Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake

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Abstract

In Lake Okeechobee (Florida), above average water depths from 1994 to early 2000 created poor light conditions on the lake bottom, leading to a widespread loss of submerged aquatic vegetation. In 2000, a controlled laboratory study quantified seedling emergence of *Vallisneria americana* ($80 \pm 20 \, \text{m}^{-2}$; mean $\pm$ S.E.) and emergence of *Chara* spp. ($504 \pm 21 \, \text{m}^{-2}$; mean $\pm$ S.E.) from sediments collected at a variety of sites confirming that a viable seed bank had persisted through years of poor light conditions. Considerable variance existed among the five sites from which seed banks were collected. Other species of submerged vegetation were hardly encountered. Additionally, a field transplant study using young *V. americana* plants examined the survival potential of *V. americana* in regions that had not supported submerged vegetation in the recent past. Although all transplants lost biomass, they produced new shoots and stolons in both sediment types. Transplants fared better in peat sediments than in the sandy sediments characteristic of areas where submerged vegetation was lost in the recent past.

In summer 2001, an extensive drought exposed thousands of hectares of near-shore lake bottom, killing much of the submerged vegetation community. The potential for recovery of submerged vegetation from a desiccated and re-inundated seed/oospore bank was examined with cores taken from areas that had previously supported submerged vegetation. Extensive emergence of *Chara* spp., including a faster rate of emergence and a greater magnitude of emergence observed in desiccated cores (mean from three sites: $2728 \, \text{m}^{-2}$; 1S.E.: ± 192) relative to cores still inundated (mean from one site: $918 \, \text{m}^{-2}$; 1S.E.: ± 165), suggests that the drought may have led to an increased germination response for *Chara*. In contrast, there was little germination

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of vascular species, except for a few seedlings of the native *V. americana* and a few plants of *Hydrilla verticillata*.

1. Introduction

Recovery of aquatic vegetation after a disturbance occurs by several mechanisms: vegetative growth (e.g. re-growth from belowground root and rhizomes, Madsen and Smith, 1999; the presence of a tuber bank); dispersal and establishment by propagules, e.g. Madsen and Smith, 1997; Madsen and Smith, 1999; Rybicki et al., 2001); or recruitment from a seed/oospore bank (hereafter referred to simply as a seed bank) (e.g. McFarland and Rogers, 1998). While emergent marsh or wetland plant communities often tolerate periodic disturbances (e.g. Mitsch and Gosselink, 1986; Williges and Harris, 1995; Wu et al., 1997; Busch et al., 1998), submerged aquatic vegetation can be significantly damaged by extreme high water events (Havens et al., 2001), or by low water (i.e. desiccation) events such as droughts or lake drawdowns (Haller and Shireman, 1984) which expose the bottom sediment. As these types of disturbances in submerged vegetation communities can limit the ability of clonal growth to contribute to population recovery, the primary mechanism for natural recovery may be through tubers or the seed bank.

Lake Okeechobee (in southern Florida, USA) is a shallow lake managed for flood control and agricultural and urban water supply, as well as for providing fish and wildlife habitat and water supply for environmental restoration (Aumen, 1995). This subtropical lake has an average depth of 2.7 m, with a littoral zone and near-shore region (shallower than 2 m depth) encompassing 600 km^2. A decade ago, there were thousands of hectares of submerged vegetation in Lake Okeechobee (Richardson and Harris, 1995; Zimba et al., 1995); common taxa included *Vallisneria americana* Michx., *Potamogeton illinoensis* Morong, *Hydrilla verticillata* (L.F.) Royle, *Najas guadalupensis* Morong, *Utricularia* spp., and the macroalgae *Chara* spp. Because the ecosystem is subtropical, native vascular plants typically do not form tubers. Therefore, the seed bank is considered the primary source for population recovery in exposed areas.

Over the past decade, there have been multiple years of high water (Havens et al., 2001), where turbid waters from the center of the lake move into the near-shore areas of Lake Okeechobee (Havens and James, 1999). Chronic effects of deep water and poor light availability during the late 1990s resulted in very sparse submerged vegetation in the lake (Havens et al., 2001). Additionally, for the past 30 years, Lake Okeechobee has experienced significant droughts on a nearly decadal time scale (Havens et al., 2001). The three most recent droughts (1981, 1989–1990, and 2001) exposed near-shore lake bottom in areas supporting submerged vegetation.

In spring 2000 (April), the South Florida Water Management District initiated a managed lake drawdown, to reduce water levels and allow native submerged vegetation to become re-established (Steinman et al., 2002). Steinman et al. (2002) reported an increase in light levels on near-shore lake bottom (pre-drawdown mean: ∼75 μmol photons m^{-2} s^{-1},

post-drawdown mean: $\sim$450 μmol photons m^{-2} s^{-1}). However, there was a delay in sub-merged vegetation response (Havens et al., 2001). Prior to observing submerged vegetation recovery in the lake, we initiated studies to examine: (1) the potential recovery of submerged vegetation from the seed bank (a laboratory study); and (2) submerged vegetation habitat suitability using *V. americana* transplants (a field study).

In summer 2001 (May–July), an historic drought exposed the majority of the submerged vegetation (and their respective seed banks) in the lake that had returned after the spring 2000 lake drawdown. Lake levels dropped exposing approximately 115 km^2 more lake bottom than was exposed during the previous significant drought (1989–1990). The viability and germination potential of submerged vegetation seeds can be negatively impacted by desicca-tion (Muenscher, 1936a,b; Forsberg, 1965). A literature survey of the maximum percent ger-mination of aquatic plant seeds of genera that are represented in Lake Okeechobee revealed that, in general, there is a lower percentage of successful germination of seeds that were desiccated relative to seeds that were held in water (Fig. 1). Given this, the viability of the submerged vegetation seed bank in the near-shore regions of the lake was examined prior to re-flooding as the drought came to an end. Desiccated cores collected from several regions of the lake that had well-developed submerged vegetation populations prior to the drought were re-inundated in an environmental chamber experiment. Submerged vegetation emergence was compared between sediment cores taken in an exposed area and cores taken from an in-undated area within one region of the lake. The overall objectives of this exercise were: (1) to
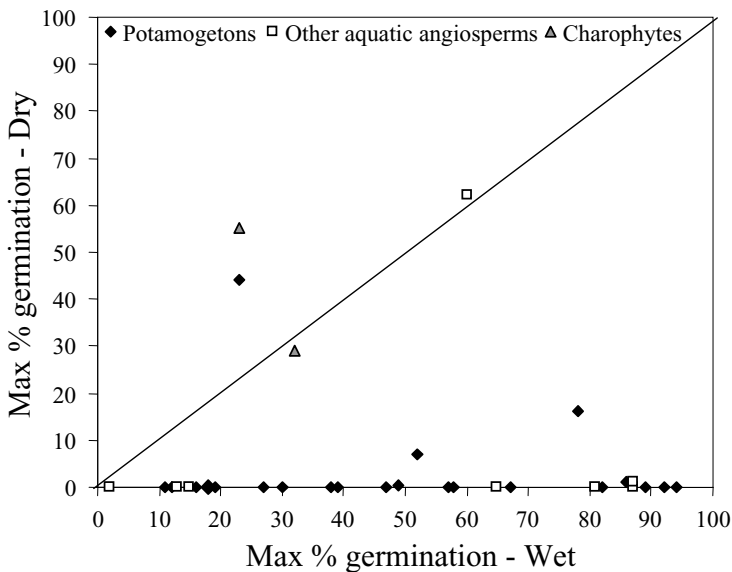

Fig. 1. Published estimates of maximum seed germination percentage of Potamogetons, other genera of submerged aquatic angiosperms found in Lake Okeechobee, and Charophytes, under dry and wet conditions from a variety of locations. Data from: Bonis and Lepart (1994); Bonis et al. (1995); Forsberg (1965); Guppy (1897); Muenscher (1936a,b); Van Wijk (1989).

determine to what extent the submerged vegetation seed bank in Lake Okeechobee remained viable after desiccation, and (2) to determine if submerged vegetation emergence after desiccation and re-inundation is species specific, site/substrate specific, or general to the entire community.

2. Methods

2.1. Emergence study—2000

In summer 2000 (July), sediment cores were taken from five sites around Lake Okeechobee: South Bay (26°43′25″N, 80°44′48″W), East Ritta (26°42′37″N, 80°47′23″W), 3-Pole Bay (26°44′19″N, 80°50′24″W), Turner's Cove (26°51′37″N, 80°57′15″W), King's Bar (27°16′12″N, 80°49′14″W). Two sites had extant vascular plants (South Bay [78 cm deep]: *V. americana*, *P. illinoensis*; East Ritta [78 cm deep]: *P. illinoensis*), while the other sites (3-Pole Bay [100 cm deep], Turner's Cove [55 cm deep], and King's Bar [49 cm deep]) had vascular submerged vegetation in the recent past (no taxa information available) but not at the time of sampling. All sites had *Chara* except King's Bar. South Bay, East Ritta, and 3-Pole Bay had peat sediments. Turner's Cove and King's Bar had sand sediments. As the peat sediments at three of our sites made it logistically impossible to sieve out seeds/oospores, we examined aquatic vegetation recovery using the emergence method (e.g. Haag, 1983; Kautsky, 1990; Boedeltje et al., 2002) rather than examining germination percentages of a known number of seeds/oospores.

At each site, six 10.2 cm diameter (81.7 cm^2) cores were taken (to ∼5 cm depth) with a PVC corer. Cores were transferred intact (to minimize manipulation artifacts) into 0.71 l plastic containers, capped, and carefully returned to the lab inside an insulated ice chest. To examine if seed bank disturbance enhances seedling emergence, six additional sediment cores were collected from each site and placed into a plastic pan (∼750 cm^2), where the sediment was mixed (exposed to air) and spread out, yielding a sediment depth of ∼2 cm. After covering the sediment with water, the pan from each site was enclosed in a plastic bag, placed in an insulated ice chest, and transported back to the lab.

To eliminate turbidity due to transporting cores from the field, the overlying water in each core was carefully suctioned out by syringe and replaced with filtered lake water (using a 3 μm fiber bag filter) to reach a level of ∼5 cm above the sediment surface. Any observed *Chara* was gently removed with forceps. The outside of each container was wrapped in double-layered aluminum foil to prevent light from reaching the core from the sides/bottom and each container was covered by plastic wrap (perforated with small holes to allow for gas exchange) to minimize evaporation. Similarly, the water in the five individual pans of mixed sediment was replaced, and covered with perforated plastic wrap.

Two light levels were chosen for this experiment (using fluorescent tubes) and reflected light data from the near-shore region (<1.5 m depth) of Lake Okeechobee before (∼100 μmol photons m^{-2} s^{-1}) and after (∼500 μmol photons m^{-2} s^{-1}) the recession (Steinman et al., 2002). Environmental chambers were set at a 14:10 L:D photoperiod and overlying water

was maintained at 30 °C (±3 °C), similar to field conditions of the subtropical Florida summer (Steinman et al., 2002).

Three cores from each sampling site were each placed in low- and high-light environmental chambers. Cores were randomly re-allocated within each environmental chamber two to three times per week to ensure uniform light exposure over time. All of the shallow pans with mixed sediments were placed in the low-light incubator and were rotated similarly. When necessary, water that had evaporated was replaced with de-ozonated, de-ionized water. The plastic wrap covering was cleaned or replaced weekly to prevent excess algal/bacterial growth that could alter light levels reaching a given core.

Vascular plant seedling and *Chara* emergence was enumerated weekly for 8 weeks (except after week 1) when terminated after no further emergence was observed for several weeks and after conditions of seedlings deteriorated.

Two-way analysis of variance (ANOVA) was used to test for significant effects of collection site (five levels), light (two levels), and interaction effects on (a) cumulative *V. americana* seedling emergence (natural-log $[x + 0.5]$ transformed; Krebs, 1989), and (b) cumulative *Chara* emergence (square-root $[x + 0.5]$ transformed; Krebs, 1989) in the undisturbed cores. When significant differences were found for a given factor (there were no interaction effects), Tukey's test were run to examine differences among treatment levels.

At the end of August 2000, the presence of vascular plant seedlings at each collection site was evaluated via 12 random ring ($81.7 \, cm^2$) tosses. At each site, ring tosses were made at the same water depth as where the seed bank cores had been collected. *Chara* presence or absence was reported for each site; however, abundance data was not calculated.

2.2. Transplant study—2000

To examine habitat suitability for submerged vegetation following multiple years of high water, we did a post-drawdown (mid-August 2000) transplant study with *V. americana* (at the same sites of the seedling emergence study). As *V. americana* was beginning to recover in the lake, young plants (rosette diameter ~3 cm) were used. Donor plants from South Bay were harvested by hand and stored in an insulated ice chest (in lake water) until return to the lab. The same day, plants were hand sorted into individual rosettes, and randomly assigned plants were tied to transplant frames using standard garden ties. Transplant frames were made of 50 cm × 36 cm (1/2 in.) PVC rectangles with five rows of waxed twine (spaced 8–10 cm apart) and two bare-rooted plants tied to each row ($n = 10$ total). Frames with plants were stored overnight in a sink of Lake Okeechobee water collected from the donor site. The following morning, frames with plants were transported to the lake in ice chests (containing lake water) and planted.

Six randomly selected frames were deployed (a total of 60 retrievable plants per site) at each transplant site and the donor site. Frames were placed several meters apart, and were anchored on diagonal corners by short sections of galvanized conduit pipe. After 2, 4, and 9 weeks, two frames from each site (containing up to 10 retrievable plants per frame) were collected. Each frame of plants was considered an experimental unit, as there was variability in number of plants recovered within a given frame (range 0–10). Thus, for each sampling date and location, biomass and morphometric characteristics were averaged for a total of up to 10 plants per quadrat, with two replicates per site.

During initial collection of transplant material, 20 additional plants (two groups of 10) were analyzed to determine initial biomass for comparison with transplant data.

Two-way ANOVAs (site: five levels; week: three levels; site × week interaction) were run for plant survival and biomass. When significant differences were found (there was no interaction effect) Tukey's tests were run to examine differences among treatments. Additionally, we evaluated the proportion of plants remaining (within each time period) that produced new stolons/shoots for each transplant site.

2.3. Emergence study—2001

In summer 2001 (July), sediment cores were taken from several areas in the near-shore region of Lake Okeechobee. Two adjacent sites (separated by <100 m) in the western part of the lake (sand bottom) were sampled to examine submerged vegetation germination differences between an exposed (desiccated) site (Cochran's Pass—dry) and an inundated site that had not dried out (Cochran's Pass—wet; both sites at approximately 26°53′52″N, 80°57′54″W). This region supported submerged vegetation (*Chara* and *V. americana*, Havens et al., 2002; *N. guadalupensis*, personal observation) in the recent past. Additionally, two sites in the southern part of the lake (South Bay, 26°44′01″N, 80°44′39″W; Kreamer Island, 26°43′05″N, 80°46′02″W) were sampled to examine the variability in submerged vegetation germination in exposed peat sediments. Both peat sites supported submerged vegetation the previous year (both sites: *Chara*, *Potamogeton*; Kreamer Island: *V. americana*, *H. verticillata*; Havens et al., 2002). The shallow slope of the lake bottom, coupled with the extent of the drought, prevented the inclusion of an inundated peat site that had supported submerged vegetation in the recent past. As with the 2000 study, the emergence method was used because of the inability to adequately sieve the peat sediments to examine a known number of seeds/oospores.

In order to minimize the influence of the inherent spatial variability of seed banks (Baskin and Baskin, 1998), a total of 16 cores (7.6 cm diameter, 10 cm long, schedule 40 PVC) were randomly collected (over an area $\sim$100 m^2) at each site. Cores were harvested, capped, and transported intact back to the laboratory in covered ice chests. Carboys of Lake Okeechobee water were collected for use in the incubation.

In the laboratory, cores were placed inside 2.8 l polyethylene containers (approximately 15 cm deep) and then filled with Lake Okeechobee water filtered through a 3 μm fiber bag filter. Incubation temperature, photoperiod, core re-distribution, and water level maintenance were as in the 2000 seed bank study. Light levels in the environmental chamber (ca. 250–350 μmol photons m^{-2} s^{-1}; 14:10 L:D) reflected typical irradiance levels observed in the field (Steinman et al., 2002). Submerged vegetation emergence was examined by enumerating sprigs of *Chara* and seedlings of vascular plants on a weekly basis over a period of 8 weeks.

Two-way repeated measures ANOVA was run separately for cores from the peat and sand sites. Each analysis examined differences between sites of a given sediment type (sand or peat) as a function of *Chara* emergence over time (time = 8, n = 16). For the peat sites, differences between sites, and among weeks, were examined with Tukey's multiple comparisons tests. A significant interaction term was present for the analysis of the sand sites, thus each of the sand sites were analyzed separately with a one-way

repeated measures ANOVA, using Tukey's multiple comparisons tests to examine differences among weeks for a given site. To examine differences between sand sites for a given week, individual *t*-tests were conducted. Since very low numbers of vascular plants germinated, repeated measures analyses were not performed on seedling emergence of vascular plants.

3. Results

3.1. Emergence study—2000

At the end of the 2000 emergence study, *V. americana* was found in 10 of 30 undisturbed cores, including those from South Bay, East Ritta, Turner's Cove, and King's Bar (Table 1; Fig. 2a). Seedling emergence lasted from 4 to 6 weeks. *Chara* emerged in 23 of 30 cores from all five sites (Table 1; Fig. 2b). One *H. verticillata* plant was found in one core from South Bay. Additionally, a single seedling of *N. guadalupensis* was found in two cores from King's Bar.

Few emerging plants were observed in the disturbed sediment. Only *Chara* emergence was observed in the pan of mixed sediments from Turner's Cove. One *H. verticillata* plant was observed in the pan from South Bay.

There were no significant differences between light levels or among sites in the number of *V. americana* seedlings observed at the end of the incubation (two-way ANOVA; all $P > 0.17$; Fig. 2a). Although there was no statistical difference between light levels at Turner's Cove, there may be a biological difference between light levels as there were zero seedlings found in the three cores incubated in low-light versus a wide range in number of seedlings found in the three cores incubated in high light.

There were no significant differences in *Chara* emergence between low- and high-light treatments (two-way ANOVA; $F = 0.06$, $P = 0.80$; Fig. 2b) regardless of site. However,

Table 1
Presence/absence of *Vallisneria americana* seedlings and *Chara* sporelings for five sites in Lake Okeechobee in 2000

	South Bay		East Ritta		3-Pole Bay		Turner's Cove		King's Bar	
	Field	Lab.	Field	Lab.	Field	Lab.	Field	Lab.	Field	Lab.
Vallisneria[a]	+[b]	+	−	+	−	−	+[c]	+	−[d]	+
Chara[e]	NA	+	+	+	+	+	+	+	+	+

(+): Present; (−): absent; NA: no information available. Field: seedling presence in the field near the end of the 2000 seedling emergence study; Lab.: seedling response observed in the laboratory at the end of the 2000 seedling emergence study.

  [a] *Vallisneria* seedling numbers for incubation experiment given in Fig. 1.
  [b] *Vallisneria* seedlings were observed in the field, but not enumerated.
  [c] Seven *Vallisneria* seedlings were found in 12–81.7 cm^2 rings.
  [d] Seedlings were observed in the field later in the summer.
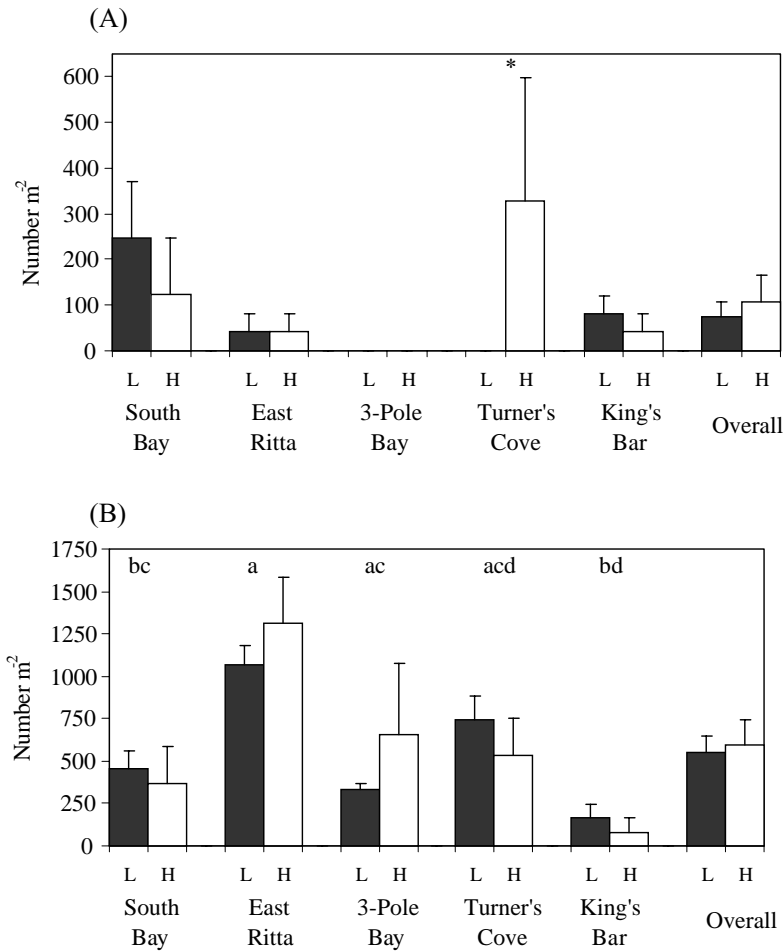 [e] Density of *Chara* in the field was not recorded.

Fig. 2. Average number (+1S.E.) of seedlings/sporelings from each site (and all sites combined [overall]) found in cores incubated under low (L)- and high (H)-light conditions (*n* = 3 for each bar) from the 2000 emergence study. (A) *Vallisneria americana* seedlings. An asterisk (*) at Turner's Cove indicates a potential biological difference between light treatments; however, there was no statistical difference found. (B) *Chara* sporelings. Different letters denote significant differences among sites; no light differences (Peat—SB: South Bay; ER: East Ritta; 3P: 3-Pole Bay. Sand—TC: Turner's Cove, KB: King's Bar).

there were significant differences in emergence among sites (two-way ANOVA; $F = 7.88$, $P < 0.001$, 59% of total variation). *Chara* emergence at East Ritta was significantly greater than at South Bay and King's Bar, while emergence at 3-Pole Bay was significantly greater than at King's Bar (Tukey's HSD; all $P < 0.05$).

Seedlings of *V. americana* were observed in the field at South Bay, Turner's Cove, and King's Bar, while no seedlings of *P. illinoensis* were observed. *Chara* was observed at all sites; no field records were made for *Chara* at South Bay.
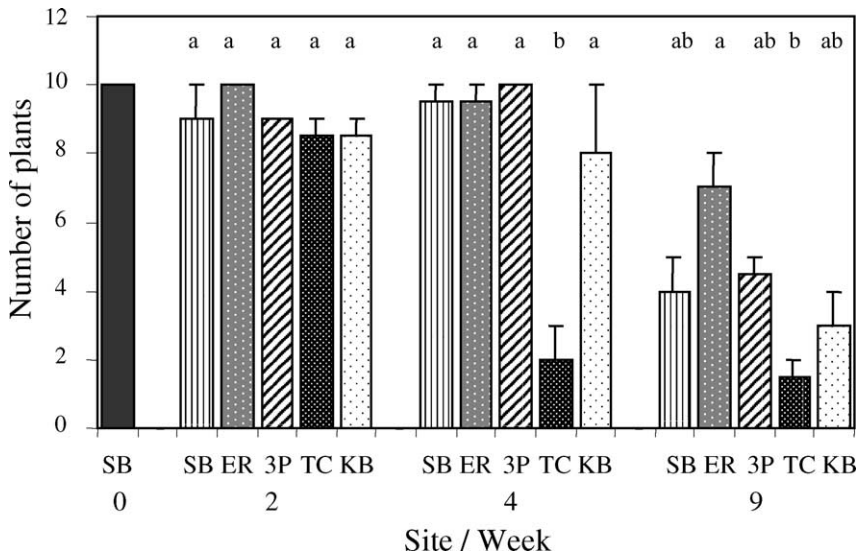
Fig. 3. *Vallisneria americana* transplant survival (mean + 1 S.E.) as a function of site and week. Different letters above bars represent significant differences among stations within a given week (Peat—SB: South Bay; ER: East Ritta; 3P: 3-Pole Bay. Sand—TC: Turner's Cove; KB: King's Bar).

3.2. Transplant study—2000

There were significant differences in *V. americana* plant survival over time ($F_{2,15} = 48.67$, $P < 0.0001$, 48% of total variation) and among sites ($F_{4,15} = 14.5$, $P < 0.0001$, 28% of total variation; Fig. 3). In general, there was no difference in survival between weeks 2 and 4, but a significant decline in survival (~50%) had occurred by week 9 (Fig. 3). By week 4, fewer plants survived at Turner's Cove than all other sites, but by week 9, survival of plants at Turner's Cove was only significantly lower than that at East Ritta (Fig. 3). A significant interaction effect ($F_{8,15} = 3.88$, $P = 0.01$, 15% of total variation) was driven exclusively by possible herbivory (from turtles) observed only at Turner's Cove between weeks 2 and 4).

There were significant differences in *V. americana* biomass over time ($F_{2,15} = 17.41$, $P = 0.001$, 36% of total variation) and among sites ($F_{4,15} = 10.1$, $P = 0.0004$, 42% of total variation; Fig. 4). Biomass decreased between weeks 2 and 4, but no difference in biomass was observed between weeks 4 and 9 (Fig. 4). By week 2, the lowest biomass was found at Turner's Cove; plants at Turner's Cove and King's Bar (sand sites) had the lowest biomass by week 4. By week 9, biomass at all sites was 50% of initial (Fig. 4).

Except for the herbivory event at Turner's Cove and week 9 plants at King's Bar, the percent of transplants producing new stolons for a given sampling period was greater at transplant sites than at the donor site (Table 2a). A similar pattern was observed for new shoot development, except that by week 9, only plants at 3-Pole Bay had a higher proportion of new shoot development than those at the donor site (Table 2b).
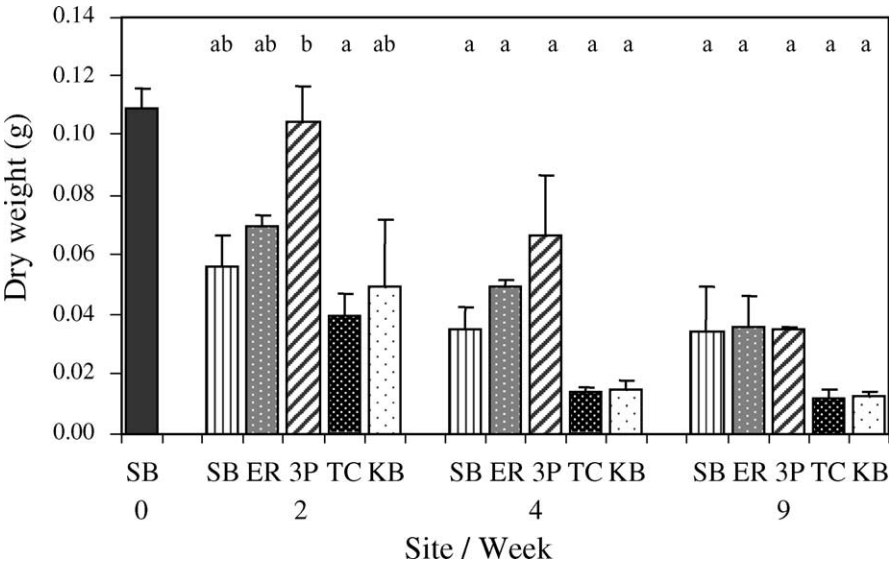
Fig. 4. *Vallisneria americana* biomass (mean + 1 S.E.). Different letters above bars represent significant differences among stations within a given week (Peat—SB: South Bay; ER: East Ritta, 3P: 3-Pole Bay. Sand—TC: Turner's Cove; KB: King's Bar).

3.3. Emergence study—2001

At the end of the 2001 emergence study, sprigs of *Chara* emerged in nearly every core, regardless of sediment type or desiccation/inundation status (mean = 15.5 out of 16 cores; S.E. = 0.25). At least one core from every site had *Chara* emerging after 1 week (Fig. 5). The total number of *Chara* sprigs in cores from all sites declined near the end of the

Table 2
Percentage (%) of *Vallisneria americana* transplants in Lake Okeechobee producing (A) new stolons or (B) new shoots, as a function of site and week during the 2000 field transplant experiment

Week	South Bay	East Ritta	3-Pole Bay	Turner's Cove	King's Bar
(A) Stolons					
2	25	**35**	**83**	**59**	**47**
4	11	**42**	**40**	0	**44**
9	50	**57**	**78**	33	17
(B) Shoots					
2	0	**15**	**61**	**35**	**6**
4	11	**11**	**35**	0	**25**
9	25	14	**56**	0	17

Proportion for each site at a given time was calculated using number of shoots recovered at that sampling time (*n* = 20 maximum). Instances where transplants produced the same or more stolons/shoots than transplants at the donor site (South Bay) are shown in bold.
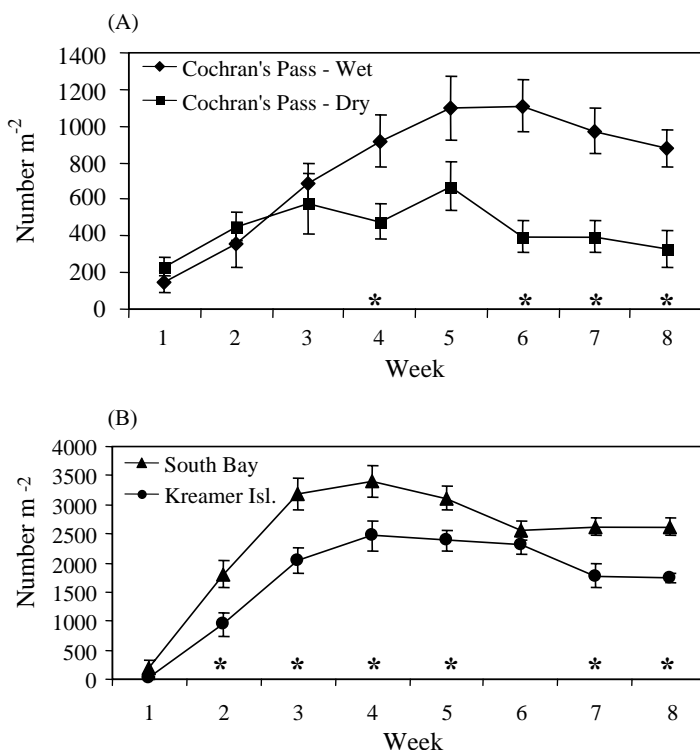
Fig. 5. *Chara* emergence over time: (A) at the sand sites (Cochran's Pass) comparing desiccated (dry) and inundated (wet) cores. (B) at the peat sites (South Bay, Kreamer Island; both desiccated) from the 2001 emergence study. For a given week, significant differences between sites (by *t*-test, $\alpha = 0.05$) are show by an asterisk (*), ($n = 16$; mean ± 1 S.E.).

incubation. *Chara* emergence was greater at the two previously desiccated peat sites than at the sand sites, regardless of inundation history (Fig. 5).

Site, week, and the interaction between site and week were statistically significant for *Chara* emergence (two-way ANOVA, $P < 0.001$ for each; all combined accounted for 31% of total variation). Among the sand sites, there was greater *Chara* emergence among desiccated cores than inundated cores after 4 weeks of incubation (*t*-test, $P = 0.015$; Fig. 5a), and for every subsequent week, except week 5 ($P < 0.05$ for all). Given no difference in *Chara* emergence between desiccated and inundated cores at week 1, there was a faster rate of emergence in cores from Cochran's Pass—dry (one-way repeated measures ANOVA, $P < 0.001$; Tukey results: weeks $1 < 2 < 3$) than at Cochran's Pass—wet (one-way repeated measures ANOVA; $F = 57.92$, $P = 0.013$; Tukey results: weeks $1 = 2 = 3$).

Among the sites with peat, the number of *Chara* sprigs was significantly greater overall at South Bay than at Kreamer Island (two-way repeated measures ANOVA, $P < 0.0001$, 9% of total variation; Fig. 5b). Over the first 3 weeks, *Chara* exhibited a continual increase

in emergence in peat sediments from both sites (Fig. 5); time accounted for almost 52% of total variation.

Only the cores from Kreamer Island had any germination of vascular submerged vegetation. Of 16 cores, *V. americana*, the dominant taxon in the lake, germinated in 10 of them (0.7 ± 0.7 seedlings per core). Three of the 16 cores from Kreamer Island produced *Hydrilla* (0.2 ± 0.9 seedlings per core); all three cores also contained *V. americana*. There was no emergence of other vascular submerged aquatics. Terrestrial and/or emergent aquatic vegetation was observed in cores from all three desiccated sites, but not from the inundated site. Taxa were not identified, but field observations in the western and southern ends of Lake Okeechobee during this period identified, among others, the presence of *Polygonum*, *Typha*, and *Panicum*.

4. Discussion

The successional state of submerged vegetation in Lake Okeechobee appears to be disturbance-mediated. Years of above average lake stages in the late 1990s almost eliminated submerged vegetation in Lake Okeechobee. Water transparency (i.e. lower TSS and chlorophyll *a*; Steinman et al., 2002) improved after the 2000 drawdown and a Secchi disk was always visible on the bottom of each site. Our 2000 emergence study predicted a rapid recovery of *Chara* from the oospore bank, with a longer recovery period of vascular aquatics led by germination of *V. americana*. Field transplants of *V. americana* showed new stolon and shoot production at all sites even though they lost biomass during the short experiment. By the end of summer, *Chara* was present at all experimental sites, whilst vascular aquatic plants were present at four of the five sites. Lake-wide, there was an overall increase in both vascular submerged aquatics (Havens et al., 2002) and *Chara* (Steinman et al., 2002) distribution and abundance.

The historic drought of 2001 desiccated approximately 70% of the lake bottom that supported submerged vegetation in 2000. Extensive emergent marsh and terrestrial vegetation (e.g. *Polygonum*, *Typha*, *Panicum*) colonized the exposed lake bottom, mirroring prior experimental research results (Williges and Harris, 1995), creating potential space/light limitation issues for initial recovery of submerged vegetation. The 2001 emergence study demonstrated a high recovery potential of *Chara* after re-wetting, and minimal response from vascular submerged aquatics. Desiccation of sediments in Lake Okeechobee appears to enhance charophyte germination. In contrast, desiccation may have negatively impacted seed viability (and subsequent germinability) of the *V. americana* seed bank. In the field, significant *Chara* emergence was observed, and some initial recovery of *V. americana* and *H. verticillata* in several regions of the lake that were exposed during the drought. After the 1989–1990 drought in Lake Okeechobee, recovery was characterized by an increase in *Chara* and the ephemeral colonizer *N. guadalupensis* (Hopson and Zimba, 1993). A decrease in *V. americana* and *P. illinoensis* was also documented (Zimba et al., 1995). The low maximum germination percentage of desiccated seeds relative to seeds held in water from the literature survey (Fig. 1) supports the observation of a limited initial response of vascular submerged species after re-flooding.

4.1. Chara

Chara was found abundantly in incubator cores and in the field at the end of both emergence studies. In spite of *Chara* emergence in disturbed sediments being less than undisturbed sediments, the greater magnitude of oospores in the seed bank than for vascular submerged vegetation (Bonis and Grillas, 2002) is hypothesized to explain the rapid recovery of *Chara* in Lake Okeechobee. Experimental irradiance levels had no effect on *Chara* emergence, suggesting that pre-recession low-light availability may have been more critical to growth of *Chara* (Steinman et al., 2002) than germination from the oospore bank.

In the 2001 re-wetting study, the density of *Chara* sprigs from two desiccated peat sites was notably greater than densities reported in inundated peat sediments from four sites in the 2000 emergence study (Table 3). In sand sediments, the average number of *Chara* emergents in 2000 (at Turner's Cove, a site near Cochran's Pass) was of the same magnitude as those in the 2001 study (Table 3); however, the 2001 study documented a difference in *Chara* emergence between desiccated and inundated cores. A greater number of newly emerged *Chara* sprigs in the desiccated cores (Fig. 5) suggest that some aspect of desiccation resulted in an enhanced *Chara* response (e.g. absolute numbers, rate of emergence, or both). Although the sand sites were in close proximity of each other (<100 m apart), spatial variability in the size of the seed bank cannot be discounted (Bonis and Grillas, 2002). With both sites having the same number of *Chara* emergents at week 1, they essentially were at the same "starting point". Repeated measures ANOVA at each site showed a different temporal response between sites (Cochran's Pass—dry: weeks $1 < 2 < 3$ versus Cochran's Pass—wet: weeks $1 = 2 = 3$). This suggests that there may be an increase in germination rate for *Chara* oospores that have been desiccated as opposed to oospores that remain wet.

Unless there is a density-dependent germination response in *Chara*, rate of emergence should not be influenced by spatial differences in oospore density. We are unaware of any studies examining whether there is a density-dependent function influencing *Chara* germination.

Table 3
Maximum *Chara* emergence data from both Lake Okeechobee emergence studies run under similar incubation conditions (8 week incubation; scaled up to per m^2)

Site	Bottom	*n*	Average[a]	S.E.
South Bay—wet (2000)	Peat	6	411	109
3-Pole Bay—wet (2000)	Peat	6	493	201
East Ritta—wet (2000)	Peat	6	1192	141
South Bay—dry (2001)	Peat	16	3920	184
Kreamer Island—dry (2001)	Peat	16	2988	222
Turner's Cove—wet (2000)	Sand	6	637	125
King's Bar—wet (2000)	Sand	6	123	55
Cochran's Pass—wet (2001)	Sand	16	918	165
Cochran's Pass—dry (2001)	Sand	16	1275	157

[a] Averages are calculated using the maximum number of *Chara* sprigs seen in each core for each site, regardless of when during the incubation the maximum number was recorded. This maximum is considered the peak of a germination flush, and hence is a conservative estimate of the germinated cohort size.

4.2. Vallisneria

V. americana emergence occurred at four of the five sites examined in 2000, suggesting widespread distribution of propagules. *V. americana* seedling emergence occurred at both light levels tested in the 2000 study, suggesting that an average light level of ∼75 μmol photons m^{-2} s^{-1} pre-recession (Steinman et al., 2002) may not have been necessarily inhibitory to *V. americana* seedling emergence. However, Steinman et al. (2002) reported *median* light levels ∼25 μmol photons m^{-2} s^{-1} in the lake. Whether light levels this low are inhibitory to *V. americana* germination in our system remains to be tested experimentally. In a northern ecotype of *V. americana*, Kimber et al. (1995) found successful seed germination across a range of light levels, including for seeds incubated in the dark, suggesting that light availability was more important for juvenile plant survival than for seed germination.

All transplants of young *V. americana* lost biomass throughout the experiment. Although Carter and Rybicki (1985) attributed *V. americana* transplant survival in the Chesapeake Bay to light levels, light is not presumed to be the primary limiting factor on transplant survival in this short-term experiment. Light measurements recorded at various times of day from were examined between April 1999 and April 2000 (pre-drawdown) at 35 sites in the near-shore region of Lake Okeechobee (Steinman et al., 2002). The proportion of light reaching the bottom in water depths shallower than the ∼1.5 m maximum depth of submerged vegetation in our system was almost always greater than the apparent light compensation point of 4% for *V. americana* in Lake Okeechobee (Grimshaw et al., 2002). This suggests that there appeared to be enough light reaching the bottom to support *V. americana* survival prior to the drawdown.

In this experiment, new stolon and new shoot development was observed for transplants at all locations, except Turner's Cove (herbivory observed by week 4) (Table 1). Given an increase in daughter shoot production, the decline in transplant biomass may be partially attributed to a combination of resource allocation (Madsen, 1991), transplantation stress (Biernacki et al., 1997; Kraemer et al., 1999), and the short duration of the experiment. Additionally, placing transplant frames on the sediment surface without burying the stolons may have delayed rooting. It is possible that *V. americana* survival would have been greater by transplanting multiple rosettes on a single stolon (or even an intact, but undeveloped bud). In examining the apparent light compensation point for young *V. americana* plants from Lake Okeechobee, Grimshaw et al. (2002) utilized a similar approach by starting with small bare-rooted individual rosettes as in this study. Under controlled mesocosm conditions, they had 100% survival of rosettes, and net growth in most light treatments, with some blades reaching the surface of the ∼0.8 m deep tank at the end of a 7 week experiment (Grimshaw et al., 2002).

Sediment type may play a role in long-term establishment and survival, as there are interactions between submerged vegetation dynamics and sediment type (e.g. for review, see Barko et al., 1991). While there did not appear to be any significant effects of sediment type on submerged vegetation seedling/sporeling emergence here, total biomass was greater in *V. americana* transplants placed in peat rather than sand regardless of water depth at a location. Submerged vegetation recruitment, survival and growth as a function of sediment type needs to be examined further.

The hypothesis that seed bank desiccation reduces the resultant submerged vegetation germination response may be applicable for *V. americana* in Lake Okeechobee. While variable,

germination of *V. americana* in the 2000 emergence study was as high as 1.5 seedlings per core in inundated peat cores from South Bay. This contrasts to the complete absence of any germination response in sediments from the same site following desiccation in this study. Unlike air-drying seeds in a laboratory setting, moisture content of lake sediments does not necessarily drop to zero immediately after exposure, but may instead decline over a period of time. Moisture content of the seed bank also can increase when re-wetted by rain events, potentially influencing seed/tuber viability. For example, varying soil moisture content in exposed lake bottom is thought to influence recovery response of torpedograss (*Panicum repens*, an emergent aquatic plant) from belowground root rhizomes (and possibly the seed bank; Hanlon, personal communication) in the littoral zone of Lake Okeechobee (Hanlon and Langeland, 2000).

4.3. Conclusions

If average water levels (SFWMD, 2001) persist for several years, submerged vegetation abundance and distribution is predicted to increase in this lake, with the most rapid recovery expected to occur in peat sediment regions. The first expected re-colonizer after recovery from high water levels or drought conditions in this shallow subtropical lake is *Chara* (Havens et al., 2001; Steinman et al., 2002), with vascular plants (primarily *V. americana*) most likely taking longer to re-establish because recruitment will be primarily from small remnant populations, ex situ sources, or highly variable seed banks.

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