Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL



RESEARCH ARTICLE

# The Role of Habitat and Herbivory on the Restoration of Tidal Freshwater Submerged Aquatic Vegetation Populations

Kenneth A. Moore,[1,2] Erin C. Shields,[1] and Jessie C. Jarvis[1]

## Abstract

**Submerged aquatic vegetation (SAV) has declined precipitously throughout coastal areas and its reestablishment has long been an important objective of coastal management. We investigated restoration success of *Vallisneria americana* (wild celery) using seeds, seed pods, and whole shoot transplants at sites in the Chesapeake Bay in the United States where historical aerial photography has indicated that the species once grew. In addition, we evaluated habitat conditions and established herbivore exclosures to assess the impacts of water quality, sediment conditions, and grazers on planting success. Whole shoot transplants resulted in the most rapid cover of the bottom, but required greater planting effort. Direct dispersal of individual seeds was generally more successful than dispersal of intact seed pods, resulting in more rapid initial seedling growth. Overall, 100% bottom cover of whole shoot transplant plots could be reached in approximately 3 years, despite light attenuation coefficients ($K_d$) of 3.0 to 4.0. Transplants at shallow depths (<0.5 m) were able to rapidly grow and elongate to the surface at mid-to-low tidal heights. Transplants were successful in both muddy (8% organic) and sandy (<2%) substrates. Using mesh exclosures to protect the plants from herbivory was critical to restoration success. Although water quality and other habitat conditions are important for SAV growth and survival, restoration in the unvegetated areas studied here was limited by grazing of initial recruits. The establishment of protected founder colonies of sufficient size to withstand initial grazing pressures may be required to reestablish SAV in similar areas.**

**Key words:** **Chesapeake Bay, nutrients, plant growth, seedlings, seeds, turbidity, underwater grasses, *Vallisneria americana*.**

## Introduction

Global loss of submerged aquatic vegetation (SAV) has been significant in coastal areas such as the Chesapeake Bay in the United States, where SAV die-offs have been observed in marine, brackish, and freshwater communities (Orth & Moore 1983; Orth et al. 2006*a*; Waycott et al. 2009). Freshwater tributaries have proportionally experienced the greatest declines, due to direct watershed inputs of nutrients, sediments, and dissolved organic matter (Cerco & Moore 2001; Kemp et al. 2004; Dobberfuhl 2007). Although there has been some regrowth of SAV in the Chesapeake Bay, particularly in low-salinity and tidal freshwater regions, current abundances are still well below historical levels (Moore et al. 2004; Orth et al. 2008). Many areas that were historically dominated by the native species *Vallisneria americana* (wild celery) are now unvegetated or vegetated with non-native species, such as *Hydrilla verticillata* or *Myriophyllum spicatum* (eurasian watermilfoil) (Davis 1985; Moore et al. 2000; Orth et al. 2008). The establishment of similar weedy SAV species in place of native species such as *V. americana* have also been observed in turbid reservoirs (Smart et al. 1996).

In North America, *V. americana* is distributed from Canada to Florida, United States in the east, and from British Columbia, Canada to California, United States in the West (USDA NCRS Plants National Database 2009). Unlike many other freshwater SAV species, which are canopy forming, *V. americana* is meadow forming, growing from a basal meristem (Catling et al. 1994). Reproduction occurs both sexually and asexually, with asexual reproduction being the most dominant form (Sculthorpe 1967). Asexual reproduction occurs through the development of rhizomes and stolons, which create new shoots (McFarland & Shafer 2008). When leaf production stops, which occurs in early fall in the Chesapeake Bay, United States winter buds are produced, giving rise to new plants the next spring (Sculthorpe 1967). Sexual reproduction occurs when female flowers are pollinated at the water surface (Sculthorpe 1967; McFarland & Shafer 2008), and flowering occurs from July to August, with fruits maturing

[1]Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester Point, VA 23062, U.S.A.
[2]Address correspondence to K. A. Moore, email moore@vims.edu


doi: 10.1111/j.1526-100X.2010.00699.x

by September–October (Moore & Jarvis 2007). These fruits consist of seed pods, which contain approximately 100–300 seeds stored in a gelatinous mass (Lokker et al. 1997).

*Vallisneria americana* is an important component of aquatic ecosystems for a variety of reasons. Meadows provide shelter for numerous fauna, improve water clarity through the trapping and stabilization of sediments, and serve as a biological indicator for local water quality conditions (Killgore et al. 1989; Dennison et al. 1993; Catling et al. 1994). This species has been reported to be an important food source for waterfowl throughout its geographic distribution (Korschgen et al. 1988; Sponberg & Lodge 2005), and the feeding habits and populations of many waterfowl species in the Chesapeake Bay, United States have been linked to changes in SAV abundance (Perry & Deller 1996; Rybicki & Landwehr 2007).

Due to the ecological importance of *V. americana* in the Chesapeake Bay, United States and elsewhere, recent restoration efforts have focused on reestablishing this species in areas where it once thrived. Successful restoration efforts with SAV species have relied on defining suitable habitat requirements for their growth (Kemp et al. 2004; Shafer & Bergstrom 2008). For freshwater species, the primary focus has been placed on quantifying abiotic factors, such as light, temperature, salinity, and sediment type (Rybicki & Carter 1986; Carter et al. 1996; Kraemer et al. 1999; French & Moore 2003; Dobberfuhl 2007; Kreiling et al. 2007; McFarland & Shafer 2008), whereas biotic factors such as herbivory that may affect restoration success have received less attention (Doyle et al. 1997).

The objective of this study was to investigate several methods for restoring *V. americana* into currently unvegetated regions of the estuarine James River in Virginia, United States. Plantings were conducted from 2001 to 2007 at sites that had previously supported the growth of SAV until the 1940s (Moore et al. 1999). We used a variety of restoration methods, incorporating the use of seeds, seed pods, and whole shoots, both inside and outside of herbivore exclosures, to evaluate the most successful planting methods and to quantify any potential herbivory effects. In addition, we monitored local water quality and sediment conditions to quantify the relationships between habitat conditions, herbivory, and SAV survival.

## Methods

### Study Sites

Four shallow-water sites were selected for transplanting and water quality monitoring in the James River, Virginia, United States, a tributary to the Chesapeake Bay, from 2001 to 2007 (Fig. 1). Site selection was based on water depth (approximately 0.5 m MSL), site orientation and location (low erosion shoreline), photographic evidence of historical SAV occurrence, and general water quality conditions in the area. Selected sites include Turkey Island (37.3826N 77.2527W), Tar Bay (37.3075N 77.1902W), Powell's Creek (37.2929N 77.1622W), and Westover Plantation (37.3105N 77.1558W). Mean tidal range for this region (37.3133N 77.2700W) for the 1983–2001 epoch was 0.73 m (National Oceanic and Atmospheric Administration [NOAA] 2009).

### Water Quality Monitoring

Water quality sampling was conducted at biweekly to monthly intervals at each of the four transplant sites. Measurements included: water temperature (°C), conductivity (μmhos), light attenuation to 1.0 m ($K_d$), secchi depth (m), pH, dissolved inorganic phosphorus (DIP), and nitrogen (DIN) (μmol $l^{-1}$), chlorophyll a (CHL) (μg $l^{-1}$), and total suspended solids (TSS) (mg $l^{-1}$). In situ water temperature, conductivity and pH were determined using a YSI-600XL sampling sonde (YSI, Inc. Yellow Springs, OH, U.S.A.). Water samples were collected at water depths between 0.5 and 1.0 m in the shallow littoral area immediately adjacent to the transplant locations. Samples were stored on ice in the dark until the end of each sampling cruise. Laboratory analyses of water samples were conducted by Hopewell Regional Wastewater Treatment Facility. DIP and DIN were measured according to method 4500-P, CHL according to method 10200-H, and TSS according to method 2540-D (American Public Heath Association, American Water Works Association, & Water Environment Federation 1995). Light attenuation profiles of photosynthetically available radiation (PAR) were made from 10 cm below the surface to 10 cm above the bottom using a $2\pi$ cosine-corrected quantum sensor (LI-COR, Inc., Lincoln, NE, Type LI-192SA). All water column light data were corrected for changes in surface irradiance using simultaneous measures of downwelling surface solar PAR irradiance with a similar terrestrial sensor (LI-COR, Inc. Type LI-190SA).

### Sediment Characterization

Sediment was characterized by taking three replicate cores at each transplant site prior to planting. The top 15 cm of the cores were homogenized, a 10 g sample was dried at 50°C, then weighed three times or until a constant dry weight was reached, combusted for 5 hours at 550°C, and then weighed a final time to determine organic content thought loss on ignition (Erftemeijer & Koch 2001).

### SAV Transplanting and Monitoring

All transplanting activities were undertaken in spring and early summer when water temperatures were ≥20°C. *Vallisneria americana* shoots were obtained from nursery grown stock established in culture ponds at the campus of the Virginia Institute of Marine Science (VIMS) in Gloucester Point, Virginia, United States (see Moore & Jarvis 2007). Shoots were gently dug from the sandy substrate in the ponds, separated into individual shoot rosettes, and submersed in freshwater in insulated coolers for transplantation within 24 hours. Mature seed pods were collected from established *V. americana* beds in Nanjemoy Creek, Maryland, United States (38.4317N, 77.1200W) in the fall of 2004, stored in river water and refrigerated in the dark at 4°C until being transplanted the following May.

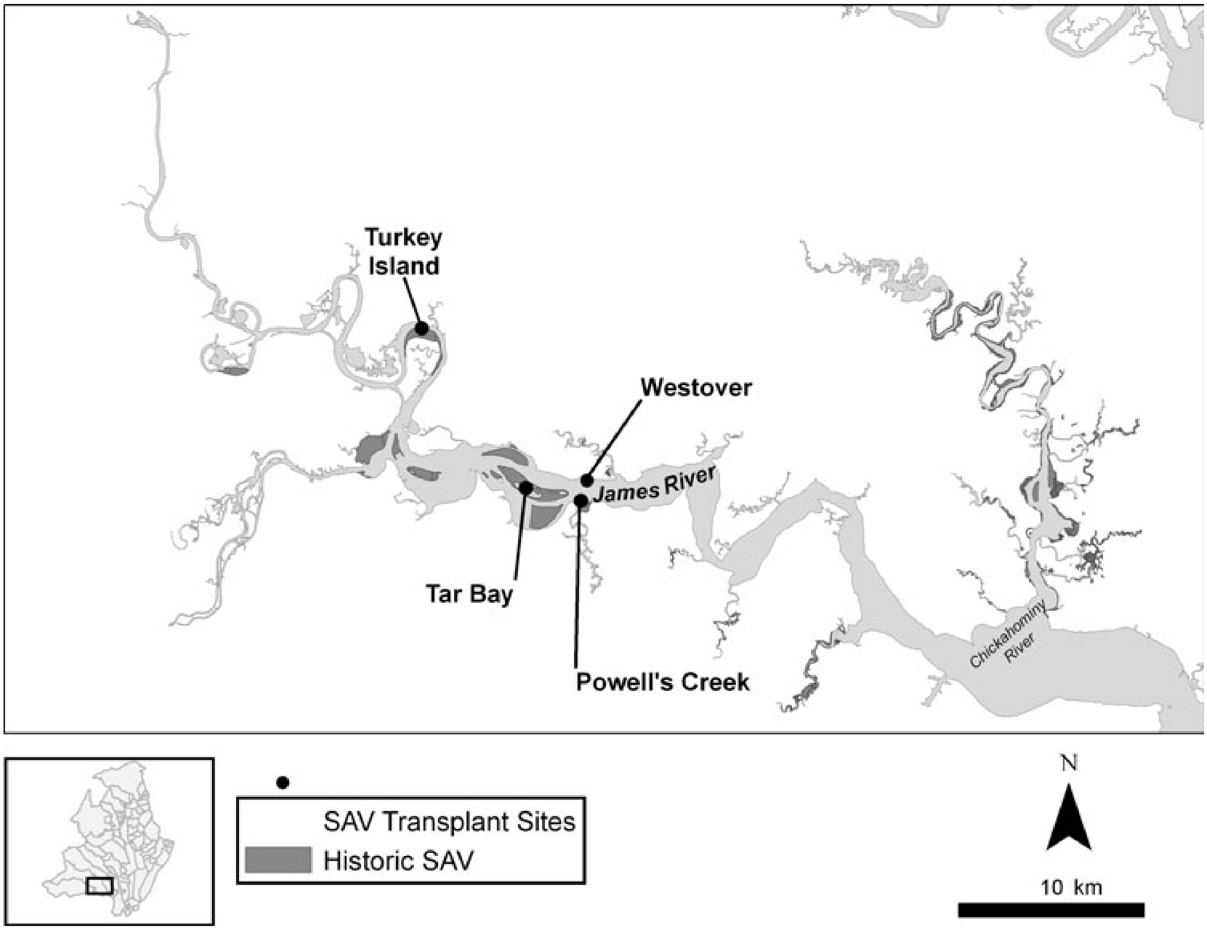


Figure 1. SAV transplant sites located in the tidal freshwater James River, Virginia. Dark gray areas indicated mapped historical SAV beds.

In 2005, one large 4 × 10–m fenced exclosure was constructed per site prior to transplanting (four exclosures total). Exclosures consisted of PVC staked plastic fencing (2.5 × 2.5–cm mesh), which extended from the sediment surface to above the high water line. To ensure that herbivores did not burrow under the exclosure a 0.25 m skirt of the plastic fencing was laid outside perimeter of the exclosure, buried slightly in the sediment, and weighted down with sections of metal fence posts secured to the fencing with cable ties. Exclosures were checked for openings monthly from May to October in all years and repaired with new fencing material when necessary. For the seed plantings, seed pods were gently broken apart by hand and all seeds were removed just prior to planting. Both intact seed pods and separated seeds were haphazardly dispersed onto the bottom and gently patted into the sediment within separate 2 × 2–m plots in each exclosure. Whole shoots were planted directly into the sediment at approximately 0.2 m intervals in a third 2 × 2–m plot in each exclosure. The three individual treatment plots were separated by approximately 1.5 m. Immediately outside of the exclosures, three identical 2 × 2–m treatment plots were established at the same water depths and distances from shore as the exclosure plots. During years other than 2005 whole shoots were transplanted within exclosures at each of the sites and occasionally in small test areas immediately outside of the exclosures. To ensure that buoyant shoot transplants did not float away, all shoots were planted to depths of 2–4 cm.

Biweekly to monthly surveys were conducted at each site to assess the transplant success both within and outside exclosures. In 2005, divers recorded percent bottom cover within 2 × 2–m sampling quadrats of whole shoots, as well as growth, measured as maximum leaf length, throughout the season (May–October). Germinated seedlings were also monitored for size and cover using similar procedures. Bottom cover was measured independent of shoot density.

#### Statistical Analysis

Effects of treatments on percent cover were analyzed with each site as a replicate ($n = 4$) using repeated measures Analysis of Variance (SPSS, Inc., Chicago, IL, U.S.A.). For this analysis, time (month), exclosure (inside or outside), and propagule type (seed, seed pod, whole shoots) were quantified as factors. Prior to analysis, data were transformed using arcsine square root transformation methods, normality was confirmed, and homogeneity of variances was verified with Cochran's test (Zar 1999). If significant time interactions were found, treatment effects were analyzed on each date using either two-way, if there were no other significant interactions, or one-way analysis of variance. Post hoc comparisons between treatments were made with Tukey's honestly significant difference (HSD) test using a significance level of 5%. Regression analysis was conducted (Minitab, Inc., State College, PA, U.S.A.) to test for a relationship between sediment organic content and end-of-season percent cover.

## Results

Overall, there were significant ($p < 0.05$) increases in SAV cover inside compared to outside of the exclosures for all methods and significant ($p < 0.05$) interactions between time and propagule type as well as location (inside or outside the exclosures). Patterns of growth and survival for the transplants were different among the three propagule types over time, but similar among all the sites. Within the first month after transplanting, there was a 20–40% loss of whole shoot planting units within the exclosures (Fig. 2a), which was attributed to physical disruption by waves or tidal currents and/or to stress related to transplanting. Little evidence of herbivory or biological disturbance was observed within the exclosures.

Following this initial loss, the transplants expanded cover by vegetative spread of stolons producing new rosettes. In contrast, outside of the exclosures there was a rapid loss of plants through herbivory. This was evident due to the apparent clipping or cutting of all leaves on a rosette at approximately 2–3 cm above the bottom. On 29 June (Fig. 2a–c), there was significantly greater SAV cover within the exclosures compared to outside ($p < 0.001$), whereas cover of shoots from seed and seedpods was significantly less than that of shoots ($p < 0.010$; $p < 0.001$). By this time, plants within the exclosures had grown from approximately 10–30 cm in shoot length compared to only 2–3 cm for those shoots transplanted outside. Some regrowth of grazed shoots outside the exclosures was evident throughout the remainder of the summer; however, the combination of limited leaf growth and continued grazing eliminated nearly all plants within 2 months and transplant cover within the exclosures was always significantly greater than outside ($p < 0.010$). Although there was some belowground plant material present outside of the exclosure, there was no evidence of new rosette production by the grazed plants.

Seed pods and seed transplant methods showed similar patterns of growth and survival (Fig. 2b & 2c). No germination was observed for either treatment by the end of the first week; however, by the end of 3 weeks there was seedling emergence from both seeds and seed pods planted inside the exclosures. By August, the seed treatments (40–45%) had significantly greater ($p = 0.023$) cover than the seed pod treatments (35–40%). In contrast to the patterns of germination and growth of the seed and seedpod seedlings inside of the exclosures, those planted outside the exclosures showed delayed

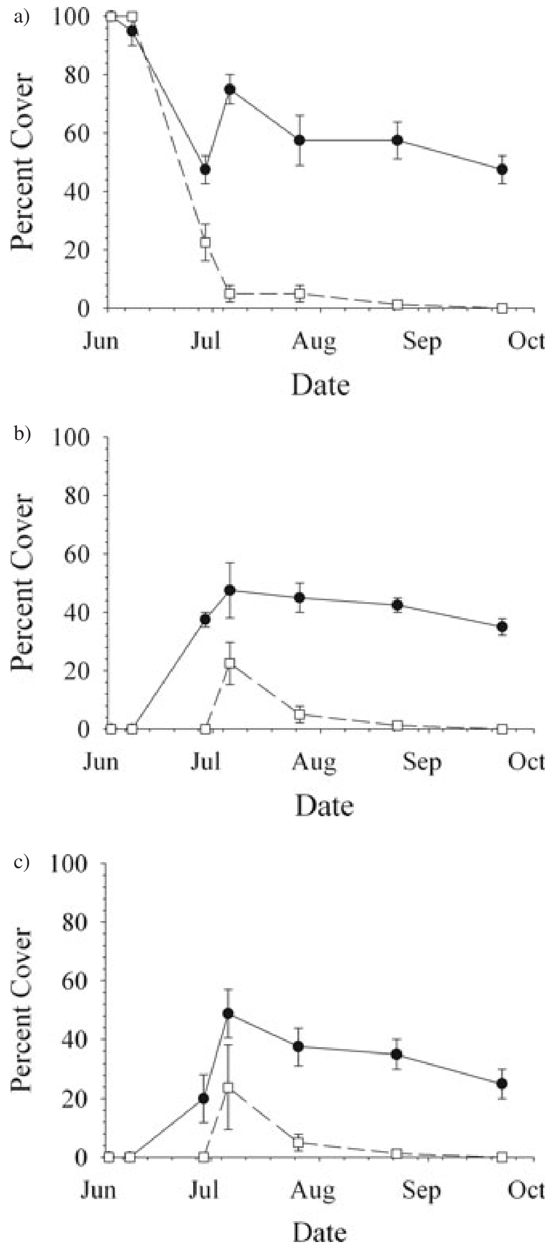


Figure 2. Mean (±SE) 2005 transplant bottom cover at all James River restoration sites. (a) Whole shoots, (b) seeds, and (c) seed pods. Open boxes—outside exclosures. Closed circles—inside exclosures.

seedling emergence by at least 1 week and significantly lower initial cover than those inside the exclosures by early July (Fig. 2b & 2c). Within 3 weeks of emergence, the bottom cover by seedlings outside the exclosures was reduced from 20–25% to 5% in both the seed and seed pod treatments. As with whole shoot transplants, individual seedling shoots outside of the exclosures were clipped or grazed to lengths of 2–3 cm. When protected from herbivory, approximately 3 years of growth were required for the transplants to reach 100% bottom cover at maximum densities of 100–150 shoots $m^{-2}$ at Turkey Island (Fig. 3). Growth of Vallisneria *americana* transplanted at all

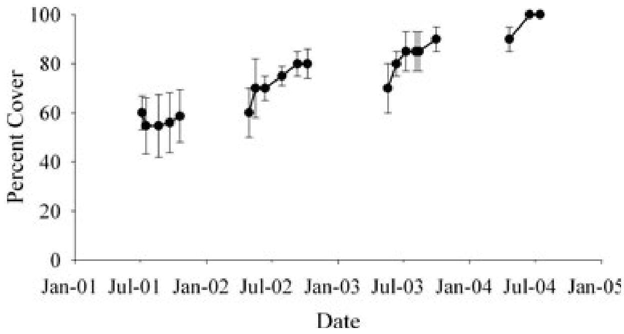


Figure 3. Mean (±SE) percent bottom cover of *Vallisneria americana* in exclosures at Turkey Island restoration site.

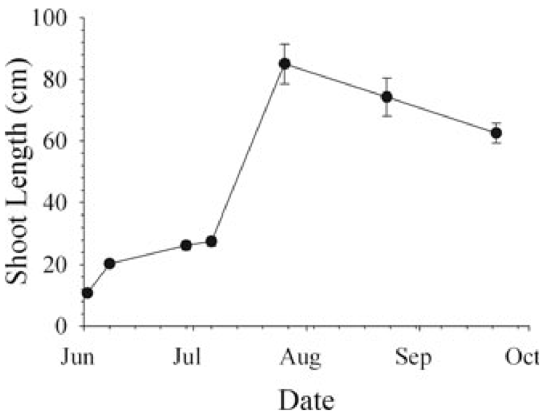


Figure 4. Mean (±SE) 2005 shoot length for whole shoot transplants inside exclosures at all James River restoration sites.

sites in this region was characterized by rapid elongation of the shoots within the exclosures with shoots reaching over 80 cm by July (Fig. 4). In contrast, the shoots outside of the exclosures were rapidly cropped to 2–3 cm or less in length.

Overall, the interannual variation in water quality and differences between sites with sediment organic content had no demonstrable effect on transplant survival as transplants were successful during each year at all sites when protected from herbivory (Table 1). Regardless of restoration method, plants were successful in both muddy (8% organic) and sandy (<2% organic) substrates with no relationship ($p = 0.36$, $r^2 = 0.095$) between sediment organic content and SAV end-of-season percent cover. For all study sites, seasonal light attenuation (to a depth of 0.5 m), CHL, and DIP levels met the criteria identified for growth and survival of freshwater SAV habitats in the Chesapeake Bay, United States (Batiuk et al. 2000) during approximately 50% of all sampling years (2001–2007), whereas the TSS levels were never met (Table 2). Water temperatures during the growing season ranged from 15°C at initiation of growth in the spring, to maximums of 30–32°C during July and August with rapid die-back of plants in the fall as temperatures dropped again below 15°C. Minimum water temperatures in the winter were 2–4°C. Typically, salinities during most years were less than 0.5 with conductivity of less than 100 μmhos. During October 2001, and again in September 2002, summer long droughts elevated conductivity to 1000–3000 μmhos for several weeks. Increased freshwater flows rapidly returned levels back to normal conditions. pH varied from 7.5 to 9.0 with little seasonal or annual trends evident.

## Discussion

We have demonstrated that *Vallisneria americana* can be planted successfully in temperate tidal freshwater sites using seeds, seed pods, and vegetative propagules. As with all direct seeding approaches used for SAV restoration, there are benefits of reduced labor and removal of the requirement for in-water restoration by divers or other personnel with water skills (Orth et al. 2006*b*). However, because of the low rates of germination success and the potential for herbivory or other sources of seedling loss, the success rate of seedlings produced by transplanted seeds can be very low. In the results presented here, seeding rates of only 2,500 seeds $m^{-2}$, well within the 1,000–16,000 seeds $m^{-2}$ produced in established *V. americana* beds in this region (Jarvis & Moore 2008), were used with success when shoots were protected from herbivory. An intermediate step to large-scale restoration of freshwater SAV populations may include using seeds (Alistock & Shafer 2004) to produce smaller, scattered founder colonies that would then re-propagate nearby unvegetated areas naturally through the dispersal of seeds and clonal expansion if shoot herbivory is low. Similar approaches are currently being used for the restoration of *Zostera marina* (eelgrass) beds (Orth et al. 2006*b*).

**Table 1.** Survival (%) of exclosure protected whole shoot transplants of *Vallisneria americana* for individual transplant years 2001–2007 at each transplant site.

| | *Year* | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *2001* | | *2002* | | *2003* | | *2004* | | *2005* | | *2006* | | *2007* | |
| *Site* | *In* | *Out* | *In* | *Out* | *In* | *Out* | *In* | *Out* | *In* | *Out* | *In* | *Out* | *In* | *Out* |
| Turkey Island | 60 | — | 93 | — | 55 | 0 | 60 | 0 | 70 | 0 | 10 | — | — | — |
| Tar Bay | 100 | — | 55 | — | 100 | 0 | 100 | 0 | 40 | 0 | 80 | — | 30 | — |
| Powell's Creek | 65 | — | 45 | — | 85 | 0 | 85 | 0 | 60 | 0 | 80 | — | 100 | — |
| Westover | — | — | 40 | — | 65 | 0 | 60 | 0 | 60 | 0 | 25 | — | 50 | — |

In = inside exclosure; Out = outside exclosure; — = not planted.

**Table 2.** SAV growing season (April–October) median water quality.

| Site | Water Quality Parameter | SAV Habitat Criteria | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|
| Turkey Island | Light Atten.($K_d$; $m^{-1}$) | ≤3.6 | — | 3.9 | 3.4 | 3.7 | 3.6 | 3.4 | 3.4 |
| | TSS (mg $l^{-1}$) | ≤15 | 32 | 30 | 26 | 35 | 32 | 28 | 31 |
| | CHL (μg $l^{-1}$) | ≤15 | 30 | 45 | 7 | 9 | 12 | 39 | 76 |
| | DIP (mg $l^{-1}$) | ≤0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.02 | 0.01 | 0.01 |
| Tar Bay | Light Atten.($K_d$; $m^{-1}$) | ≤3.6 | — | 3.9 | 3.7 | 3.5 | 3.6 | 3.3 | 3.5 |
| | TSS (mg $l^{-1}$) | ≤15 | 30 | 35 | 24 | 32 | 28 | 34.5 | 33 |
| | CHL (μg $l^{-1}$) | ≤15 | 39 | 42 | 5 | 5 | 15 | 33 | 93 |
| | DIP (mg $l^{-1}$) | ≤0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.02 | 0.01 | 0.01 |
| Powell's Creek | Light Atten.($K_d$; $m^{-1}$) | ≤3.6 | — | 3.9 | 3.5 | 4.0 | 4.4 | 3.8 | 3.4 |
| | TSS (mg $l^{-1}$) | ≤15 | 36 | 36 | 31 | 38 | 38 | 44 | 33 |
| | CHL (μg $l^{-1}$) | ≤15 | 24 | 42 | 6 | 6 | 14 | 44 | 103 |
| | DIP (mg $l^{-1}$) | ≤0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.01 | 0.02 | 0.01 |
| Westover | Light Atten.($K_d$; $m^{-1}$) | ≤3.6 | — | 3.8 | 3.0 | 4.0 | 3.7 | 3.4 | 3.0 |
| | TSS (mg $l^{-1}$) | ≤15 | 30 | 30 | 26 | 32 | 36 | 34 | 27 |
| | CHL (μg $l^{-1}$) | ≤15 | 32 | 41 | 6 | 7 | 11 | 42 | 66 |
| | DIP (mg $l^{-1}$) | ≤0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.01 | 0.01 | 0.01 |

Shaded cell indicates SAV criteria met for SAV growth to 0.5 m. (—) indicates data not collected.

There was no significant effect of water quality on *V. americana* restoration here despite light attenuation values, which only met the SAV habitat criteria requirements approximately 50% of the time for all sites combined. Lower light conditions within this region may be related to increased total suspended solids levels, which were greater than the habitat criteria of less than 15 mg $l^{-1}$ throughout the entire sampling period (2001–2007). Although light requirements were not always met, SAV was still able to survive and grow. This was likely because that the sites were shallow (0.5 m MSL) and the plants are able to reach the water surface at lower tide levels. During mid-to-low tides, *V. americana* leaves were able to lie at the water surface, thus enhancing its light capturing capacity. Canopy-forming plants such as *Hydrilla verticillata* and *Myriophyllum spicatum* have been found to respond to low light conditions by increasing their shoot length and forming a dense canopy at the water surface, concentrating their photosynthetic tissues in areas of greater light availability (Titus & Adams 1979; Barko & Smart 1981). Titus and Adams (1979) noted that *V. americana* did not form a canopy, but was able to grow in low light conditions through efficient carbon fixation. Rybicki and Carter (2002) found that *V. americana* growing in turbid conditions had increased elongation potential compared to *H. verticillata*, and was able to outcompete this species in the Potomac River, Maryland, United States during a period of low light by expanding its leaves to the water surface. The cropping of the shoots outside of the exclosures reported here not only reduced the total leaf length but also increased the effective water depth for the leaves, resulting in less light available for photosynthesis and significantly lower shoot survival.

Along with light, sediment composition has been shown to affect *V. americana* populations, with higher sediment organic content inhibiting growth (Barko & Smart 1983; Barko & Smart 1986). In the results reported here, sediment organic content, ranging from 2 to 8%, did not inhibit SAV growth and there was no significant relationship between sediment organic content and transplant survival. Kreiling et al. (2007) found similar results in the Mississippi River, United States where there was no relationship between *V. americana* distribution and sediment organic content within the range of 0.29–5.68%. Makkay et al. (2008) measured organic content on a much wider scale (0.5–44.1%) in the Rideau River, Canada, where *V. americna* is a dominant species, and found no relationship between sediment type and SAV distribution. Batiuk et al. (2000) suggested a habitat requirement of less than 5% organic content for SAV in the Chesapeake Bay, United States based on a literature review of a variety of species. It appears that for *V. americana* this may be a conservative number, and restoration of *V. americana* in the tidal freshwater regions may not be limited by sediment organic content within the range reported here.

In areas where water quality conditions are not limiting to freshwater SAV restoration, successful plant establishment and survival may still be reduced by external factors such as herbivory. Results here indicate that it can take at least 3 years for complete bed development, allowing ample opportunity for grazers to impact the developing beds. Because of this, transplants at these sites were only successful when planted inside herbivore exclosure fences. Doyle et al. (1997) similarly conducted test plantings to develop founder colonies of freshwater SAV including *V. americana* in two turbid Texas, U.S. reservoirs. Expansion of the SAV outside of the protective exclosures occurred only when herbivore pressure was low. Several of their exclosures were breached and most of the plants within these exclosures were destroyed. We similarly have experienced herbivorous cropping and destruction of founder patches where integrity of the exclosures was breached during the growing season.

Usually, waterfowl have been observed to be the most significant grazers, as their populations have been shown to be highly dependent on SAV as a food source (Perry & Deller 1996; Søndergaard et al. 1996; Rybicki & Landwehr 2007), but grazing by manatees (Hauxwell et al. 2004), crayfish (Nystrom & Strand 1996), and a variety of fish species and turtles (Prejs 1984; Wright & Phillips 1992; Van Donk et al. 1994; Smart et al. 1996; Doyle et al. 1997; Harwell & Havens 2003) have also been reported. In the Chesapeake Bay, United States, Carter and Rybicki (1985) also reported grazing on *V. americana* transplants in the Potomac River by turtles or fish. In their study, transplants did not survive outside of exclosures for the first 2 years. After this time period, transplants that were exposed to relatively high light levels were able to survive without further protection. One difference between their Chesapeake Bay sites and those of this study is that there were surrounding SAV beds in the vicinity of their study sites to potentially diffuse the grazing pressure, whereas no SAV were present in the area surrounding our study sites.

Hauxwell et al. (2004) also found that unfenced *V. americana* transplant plots in Kings Bay, Florida, United States were completely consumed by herbivores (manatees) within 1 month of planting. In addition, Hauxwell et al. (2004) concluded that allowing plants to become established for 5 months in fenced plots did not affect their ability to survive once opened to grazing pressures. The transplant studies presented here were not set up to test for a time threshold in which *V. americana* would be able to survive without protection from grazers, but the results suggest that protection for more than one growing season is necessary before the plants are able to withstand grazing pressures. The appropriate size and density of restoration founder colonies, especially relative to the abundance of existing vegetation, is an area for future research.

Along with reports of initial plant establishment thresholds, density-dependent foraging thresholds have been reported for grazers in a variety of systems. Sponberg and Lodge (2005) observed a density-dependent response of waterfowl to *V. americana* belowground tubers in a North Carolina, United States lake. They found no impact of grazers in plots where tuber densities were less than 234 tubers $m^{-2}$, indicating that it is not energetically efficient for these grazers (primarily Tundra Swans and diving ducks) to feed at low tuber densities. Similar density-dependent grazing thresholds have been reported on *Potamogeton pectinatus* shoots in a Denmark Lake (Søndergaard et al. 1996) and *P. pectinatus* tubers in the Baltic Sea (Idestam-Almquist 1998), in which SAV was never grazed to extinction due to the high energetic cost of foraging. All of these studies reported waterfowl as the grazers. We did not find evidence of a foraging threshold in our transplants, as plants outside exclosures were completely grazed regardless of planting densities. This may indicate that the primary grazers in our system were not waterfowl, but possibly turtles or fish, which may not have similar energetic constraints.

Here, we demonstrate that *V. americana* can be successfully restored to tidal freshwater areas of the Chesapeake Bay, United States that have been unvegetated for 60 years. However, continued spreading of the transplanted plots outside of protective exclosures is limited by grazing pressure. This indicates that restoration of larger founder beds in this region may be required to reduce herbivore pressure given the large areas of potential habitat for waterfowl, turtles, fish, and crabs that would be drawn to graze in these patches of SAV. Multispecies restoration plantings may also provide increased success in SAV restoration in these areas. It has been observed that in some freshwater tidal regions of the Chesapeake Bay experiencing regrowth of SAV that *V. americana* can be found growing in combination with other species (Moore et al. 2000). This suggests that mixed plantings may improve restoration success by reducing grazing pressure and/or providing a broader range of bed tolerance to varying environmental conditions.

## Conclusions

Although habitat conditions such as physical setting, sediments, and water quality are important components of SAV restoration success (Kemp et al. 2004), the effects of herbivory on transplant success may be a bottleneck to SAV recovery, especially in freshwater areas. It may be that in many areas, recovery and restoration of native SAV species is limited by direct herbivory of the propagules or transplants. Protection of small founder colonies by mesh exclosures have been shown to be effective in reducing or eliminating herbivory inside of the exclosures; however, significant expansion of SAV outside of small scale exclosures has been problematic in many areas. The use of seeds as an alternative to whole shoots or overwintering buds or tubers to expand the size of the initial restoration areas is a promising avenue for future restoration efforts.

### Implications for Practice

- *Vallisneria americana* can be successfully planted in unvegetated sites using whole shoots, seeds, and seed pods. Restoration methods using whole shoots provided the greatest establishment success, but the use of whole shoots required more time, infrastructure (growout ponds), and effort than seeds and seed pods.
- In tidal freshwater regions, *V. americana* can be successfully restored in sediments with organic content ranging from 2 to 8%.
- Semilimiting environmental conditions such as light availability and sediment condition can be ameliorated in shallow (0.5 m MSL) restoration sites for freshwater SAV species such as *V. americana*.
- Herbivory, not water quality or sediment condition, limited the expansion of SAV outside mesh exclosures at all James River, Viriginia, United States sites. Future SAV restoration efforts in this area need to consider herbivore stress as a potential limiting factor on restoration success.
- Large founder colonies may need to be established to withstand grazing pressures for expansion outside of herbivore exclosures. The potential effects of size, density, and species diversity of founder colonies on reducing herbivore pressure is not well understood and requires further investigation.

## Acknowledgments

This work was supported by grants from the U.S. Army Corps of Engineers, Engineering Research and Development Center, the City of Hopewell, Virginia, and the Chesapeake Bay Restoration Fund. Special thanks to B. Neikirk and J. Grandstaff for assistance with the water quality monitoring and to many others for assistance in sampling and field restoration. This is contribution No. 3046 from the Virginia Institute of Marine Science, College of William & Mary.


## LITERATURE CITED


Ailstock, M. S., and D. Shafer. 2004. Restoration potential of *Ruppia maritima* and *Potamogeton perfoliatus* by seed in the mid-Chesapeake Bay. ERDC/TN EL-04-02. U.S. Army Corps of Engineers, Engineer Research and Development Center, Vicksburg, Mississippi (available from http://el.erdc.usace.army.mil/sav/index.html).

American Public Heath Association (APHA), American Water Works Association (AWWA), and Water Environment Federation. 1995. Standard methods for the examination of water and waste-water. 19th edition. APHA, Washington, D.C.

Barko, J. W., and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecological Monographs **51:**219–236.

Barko, J. W., and R. M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. Journal of Ecology **71:**161–175.

Barko, J. W., and R. M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology **67:**1328–1340.

Batiuk, R. A., P. Bergstrom, M. Kemp, E. Koch, L. Murray, J. C. Stevenson, et al. 2000. Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. CBP/TRS 245/00. EPA 903-R-00-014, U.S. EPA, U.S. Environmental Protection Agency Chesapeake Bay Program, Annapolis, Maryland.

Carter, V., and R. 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.

Catling, P. M., K. W. Spicer, M. Biernacki, and J. Lovett-Doust. 1994. The biology of Canadian weeds. 103. *Vallisneria americana* Michx. Canadian Journal of Plant Science **74:**883–897.

Cerco, C. F., and K. Moore. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. Estuaries **24:**522–534.

Davis, F. W. 1985. Historical changes in submerged macrophyte communities of upper Chesapeake Bay. Ecology **66:**981–993.

Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation: Habitat requirements as barometers of Chesapeake Bay health. BioScience **43:**86–94.

Dobberfuhl, D. R. 2007. Light limiting thresholds for submerged aquatic vegetation in a blackwater river. Aquatic Botany **86:**346–352.

Doyle, D. D., and R. M. Smart. 1997. Establishment of native aquatic plants for fish habitat: test plantings in two north Texas reservoirs. Journal of Lake and Reservoir Management **13:**259–269.

Erftemeijer, P. L. A., and E. W. Koch. 2001. Sediment geology methods for seagrass habitat. Pages 345–367 in F.T. Short and R.G. Coles, editors. Global seagrass research methods. Elsevier Science B.V., Amsterdam, the Netherlands.

French, G. T., and K. A. Moore. 2003. Interactive effects of light and salinity stress on the growth, reproduction, and photosynthetic capabilities of *Vallisneria americana* (wild celery). Estuaries **26:**1255–1268.

Harwell, M. C., and K. E. Havens. 2003. Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. Aquatic Botany **77:**135–151.

Hauxwell, J., T. K. Frazer, and C. W. Osenberg. 2004. Grazing by manatees excludes both new and established Wild Celery transplants: Implications for restoration in Kings Bay, FL, USA. Journal of Aquatic Plant Management **42:**49–53.

Idestam-Almquist, J. 1998. Waterfowl herbivory on *Potamogeton pectinatus* in the Baltic Sea. Oikos **81:**323–328.

Jarvis, J. C., and K. A. Moore. 2008. Influence of environmental factors on *Vallisneria americana* seed germination. Aquatic Botany **88:**283–294.

Kemp, W. M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C. Gallegos, et al. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. Estuaries **27:**363–377.

Killgore, K. J., R. P. Morgan II, and N. B. Rybicki. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River.North American Journal of Fisheries Management **9:**101–111.

Korschgen, C. E., L. S. George, and W. L. Green. 1988. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River. Pages 237–249 in M. W. Weller editor. Waterfowl in winter. University of Minnesota Press, Minneapolis.

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 (Southwestern Florida). Estuaries **22:**138–148.

Kreiling, R. M., Y. Yin, and D. T. Gerber. 2007. Abiotic influences on the biomass of *Vallisneria americana* Michx. in the upper Mississippi River. River Research and Applications **23:**343–349.

Lokker, C., L. Lovett-Doust, and J. Lovett-Doust. 1997. Seed output and the seed bank in *Vallisneria americana* (Hydrocharitaceae). American Journal of Botany **84:**1420–428.

Makkay, K., F. R. Pick, and L. Gillespie. 2008. Predicting diversity versus community composition of aquatic plants at the river scale. Aquatic Botany **88:**338–346.

McFarland, D. G., and Shafer, D. J. 2008. Factors influencing reproduction in American wild celery: a synthesis. Journal of Aquatic Plant Management **46:**129–143.

Moore, K. A., and J. C. Jarvis. 2007. Using seeds to propagate and restore *Vallisneria americana* Michaux. (Wild Celery) in the Chesapeake Bay. ERDC/TN SAV-07-3. U.S. Army Corps of Engineers, Engineer Research and Development Center, Vicksburg, Mississippi (available from http://el.erdc.usace.army.mil/sav/index.html).

Moore, K. A., D. Wilcox, R. J. Orth, and E. Bailey. 1999. Analysis of historical distribution of submerged aquatic vegetation (SAV) in the James River. Special Report no. 355 in Applied Marine Science and Ocean Engineering. The Virginia Institute of Marine Science, Gloucester Point, Virginia.

Moore, K. A., D. L. Wilcox, and R. J. Orth. 2000. Analysis of abundance of submersed aquatic vegetation communities in the Chesapeake Bay. Estuaries **23:**115–127.

Moore, K. A., D. J. Wilcox, B. A. Anderson, T. A. Parham, and M. D. Naylor. 2004. Historical analysis of submerged aquatic vegetation (SAV) in the Potomac River and analysis of bay-wide SAV data to establish a new acreage goal. CB983627-01. U.S. Environmental Protection Agency Chesapeake Bay Program, Annapolis, Maryland.

National Oceanic and Atmospheric Administration. 2009. Tides and Currents. Station Information, City Point, Hopewell, NOAA, Virginia. [accessed 1 October 2009].

Nystrom, P., and J. A. Strand. 1996. Grazing by a native and an exotic crayfish on aquatic macrophytes. Freshwater Biology **36:**673–682.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, Jr., et al. 2006*a*. A global crisis for seagrass ecosystems. BioScience **56:**987–996.

Orth, R. J., and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. Science **222:**51–53.

Orth, R. J., and K. A. Moore. 1988. Distribution of *Zostera marina* and *Ruppia maritima* sensu lato along depth gradients in the Lower Chesapeake Bay, U.S.A. Aquatic Botany **32:**291–305.

Orth, R. J., J. Bieri, J. R. Fishman, M.C. Harwell, S. R. Marion, K. A. Moore, J. F. Nowak, and J. van Montfrans. 2006*b*. A review of techniques using adult plants and seeds to transplant eelgrass (*Zostera marina* L.) in Chesapeake Bay and the Virginia Coastal Bays. Pages 1–17 in S. F. Treat and R. R. Lewis, editors. Seagrass restoration: success, failure and the cost of both. Proceedings of the Conference. Lewis Environmental Services, Inc., Tampa, Florida.

Orth, R. J., D. J. Wilcox, J. R. Whiting, L. S. Nagey, A. L. Owens, and A. K. Kenne. 2008. 2007 Distribution of submerged aquatic vegetation in Chesapeake Bay and coastal bays. Virginia Institute of Marine Science Special Scientific Report #151, Gloucester Point, Virginia.

Perry, M. C., and A. S. Deller. 1996. Review of factors affecting the distribution and abundance of waterfowl in shallow-water habitats of Chesapeake Bay. Estuaries **19:**272–278.

Prejs A. 1984. Herbivory by temperate fishes and its consequences. Biology of Fish **10:**281–296.

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.

Rybicki, N. B., and V. Carter. 2002. Light and temperature effects on the growth of Wild Celery and Hydrilla. Journal of Aquatic Plant Management **40:**92–99.

Rybicki, N. B., and J. M. Landwehr. 2007. Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. Limnology and Oceanography **52:**1195–1207.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York.

Shafer, D., and P. Bergstrom. 2008. Large scale submerged aquatic vegetation restoration in the Chesapeake Bay. ERDC/EL TR-09-20, U.S. Army Corps of Engineers, Engineer Research and Development Center, Vicksburg, Mississippi (available from http://el.erdc.usace.army.mil/sav/index.html).

Smart, R. M., R. D. Doyle, and G. O. Dick. 1996. Establishing native submersed aquatic plant communities for fish habitat. Multidimensional Approaches to Reservoir Fisheries Management. American Fisheries Society Symposium **16:**347–356.

Søndergaard, M., L. Bruun, T. Lauridsen, E. Jeppesen, and T. V. Madsen. 1996. The impact of grazing waterfowl on submerged macrophytes: In situ experiments in a shallow eutrophic lake. Aquatic Botany **53:** 73–84.

Sponberg, A. F., and D. M. Lodge. 2005. Seasonal belowground herbivory and a density refuge from waterfowl herbivory for *Vallisneria americana*. Ecology **86:**2127–2134.

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.

U.S. Department of Agriculture, Natural Resources Conservation Service (USDA NRCS). 2009. Plants national database. Profile for *Vallisneria americana* Michx (available from http://plants.usda.gov/, accessed 1 September 2009.

Van Donk, E., E. De Deckere, J. P. G. Breteler, and J. T. Meulemans. 1994. Hervivory by water fowl and fish on macrophytes in a biomanipulated lake: effects on long term recovery. Verhandlungen des Internationalen Verein Limnologie **25:**2139–2143.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyanik, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America **106:** 12377–12381.

Wright, R. M., and V. E. Phillips. 1992. Changes in the aquatic vegetation of two gravel pit lakes after reducing the fish population density. Aquatic Botany **43:**43–49.

Zar, J. H. 1999. Biostatistical analysis. 4th edition. Prentice Hall, Upper Saddle River, New Jersey.