al. 2003b) were estimated to be approximately twice that of the *maximum* growth rate of a “highly productive” seagrass (*Thalassia testudinum*) meadow off of Florida’s central Gulf coast (Zieman et al. 1989). These data suggest that, first, on an ecosystem scale, the magnitude of carbon fixed by *Vallisneria* and available as standing biomass for heterotrophic consumption may be relatively large, emphasizing the importance of *Vallisneria* to whole ecosystem functioning in springs, lakes, and oligohaline reaches of many estuaries.

In comparison with productivity of natural stands, transplants exhibited similar relative growth rates (0.8–1.8% per day). At no point during our yearlong experiment, however, did overall productivity reach values exhibited by natural stands, due to lower shoot densities in transplanted plots. It is not yet clear how long (if ever) it might take a transplanted plot to achieve productivity of a natural stand. However, productivity may not be the appropriate benchmark from

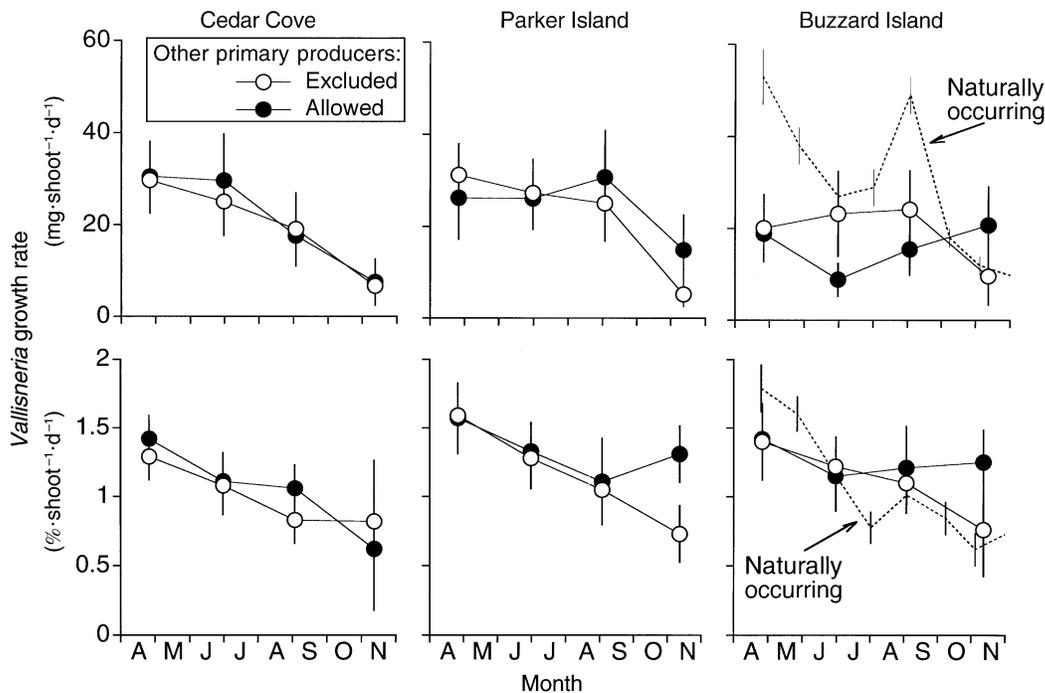


FIG. 6. Absolute (top, in mg dry mass) and mass-specific (bottom) growth rates of *Vallisneria americana* shoots over time (midpoint of punching and retrieval dates) in plots in which we excluded or allowed colonization by other primary producers during 2001 at the three study sites in Kings Bay, Florida (means ± 1 SE). The dashed lines in the right panels indicate growth rates of naturally occurring *Vallisneria* in a patchy meadow adjacent to the transplanted plots at Buzzard Island.

TABLE 4. Results of three-factor (treatment, site, and time) repeated-measures ANOVAs used to test for differences in absolute and mass-specific growth rates of *Vallisneria americana* over time in plots that either excluded or allowed colonization by other primary producers at the three study sites in Kings Bay, Florida (depicted in Fig. 6).

Factor	df	MS	F	P
Absolute growth rate				
Treatment	1	0.000002	0.07	0.7984
Site	2	0.000103	2.89	0.1020
Treatment \times site	2	0.000024	0.67	0.5332
Plots within treatments	10	0.000036		
Time	3	0.001000	31.17	<0.0001
Time \times treatment	3	0.000071	2.78	0.0581
Time \times site	6	0.000167	6.58	0.0002
Time \times treatment \times site	6	0.000063	2.49	0.0448
Time \times plots within treatments	30	0.000025		
Mass-specific growth rate				
Treatment	1	0.251	4.1	0.0699
Site	2	0.312	5.1	0.0295
Treatment \times site	2	0.036	0.6	0.5699
Plots within treatments	10	0.061		
Time	3	0.862	23.3	<0.0001
Time \times treatment	3	0.050	1.4	0.2745
Time \times site	6	0.020	0.5	0.7720
Time \times treatment \times site	6	0.071	1.9	0.1101
Time \times plots within treatments	30	0.037		

which to judge "success." Indeed, there are many aspects of habitat restoration (physical, chemical, biological, as well as aesthetic and educational) that various audiences representing different interests consider favorable targets.

Effect of herbivores on Vallisneria restoration

Experimental results demonstrate strong effects of manatees on *Vallisneria* restoration efforts in Kings Bay, and potentially in other spring-fed systems along the Gulf coast of Florida. Although natural *Vallisneria* beds adjacent to transplanted plots remained intact over the course of our experiment, grazing by manatees on newly transplanted *Vallisneria* in Kings Bay was targeted and intense, regardless of site, and would be a vital element to consider when formulating a restoration strategy. From grazing scars on leaves, we roughly estimate small invertebrate grazing to be minimal ($\sim <0.1\%$ standing biomass; J. Hauxwell, unpublished data). Field observations of turtles, a class of herbivore shown to significantly reduce success of *Vallisneria* transplants in other systems in Florida (Lake Monroe; Jagers 1994), Alabama (Guntersville Reservoir; Doyle and Smart 1993), and Maryland (Potomac River; Carter and Rybicki 1985), were also minimal; while we encountered manatees daily, in the collective >4000 hours spent diving for this and other experiments, we observed only one turtle. Also, herbivorous waterfowl were never observed in the vicinity of plots.

Despite the marked effect of manatees on *Vallisneria* in our experimental plots, we do not, however, suggest that the presence of manatees (1) was the cause for long-term decline of *Vallisneria* in Kings Bay, or (2) necessarily precludes restoration of *Vallisneria* in

Kings Bay. While feeding within natural meadows of *Vallisneria*, manatees primarily crop plants (T. K. Frazer, personal observation), leaving the belowground portion, along with several centimeters of leaf material, intact. *Vallisneria* and other true seagrasses (e.g., *Thalassia* and *Halodule*) have evolved to cope with herbivory by large herbivores (including manatees, dugongs, turtles, waterfowl), and can repeatedly regrow the cropped leafy portion (Cebrián et al. 1998), presumably using within-shoot belowground energy reserves or translocated energy reserves from a neighboring clone. In several studies, seagrasses have been documented to persist, and in some cases, even increase productivity (Valentine et al. 1997), despite extensive, sometimes repeated, grazing by sea turtles, manatees, dugongs, or sea urchins (Greenway 1976, Ogden et al. 1983, Zieman et al. 1984, Williams 1988, Masini et al. 2001). We, in fact, have conducted simulated grazing experiments within natural stands of *Vallisneria* in Kings Bay and have found that, one week after clipping, we could not recognize clipped plants from controls (J. Hauxwell, personal observation). In the experiment described here, however, newly planted shoots were completely uprooted by manatees. It is possible that transplanted *Vallisneria* must be protected during some initial acclimatization period (e.g., enough time to allow plants to become well-rooted and to develop a more mature belowground rhizome system), and if so, it would be a relatively simple task to exclude herbivores during this period, using spatial (fencing, necessary year-round; Smart et al. 1998) combined with temporal strategies (planting in summer when manatee abundances are lowest, although still present). If this is indeed the case, however, the time required

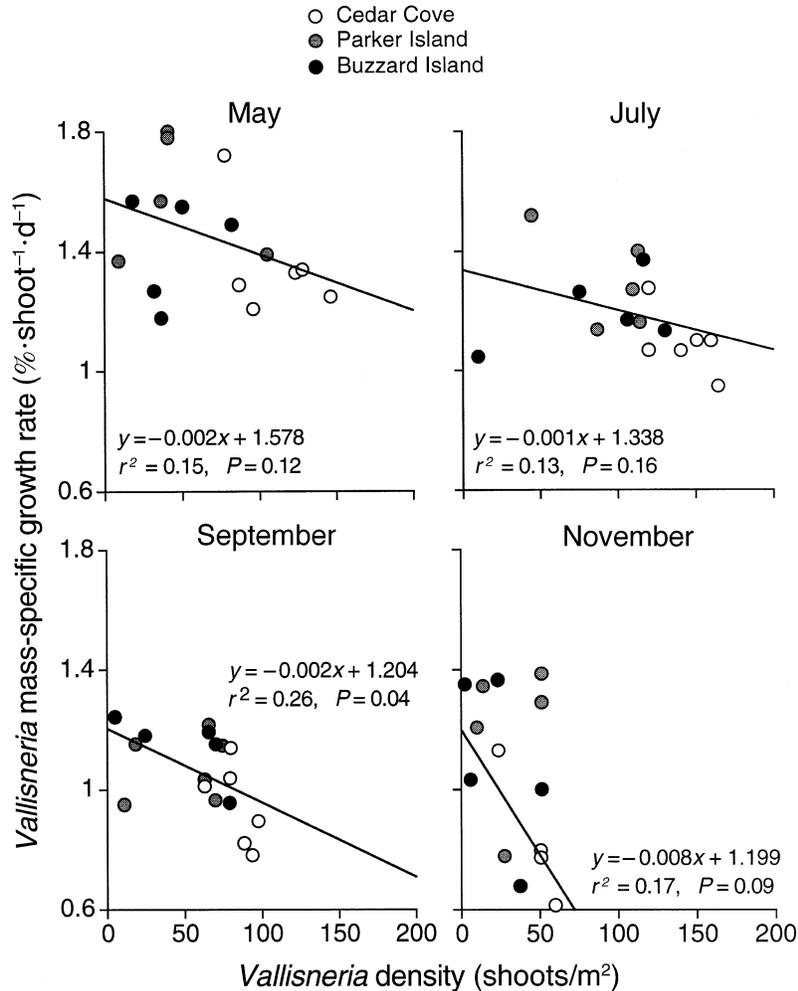


FIG. 7. Mass-specific growth rates of *Vallisneria americana* shoots vs. *Vallisneria* shoot densities in plots in which we excluded or allowed colonization by other primary producers for four dates in 2001 at the three study sites in Kings Bay, Florida (symbols represent means within plots; treatments not distinguished).

for plants to establish is beyond the five-month period tested in a follow up experiment (Hauxwell et al., *in press*).

Results from this experiment illustrate a potentially difficult management scenario and a topic of ongoing debate: “save the ecosystem, [vs.] save the species” (Senior 2003). The manatee, a federally endangered species, negatively affected restoration of a native aquatic plant. Though simultaneous protection of manatees and potential restoration of *Vallisneria* would require creative solutions that are not necessarily mutually exclusive, results of this experiment illustrate the potential conflicts that can arise when species-specific approaches to management are employed within ecosystems.

Effect of other primary producers on Vallisneria restoration

Recently planted shoots of *Vallisneria* in Kings Bay may be competitively reduced by other plants, espe-

cially the nonnative macrophyte *Myriophyllum spicatum*. In plots where these competitors were routinely removed, or where natural densities of *Myriophyllum* remained low (Cedar Cove), there remained relatively dense and productive stands of *Vallisneria*. Therefore, the recent status of water clarity in Kings Bay does not appear to preclude *Vallisneria* restoration. *Lyngbya*, though abundant in the vicinity of enclosures at Cedar Cove, was not common in our experimental plots. *Hydrilla verticillata* was present but did not achieve nuisance levels. Compared to herbivory, competition with *Myriophyllum* likely represents a much more chronic and difficult problem to confront in restoration, and may have been a factor related to the initial decline of *Vallisneria* in Kings Bay. *Myriophyllum* has been shown to competitively exclude native vegetation, including *Vallisneria*, in other systems in North America (Lind and Cottam 1969, McFarland and Rogers 1998).

Potential mechanisms by which *Myriophyllum* reduces *Vallisneria* in shallow-water systems might in-

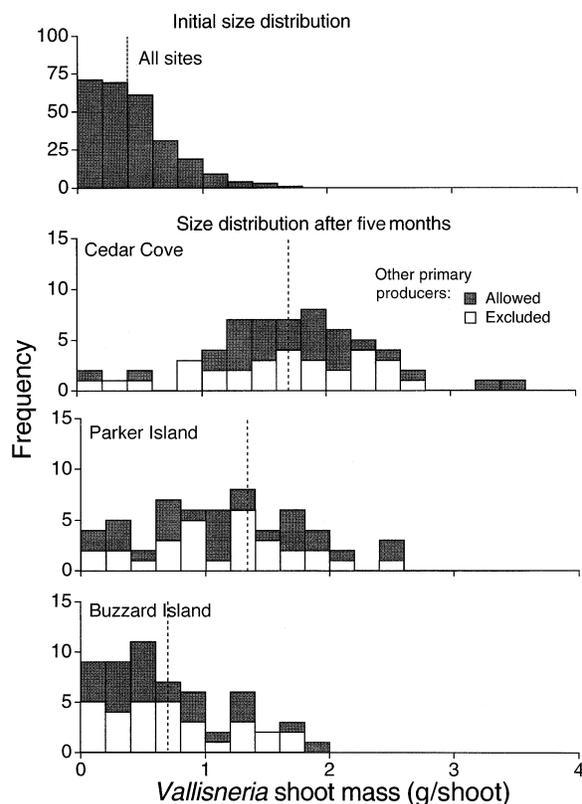


FIG. 8. Histograms showing the size distribution of *Vallisneria americana* shoots (aboveground modeled values, all in g dry mass) that were initially planted in all plots (top panel) and five months after planting in plots in which we excluded or allowed colonization by other primary producers during 2001 at the Cedar Cove (second panel), Parker Island (third panel), and Buzzard Island sites (bottom panel) in Kings Bay, Florida. Extended dashed lines indicate means (pooled for treatments within a site).

clude (1) competition for space and (2) light limitation of newly recruiting shoots. Established tall plants of *Vallisneria* grew similarly whether in monospecific stands or in mixed stands with *Myriophyllum*. Densities of *Vallisneria*, however, decreased rapidly as *Myriophyllum* stem density increased. It is possible that *Myriophyllum* affects growth of short, newly recruiting *Vallisneria* shoots as a result of inherent differences between their growth forms. Titus and Adams (1979) demonstrated that in one meter depths (similar to Kings Bay), *Myriophyllum* formed a leafy canopy concentrated at the surface (68% of its aboveground biomass was within 30 cm of the surface), whereas young shoots of *Vallisneria* concentrated the majority of leaf biomass near the bottom (62% of its biomass was within only 30 cm of the bottom; see also Duarte and Roff 1991). Growth of *Vallisneria* in systems with degraded water clarity can be stimulated by increased light, demonstrating general light limitation of growth (Carter et al. 1996). Therefore, it is possible that in Kings Bay, growth of young, newly recruiting plants may be re-

duced by competition with *Myriophyllum*, although growth of taller *Vallisneria* (which extend to the water's surface) is not (Figs. 5 and 6). This mechanism would also affect the number of plants recruiting to larger size classes. In our experiment, where *Myriophyllum* colonization was negligible (Cedar Cove), size distributions of *Vallisneria* spanned the greatest range, and after five months, a large percentage of plants extended to the surface, even at high tide (>1.5 m tall). It is possible, that plants at Cedar Cove reached high enough densities (Fig. 2) and attained large enough sizes (Fig. 8) for growth to be limited due to self-shading (Fig. 7). Alternatively, increased allocation of carbon reserves to belowground growth in the absence of interspecific competition might account for the absence of an effect of competitors on aboveground growth.

Implications for *Vallisneria* restoration and management of aquatic habitats

Based on results of this study, we propose the following recommendations regarding potential future restoration of *Vallisneria* in Kings Bay. First, transplants must be protected from manatees. Second, effects of competition must be relatively small. As a result of spatial variation in competition, success of restoration is likely to be highly site specific. For example, we observed large spatial heterogeneity in overall success of transplants in the experiment, due to site-specific differences in natural abundances of other primary producers. At two of our three sites, restoration does not appear to be feasible without considerable site maintenance (i.e., routine mechanical or targeted chemical removal of potential competitors); colonization by *Myriophyllum* was rapid, and it was able to competitively reduce densities of *Vallisneria* transplants. At the Cedar Cove site, however, natural densities of competitors were low (Figs. 3 and 4) and we observed: (1) generally high densities of plants (Fig. 2), (2) generally high absolute growth rates (Fig. 6), (3) greatest recruitment of small shoots into larger size classes (Fig. 8), and (4) general extension of *Vallisneria* coverage beyond original plot perimeters. Many factors may contribute to the site-to-site differences in colonization by

TABLE 5. Results of a two-factor ANOVA comparing mean sizes of shoots of *Vallisneria americana* (modeled aboveground shoot mass, depicted in Fig. 8) in transplanted plots in which we either excluded or allowed colonization by other primary producers at the three experimental sites (Cedar Cove, Parker Island, and Buzzard Island) in Kings Bay, Florida.

Factor	df	MS	F	P
Site	2	0.323	16.83	0.0003
Treatment	1	0.001	0.07	0.8030
Site × treatment	2	0.005	0.25	0.7803
Residual	12	0.019		

Note: Data were log transformed.

other primary producers and the general success of *Vallisneria* in transplanted plots, including physical, geological, and geochemical differences among sites (Titus and Adams 1979, Titus and Stone 1982, Barko and Smart 1986, Twilley and Barko 1990, Sullivan and Titus 1996, Kraemer et al. 1999, Van et al. 1999, Koch 2001).

It is important to note that these results are from a highly "managed" system (as are most freshwater systems), and may be affected if any one of the many management practices were altered or if new strategies were implemented. During our experiment, the herbicide endothal (Aquathol, Cerexagri, King of Prussia, Pennsylvania, USA) was applied in back canals to limit growth of hydrilla (Mark Edwards, Citrus County Aquatic Services, Citrus County, Florida, USA, *personal communication*). In addition, mechanical removal of vegetation assemblages in the littoral zone (primarily hydrilla, *Lyngbya*, and Eurasian watermilfoil) occurred sometimes daily. These management strategies are not specific to Kings Bay, and may, in many cases, be the norm in many freshwater environments around the world. Indeed, there exists a very full and imaginative toolbox accessible to those interested in ameliorating recreational or aesthetic problems stemming from cultural eutrophication in freshwaters, including: application of herbicides, application of alum or lime to bind nutrients, withdrawal of nutrient-rich hypolimnetic waters, water level manipulation, imposing light limitation using dyes or opaque screens, lining the bottom with plastic to inhibit plant growth, whole-lake aeration to reduce internal phosphorus loading, dredging, introduction of herbivores (e.g., grass carp, milfoil weevil), mechanical harvesting, and repeated disturbance of sediments ("weed rollers") (Holdren et al. 2001). In best cases, these methods may be used in conjunction with improved watershed management practices; in many cases they are used in lieu of longer-term solutions. As is the case for many other water bodies, numerous management agencies, representing city, county, regional, state, and federal interests are presently active within the Kings Bay system. Hence, experimental results for Kings Bay and other highly managed systems must be viewed within this context and the limitations of extrapolating these results to other systems—and the importance in site-specific pilot experiments—should also be recognized, particularly for freshwater environments.

In conclusion, we argue that only by understanding the ecological factors that affect the successful re-establishment of *Vallisneria*, can we develop the most successful, cost-effective techniques for restoration. Restoration might not be feasible in many targeted systems, and it is important to understand not only the causes of initial degradation and factors that might affect future restoration, but also, to characterize the appropriate measures of "success." Detailed demographic studies of natural populations of *Vallisneria* must at

least accompany, if not precede, investment in large-scale restoration efforts, and the possibility that "re-stored" systems may differ significantly from natural systems in terms of productivity, habitat complexity, and genetic diversity (Williams 2001), should also be recognized.

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LITERATURE CITED

- Barko, J. W., M. S. Adams, and N. L. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. *Journal of Aquatic Plant Management* **24**:1–10.
- Barko, J. W., and R. M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* **67**:1328–1340.
- Bayley, S., V. D. Stotts, P. F. Springer, and J. Steenis. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958–1975. *Estuaries* **1**:73–84.
- Belanger, T., H. Heck, M. Sohn, P. R. Sweets, M. Morris, and N. Julien. 1993. Sediment mapping and analysis in Crystal River/Kings Bay and Lake Panasoffkee. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Blackburn, R. D., and L. W. Weldon. 1967. New underwater menace—Eurasian watermilfoil. *Weeds Trees and Turf* **November 1967**:10–13.
- Carter, V., and N. B. Rybicki. 1985. The effects of grazers and light penetration on the survival of transplants of *Vallisneria americana* Michx. in the tidal Potomac River, Maryland. *Aquatic Botany* **23**:197–213.
- Carter, V., N. B. Rybicki, and M. Turtora. 1996. Effect of increasing photon irradiance on the growth of *Vallisneria americana* in the tidal Potomac River. *Aquatic Botany* **54**:337–345.
- Cebrián, J., C. M. Duarte, N. S. R. Agawin, and M. Merino. 1998. Leaf growth response to simulated herbivory: a comparison among seagrass species. *Journal of Experimental Marine Biology and Ecology* **220**:67–81.
- Chambers, P. A., M. Guy, E. S. Roberts, M. N. Charleton, R. Kent, C. Gagnon, G. Grove, and N. Foster. 2001. Nutrients and their impact on the Canadian environment. *Agriculture*

- and AgriFood Canada, Environment Canada, Fisheries and Oceans Canada, Health Canada and Natural Resources Canada, Hull, Quebec, Canada.
- Chambers, P. A., and J. Kalf. 1985. Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi depth. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:1010–1017.
- Davis, R. C., and F. T. Short. 1997. Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. *Aquatic Botany* **59**:1–15.
- Davis, R. C., F. T. Short, and D. M. Burdick. 1998. Quantifying the effects of green crab damage to eelgrass transplants. *Restoration Ecology* **6**:297–302.
- Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* **27**:15–26.
- Doyle, R. D., and R. M. Smart. 1993. Potential use of native aquatic plants for long-term control of problem aquatic plants in Guntersville Reservoir, Alabama. Report 1. Establishing native plants. Technical Report **A-93-6**. U.S. Army Corps of Engineers, Environmental Laboratory, Vicksburg, Mississippi, USA.
- Duarte, C. M., and R. A. Roff. 1991. Architectural and life history constraints to submersed macrophyte community structure: a simulation study. *Aquatic Botany* **42**:15–29.
- Duffy, K. C., and D. M. Baltz. 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Ponchartrain estuary, USA. *Journal of Experimental Marine Biology and Ecology* **223**:199–221.
- Frazer, T. K., and J. A. Hale. 2001. An atlas of submersed aquatic vegetation in Kings Bay (Citrus County, Florida). Southwest Florida Water Management District, Brooksville, Florida, USA.
- Frazer, T. K., M. V. Hoyer, S. K. Notestein, J. A. Hale, and D. E. Canfield, Jr. 2001a. Physical, chemical and vegetative characteristics of five Gulf coast rivers. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Frazer, T. K., S. K. Notestein, M. V. Hoyer, J. A. Hale, and D. E. Canfield, Jr. 2001b. Frequency and duration of pulsed salinity events in Kings Bay. Southwest Florida Water Management District, Brooksville, Florida, USA.
- GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Pollution). 1990. State of the Marine Environment. Reports and Studies Number 39. United Nations Environment Programme, Nairobi, Kenya.
- Greenway, M. 1976. The grazing of *Thalassia testudinum* in Kingston Harbour, Jamaica. *Aquatic Botany* **2**:117–126.
- Harrison, P. G. 1990. Variations in success of eelgrass transplants over a five-year period. *Environmental Conservation* **17**:157–163.
- Hauxwell, J., J. Cebrián, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* **82**:1007–1022.
- Hauxwell, J., J. Cebrián, and I. Valiela. 2003a. Eelgrass (*Zostera marina* L.) loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* **247**:59–73.
- Hauxwell, J., T. K. Frazer, and C. W. Osenberg. *In press*. Grazing by manatees excludes both new and established wild celery transplants: implications for restoration in Kings Bay, Florida, USA. *Journal of Aquatic Plant Management*.
- Hauxwell, J., C. W. Osenberg, and T. K. Frazer. 2003b. Factors affecting restoration of *Vallisneria americana* in Kings Bay. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Hestand, R. S., and C. C. Carter. 1978. Comparative effects of grass carp and selected herbicides on macrophyte and phytoplankton communities. *Journal of Aquatic Plant Management* **16**:43–50.
- Holdren, C., W. Jones, and J. Taggart. 2001. Managing lakes and reservoirs. North American Lake Management Society and Terrene Institute, in cooperation with the Office of Water, Assessment and Watershed Protection Division of the U.S. Environmental Protection Agency, Madison, Wisconsin, USA.
- Hoyer, M. V., T. K. Frazer, D. E. Canfield, Jr., and J. M. Lamb. 2001. Vegetation evaluation in Kings Bay/Crystal River. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Hoyer, M. V., L. K. Mataraza, A. B. Munson, and D. E. Canfield, Jr. 1997. Water clarity in Kings Bay/Crystal River. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Jagers, B. V. 1994. *Vallisneria americana*: considerations for restoration in Florida. Technical report. Florida Game and Fresh Water Fish Commission, Eustis, Florida, USA.
- Johansson, J. O. R., and H. S. Greening. 2000. Seagrass restoration in Tampa Bay: a resource-based approach to estuarine management. Pages 279–293 in S. A. Bortone, editor. *Seagrasses: monitoring, ecology, physiology, and management*. CRC Press, New York, New York, USA.
- Kemp, W. M., R. R. Twilley, J. C. Stevenson, W. R. Boynton, and J. C. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. *Marine Technology Society Journal* **17**:78–89.
- Kenworthy, W. J., and M. S. Fonseca. 1992. The use of fertilizer to enhance growth of transplanted seagrasses *Zostera marina* L. and *Halodule wrightii* Aschers. *Journal of Experimental Marine Biology and Ecology* **163**:141–161.
- Kimber, A., J. L. Owens, and W. G. Crompton. 1995. Light availability and growth of wildcelery (*Vallisneria americana*) in Upper Mississippi River backwaters. *Regulated Rivers: Research and Management* **11**:167–174.
- Koch, E. W. 2001. Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* **24**:1–17.
- Korschgen, C. E., and W. L. Green. 1988. American wildcelery (*Vallisneria americana*): ecological considerations for restoration. Fish and Wildlife Technical Report **19**. U.S. Fish and Wildlife Service, Northern Prairie Research Center, Jamestown, North Dakota, USA.
- Kraemer, G. P., R. H. Chamberlain, P. H. Doering, A. D. Steinman, and M. D. Hanisak. 1999. Physiological responses of transplants of the freshwater angiosperm *Vallisneria americana* along a salinity gradient in the Caloosahatchee estuary (southwest Florida). *Estuaries* **22**:138–148.
- Langeland, K. A. 1990. Hydrilla (*Hydrilla verticillata* (L. F.) Royle). A continuing problem in Florida waters. Circular No. **884**. Cooperative Extension Service/Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida, USA.
- Lind, C. T., and G. Cottam. 1969. The submerged aquatics of University Bay: a study in eutrophication. *American Midland Naturalist* **81**:353–369.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina, USA.
- Masini, R. J., P. K. Anderson, and A. J. McComb. 2001. A *Halodule*-dominated community in a subtropical embayment: physical environment, productivity, biomass, and impact of dugong grazing. *Aquatic Botany* **71**:179–197.
- McFarland, D. G., and S. J. Rogers. 1998. The aquatic macrophyte seed bank in Lake Onalaska, Wisconsin. *Journal of Aquatic Plant Management* **36**:33–39.

- National Research Council. 1994. Priorities for coastal science. National Academy Press, Washington, D.C., USA.
- Ogden, J. C., L. Robinson, K. Whitlock, H. Daganhardt, and R. Cebula. 1983. Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **66**:199–205.
- Orth, R. J., M. C. Harwell, and J. R. Fishman. 1999. A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquatic Botany* **64**:77–85.
- Roberts, J., A. Chick, L. Oswald, and P. Thompson. 1995. Effect of carp, *Cyprinus carpio* L., an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. *Marine and Freshwater Research* **46**:1171–1180.
- Rogers, S. J., D. G. McFarland, and J. W. Barko. 1997. Evaluation of the growth of *Vallisneria americana* Michx. in relation to sediment nutrient availability. *Lake and Reservoir Management* **11**:57–66.
- Romie, K. F. 1990. An evaluation of factors contributing to the growth of *Lyngbya* sp. in Kings Bay/Crystal River, Florida. Final Report. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Rybicki, N. B., and V. Carter. 1986. Effect of sediment depth and sediment type on the survival of *Vallisneria americana* Michx grown from tubers. *Aquatic Botany* **24**:233–240.
- Schlosser, D. W., and B. A. Manny. 1990. Decline of wild celery buds in the lower Detroit River, 1950–1985. *Journal of Wildlife Management* **54**:72–76.
- Senior, K. 2003. Save the ecosystem, save the species. *Frontiers in Ecology and the Environment* **1**:116.
- Sheridan, P., G. McMahan, K. Hammerstrom, and W. Pulich, Jr. 1998. Factors affecting restoration of *Halodule wrightii* to Galveston Bay, Texas. *Restoration Ecology* **6**:144–158.
- Short, F. T., D. M. Burdick, J. S. Wolf, and G. E. Jones. 1993. Eelgrass in estuarine research reserves along the East Coast, USA., Part I, Declines from pollution and disease, and Part II, Management of eelgrass meadows. Publication **M1–M24**. National Oceanic and Atmospheric Administration, Coastal Ocean Program Publication, Rockville, Maryland, USA.
- Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* **23**:17–27.
- Smart, R. M., G. O. Dick, and R. D. Doyle. 1998. Techniques for establishing native aquatic plants. *Journal of Aquatic Plant Management* **36**:44–49.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third edition. W. H. Freeman, New York, New York, USA.
- Sullivan, G., and J. E. Titus. 1996. Physical site characteristics limit pollination and fruit set in the dioecious hydrophilous species, *Vallisneria americana*. *Oecologia* **108**:285–292.
- SWFWMD (Southwest Florida Water Management District). 2001. Crystal River/Kings Bay Surface Water Improvement and Management Plan. Southwest Florida Water Management District, Brooksville, Florida, USA.
- Terrell, J. B., and D. E. Canfield, Jr. 1996. Evaluation of the effects of nutrient removal and the “Storm of the Century” on submersed aquatic vegetation in Kings Bay–Crystal River, Florida. *Journal of Lake and Reservoir Management* **12**:394–403.
- Titus, J. E., and M. S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia* **40**:273–286.
- Titus, J. E., and W. H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH. *Limnology and Oceanography* **27**:151–160.
- Tomasko, D. A., C. J. Dawes, and M. O. Hall. 1991. Effects of the number of short shoots and presence of the rhizome apical meristem on the survival and growth of transplanted seagrass *Thalassia testudinum*. *Contributions in Marine Science* **32**:41–48.
- Twilley, R. R., and J. W. Barko. 1990. The growth of submersed macrophytes under experimental salinity and light conditions. *Estuaries* **13**:311–321.
- U.S. Geological Survey. 1999. The quality of our nation’s waters—nutrients and pesticides. U.S. Geological Survey Circular **1225**.
- Valentine, J. F., K. L. Heck Jr., J. Busby, and D. Webb. 1997. Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. *Oecologia* **112**:193–200.
- Valiela, I., and M. L. Cole. 2002. Comparative evidence that salt marshes and mangroves may protect seagrass meadows from land-derived nutrient loads. *Ecosystems* **5**:92–102.
- Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* **42**:1105–1118.
- Van, T. K., W. T. Haller, and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology* **58**:761–768.
- Van, T. K., G. S. Wheeler, and T. D. Center. 1999. Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility. *Aquatic Botany* **62**:225–233.
- West, R. J., N. E. Jacobs, and D. E. Roberts. 1990. Experimental transplanting of seagrasses in Botany Bay, Australia. *Marine Pollution Bulletin* **21**:197–203.
- Williams, S. L. 1988. *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Marine Biology* **98**:447–455.
- Williams, S. L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population and individual fitness. *Ecological Applications* **11**:1472–1488.
- Wilson, K. A. 2002. Impacts of the invasive rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Zieman, J. C., J. W. Fourqurean, and R. L. Iverson. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* **44**:292–311.
- Zieman, J. C., R. L. Iverson, and J. C. Ogden. 1984. Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Marine Ecology Progress Series* **15**:151–158.
- Zieman, J. C., and R. G. Wetzel. 1980. Productivity in seagrasses: methods and rates. Pages 87–116 in R. C. Phillips and C. P. McRoy, editors. *Handbook of seagrass biology*. Garland Press, New York, New York, USA.
- Zimmerman, R. C., J. L. Reguzzoni, and R. S. Alberte. 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: role of light availability on metabolism, growth and survival. *Aquatic Botany* **51**:67–86.