Kings Bay vegetation evaluation 2010: historical narrative and ecological synthesis

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EXECUTIVE SUMMARY

Kings Bay comprises approximately two square kilometers (500 acres) of embayments and canals in Citrus County, Florida, with Crystal River originating from its northwest end to flow approximately six miles northwestward to the Gulf of Mexico. The bay and river constitute a tidally influenced, spring-fed system that ranks first among Florida's springs in terms of extent and second or third in terms of discharge. Citrus County has experienced rapid population growth, with an increase from approximately 9 thousand to over 140 thousand residents between 1960 and 2010. To meet the demand for waterfront, residential property and boat access, extensive dredging and filling began in the 1950s, and ultimately, these activities altered much of the Kings Bay shoreline and Crystal River. The public has voiced their concerns regarding water quality and proliferation of undesirable plant and algal species in the Kings Bay-Crystal River system since the late 1980s. Declining water clarity represented a widespread and high priority concern, although it was supported only by anecdotal evidence. Nevertheless, this concern merits attention because even a perceived loss of aesthetics can impact eco-tourism, especially diving activities. Over time, the biomass of vegetation in Kings Bay has varied widely, peaking in the mid-1990s when invasive plants were widespread and declining during the last decade. The spatial and temporal patterns of submersed aquatic vegetation in Kings Bay and the influence of these patterns on the ecology of the bay and Crystal River reflect interactions between a complex suite of physical, chemical and biological factors and key ecological processes. Historically, non-native plants, e.g., Hydrilla verticillata and Myriophyllum spicatum, have exerted undesirable pressure on native macrophytes. Acute variations in salinity caused by tropical storms and hurricanes led to marked changes in the submersed aquatic vegetation within Kings Bay, and similar events can be expected to reoccur. Grazing by manatees exerts pressure on native macrophytes, with major reductions in biomass and coverage recorded during winters when manatees seek a thermal refuge. In addition, evidence suggests complex feedbacks between diminished water clarity and decreased coverage of rooted aquatic macrophytes. Based on available evidence, flows in the Kings Bay-Crystal River system will interact with multiple aspects of the ecology of submersed aquatic vegetation. Lower flows will increase residence times, which will promote accumulation of phytoplankton biomass leading to reduced light penetration and stress on vegetation, including Vallisneria americana. Lower flows also will increase salinities, which will decrease competition between V. americana and other less tolerant vegetation potentially leading to an expansion of this desirable macrophyte. Lower flows also may benefit V. americana if water temperatures in Kings Bay become less stable, which will make it a less desirable thermal refuge for manatees leading to reduced grazing pressure. Ultimately, establishing a balanced and self-sustaining assemblage of submersed aquatic vegetation in the Kings Bay-Crystal River system will require ongoing management that maintains suitable, background environmental conditions, including appropriate residence times for water, concentrations of nutrients, concentrations of suspended particles and sediment conditions. Success also may require more drastic, short-term interventions to remove the legacy of past events and reset the system, e.g., sediment removal and the transplanting of V. americana or other native macrophytes. In all cases, the efficiency and effectiveness of management actions will be improved by science that evaluates options, guides implementation, and assesses success to inform adaptation.

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THE KINGS BAY-CRYSTAL RIVER SYSTEM

Kings Bay comprises approximately two square kilometers (500 acres) of embayments and canals in Citrus County, Florida, with Crystal River originating from its northwest end to flow approximately six miles northwestward to the Gulf of Mexico (Figure 1). The bay and river constitute a tidally influenced, spring-fed system that contains at least 70 unique vents or vent-clusters (Vanasse Hangen Brustlin, Inc. 2009). Geographically, the spatial extent and total number of vents make it Florida's largest spring-fed system. In terms of discharge, the complex ranks second or third among Florida's springs. The groundwater feeding the springs originates from the upper Floridan aquifer (Jones and Upchurch 1994).



Figure 1. Map showing the location of Kings Bay and Crystal River in Citrus County, Florida.

The system's springshed is bordered by the Withlacoochee River to the north, a line of divergence in groundwater flow in south-central Citrus County to the south, and the Tsala Apoka chain of lakes to the east (Jones and Upchurch 1994). Recharge rates are highest along the Brooksville Ridge that lies east of the system, where well-drained soils overlay karst. Due to low topography and the proximity of a saltwater-freshwater transition zone in the underlying aquifer, the quantity and chemistry of water discharged into Kings Bay varies. Historic measurements, made approximately three miles downstream from Kings Bay over a 13-year period (1965 to 1977), estimated average discharge at 975 cubic feet per second (Yobbi and Knochenmus 1989). During the summer of 2009, measurements taken in spring vents, vent complexes and canals with acoustic Doppler current meters and other methods estimated aggregated discharge as 488 cubic feet per second (Vanasse Hangen Brustlin, Inc. 2010). The number, complex geometry and variable flow rates of springs and spring vents in Kings Bay and Crystal River make assessing discharge rates challenging.

CHANGES IN LAND USE

Like most coastal areas in the United States, Citrus County has experienced rapid population growth. Between 1960 and 2010, the population of Citrus County grew from little more than 9 thousand to over 140 thousand residents, which ranked among the six fastest percentage growth rates for coastal counties in the country (Wilson and Fischetti 2010). To meet the demand for waterfront, residential property and boat access, extensive dredging and filling began in the 1950s, and ultimately, these activities altered much of the Kings Bay shoreline and Crystal River (Figures 2, 3 and 4). During this time, extensive deadend canal systems were created, significant amounts of natural fringing marsh were converted to hardened shorelines, and about 40 percent of the Kings Bay springshed became urbanized (Southwest Florida Water Management District 2004).

Similar urbanization throughout the jurisdiction of the Southwest Florida Water Management District resulted in increased nutrient loading to all regional springs (Jones and Upchurch 1994; Champion and Starks 2001; Frazer et al. 2001a). Eventually, concerns about groundwater contamination and resulting degradation of aquatic ecosystems pervaded all water management districts with substantial spring resources (see Chellette et al. 2002 for the Northwest Florida Water Management District; Cohen et al. 2007 for the St. Johns River Water Management District; and Hornsby and Ceryak 1999 for the Suwannee River Water Management District).

The public has voiced their concerns regarding water quality and proliferation of undesirable plant and algal species in the Kings Bay–Crystal River system since the late 1980s (Citrus County Chronicle 1985a, 1985b and 1986). Declining water clarity represented a widespread and high priority concern, although it was supported only by anecdotal evidence. Nevertheless, this concern merits attention because even a perceived loss of aesthetics can impact eco-tourism, especially diving activities.

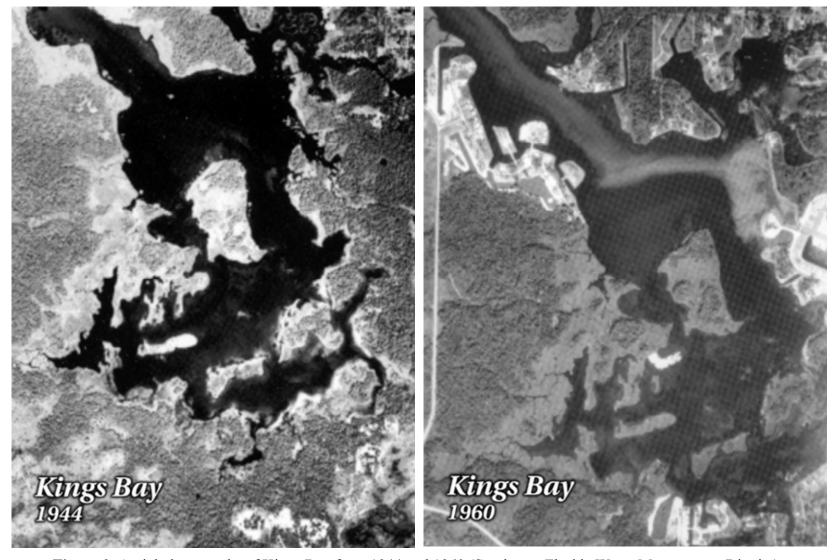


Figure 2. Aerial photographs of Kings Bay from 1944 and 1960 (Southwest Florida Water Management District). Between 1944 and 1960, portions of the shoreline and marshes were modified for residential and commercial development.

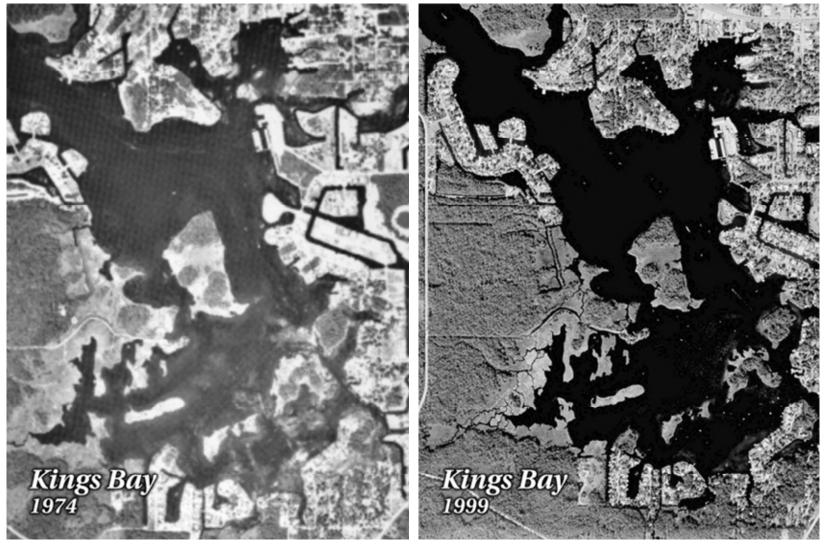


Figure 3. Aerial photographs of Kings Bay from 1974 and 1999 (Southwest Florida Water Management District). Dredging, filling, development and in-fill continued.



Figure 4. Aerial photographs of Kings Bay from 1944 (inset) and 2011 (Southwest Florida Water Management District and Google). Modifications from 65 years of development are extensive.

MANAGEMENT ACTIONS

The Kings Bay–Crystal River system was designated as an Outstanding Florida Water in 1983 by the State, and in 1989 the Southwest Florida Water Management District designated the area as a Surface Water Improvement and Management (SWIM) Priority Water Body (Southwest Florida Water Management District 2000). In the resulting SWIM plans, the district identified establishing a favorable submersed plant assemblage in Kings Bay as a primary management objective required for improved water clarity and wildlife habitat (Southwest Florida Water Management District 2000, 2004). SWIM plans also addressed related issues, including the spread of invasive and exotic submersed aquatic vegetation, increased groundwater pollution within the region, reduced water clarity, and increased use of the bay as a thermal refuge during winters by the largest population of manatees along the west coast of Florida.

A subsequent management action targeting these issues bears on the status of submersed aquatic vegetation in the Kings Bay–Crystal River system. Prior to March 1992, the City of Crystal River discharged 0.75 million gallons of treated wastewater per day into Cedar Cove, an embayment along the northern shoreline of Kings Bay. These discharges were blamed for declines in water clarity and concomitant proliferation of *Lyngbya* sp. and other filamentous algae (Nearhoof 1989; Romie 1990). In response, the City of Crystal River diverted the effluent to an upland spray field. Elimination of the discharges did lead to a four-fold decrease in total phosphorus concentrations and a three-fold reduction in total nitrogen concentrations within Cedar Cove and at sites considered to be downstream (Bishop and Canfield 1995; Terrell and Canfield 1996). Nutrient concentrations in the southern portion of the bay, considered to be upstream of Cedar Cove, remained similar to those measured in the discharges of springs found there, which indicated they had never been affected by the wastewater inputs (Bishop and Canfield 1995; Terrell and Canfield 1996).

Many concerns expressed by the public and managers revolve around the distribution and composition of the submersed aquatic vegetation in the Kings Bay–Crystal River system. In particular, loss of native macrophytes, such as *Vallisneria americana*, and proliferation of invasive or nuisance plant and algal species, e.g., *Myriophyllum spicatum* and *Lyngbya* sp., form the core of many claims citing environmental degradation in this system (Frazer and Hale 2001b; Hauxwell et al. 2003; Jacoby et al. 2007).

HISTORICAL CHANGES IN THE VEGETATIVE ASSEMBLAGE

Submersed aquatic vegetation includes species that grow or float to the surface and reduce open water areas (e.g., *Hydrilla verticillata*, *Myriophyllum spicatum* and filamentous algae, such as *Lyngbya* sp.). Categories of submersed aquatic vegetation (SAV) include rooted macrophytes, large bodied "macroalgae" and filamentous algae. Exotic, introduced or non-indigenous refer to vegetation that is not native to the system, and invasive typically applies to introduced species that grow rapidly.

There are no published reports describing the aquatic vegetation in the Kings Bay-Crystal River system prior to the 1960s; however, recent collections, including those from nearby, spring-fed systems yield insights into the native assemblage. The assemblage likely included flowering plants, such as tape grass or wild celery (*Vallisneria americana*), pondweeds (*Potamogeton pectinatus* and *P. pusillus*), southern naiad (*Najas guadalupensis*), hornwort (*Ceratophyllum demersum*), and widgeon grass (*Ruppia maritima*). Common macroalgae probably included musk grass (*Chara* sp.) and a variety of filamentous forms (species of *Lyngbya*, *Chaetomorpha*, *Enteromorpha*, *Vaucheria* and *Gracillaria*). Filamentous

algae have become so abundant that they are considered an undesirable nuisance, but they are native to Florida and have been present in many of Florida's springs for decades (Whitford 1956).

During the first decade of large-scale development around Kings Bay, aquatic plants become an issue for managers. Interviews with long-term residents suggest that although non-native water hyacinth (*Eichhornia crassipes*) was present in Kings Bay, it was only during the mid to late 1950s that floating mats expanded rapidly throughout the bay and made boating difficult (Evans et al. 2007). In response, broadcast herbicides were applied in aggressive eradication program (Evans et al. 2007).

A second wave of problematic vegetation in Crystal River and Kings Bay arose after the introduction of *Hydrilla verticillata* in 1960 (Blackburn et al. 1969). This macrophyte was documented simultaneously in this system and a canal near Miami lending credence to a report that it was planted by tropical plant dealers as a crop (Blackburn et al. 1969; Langeland 1990). By 1965, the abundance of *H. verticillata* was so problematic that it prompted dramatic control measures. In one notable example, 3,600 gallons of concentrated sulfuric acid were introduced into canals along the east side of Kings Bay and north of Paradise Point Road (Phillippy 1966). Although the local abundance of *H. verticillata* was reduced, the application was not repeated.

During the 1970s and 1980s, Hydrilla remained a problem in Kings Bay and Crystal River, and it was joined by *Myriophyllum spicatum* or Eurasian watermilfoil, a new exotic species (Haller 1978; Langeland 1990). Eurasian watermilfoil appears to have been introduced into the system as early as the 1960s (Blackburn and Weldon 1967; Southwest Florida Water Management District 2004). Efforts to control these plants primarily relied on copper-based herbicides that did not yield long-term success (Haller et al. 1983; Dick 1989). Application of copper based herbicides was discontinued by the middle of the 1980s in response to concerns about bioaccumulation and toxicity in manatees grazing within Kings Bay (Haller et al. 1983; Facemire 1991, 1992).

During the latter half of the 1980s and throughout the 1990s, aquatic herbicides containing photosynthetic inhibitors (e.g., diquat, endothall and fluridone) were applied by multiple agencies, including the Southwest Florida Water Management District, the Florida Department of Natural Resources and the United States Army Corps of Engineers. In the last decade, herbicides have been applied primarily to small beds of floating water hyacinth and water lettuce (*Pistia stratiotes*), which may have been introduced to Florida before 1765 (http://www.invasivespeciesinfo.gov/aquatics/waterlettuce.shtml). Mechanical harvesters, which were first employed by the Citrus County Division of Aquatic Services in 1978, have replaced herbicide applications as a means of maintaining navigable paths.

During the middle 1980s, filamentous algae became a nuisance within Kings Bay leading to complaints from citizens. Filamentous algae form dense mats that trap gasses, which eventually accumulate to the point where the mats float to the surface. These floating mats are unaesthetic, and filamentous algae may outcompete rooted macrophytes leading to a loss of vertically complex habitats. *Lyngbya* sp. (a cyanobacterium or blue-green alga) has received the most attention, but other species contribute to the formation of mats (Jacoby et al. 2007). By the end of 1980s, *Lyngbya* and other filamentous algae represented a key concern for the public and managers (Southwest Florida Water Management District 2004).

In parallel with changes in the composition of the submersed aquatic vegetation assemblage in the Kings Bay-Crystal River system, various short-term perturbations have been noted. In particular, decreases in vegetative cover and biomass follow salinity intrusions caused by storms and hurricanes (Bishop 1995; Terrell and Canfield 1996; Mataraza et al. 1999; Frazer et al. 2001b, 2006a; Jacoby et al. 2007) and grazing by manatees (Hauxwell et al. 2003, 2004a, 2004b; Jacoby et al. 2007). Species differ in their

susceptibility to these pressures and their resilience, but most species recover once salinities or grazing decrease.

Over time, the biomass of vegetation in Kings Bay has varied widely, with a recent peak in the mid-1990s when invasive plants were widespread and a decline during the last decade (Figure 5; Haller et al. 1983; Terrell and Canfield 1996; Mataraza et al. 1999; Hoyer et al. 2001; Jacoby et al. 2007). After 1994, samples typically yielded less than 5 kg wet weight m⁻². In addition, the composition of the submersed aquatic vegetation assemblage appears to have changed, with filamentous algae that was limited to the northern edge of Kings Bay in the early 1980s (Haller et al. 1983) becoming more widespread and abundant in 2004–2006 (Jacoby et al. 2007). Overall, available data corroborate claims by residents and resource managers that submersed aquatic vegetation has declined in Kings Bay over the past decade.

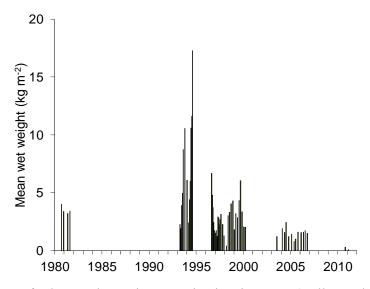


Figure 5. Biomass of submersed aquatic vegetation in Kings Bay (Haller et al. 1983; Terrell and Canfield 1996; Mataraza et al. 1999; Hoyer et al. 2001; Jacoby et al. 2007). Gaps are months within years that lack data.

The mean biomass of submersed aquatic vegetation in nearby, tidally influenced, spring-fed systems also has declined, although these systems typically support less biomass than Kings Bay. Since 1998–2000, biomass of all submersed aquatic vegetation has declined from 4.0 to 1.0 kg wet weight m⁻² in the Weeki Wachee River, 0.7 to 0.2 kg wet weight m⁻² in the Homosassa River, and 1.4 to 0.9 kg wet weight m⁻² in the Chassahowitzka River (Frazer et al. 2006b). In the upper half of the Homosassa, Chassahowitzka and Weeki Wachee rivers (reaches with conditions comparable to Kings Bay), the average biomass of all submersed aquatic vegetation in August 2004 was 0.3, 1.3 and 0.9 kg wet weight m⁻², with angiosperms contributing 24%, 72% and 30% of this biomass, respectively (Frazer unpublished data). In July 2004, the mean biomass for all submersed aquatic vegetation in Kings Bay was 2.4 kg wet weight m⁻², with angiosperms accounting for approximately 10% of this value (Jacoby et al. 2007). In comparison to the Ichetucknee River, which is less affected by salinity but does harbor manatees, Kings Bay supports far lower average biomass per unit area. In 2004, the average biomass for all submersed aquatic vegetation in the Ichetucknee was 5.3 kg wet weight m⁻², more than double the estimate for Kings Bay (Kurz et al. 2004). In addition, samples from the Ichetucknee comprise two native angiosperms, Vallisneria americana and Sagittaria kurziana almost entirely. The standardized areal biomass of Vallisneria americana in the Ichetucknee River was approximately 15-fold greater than in Kings Bay, 0.47 kg dry weight m⁻² and 0.03 kg dry weight m⁻², respectively (Kurz et al. 2004; Jacoby et al. 2007).

ECOLOGY OF SUBMERSED AQUATIC VEGETATION IN THE KINGS BAY-CRYSTAL RIVER SYSTEM

The spatial and temporal patterns of submersed aquatic vegetation in Kings Bay and the influence of these patterns on the ecology of the bay and Crystal River reflect interactions between a complex suite of physical, chemical and biological factors and key ecological processes. Historically, an over-abundance of non-native plants, e.g., *Hydrilla verticillata* and *Myriophyllum spicatum*, has been problematic. Acute variations in salinity caused by tropical storms and hurricanes have led to repeated and marked changes in submersed aquatic vegetation within Kings Bay, and similar events can be expected to reoccur (Mataraza et al. 1999; Frazer et al. 2001b, 2006a). Grazing by manatees exerts additional pressure on native plants (Hauxwell et al. 2004a, 2004b), with major reductions in biomass and coverage recorded during winters when manatees seek a thermal refuge (Jacoby et al. 2007). In addition, evidence suggests complex feedbacks between diminished water clarity and decreased coverage of rooted aquatic macrophytes (Hoyer et al. 2001).

Interactions with light availability

The distribution and abundance of submersed aquatic vegetation is influenced by the prevailing light regime. Species vary in their capacity to cope with reduced light, but all species require light to support photosynthesis.

Non-volatile, algal and detrital suspended solids all are inversely related to horizontal Secchi distance, a measure of water clarity and available light (Hoyer et al. 1997; Munson 1999). For example, chlorophyll concentrations below 6 µg L⁻¹ yield horizontal Secchi distances greater than 10 m (Hoyer et al. 2001). During a period of low visibility in Kings Bay, surface water collected near Kings Spring contained suspended particles comprised primarily of microscopic algal cells (Bishop 1995, Bishop and Canfield 1995). Horizontal Secchi distances were negatively correlated with chlorophyll concentrations, with minimum (10 ft) and maximum (58 ft) readings recorded on days when chlorophyll concentrations were 20 µg L⁻¹ and 1.7 µg L⁻¹, respectively. In other data, non-volatile and detrital solids accounted for 30% and 12% of the variance in horizontal Secchi readings, respectively, whereas algal solids accounted for approximately 40% of the variance (Hoyer et al. 1997; Munson 1999). Overall, these findings indicated that phytoplankton abundance was the primary factor determining water clarity in Kings Bay during the 1990s. Although the source of the algae was not determined, several mechanisms might explain the occurrence of elevated chlorophyll concentrations in Kings Bay.

Phosphorus and nitrogen are often primary factors determining the abundance of algal cells in waters around the world (Aizaki et al. 1981). Data from seven Florida LAKEWATCH stations sampled monthly from 1992 to 2000 showed that both total phosphorus and total nitrogen concentrations correlated positively with chlorophyll concentrations in Kings Bay–Crystal River system (Florida LAKEWATCH 2000; Hoyer et al. 2001). Total phosphorus, total nitrogen and chlorophyll concentrations averaged 28 μg L⁻¹, 229 μg L⁻¹, and 8 μg L⁻¹, respectively (Florida LAKEWATCH 2000). Compared to other LAKEWATCH water bodies, chlorophyll concentrations in the Kings Bay–Crystal River system were low relative to total phosphorus concentrations (Brown et al. 2000). In contrast, chlorophyll concentrations were near the predicted maximum given the observed total nitrogen concentrations. In Crystal River, both nitrogen and phosphorus limited phytoplankton growth in nutrient bioassays, with the frequency of nitrogen limitation being relatively high compared to other spring-fed, coastal rivers (Frazer et al. 2002). Thus, changes in nutrient concentrations, especially nitrogen, may influence phytoplankton abundance, which, in turn, influences water clarity in Kings Bay–Crystal River system. Dissolved, inorganic nitrogen concentrations in Kings Bay typically have been low relative to the Weeki Wachee,

Chassahowitzka and Homosassa systems (Frazer et al. 2001a). However, ongoing monitoring by the Southwest Florida Water Management District indicates that nitrogen concentrations have increased recently. These increases were predicted by Jones and Upchurch (1994) who stated, "The many nitrogen releases resulting from land uses that exist in the [Kings Bay] study area are elevating ground-water nitrogen concentrations. Ground water that has been enriched in nitrogen from both development-related and natural sources [Tsala Apopka Lake chain] is moving toward the coast in well-defined plumes from the east-central and north-central portions of the study area. Within 20 years this nitrogen will reach the King's Bay Springs and probably increase nitrogen concentrations significantly."

Flushing can remove phytoplankton before standing crops reach levels limited by nutrient concentrations (Swanson and Bachmann 1976). Chlorophyll bioassays using samples from 20 Florida rivers suggested that chlorophyll concentrations can approach levels limited by nutrients within 3-7 days (Canfield and Hoyer 1988). Other controlled bioassays using samples from Kings Bay suggested that maximum chlorophyll concentrations are reached in 2 to 3 days (Frazer et al. 2002). Flushing rates vary with spring discharge, rainfall and tides, with tides adding an oscillatory component to spring discharge that is the dominant flushing force in Kings Bay because it supplies approximately 90% of the freshwater and (Hammett et al. 1996). A model calibrated with data collected during a period of low rainfall and spring discharge estimated at 735 cfs predicted that water in Kings Bay was replaced in 2-4 days (Hammett et al. 1996). This estimated discharge was about 25% less than a previously calculated long-term average of 975 cfs (Yobbi and Knochenmus 1989), which would have generated faster flushing. Nevertheless, recent periods of low rainfall and apparent decreases in spring discharge, as suggested by increases in salinity and an estimated median daily discharge of 490 cfs for August 2002 through October 2011 (http://waterdata.usgs.gov/usa/nwis/uv?site no=02310747), may mean the flushing rate is at or above 4 days. Overall, flushing rates appear to be low enough for chlorophyll concentrations to reach levels where nutrients become limiting, which will decrease water clarity (Hoyer et al. 2001).

Analysis of data from 1993–1994, 1996–1997 and 1997–2000 indicated that chlorophyll concentrations decreased as aquatic plant biomass increased (Terrell and Canfield 1996; Hoyer et al. 1997; Hoyer et al. 2001). Aquatic plant biomass accounted for 11% of the variance in chlorophyll concentrations suggesting that nutrients and other factors also affected phytoplankton production in this system (Hoyer et al. 2001). A similar inverse relationship was found in a study of two macrophyte dominated lakes in central Florida (Lamb 2000). Several mechanisms can contribute to the inverse relationship between biomass of benthic plants and chlorophyll concentrations in the water column: (1) aquatic plants and their associated epiphytic algae compete for nutrients that might otherwise be assimilated by phytoplankton, (2) aquatic plants dampen wave energy and cause phytoplankton to settle, and (3) aquatic plants stabilize sediments and lessen the likelihood of resuspension of benthic microalgae (Hoyer et al. 2001). Two of these mechanisms involve wind, which suggests that wind speed could be a factor determining water clarity in Kings Bay–Crystal River system.

Average daily wind speed at the mouth of Crystal River was related positively to concentrations of chlorophyll and total suspended solids in the water of Kings Bay and Crystal River (Hoyer et al. 1997). Given water depths and fetch in Kings Bay, very few wind events would create waves capable of resuspending bottom sediments in the bulk of Kings Bay; therefore, increases in chlorophyll and suspended solids most likely arise from previously settled algae, previously settled detritus, or periphyton being dislodged from the surfaces of aquatic vegetation (Bachmann et al. 2001; Hoyer et al. 2001). A positive relationship between wind and concentrations of chlorophyll and suspended solids also was found in a study of two macrophyte dominated lakes in central Florida (Lamb 2000). Additional periphyton and detritus can be dislodged by power boats, swimmers, divers and foraging manatees.

Effects of high salinity

Salinity represents a primary determinant of long-term patterns in the abundance and distribution of plants in spring-fed rivers along Florida's Gulf coast (Hoyer et al. 2004). For example, in Crystal River, both Hydrilla verticillata and Myriophyllum spicatum were present at the head of the river near Kings Bay, but H. verticillata disappeared in the lower river and M. spicatum became dominant, with evidence from laboratory experiments pointing to salinity tolerance as the likely cause of these distributions (Haller et al. 1974). Survival of H. verticillata was decreased in salinities as low as 7% in a study using static conditions for 4 weeks, whereas, M. spicatum tolerated 13\% and died when exposed to 17\% (Haller et al. 1974). Growth of Vallisneria americana was suppressed by salinities as low as 7% and mortality was observed at 13% in a study using static conditions for 4 weeks (Haller et al. 1974). In experiments with plants from Kings Bay, H. verticillata was particularly sensitive because all plants died following 1-d exposures to 15% (Table 1; Frazer et al. 2006a). In contrast, V. americana and M. spicatum survived 1-d and 2-d exposures to 15‰, but 25–100% of these plants died following 7-d exposures to 15‰ or any exposure to 25‰ (Table 1; Frazer et al. 2006a). In addition, V. americana exposed to salinities $\geq 15\%$ exhibited less blade elongation, added fewer blades, generated fewer clones, and produced less aboveground and belowground biomass (Frazer et al. 2006a). Overall these results lead to a prediction that this species would be stressed, but able to tolerate rapid, short-lived (< 2 d) pulses of high salinity water. Similar tolerances were observed in studies done elsewhere. For example, results of multiple studies of V. americana were summarized, with extreme stress reported from 1 d exposure to 18‰ and essentially no evidence of stress from exposures to 10‰ over 128 d (Figure 6; Dobberfuhl et al. 2012; Jacoby 2012). Growth of V. americana was not affected by salinities up to 12-15‰, and mortality was recorded at 18% only in longer exposures (Twilley and Barko 1990; Doering et al. 1999, 2001; Kraemer et al. 1999). Field observations also suggested that M. spicatum can withstand salinities up to 15‰, with growth reduced at 16‰ (Twilley and Barko 1990; McGahee and Davis 1971).

Table 1. Percent mortality of *Vallisneria americana*, *Hydrilla verticillata* and *Myriophyllum spicatum* after exposures to different salinities and a 28-d recovery period (Frazer et al. 2006a).

Salinity	Vallisneria			Hydrilla			Myriophyllum			
	1 d	2 d	7 d	1 d	2 d	7 d	1 d	2 d	7 d	
Control	0	0	0	0	0	0	0	0	0	
5‰	0	0	0	0	0	0	0	0	0	
15‰	0	0	75	100	100	100	0	0	50	
25‰	100	100	100	100	100	100	100	100	100	

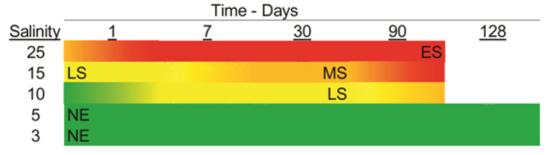


Figure 6. Impacts of salinity on *Vallisneria americana* (Jacoby 2012). ES = extreme stress; MS = moderate stress; LS = low stress; NE = no effect

Experimental observations appeared to translate to real-world events. The Kings Bay-Crystal River system is tidally influenced, flow reversals are common and they reach the manmade canals (Mann and Cherry 1969; Yobbi and Knochenmus 1989; Hammet et al. 1996; Frazer et al. 2001b). In response to typical tidal oscillations, water in Kings Bay stages up and down less than 1.2 m (Hammett et al. 1996). In contrast, Hurricane Donna in 1964 generated a stage of 1.5 m above mean sea level, which demonstrates that large amounts of saline water can be forced up the river and into Kings Bay by storms and high winds (Mann and Cherry 1969). Based on such phenomena, a series of studies related noticeable decreases in vegetation in Kings Bay to the "Storm of the Century" in 1993, Hurricane Elena in 1985, and Tropical Storm Josephine in 1996 (Bishop 1995; Terrell and Canfield 1996; Mataraza et al. 1999; Hoyer et al. 2001). These early attempts to link changes in vegetation to storm surges remained speculative because measurements of salinity were not available.

Salinity was measured at two locations in Kings Bay in 1999–2001 and 2004, with the results clearly capturing pulses of salinity that influenced the vegetation in Kings Bay (Figure 7; Frazer et al. 2001b; Frazer et al. 2006a; Jacoby et al. 2007). Hurricanes Frances, Ivan and Jeanne forced dense, saline water into the bay, and the shallow sill near the mouth of the bay acted as a natural barrier to its exit. In the bay's interior, salinities near the bottom remained elevated for more than 2 d following each storm, with a gradual decrease attributed primarily to dilution by groundwater discharging from springs. Aboveground biomass and percent cover of vascular plants were reduced after the series of hurricanes. *Myriophyllum spicatum* exhibited an 83% decrease in aboveground biomass and an 80% decrease in percent cover. *Hydrilla verticillata* exhibited 47% and 15% declines in biomass and percent cover, respectively. *Vallisneria americana* exhibited an 18% increase in aboveground biomass and a 37% increase in percent cover, which suggests greater tolerance of salinity pulses and release from competition with the invasive *H. verticillata* and *M. spicatum* as has been suggested by field observations and laboratory experiments (Lind and Cottam 1969; McFarland and Rogers 1998; Van et al. 1999; Rybicki and Carter 2002; Hauxwell et al. 2003).

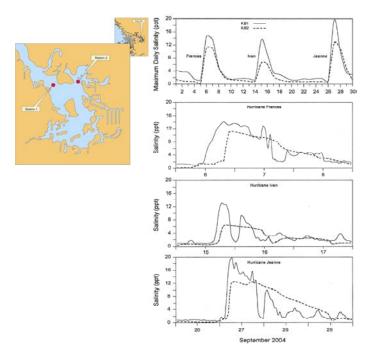


Figure 7. Locations of sondes recording salinity data and values recorded during hurricanes Frances, Ivan, and Jeanne (Frazer et al. 2001b). Station 1 = KB1; Station 2 = KB2

More subtle variations in salinity, which arise when weather patterns alter rainfall, groundwater supply and spring discharge, also affect the ecology of this system. For example, ten species of submersed aquatic plants were found in the Kings Bay-Crystal River between July 1999 and July 2000, with over 98% of the quadrats containing some vegetation (Hoyer et al. 2001). During this time, Myriophyllum spicatum, Hydrilla verticillata, Lyngbya sp., and Vallisneria americana occurred in 90, 85, 64, and 59% of the quadrats, respectively. Locations with higher mean specific conductances yielded more M. spicatum and V. americana than H. verticillata or Lyngbya sp. Thus, elevated salinities may favor the expansion of M. spicatum and V. americana. In addition, multivariate ordinations of quarterly data collected in 2004-2006 indicated that 71 stations fell into three groups distinguished by patterns in the percentage cover and biomass of vegetation (Figure 8; Jacoby et al. 2007). Vegetation comprised filamentous algae; non-native H. verticillata and M. spicatum; and native Chara spp., Ceratophyllum demersum, Najas guadalupensis, Potamogeton pectinatus, Potamogeton pusillus, Ruppia maritima, Vallisneria americana, and Zannichellia palustris. Analyses based on percentage cover and biomass separated 63 stations into a group of 35 stations and a group of 28 stations, with the remaining 8 stations alternating between these groups depending on whether percentage cover or biomass data were analyzed. Submersed aquatic vegetation of some type was found in approximately 90% of the quadrats sampled at 71 stations over 3 years, but quadrats from stations in the group of 35 contained native plants and algae about 1.6 times as often and non-native plants and algae about 1.2 times as often as quadrats from stations in the group of 28. In contrast, quadrats from stations in the group of 28 contained filamentous algae about 2.0 times as often as quadrats from stations in the group of 35. Multivariate ordinations of water quality data indicated that the spatial patterns in vegetation within Kings Bay were most strongly related to variation in freshwater inputs from springs located primarily among the 28 stations with large quantities of filamentous algae (Figure 8). Near springs, horizontal Secchi readings and concentrations of nitrate and nitrite were higher, whereas conductivities were lower. Analyses based on available data did not indicate a relationship to sediments (Belanger et al. 2005; Jacoby et al. 2007).

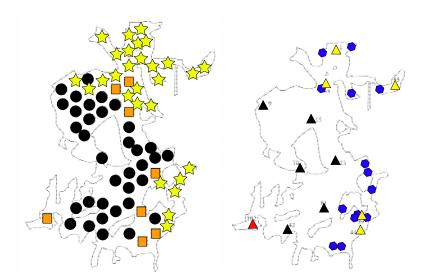


Figure 8. Groups of stations derived from multivariate ordinations of percentage cover and biomass data for 11 types of vegetation (left-hand map) and water quality data (right-hand map). Black circles = group of 35 stations; Yellow stars = group of 28 stations; Orange boxes = group of 8 stations; Blue hexagons = springs; Triangles = water quality sites, with sites marked by yellow triangles having longer horizontal Secchi readings, higher nitrate and nitrite concentrations and lower conductivities than sites marked by black triangles and the site marked by a red triangle being very shallow, surrounded by marshes and characterized by lower temperatures and higher color readings

Responses to grazing

The 2004–2006 surveys of vegetation in Kings Bay also identified a repeated temporal pattern in percentage cover and biomass (Figure 9; Jacoby et al. 2007). In February of all years, percentage cover and biomass decreased at the stations with less filamentous algae, with those decreases corresponding to times when large numbers of manatees sought refuge and food in the bay. Stations characterized by filamentous algae exhibited less of a response, suggesting that manatees primarily feed on other plants and algae.

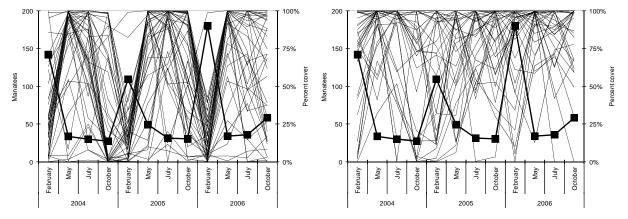


Figure 9. Mean percentage cover for total submersed aquatic vegetation for stations in Kings Bay without (left-hand graph) and with (right-hand graph) large amounts of filamentous algae, along with mean numbers of manatees observed in the bay. Black lines without symbols = percentage cover; Black lines with boxes = numbers of manatees

The effects of manatee grazing were examined directly in an experiment assessing the feasibility of large-scale restoration of Vallisneria americana in Kings Bay (Hauxwell et al. 2003, 2004a and b). To determine the effects of herbivores and other primary producers on V. americana transplants, a 2 × 2 factorial experiment was conducted in Cedar Cove, south of Buzzards Island and north of Parkers Island (Figure 10). At each site, 1.5×1.5 m plots of transplanted V. americana were either subjected to or protected from grazing by relatively large herbivores (e.g., manatees, turtles, waterfowl and large fishes) and the presence of other primary producers (e.g., Myriophyllum spicatum, Hydrilla verticillata and filamentous algae that included Lyngbya sp.). Plants not protected by cages were consumed by manatees, with 80% of the V. americana removed in one month (Figure 11). Densities of Vallisneria americana were reduced by 0-50% in plots that included other plants, with the strongest effects at Buzzard Island and Parker Island where more M. spicatum was present. Established V. americana grew even though M. spicatum was present, so competition for space was more likely than competition for light. Given the abundance of manatees in 2003, their energetic requirements, and the productivity of V. americana, it was estimated that 18,400,000 shoots would be required to meet the needs of the existing population. Extant V. americana beds contained approximately 730,000 shoots or only 4% of the required standing crop. Therefore, approximately 18 million shoots would need to be transplanted to Kings Bay if the goal was to create a self-sustaining population that could cope with existing grazing pressure. Based on an average dry mass of 1 g and an average density of 200 shoots m⁻², successful restoration would require planting 90,000 m² or 22.2 acres of V. americana.

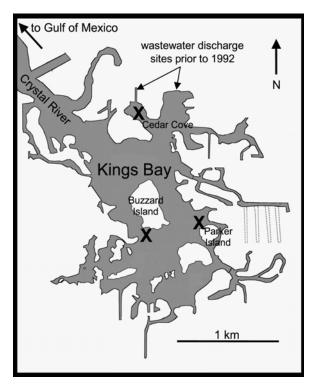


Figure 10. Locations of plots containing transplanted *Vallisneria americana* (Hauxwell et al. 2003, 2004a).

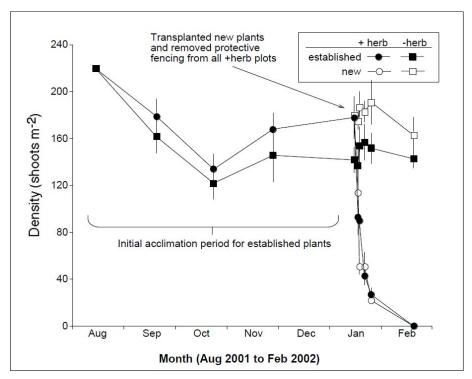


Figure 11. Mean densities of transplanted *Vallisneria americana* shoots \pm standard errors (n = 3) in plots in Kings Bay (Hauxwell et al. 2003, 2004b). + herb = manatees allowed access; - herb = manatees excluded by cages

In summary, anecdotal accounts describe *Vallisneria americana* as the dominant species of submersed aquatic vegetation in Kings Bay, but this native macrophyte is now restricted to limited, patchy meadows (Jacoby et al. 2007). Decreased water clarity and light availability, stress from storm-induced salinity events, grazing by herbivores, and competitive exclusion by macroalgae and non-indigenous macrophytes probably all contributed to the displacement of this native macrophyte (Haller and Sutton 1975; Bowes et al. 1977; Barko et al. 1991; Blanch et al. 1998; Hauxwell et al. 2004a).

THE FUTURE OF SUBMERSED AQUATIC VEGETATION IN THE KINGS BAY-CRYSTAL RIVER SYSTEM

Based on available evidence, flows in the Kings Bay-Crystal River system will interact with multiple aspects of the ecology of submersed aquatic vegetation. Lower flows will increase residence times, which promotes the accumulation of phytoplankton biomass that can lead to reduced light penetration and stress on vegetation, including *Vallisneria americana*. Lower flows also will increase salinities, which will decrease competition between *V. americana* and other less tolerant vegetation potentially leading to an expansion of this desirable macrophyte.

Ultimately, establishing a balanced and self-sustaining assemblage of submersed aquatic vegetation in the Kings Bay–Crystal River system will require ongoing management that maintains suitable, background environmental conditions, including appropriate residence times, concentrations of nutrients, concentrations of suspended particles, and sediment conditions. Success also may require more drastic, short-term interventions to remove the legacy of past events and reset the system, e.g., sediment removal and the transplanting of *Vallisneria americana* or other native macrophytes. In all cases, the efficiency and effectiveness of management actions will be improved by science that evaluates options; guides implementation, including scaling from pilot studies; and assesses success to inform adaptation.

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