An annual cycle of biomass and productivity of *Vallisneria americana* in a subtropical spring-fed estuary

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Abstract

An annual cycle of biomass and productivity of wild celery (*Vallisneria americana*) was studied in Kings Bay, FL, USA. *In situ* growth rates were measured monthly between March 2001 and June 2002 in high-density stands, using a modified hole-punching technique, and applied to shoot density data to obtain areal estimates of production. Mean shoot density varied greatly over the study period, ranging between 200 and 800 shoots m^{-2}. Mean total biomass ranged between 162 and 1013 g m^{-2}, with aboveground material comprising, on average, 70% of total biomass. Total annual estimated production of new attached shoots was 519 g m^{-2}. Leaf growth rates peaked at >50 mg shoot^{-1} d^{-1}, and mass-specific leaf growth ranged 0.6–1.8% d^{-1}. Annually, individual shoots produced 7.4 g of leaf material and completely replaced standing leaf biomass 3.5 times. Areal leaf production was highest in late spring/summer of 2001, and ranged between 3.6 and 23.0 g m^{-2} d^{-1}. Annual total leaf production was 2704 g m^{-2}. Seasonality was not apparent in most variables monitored monthly; only 1 of the 64 relationships we examined between environmental variables (nutrients, chlorophyll a, and irradiance) and *Vallisneria* biological variables were significant, with relative growth rate increasing linearly with irradiance. Peak biomass and productivity of *Vallisneria* in Kings Bay were high compared to literature values for other *Vallisneria* populations as well as global averages for well-studied seagrasses, emphasizing the potential importance of *Vallisneria* to whole ecosystem functioning in springs, lakes, and oligohaline reaches of many estuaries.
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1. Introduction

Wild celery (*Vallisneria americana* Michx) is a dioecious, perennial, aquatic angiosperm, distributed from Central America to Canada (Korschgen and Green, 1988), and found in freshwater to mesohaline environments. *Vallisneria* is a stoloniferous species, capable of rapid clonal extension and often forms expansive meadows. Such meadows are important biological, physical, and chemical components of these ecosystems, providing both refuge and foraging habitat (Persson and Crowder, 1998; Diehl and Kornijów, 1998; Jeppesen et al., 1998; Mitchell and Perrow, 1998), promoting sedimentation and sediment stability (Barko and James, 1998),

hence affecting water column chemistry (Carpenter, 1980; Graneli and Solander, 1988; Wetzel and Søndergaard, 1998; Caraco and Cole, 2002) and sediment biogeochemistry (Wigand et al., 1997; Barko and James, 1998).

Vallisneria has declined in abundance in several lakes, rivers, and estuaries in Florida—in many cases, as a result of degraded water quality (Jaggers, 1994). Reduced water clarity in the Potomac River probably contributed to the loss of *Vallisneria* from the freshwater tidal river (Haramis and Carter, 1983). Similarly, loss of large beds of *Vallisneria* from the backwaters of the upper Mississippi River also has been associated with reduced light availability (Kimber et al., 1995). An opposite and rapid response of *Vallisneria* to increased light availability was noted in Put-in-Bay Harbor, Lake Erie; within 5 years of the zebra mussel introduction in 1988 and the resulting clarification of lake water, *Vallisneria* had increased to such abundance that it became the dominant submersed species in the Bay (Stuckey and Moore, 1995). A similar recovery in response to zebra mussel invasion was observed in Long Point

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Bay, Lake Erie (Knapton and Petrie, 1999), and Saginaw Bay, Lake Huron (Skubinna et al., 1995), where *Vallisneria* expanded in coverage, most likely as a result of improved water clarity. Increases in water clarity in the Potomac River following improved wastewater treatment have been attributed to cause the resurgence of populations in the mid 1980s (Carter and Rybicki, 1986).

Though similar in function to many seagrass species (*e.g.*, *Zostera marina*, *Thalassia testudinum*, *Halodule wrightii*, *etc.*) for which annual estimates of productivity have been made (reviewed by Duarte and Chiscano, 1999), we found no published reports based upon reliable methods that documented net production of *Vallisneria in situ*. As responses of seagrasses have been developed as indicators of change to coastal marine systems, long-term production data for *Vallisneria* may provide a tool for detecting watershed effects as well as transplant performance in restoration efforts.

We sought to determine the monthly dynamics of *Vallisneria* biomass and productivity over an annual cycle in Kings Bay, FL, USA, and examine the relationship of *Vallisneria* biological variables with environmental variables including nutrients, water column chlorophyll a, and surface irradiance. Although there are anecdotal accounts that *Vallisneria* once dominated the benthic vegetation of Kings Bay, this native macrophyte is recently restricted to high-density nearly monospecific patchy meadows ranging in size from a few square meters to hectares (Frazer and Hale, 2001; Hauxwell et al., 2003). Additional species that could be found interspersed around high-density *Vallisneria* stands included *Myriophyllum spicatum* (L.), *Hydrilla verticillata* (L.F.) Royle, *Lyngbya* sp., *Stuckenia pectinata* (L.), *Najas guadalupensis* (Spreng.) Magnus, and *Ceratophyllum demersum* (L.). Over the past decade, local management agencies achieved reductions in nutrient concentrations following improvements in wastewater management within the Kings Bay watershed (Terrell and Canfield, 1996), and are now interested in the potential for restoration of *Vallisneria* in the system. Data generated as a result of this study provide estimates of *Vallisneria* biomass and productivity over an annual cycle and could be used as a benchmark from which to compare restoration success.

2. Methods

2.1. Study site and environmental data

Kings Bay (Citrus County, FL, approximately 97 km north of Tampa) is a spring-fed, tidally influenced freshwater-oligohaline system (see Hoyer et al., 2001; Frazer et al., 2001a, 2006) and headwater for the 11-km long Crystal River, which discharges to the Gulf of Mexico (Frazer et al., 2001b). Because groundwater flow, primarily from spring discharge, contributes up to 99% of the freshwater entering the 1.8-km^2 Bay (Hammett et al., 1996), water temperature remains ~25 °C year-round. Throughout our study period (March 2001–June 2002), bay-wide monthly average concentrations of total phosphorus, total nitrogen, and chlorophyll ranged from 16 to 41 μg P L^{-1}, 135–283 μg N L^{-1}, and 3–24 μg chl a L^{-1},

respectively (Florida LAKEWATCH, 2001, 2002). Mean monthly surface irradiance peaked in May of both years and ranged from 1076–2384 μmol photons m^{-2} s^{-1}. Values were determined by converting solar radiation values collected every 15 min over the study period by the Florida Automated Weather Network station in Brooksville, FL (FAWN, 2006) and averaged over daylight hours (6:00 am to 6:00 pm), using a conversion factor of 4.6 (W m^{-2} to μmol photons m^{-2} s^{-1}, Duncan, 1990). Tidal range is ~1 m and mean salinity is generally <2‰ (Frazer et al., 2001b and references therein).

2.2. Measurements of Vallisneria biomass and production

Measurements were taken within the largest continuous *Vallisneria* meadow in Kings Bay located just south of Buzzards Island (28.885°N, 82.601°W), in a depth of ~1 m (mean low water). The meadow was approximately 9 ha in size, dominated by *Vallisneria*, and consisting of monospecific stands of *Vallisneria* in the areas selected for monitoring. Variables monitored monthly from March 2001 through June 2002 included: shoot density, height, number of leaves, mass, flowering frequency and sex, areal biomass (above- and belowground), absolute and relative *in situ* aboveground growth rates, production of new attached shoots, and areal leaf production.

To quantify shoot densities and biomass of *Vallisneria* within the meadow, SCUBA divers hand-collected all shoots and associated belowground material within three haphazardly tossed 20-cm diameter cores (0.03 m^2) during each monthly sampling event. Samples were stored frozen and subsequently processed in the laboratory, where number of shoots was counted. After measuring shoot height and counting number of leaves per shoot, samples were separated as new leaves, senescent leaves, flowers, stems and stolons and roots. Each component was dried at 60 °C to constant weight and mass determined to the nearest 0.001 g with an electronic balance.

To measure *in situ* aboveground growth by shoots, we modified a leaf-marking technique commonly used for seagrasses (Odum, 1957; Zieman, 1968; Zieman and Wetzel, 1980), and appropriate for many wide-bladed aquatic plants exhibiting a basal meristem. To ensure that a representative range of size classes of shoots were included, SCUBA divers tagged the 15 closest shoots to a randomly tossed buoy, and carefully punched two needle holes (18 gauge) in each leaf per shoot, at a common reference point, approximately 3 cm above the sediment/water interface (Hauxwell et al., 2004). Divers severed all stolon connections with other shoots, so that the appearance and production of new attached shoots could also be assessed. Tagged shoots, and along with any newly formed attached shoots, were retrieved 1 month after punching, at which time a new batch of shoots was tagged and punched; this continuous mark/retrieval provided 13 sets of measurements over the study period. Shoots were transported to the laboratory and frozen until leaf elongation from the original markings for each leaf on each shoot could be measured, and number and dry mass of new shoots recorded. In the laboratory, we ranked the leaves on each shoot by age and measured total length and

width. Because there were generally 3–12 older, senescent leaves on a given shoot, all bearing punching scars at the same height from the shoot base (no observed growth), this height served as the final reference point for initial punching. Growth of younger leaves (typically the newest 3 or 4 leaves) was determined as the distance between their punching scars and the reference point. Growth of new attached shoots was calculated as final biomass, based on the reasonable assumption that these young (<1 month old) shoots had not yet sloughed leaves.

To convert aboveground shoot characteristics and leaf growth from units of surface area to dry mass, we applied a conversion factor of 0.0034 g cm^{-2} (Hauxwell et al., 2004: regression analysis, $N = 120$ shoots, $P < 0.0001$, $r^2 = 0.92$) to length and width data to obtain aboveground shoot mass (mg shoot^{-1}), and to leaf growth measurements to obtain daily leaf growth rates (mg shoot^{-1} d^{-1}). Mass-specific daily leaf growth rates (% d^{-1}) were determined by dividing daily growth rates per shoot by final aboveground shoot dry mass $\times$ 100 (Dennison, 1987).

Estimates of areal net production of *Vallisneria* over an annual cycle were made by multiplying mean leaf growth rates and growth of new attached shoots (per shoot) by interpolated mean densities of shoots for the midpoint between consecutive sampling dates. Annual estimates were derived by taking the sum of production during all growth intervals between May 2001 and May 2002.

Regression analyses were conducted to determine whether there was a coupling between environmental variables (including total phosphorus, total nitrogen, chlorophyll a, and surface irradiance) and *Vallisneria* biological variables (including individual shoot variables such as shoot mass, shoot height, number of leaves, shoot absolute growth rates, shoot relative growth rates, appearance of new shoots, and areal estimates of shoot density, total biomass, aboveground biomass, belowground biomass, flowering frequency, frequency of female or male flowers, productivity via leaf elongation, productivity via the appearance of new shoots, and total production). Using monthly averaged environmental ($n = 4$) and biological data ($n = 16$), we determined 64 regression models.

3. Results

Mean shoot density varied greatly over the study period, ranging between 200 and 800 shoots m^{-2} (Fig. 1, top); individual cores yielded values between 90 and 1140 shoots m^{-2}. Although it was not possible to discern any consistent seasonal pattern in Kings Bay, peaks in density occurred between April and June of both study years. Some indication of interannual variation is also discernible by comparing the March–July interval of both years; shoot densities were generally higher in 2002.

We compiled morphological and biomass data for the shoots retrieved from cores (Fig. 1, panels 2–4). Shoot height peaked in late summer (2001), at which time shoots were approximately 80 cm tall and extended to the water's surface at low tide. Throughout the study period, individual height ranged from 3 to 134 cm, with number of leaves per shoot ranging from 1 to 26 (on average, ranging between 6 and 11). Mean shoot
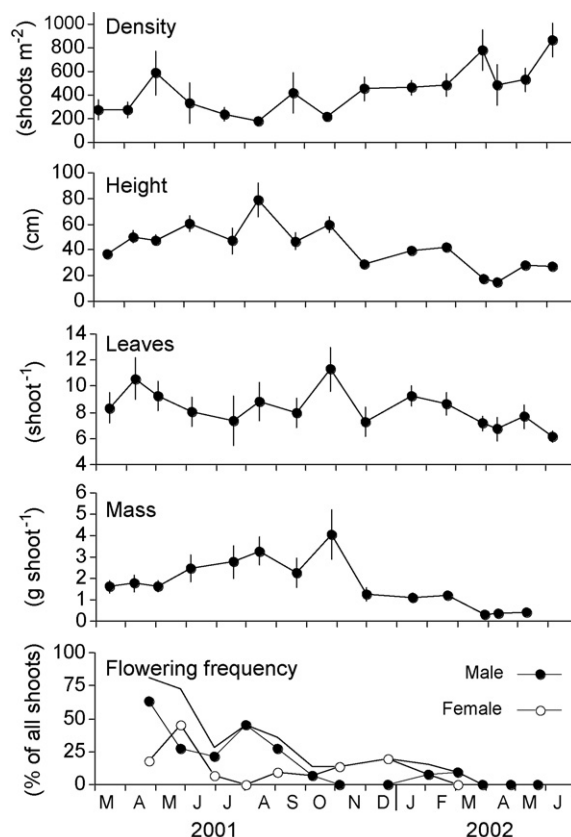

Fig. 1. Monthly measurements of *Vallisneria americana* shoot density, shoot height, number of leaves shoot^{-1}, shoot dry mass, and flowering frequency (as percentage of all shoots and sex, solid line indicates total) in Kings Bay, FL (all expressed as means ± S.E.).

mass ranged from 0.4–4.0 g shoot^{-1}, with the highest value in fall (2001).

Flowering shoots were collected throughout much of the study period (Fig. 1, bottom), with the highest frequency of occurrence in April 2001 (82% of shoots flowering). None of the shoots collected for growth measurements in April 2002 were flowering, indicating substantial interannual variability in sexual reproduction.

Mean total biomass also varied over the study period, ranging between 162 and 1013 g m^{-2} (Fig. 2, top). Aboveground material comprised the majority of total biomass, on average 70% (Fig. 2, top). Of the aboveground material, new leaves, senescent leaves, and flowers comprised 83, 16, and 1%, respectively (Fig. 2, middle). Of the belowground material, roots, stems, and stolons comprised 45, 41, and 14% of the biomass, respectively (Fig. 2, bottom).

Production of new shoots by tagged shoots was relatively rapid (Fig. 3). In January 2002, at peak rates, mean production of new attached shoots was >1 shoot^{-1} over the 30-d sampling interval (Fig. 3, top). Throughout the study period, maximum production of new shoots over sampling intervals by individual shoots ranged from 0 to 4. When applied to shoot densities, estimated mean new shoot leaf production fluctuated greatly over the annual cycle, ranging from 0 to 6.6 g m^{-2} d^{-1} (Fig. 3, bottom). Total annual estimated production by the appearance
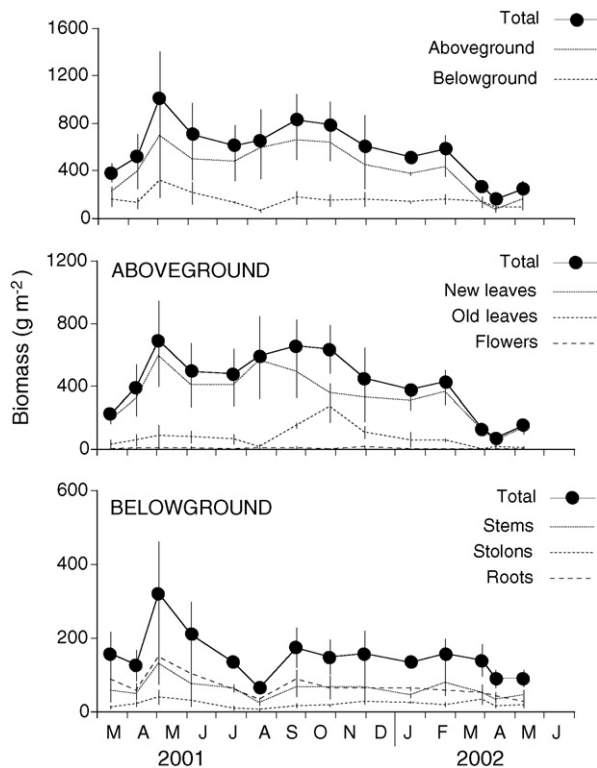
Fig. 2. Monthly measurements of *Vallisneria americana* total (top), above-ground (middle), and belowground (bottom) dry biomass, and associated components, in Kings Bay, FL (means ± S.E.).
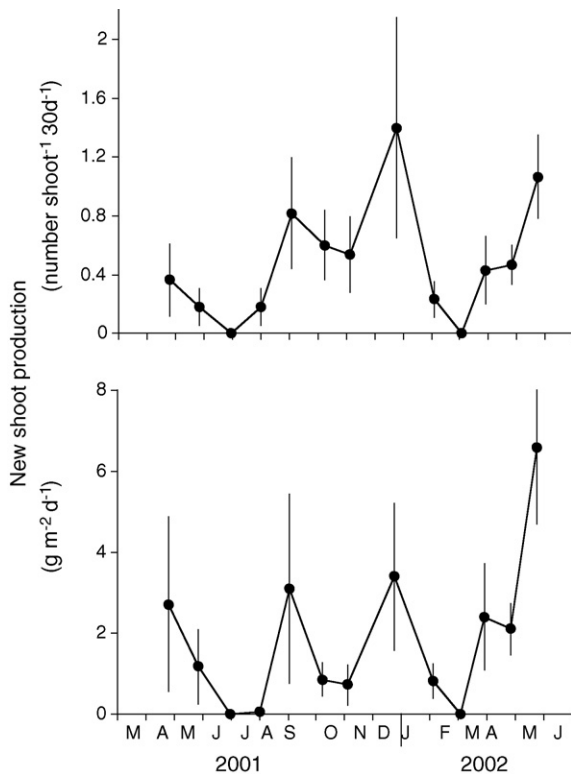
of new shoots alone was 519 g m^{-2}. Belowground biomass of new attached shoots accounted for 25% of their total mass.

Leaf growth rate by *Vallisneria* shoots increased as a function of shoot mass (data not shown). For 10 of the 13 months over which we monitored growth, there was a significant positive relationship between leaf production by tagged shoots and shoot mass, with leaf growth rates (log transformed) increasing as the 0.5–1.9th power of shoot mass (log transformed) (monthly regression analyses, $P < 0.05$). There were two possible outliers, in which shoots grew an order of magnitude less than others of similar size (March and June 2002), possibly indicating senescence or another factor limiting growth of certain shoots.

Leaf growth rates were highest in spring and late summer in 2001 (>50 mg shoot^{-1} d^{-1}) and generally lower in 2002 than in 2001 (Fig. 4, top). Because growth of leaf material by shoots increases with shoot mass (see above, Hauxwell et al., 2004), a temporal pattern in growth became more apparent after incorporating the effect of shoot mass; mass-specific leaf growth rates were highest in late spring during both years, and ranged 0.6–1.8% d^{-1} over the study period (Fig. 4, middle). On an annual basis, a shoot in Kings Bay produced 7.4 g of dry leaf material and completely replaced standing leaf biomass 3.5 times. Areal leaf production (via leaf elongation) was highest in late spring and late summer of 2001, with a maximum mean value of 23.0 and minimum of 3.6 g m^{-2} d^{-1}. Annual total leaf production was 2704 g m^{-2}, more than 5 times that due to the production of new attached shoots (519 g m^{-2}).

Fig. 3. Monthly measurements of *Vallisneria americana* production of new attached shoots expressed as number of new shoots shoot^{-1} over the 30-d sampling interval (top) and as areal production (bottom) in Kings Bay, FL (means ± S.E.).
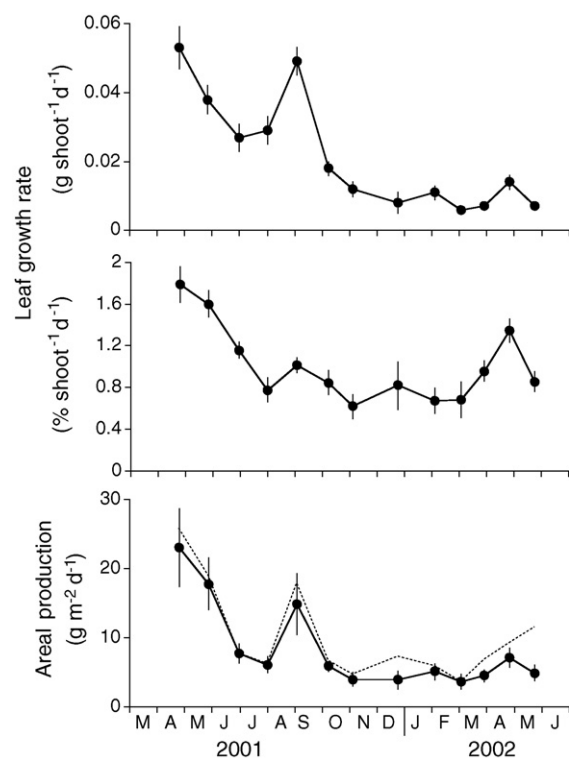

Fig. 4. Monthly measurements of daily *Vallisneria americana* leaf growth rate (top), mass-specific leaf growth rate (middle), and areal production (bottom, dashed line indicates leaf production of tagged shoots plus total production of new attached shoots) in Kings Bay, FL (means ± S.E.).

Of the 64 regression models adjusted between monthly averaged environmental data and biological data (both absolute and log-transformed), we found only 1 significant relationship. Relative growth rate of shoots (% d^{-1}) increased linearly with surface irradiance ($y = -0.19 + 0.001x$, $r^2 = 0.57$; $P = 0.003$).

4. Discussion

Unlike northern populations which overwinter as below-ground tubers, *Vallisneria* grew year-round in Kings Bay, as it does in other southern populations (Bortone and Turpin, 2000; Doering et al., 2001). Shoot densities in Kings Bay (200–800 shoots m^{-2}) were comparable to those reported by Bortone and Turpin (2000), in which mid-summer peak densities of 600–1200 shoots m^{-2} were documented for a south Florida system (Caloosahatchee River, FL). Peak densities in these southern Florida populations were 2–5 times higher than densities reported in monocultures in more northern populations (280 shoots m^{-2} in the Pamlico River Estuary, North Carolina (Zamuda, 1976); 253 in Navigation Pool 7 of the Mississippi River (Korschgen and Green, 1988); and 214 in Navigation Pool 9 (Donnermeyer and Smart, 1985)).

In Table 1, we provide a list of peak biomass values for naturally occurring monospecific beds of *Vallisneria* in a variety of locations. Peak biomass of *Vallisneria* in Kings Bay (1013 g m^{-2}) was the highest observed so far, with a similar observation at Lake Mattamuskeet, North Carolina, where aboveground *Vallisneria* biomass peaked at approximately 900 g m^{-2} (Sponberg and Lodge, 2005). Measurements from other sites ranged 50–400 g m^{-2}. Peak areal biomass values in Kings Bay were 5–20 times greater than those in the Caloosahatchee, despite similar shoot densities; the mass of individual shoots in Kings Bay approached 5 g while the maximum in the Caloosahatchee was <0.4 g.

Although seasonal patterns in shoot density and biomass have been documented for other southern *Vallisneria* populations (e.g., Bortone and Turpin, 2000), our data provided little indication of seasonality for the *Vallisneria* population in Kings Bay, except for significantly relating relative growth rate to irradiance. Due to the spring-fed nature of this system, water temperatures do not fluctuate widely over the year as they do in

most other systems (~25 °C year-round). In addition, waters are relatively clear (annual average chlorophyll concentrations = 9 ± 5 μg L^{-1}; Florida LAKEWATCH, 2001, 2002), and the plants we monitored were in relatively shallow waters. Hence, surface irradiance is likely the most important physical variable that fluctuates over an annual cycle. Because both temperature and irradiance influence growth (Barko et al., 1982), it is possible that uniform temperatures in Kings Bay dampened the signal associated with seasonal changes in irradiance observed in thermally variable environments. Also, at certain times leaf growth may be supported by previously stored carbohydrates re-allocated to new leaves (Titus and Adams, 1979). Storage of energy reserves by *Vallisneria* in the Kings Bay system during non-limiting periods of growth may also mask seasonality.

Despite observing flowering shoots year-round (Fig. 1, bottom), most recruitment of new shoots occurred via vegetative reproduction (Fig. 3; Hauxwell pers. obs.). Over an annual cycle, seedlings accounted for 7% only of new shoots (ranged 0–18%; Hauxwell pers. obs.), and clonal growth resulted in an average of 56 new shoots annually per square meter (adapted from Fig. 3). It is not uncommon for aquatic angiosperms, and specifically *Vallisneria*, to reproduce primarily *via* clonal growth aiding in the maintenance and expansion of established beds (Fig. 3; Titus and Stephens, 1983; Lovett-Doust and Laporte, 1991), and to rely on emergence of seedlings for colonizing new areas (McFarland and Rogers, 1998). The lack of synchrony in the presence of male and female flowers was notable (Fig. 1, bottom), and might be indicative of spatial heterogeneity not well captured with our sampling protocol. For example, given the clonal extension of *Vallisneria*, there may be "patches" of female or male plants. In fact, "spatial segregation" of the sexes of clonal, dioecious plants is not uncommon (Bierzychudek and Eckhart, 1988), and has been documented for *Vallisneria* (Lovett-Doust and Laporte, 1991).

To our knowledge, this is the first study to provide *in situ* annual estimates of *Vallisneria* production. To provide some comparison for growth of *Vallisneria* in Kings Bay to that of other populations, we searched the literature and found a total of three reports that gave estimates of growth using a variety of

Table 1
Compilation of published maximum total areal biomass values measured in monospecific beds (>90%) of *Vallisneria americana* and results of this study

Source	Study location	Time period	Biomass (g m^{-2})
This study	Kings Bay, FL, USA	May 2001	1013
Sponberg and Lodge (2005)	Lake Mattamuskeet, NC, USA	September 1996	~900[*]
Donnermeyer and Smart (1985)	Pool 9, Upper MS, USA	September 1980	217
Sponberg and Lodge (2005)	Lake Mattamuskeet, NC, USA	September 1997	~200[*]
Harley and Findlay (1994)	Hudson River, NY, USA	Summer 1991	~200
Bortone and Turpin (2000)	Caloosahatchee, FL, USA – Site 2	July 1998	~200
Bortone and Turpin (2000)	Caloosahatchee, FL, USA – Site 4	July 1998	~175
Bortone and Turpin (2000)	Caloosahatchee, FL, USA – Site 1	August 1998	~125
Tazik et al. (1993)	Pool 19, Upper MS, USA	July 1986	95
Bortone and Turpin (2000)	Caloosahatchee, FL, USA – Site 3	September 1998	~50
Titus and Stephens (1983)	Chenago Lake, NY, USA	August 1978	50

Asterisk ([*]) refers to aboveground biomass only. The measurement from the Hudson River site represents a single sample from a single sampling event (no seasonal data available).

Table 2
Compilation of all published leaf production values measured for *Vallisneria americana* using several methods and results from this study

Source	Study location	Time period	Method	Leaf production (mg shoot^{-1} d^{-1})	Maximum daily areal production (g m^{-2} d^{-1})	Annual areal production (g m^{-2} year^{-1})
This study	FL, USA	2001–2002	Punch and harvest	6–53	23	2700
Steller (1986)	LA, USA	1985	Biomass changes			200–473
Donnermeyer and Smart (1985)	Upper MS, USA	July 1980	Biomass changes		3.2	
Cattaneo and Kalff (1980)	Quebec, Canada	Summer 1977	^{14}C uptake	70		

All reports of production are given in dry mass.

techniques, including ^{14}C incorporation or biomass changes between consecutive sampling dates (Table 2). Although results are not directly comparable, they provide some perspective. While our estimates are similar to those obtained using measures of short-term *in situ* ^{14}C incorporation, they are an order of magnitude greater than those obtained using changes in standing crop over time. Due to the rapid turnover of leaves and loss of leaf material during growth, biomass changes on subsequent sampling dates may vastly underestimate seagrass (and *Vallisneria*) production (Dennison, 1990). Leaf marking techniques (Zieman and Wetzel, 1980), though labor-intensive, undoubtedly provide the most accurate estimates of leaf production.

To provide additional context for results of this study, we compared our estimates of *Vallisneria* production to those of commonly measured marine seagrass species. Maximum rates of *Vallisneria* production (23 g m^{-2} d^{-1}) were generally an order of magnitude greater than typical reports of "highly productive" seagrass species like *T. testudinum* (up to 3 g m^{-2} d^{-1}, Florida Bay, Zieman et al., 1989; Gallegos et al., 1993) and *H. wrightii* (up to 3 g m^{-2} d^{-1}, Indian River Lagoon, FL, Virnstein, 1982; up to 1 g m^{-2} d^{-1}, Florida Keys, Lapointe et al., 1994; Hauxwell et al., 2001). Compared to global averages of seagrass species (reviewed by Duarte and Chiscano, 1999), *Vallisneria* in Kings Bay had both the highest standing crops and rates of production of the 29 species for which data were available. For example, Duarte and Chiscano (1999) reported an average rate of total annual production (above- and belowground) for seagrasses of 1012 g m^{-2}, approximately one-third the rate of aboveground production of *Vallisneria* in Kings Bay (2704 g m^{-2} year^{-1}). The high production of *Vallisneria* at our study site is attributable to both its high standing crop (in Kings Bay, higher than the global average for any seagrass species) and its high mass-specific production (which was fifth highest of the 29 species reviewed by Duarte and Chiscano (1999)). Although *Vallisneria* production in Kings Bay was higher than most published values for seagrasses, various populations of seagrasses are similar to (see Vermaat et al., 1995; mixed Philippine seagrass bed with >624 g m^{-2} total biomass and 2143 g m^{-2} year^{-1} annual production) or even more productive than this population of *Vallisneria* (see Duarte and Chiscano, 1999; at least a dozen examples of total biomass exceeding the Kings Bay population for many species). So, while exceptions at the population level occur, these data suggest that, on an ecosystem

scale, the magnitude of carbon fixed by *Vallisneria* and available as standing biomass for heterotrophic consumption in the subtropical Kings Bay spring system may be relatively large, emphasizing the potential importance of *Vallisneria* to whole ecosystem functioning in springs, lakes, and oligohaline reaches of many estuaries.

Due to the inherent ecological value in maintaining beds of native plants, restoration efforts aimed at revegetating shallow freshwater systems with *Vallisneria* 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. Our results provide a reference from which we may begin to assess "success" of a restoration effort. By conducting this study simultaneously with a year-long experiment designed to assess similar features of transplanted plots of *Vallisneria* in potential restoration sites in Kings Bay (Hauxwell et al., 2004), we were able to compare shoot-specific morphology and growth as well as areal productivity of experimental plots with naturally-occurring *Vallisneria*. In this comparison, we found that transplanted plots achieved mass-specific growth rates that were similar to those in natural *Vallisneria* beds. Areal productivity, however, in even our most productive restoration plot (which, to the casual observer was highly successful— within a few months, 20-cm transplants had grown to the water's surface (~1 m) and shoot recruitment had extended the plot's perimeter) was only 10–40% that of a natural plot, due to lower shoot mass and density than a natural plot (Hauxwell et al., 2004). These data allowed us to assess: (1) which potential restoration sites most closely match that of a natural area (most cost-effective for investment) and (2) which features and functions of restoration sites are most able to achieve that of natural areas and which are not (from the per shoot to areal assessments of habitat structure to carbon cycling). We advocate that demographic studies of natural populations of any species should at least accompany, if not precede, investment in large-scale restoration efforts as a way to assess differences in the structure and function of "restored" systems, especially in the case of ecosystem mitigation.

Acknowledgements

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