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Grazing by Manatees Excludes Both New and Established Wild Celery Transplants: Implications for Restoration in Kings Bay, FL, USA

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ABSTRACT

We conducted a field experiment between August 2001 and February 2002 in Kings Bay, FL, USA, designed to determine whether the amount of time allowed for wild celery (Vallisneria americana Michx) transplants to establish altered the effect of herbivorous manatees (Trichechus manatus L.) on their survival. We employed a 2 by 2 factorial design in which we allowed or denied manatees access to (1) newly transplanted plots of wild celery or (2) plots that had been planted 5 months earlier and allowed to establish. Upon removal of protective fencing, a significant effect of manatees was observed in unprotected plots, regardless of level of establishment. Within 1 month, all exposed plots were void of plants. In contrast, density of plants in plots that had been protected from herbivores showed very little change over the study period. Results of this experiment indicate that success of any future larger-scale transplant effort in Kings Bay is contingent upon adequate protection from manatees. If, in fact, transplants become more resistant to uprooting by manatees over time, it is beyond the duration tested in this experiment (>5 months).

Key words: Vallisneria americana, Trichechus manatus, seagrass, macrophyte, herbivory.

INTRODUCTION

Wild celery is distributed from Central America to Canada (Korschgen and Green 1988), and occurs in freshwater to mesohaline environments. Wild celery is native to Florida and is common in most spring-fed systems throughout the state, often forming extensive meadows. Such meadows are important biological, physical, and chemical components of these ecosystems, providing both refuge and foraging habitat, while also influencing local chemical and nutrient cycles and affecting sediment biogeochemistry (Wigand et al. 1997).

Wild celery has declined in abundance in several lakes, rivers, and estuaries in Florida-in many cases, as a result of degraded water quality (Jaggers 1994). For example, residents and visitors of the Kings Bay area of Crystal River, FL, a popular tourist site for diving and snorkeling, have noted both degrading water clarity and an overall decline in areal coverage of wild celery. Although there are anecdotal accounts that wild celery once dominated the benthic vegetation of Kings Bay, this native macrophyte is recently restricted to small patch meadows (Frazer and Hale 2001). It is generally thought, albeit without historical data, that increased nutrient loads primarily from treated wastewater to Kings Bay led to the decline in water quality (Romie 1990) and wild celery. In 1992, wastewater discharged to Kings Bay was diverted and nutrient concentrations subsequently declined (Terrell and Canfield 1996). As a result of these changes, local management agencies became interested in restoration of wild celery in Kings Bay.

In 2000, we conducted an experiment in Kings Bay to determine the factors that might affect successful restoration of wild celery, and demonstrated that recently transplanted shoots were intensively grazed by manatees (Hauxwell et al. 2004). Within days of planting, manatees decimated all unprotected transplants. However, plants protected within adjacent fenced plots survived and, in fact, increased in size, flowered, and reproduced clonally over the same time period, suggesting that site-specific restoration may be feasible if plants were protected from manatees. We have observed that while feeding within natural meadows of wild celery, manatees primarily crop plants, leaving the below-ground portion along with several centimeters of leaf material intact. These plants rapidly grew new leaves and, within a week, were indistinguishable from ungrazed plants. In our initial experiment, however, new wild celery transplants were completely uprooted by manatees (Hauxwell et al. 2004), thus precluding subsequent growth and persistence. Indeed, in certain areas of the Kings Bay, wild celery persists in dense and productive stands, suggesting that established stands can persist in the presence of manatees. As a consequence of these observations, we postulated that by allowing transplants time to become well-rooted, the effect of manatees might be similar to that observed in natural meadows, where plants may be cropped, but able to recover.

In this study, we investigated whether the duration of reestablishment alters the effect of herbivores on wild celery

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survival, and thus, the efficacy of restoration efforts. Given the importance of manatees as a protected species, it is inconceivable to manipulate their abundances on large scales, but if caged plants become sufficiently established to withstand grazing, then transplantation combined with shortterm exclusion might provide a feasible way to restore wild celery without deleteriously affecting manatees. If true, such an approach could lead to a simple, cost-effective technique for restoration of Florida lakes and spring systems.

MATERIAL AND METHODS

Study Site

Kings Bay, in Citrus County, FL, is a spring-fed, tidally-influenced freshwater-oligohaline system (Hoyer et al. 2001, Frazer et al. 2001b) and headwater for the 11-km long Crystal River, which discharges to the Gulf of Mexico (Frazer et al. 2001a). The relatively constant 25 C spring waters of Kings Bay are used seasonally by manatees. Abundances peak at approximately 150 to 220 individuals between November and February, as manatees seek shelter in the relatively warm waters of the springs. Manatee abundance declines to approximately 50 individuals during summer months when they egress to coastal waters.

Experimental Design

To determine whether the effect of manatees on transplants of wild celery differed depending on the time allowed for plants to establish, we conducted a 2 by 2 factorial design field experiment in which we allowed or denied manatees access to newly transplanted plots of wild celery or plots that had been planted 5 months earlier. Two planting efforts were made, the first on August 14, 2001, and the second on January 15, 2002, yielding three replicates of each of the following treatments:

Treatment 1: Established plants, herbivores allowed (but excluded initially)

Treatment 2: Established plants, herbivores excluded

Treatment 3: New plants, herbivores allowed

Treatment 4: New plants, herbivores excluded

The first set of plants (Treatments 1 and 2, planted in August) were protected from herbivores until initiation of the experiment in January. Immediately following the second planting effort (Treatments 3 and 4, planted in January), both appropriate treatments were simultaneously exposed to herbivores (Treatments 1 and 3). Treatments 2 and 4 remained protected from large herbivores.

Transplanting Protocol

For both planting efforts, a team of divers transplanted individual wild celery rosettes, obtained from Aquatic Plants of FL, Inc., Sarasota, FL, within 1.5 m by 1.5 m plots initially void of dense vegetation. These plots were situated at the northwest inlet of Cedar Cove, a site within Kings Bay that was previously determined to have the highest likelihood of successful survival and growth of wild celery transplants (Hauxwell et al. 2004). Plots were situated approximately 2 m apart in depths of approximately 1.2 m at mean low water. Shoot planting density was approximately 200 m², and 40 to 60 cm tall plants were used. The experimental design resulted in 12 total plots, requiring approximately 5,400 transplanted shoots.

To exclude manatees, we placed plastic fencing with 2.5cm mesh around plots. This fencing was ~2 m high to extend above the water surface at high tide. The typical tidal range at this location is ~1 m. The meshed fence excluded any aquatic herbivore >3 cm, while minimally affecting water circulation and light (Hauxwell et al. 2001, Hauxwell et al. 2004).

Measurements of Response Variables

Changes in size distributions of plants within treatment plots can yield information regarding overall establishment and active growth of plants by indicating both recruitment of new shoots and recruitment of transplanted shoots into larger size classes. We determined whether the first set of plants were actively growing, by comparing the initial size distribution of plants within August-planted plots to size distributions 4 months after planting, but prior to exposure to herbivores. To obtain non-destructive estimates of wild celery individual shoot mass *in situ*, 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. We used the relationship developed in Hauxwell et al. (2004) to convert these morphological data to plant mass (above-ground shoot mass (g dm) = 0.003 (number of leaves per shoot \times length of longest leaf in $cm \times width$ of longest leaf in cm)^{0.915}) $(P < 0.0001, r^2 = 0.93)).$

To assess the effect of manatees, the primary response variable monitored within plots over time was wild celery shoot density. Measurements were taken on a monthly basis until initiation of the experiment, at which time we began taking measurements on a daily to weekly basis. Measurements were taken within the inner 1 m² of plots to allow some buffering (~25 cm) of potential edge effects. To quantify densities of wild celery within each plot, SCUBA divers counted total numbers of shoots enclosed within three randomly-placed 30 cm by 30 cm quadrats. Divers also noted the number of plants that were still rooted, but had leaves that had been cropped.

RESULTS AND DISCUSSION

We determined whether the first set of plants were successfully established within plots by (1) pooling data from plots planted in August and comparing their overall size distribution 4 months after planting to their initial condition, and (2) tracking changes in plant density over the initial 5-month acclimation period. In the absence of herbivory, the first set of transplanted plants flourished over the acclimation period (Figures 1 and 2). At planting, the size distribution of plant biomass was skewed toward smaller plants (Figure 1; on average, 0.57 ± 0.03 g and 45 cm tall). After 4 months, size distributions shifted toward larger plants

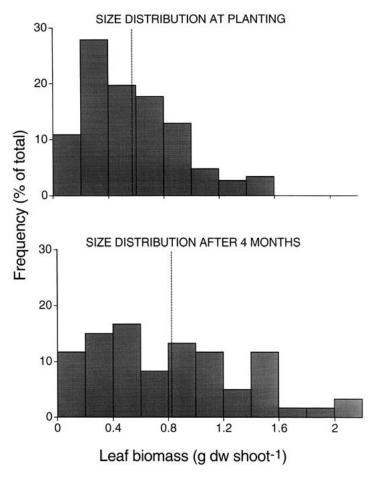


Figure 1. Histograms showing the size distribution of wild celery shoots that were planted August 2001 in plots in Kings Bay, FL, in which we allowed plants to establish. Initial distributions (top panel) and those 4 months post planting (bottom panel) are shown (pooled data for all plots). Extended dashed lines indicate means.

(Mann-Whitney U-test, U = 3311, P = 0.0049), indicating active growth of transplants (on average, 0.82 ± 0.07 g and 78 cm tall). By November, in fact, some plants extended to near the surface at low tide and were up to 1.4 m tall. The presence of very small plants in November indicated recruitment of new plants, via vegetative propagation and extension of the below-ground root-rhizome system; this was corroborated by divers' observations. Plant density data also indicated that transplants performed well. After an initial decline in plant density, most likely associated with handling involved with transplantation (Hauxwell et al. 2004), plant densities increased between October and initiation of the experiment in January (Figure 2). These results for size distributions and density mimic observations obtained the previous year in a different experiment (Hauxwell et al. 2004), reinforcing the notion that, in the absence of herbivores, the Cedar Cove site in Kings Bay is a potential site for successful wild celery restoration. Time of year of planting did not seem to affect success: i.e., protected transplants grew well whether planted in the summer or in the winter in this experiment, and in the winter in a previous experiment (Hauxwell et al. 2004).

Upon initiation of the experiment in January, a rapid and significant effect of herbivores was observed, regardless of

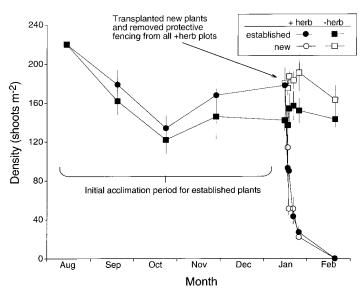


Figure 2. Density of shoots of wild celery over time in transplanted plots in Kings Bay, FL (means \pm SE, n = 3), that were either protected from herbivores (-herb) or exposed (+herb) on January 15, 2002 (established = planted August 2001, new = planted January 2002).

level of establishment (Figure 2, Table 1). Within 3 days, whether established or new, 50 to 75% of the plants in unprotected plots had been consumed by manatees. After 10 days of exposure to manatees, more than 85% of plants present in protected plots prior to removal of the fence were consumed (Figure 2). Within 1 month, all exposed plots were void of plants. In contrast, density of plants in plots that had been protected from manatees showed very little change over the study period.

Approximately 60 to 90% of the few surviving plants in the exposed plots had been cropped, although, in contrast to our expectation, there was not a significant difference in cropping in established plots versus new plots (Figure 3; P >0.05, *t*-test). Wild celery, like other relatively slow-growing seagrasses that have highly developed below-ground root-rhizome systems (e.g., Thalassia and Posidonia), are thought to have evolved to cope with herbivory by invertebrates and large herbivores such as sea urchins, manatees, dugongs, turtles, and waterfowl (Greenway 1976, Ogden et al. 1983, Zieman et al. 1984, Williams 1988, Masini et al. 2001), by repeatedly regrowing the cropped leafy portion (Cebrián et al. 1998). They are able to do this using stored within-shoot below-ground energy reserves or translocated energy reserves from neighboring clones. However, we ultimately had significant removal of whole plants in all treatments, regardless of level of establishment (Figure 2). Though it is likely that established plants in our experiment had developed more extensive below-ground biomass than new transplants, making them somewhat more difficult to uproot, these effects were not sufficient to preclude their eventual removal by herbivores.

Similarly dramatic effects have been observed in other systems that involved native or introduced animals and transplanted native plants. For example, burrowing by foraging shrimp, lugworms, rays, and green crabs can severely affect experimental seagrass transplants such as *Zostera marina* and

TABLE 1. RESULTS OF A THREE-FACTOR (EFFECT OF HERBIVORES, EFFECT OF LEVEL OF ESTABLISHMENT, AND EFFECT OF TIME) REPEATED MEASURES ANOVA USE	D TO
TEST FOR DIFFERENCES IN DENSITIES OF ESTABLISHED OR NEW TRANSPLANTED WILD CELERY OVER TIME IN PLOTS THAT EITHER EXCLUDED OR ALLOWED HERBIV	ORES
IN KINGS BAY, FL (DEPICTED IN FIGURE 2).	

Variable	df	MS	F	Р
Herbivory	1	155589	42.8	0.0002
Level of establishment	1	4125	1.1	0.3176
Herbivory \times Level of establishment	1	5391	1.5	0.2578
Plots within treatments	8	3631		
Time	5	12128	12.6	< 0.0001
Time × Herbivory	5	12935	13.4	< 0.0001
Time × Level of establishment	5	350	0.4	0.8702
Time $ imes$ Herbivory $ imes$ Level of establishment	5	351	0.4	0.8692
Time × Plots within treatments	40	962		

Posidonia oceanica (Harrison 1987, Molenaar & Meinesz 1995, Davis et al. 1998). Herbivory by turtles (*Pseudemys rubriventris*), muskrats (*Ondatra zibethicus*), and waterfowl (Carter and Rybicki 1985) have negatively affected experimental wild celery transplants in other studies. In our experiment, manatees were the herbivore causing the large effects. We not only observed manatees grazing in our plots within hours of initiating the experiment, but observed them routinely during subsequent visits. Two additional lines of evi-

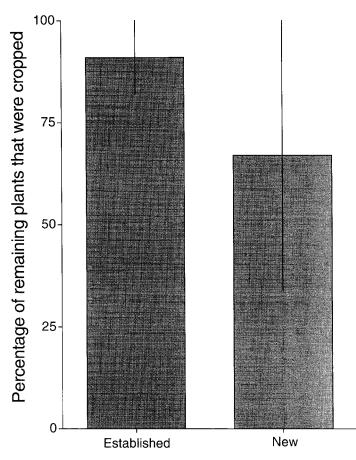


Figure 3. Percentage of remaining (as of January 25, 2002) shoots of wild celery that were cropped in transplanted plots in Kings Bay, FL (means \pm SE, n = 3), that were exposed to herbivores on January 15, 2002 (established = planted August 2001, new = planted January 2002).

dence indicate their presence in plots during our absence: (1) monofilament line tied between stakes surrounding plots was routinely broken, indicating the presence of a relatively large, heavy organism, and (2) manatee fecal material was found in our plots but rarely noticed in our 2 years of work in an adjacent natural wild celery meadow. Based upon the rapid removal of plants during this experiment, our limited observations of other grazers, and the absence of grazing scars indicative of invertebrate herbivores (J. Hauxwell, pers. obs.), we conclude that manatees are the most significant grazer in the system with regard to wild celery restoration.

Though manatees are known to consume a variety of aquatic plants, including wild celery, waterhyacinth (Eichhor*nia crassipes* Solms.), water lettuce (*Pistia stratoites* Linnaeus), Eurasian watermilfoil (Myriophyllum spicatum L.), and hydrilla (Hydrilla verticillata (L.f.) Royle) (Etheridge et al. 1985) species all commonly encountered in Kings Bay-they selectively grazed our transplanted plots of wild celery. It is possible that the relatively small, young wild celery transplants that we used were favored by manatees because of nutritional characteristics of plants in early growth stages, which include low fiber and high nitrogen content. Preen (1995), for example, observed "cultivational grazing" by dugongs in Australia in which they excluded potentially dominant seagrasses and maintained favored, more easily assimilated, species. Green turtles in the Caribbean, that graze primarily in *Thalassia testudinum* beds, have been observed to repeatedly crop the same plants, because new tissue, higher in protein and lower in lignin, is apparently more digestible (Bjorndal 1980).

Results of this experiment indicate that success of any future larger-scale transplant effort in Kings Bay is contingent upon adequate protection from manatees. Plants can be protected by fencing, by allowing enough time for plants to establish, or by planting when manatee abundances are at a minimum. If, in fact, established transplants become more resistant to uprooting by herbivores, and can thus persist without ongoing protection from herbivores, it is beyond the time period tested in this experiment (>5 months).

Due to the inherent ecological value in maintaining beds of native plants, restoration efforts aimed at revegetating shallow freshwater systems with wild celery have been initiated in several sites in Florida (including Lake Apopka, Lake Thonotosassa, Clear Lake, Lake Monroe, Newnans Lake, and Lake Lochloosa) (B. Hujik, Florida Fish and Wildlife Conservation Commission, pers. comm.; see also Jaggers 1994) at considerable cost and with variable success. Clearly, understanding the factors responsible for the initial declines of wild celery, and reducing their influence, are the first steps toward restoration. In certain cases, however, additional factors may prove problematic for restoration—in this case, the unanticipated effect of a native herbivore and the difficulty in providing a convenient larger-scale refuge for plants in space or time. Our results demonstrate the value in conducting smaller-scale pilot studies to understand what factors anticipated or not—might affect successful restoration prior to investment of considerable resources.

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