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Macrophyte colonization in a freshwater tidal wetland (Lyme, CT, USA)

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Abstract

Seed bank sampling and creation of plots cleared of standing vegetation showed that aboveground vegetative propagules were more important than seeds in colonization of a freshwater tidal wetland but that the relative importance of sexual reproduction varied among species. Nine submerged species established in colonization plots. Of these colonization events, 60% were achieved by plant fragments, either in the sediment or floating in the water, and 16% resulted from vegetative growth. Only 4 of 16 submerged species in the community were represented in the seed bank. The collection of vegetative propagules in nets demonstrated that drifting propagules were very abundant and that the relative abundance of species in the propagule stream corresponded most closely with the standing community.

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1. Introduction

Freshwater wetlands are dynamic habitats (Dawson, 1988; Wiegand, 1988), and the presence and abundance of plants at any location can change in response to disturbance or change in conditions. The ability to colonize available space and to re-establish after local extirpation is essential for long-term persistence of plant populations in such dynamic habitats (Keddy and Reznicek, 1982; Welling et al., 1988). Research by Van der Valk and others (e.g. Van der Valk, 1981, 2000) has provided valuable insights into the means by which plants respond to flood and drawdown cycles in prairie wetlands. However, this and other wetland seed bank research (Leck and Simpson, 1987, 1995; Schneider and Sharitz, 1986) has focused on the emergent community, and less quantitative information is available on

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submerged plant seed banks (Grillas et al., 1993; but see Haag, 1983; Van Wijk, 1989; Westcott et al., 1997) or on the relative importance of the ways in which submerged plants colonize (Barrat-Segretain, 1996).

As part of a long-term study of dynamics in a submerged aquatic community in a freshwater tidal wetland, I established plots free of plants to test the relative importance of the seed bank, local vegetative growth, and immigration by various kinds of vegetative propagules for recruitment to the community. I also sampled the seed bank to determine the importance of sexual reproduction among the submerged plants present. Finally, I used nets to collect vegetative propagules entering and leaving the community to determine whether propagule abundance determined the relative abundance of species. I compare the species present in these samples with the standing vegetation and interpret the results in terms of the relative importance of various colonization strategies.

2. Methods

The research was conducted in Whalebone Cove (41°25'N, 72°25'W), a freshwater tidal wetland that is in excess of 350,000 m² in area and on the east side of the Connecticut River, 16 km north of its mouth. Whalebone Cove is typical of the tidal wetlands along the river, which are listed under the Ramsar convention. It is intermediate in size, and species richness is comparable to that in other tidal wetlands on the river (Capers, unpublished). No point in the wetland is more than 4 m deep at high tide, and only two narrow channels are anywhere more than 2 m deep. The semidiurnal tide rises and falls about 80 cm, and more than half of the wetland's area is exposed at low tide.

Colonization plots were established between May and July 2000 in three locations with shallow water, sediment composed largely of silt and low water velocity. The plots were in areas where plants were exposed to the air for about 1 h each day, during low tide, although the sediment never became dry. At high tide the plants were under about 60 cm of water. Conditions in the colonization plots would be less representative of areas with deeper water, especially mid-channel areas with more sandy sediment and water velocity that can exceed 0.4 m per second. At each location, a 1 m × 1 m plot was marked out and 1 m away, a 1 m × 3 m plot was established. This larger plot was marked off, using stakes, into three separate 1 m² plots. All standing vegetation was removed from the plots, and care was taken to remove below-ground portions of plants growing in the plots at the beginning of the experiment. No effort was made to remove other below-ground material. Periodically during the growing season, I removed plants that had established in the plots, identifying each to species and determining whether it had established in the plots through germination of a seed, vegetative spread (growth of a plant from an adjacent area), or by sprouting from a vegetative fragment in the sediment. This determination was made by inspecting each shoot, looking for a seed, attached winter bud or an attached fragment from which the new shoot had sprouted. Fragments in the sediment for more than a few days typically blacken and are easily distinguished from new growth. In cases where no seed was present and the shoot had not clearly sprouted from a fragment or winter bud, the origin was recorded as unknown. Daily colonization rates were calculated for each 1 m² subplot for the period between surveys. Repeated measures analysis with the SAS Genmod procedure was

performed on the data after colonization by the different propagule types and was combined to produce a single number of colonizations for each species for each subplot.

I obtained 40 sediment samples for the seed bank analysis on March 22, 2000, by which time any stratification requirements presumably would have been met. Sampling locations were chosen haphazardly while attempting to include all parts of the wetland and to represent all habitat variation. A plastic pipe with a diameter of 5 cm was used to obtain sediment samples 10 cm deep; three samples were combined to make a single sediment sample representing the seed bank at each location. Sediment samples were washed through a 3 mm screen to remove litter, plant fragments, winter buds, turions and other vegetative propagules. On March 23, 2000, the screened sediment was placed in plastic pots 12 cm² spread to a depth of approximately 2 cm. The apparent loss of volume reflected the removal of vegetative material from the sediment plus the settling that occurred when the unconsolidated sediment was removed from the water. The pots were placed in shallow tanks in a greenhouse and maintained under ambient light through the summer and autumn of 2000. Fresh water over the sediment surface was kept at a depth of 10 cm. Tap water was added as needed to replace water lost through evaporation. Water temperature varied during the growing season from 16 to 28 °C. Observations were made daily for the first month and then every few days for the duration of the period. Plants appearing in the plots were removed as soon as they could be identified. As considered here, the seed bank includes only viable seeds and excludes all vegetative propagules, following Grime (1979) and Haag (1983).

To determine the abundance of vegetative propagules carried by water into the community, I placed nets in the channel through which all water enters and leaves the wetland. I used two nets with 1.3 mm mesh, one placed on the bottom of the channel and one floating so it would capture material on the surface. After retrieving the nets, I removed all material and refloatated it in trays of water, removing whole plants, fruits, and plant fragments while recording the number of each, by species. Only material that appeared viable and was known to be capable of establishing a new plant was considered a propagule; so, for example, pieces of leafy rhizomes of *Elodea nuttallii* were considered propagules but leaves of *Vallisneria americana* were not. Each plant or fragment was considered a separate propagule, regardless of size. The nets were used each day for the duration of the rising or falling tide. I used the nets on 21 days between 12 July 2001 and 7 September 2001, capturing surface material for 11 falling tides and 9 rising tides and capturing propagules carried along the bottom of the channel during 10 falling tides and 9 rising tides. Each net was 50 cm high and 100 cm wide, and the surface net was positioned so that the top 10 cm floated above the surface. I used measurements of channel width and depth to estimate the total number of propagules moving into and out of the wetland on each tide, based on the proportion of the total channel area intercepted by the nets.

I used repeated measures analysis implemented with SAS, Proc Mixed, to test for differences in the number of propagules carried along the surface of the water and the number carried on the bottom and to determine if species differed in propagule immigration and emigration rates. To determine how well species propagule abundance corresponded with community abundance, I performed Spearman's rank correlation analysis using the combined total of incoming and outgoing propagules for each species and relative abundance of species based on two data sets, one from 2001 and a second from 2000. The 2001 data were based on a census done in 100 quadrats, each 1 m² in area. Quadrats were arranged in 10 transects

distributed through the wetland to reflect the variety of conditions available for submerged plants, including areas with deep water that are permanently submerged and large areas of shallow water, where plants are exposed at low tide. The census was done in the water, using snorkeling equipment. Each stem in a quadrat was identified to species and counted. Because selection of the transects was not strictly random, rank correlation also was performed between propagule abundance and relative abundance of submerged species censused in 70 quadrats, each 1 m², that were selected randomly in the community during July and August 2000. Each stem in the quadrats was identified to species and counted. In the present analysis, only submerged species are considered in determining relative abundance ranks. Similarity between the propagule stream and community composition for 2000 and 2001 was assessed, using the Sørensen index, which considers only species presence or absence, and the Morasita–Horn index, which also takes into account species abundance. Composition of the propagule stream also was compared with the total submerged plant community composition as determined by numerous in-water and boat surveys of the area each year.

Nomenclature follows Gleason and Cronquist (1991). Voucher specimens of submerged species in the community were deposited in the herbarium at the University of Connecticut (CONN).

3. Results

A total of 730 plants established in the colonization plots during the 14-week observation period, including 628 submerged plants. Nine submerged species were recorded: *E. nuttallii*, *Ceratophyllum demersum*, *Potamogeton pusillus*, *P. spirillus*, *P. perfoliatus*, *V. americana*, *Zannichellia palustris*, *Najas flexilis* and a *Callitriche* sp. (Table 1). Of these, *Z. palustris*, *N. flexilis* and *Callitriche* are annuals. Three emergent plants were recorded: *Pontederia cordata*, *Sagittaria latifolia* and a grass, presumably *Zizania aquatica*, which is abundant in the wetland. An average of 61 plants appeared per 1 m² area, including 52 submerged plants.

No difference was found in the rate of colonization of 1 m² plots and 1 m by 3 m plots, after adjusting for area, even for vegetative spread, where it was thought to be most likely to make a difference (one-way ANOVA, d.f. = 1, $F = 0.61$, $P = 0.445$ for difference overall and d.f. = 1, $F = 2.90$, $P = 0.164$ for vegetative spread), and data were not distinguished by the shape of the colonization plot in subsequent analyses. Fragments, either in the sediment or floating in the water, were responsible for 60% of colonization events among submerged species, and an additional 16% resulted from vegetative spread (Table 1). Six of the seven perennial submerged species colonized by both fragments and vegetative spread. Only vegetative spread was observed as a colonizing method for *P. perfoliatus*. Establishment by fragment or vegetative spread was recorded for no emergent plant. Across all species, the origin of 29% of the colonizing propagules could not be established. Seeds accounted for 5% of colonizations overall, but 39 of the 40 seedlings were of the emergent *P. cordata*. Only a single seedling of a submerged plant, *Z. palustris*, was recorded. Even if all colonizations by annual plants are assumed to have been by seeds, converting the “unknown origin” category to instances of establishment by seed, the proportion of colonizations by seeds among submerged plants would be less than 3%.

Table 1
Colonization of plots cleared of vegetation

Species	Colonization events					Colonization rate (events m ⁻² d ⁻¹)
	Fragment	Vegetative growth	Seed	Unknown	Total	
Submerged species						
<i>Elodea nuttallii</i>	221	52	0	57	330	0.288 ± 0.068
<i>Potamogeton pusillus</i>	41	9	0	47	97	0.121 ± 0.024
<i>Ceratophyllum demersum</i>	97	12	0	22	131	0.116 ± 0.035
<i>P. perfoliatus</i>	0	16	0	3	19	0.025 ± 0.018
<i>P. spirillus</i>	4	4	0	8	16	0.020 ± 0.009
<i>Callitriche</i> sp.	10	2	0	9	21	0.019 ± 0.008
<i>Zannichellia palustris</i>	0	2	1	6	9	0.012 ± 0.006
<i>Vallisneria americana</i>	1	1	0	0	2	0.004 ± 0.003
<i>Najas flexilis</i>	3	0	0	0	3	0.003 ± 0.002
Submerged spp. Total	377	98	1	152	628	0.610 ± 0.102
Emergent species						
<i>Pontederia cordata</i>	0	0	39	51	90	0.082 ± 0.031
Grass (cf. <i>Zizania aquatica</i>)	0	0	0	11	11	0.009 ± 0.003
<i>Sagittaria latifolia</i>	0	0	0	1	1	0.002 ± 0.001
Emergent spp. Total	0	0	39	63	102	0.092 ± 0.032

Shown are the number of colonization events ("Total") observed from May to September 2000 for each species in 12 plots (each 1 m² in area) from which all standing vegetation had been removed. Also shown are the number of colonizations attributed to each kind of propagule. The final column shows the mean (±S.E.) number of colonization events per 1 m² per day for each species, averaging across all colonization plots and propagule types. In some cases, species with fewer colonization events have higher rates because all colonization plots were not maintained for exactly the same number of days.

Variation in colonization rates per 1 m² subplot increased during the growing season, with maximum rates recorded in mid-August (Fig. 1). However, time was not found to be significant in the repeated measures analysis because of high variation in colonization rates during the growing season. Colonization rates differed significantly among species, and differences among plots in variation in colonization rates with time were reflected in a significant interaction (Table 2).

Table 2
Analysis of colonization rates among wetland plants

Source	d.f.	Chi square	P
Species	11	65.21	<0.0001
Plot	2	5.94	0.0512
Day	1	0.38	0.5376
Subplot (plot)	9	4.09	0.9052
Day × Plot	2	11.40	0.0033

Repeated measures analysis was used on colonization rates recorded during a single growing season in four subplots (1 m² each) arranged in three plots. The analysis, which nested subplots within plots, found that rates differed among the 12 species that colonized. Non-significant interactions were removed from the model.

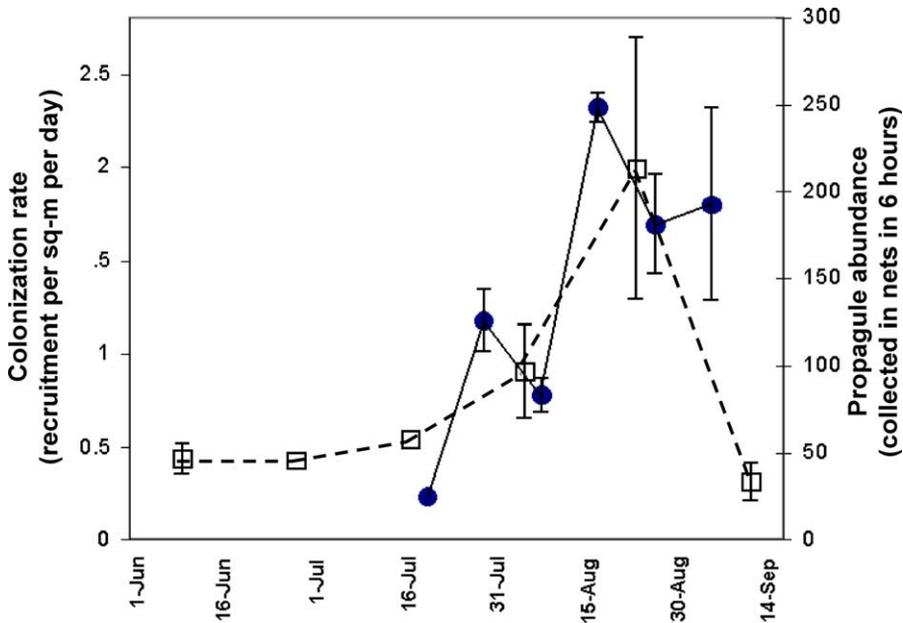


Fig. 1. The mean daily colonization rate per 1 m² among submerged species increased during the growing season, peaking in mid- to late August before declining again in September (open squares). Data for all species and plots were combined, and 20-day average rates are shown. The mean number of propagules collected in nets during a 6 h tide, averaged over 10-day periods (filled circles), also peaked in mid-August.

E. nuttallii demonstrated the greatest potential for colonization, appearing in more than 90% of the subplots and sprouting from an average of 30 fragments in each. The number of shoots appearing was actually much higher than this, because most fragments branched and produced several shoots, although each fragment was assigned responsibility for a single colonizing event. Only *E. nuttallii*, *C. demersum*, and *P. pusillus* colonized more than 10% of available habitat each day on average (Table 1). Colonization rates of individual species, averaged across all subplots for the period of the experiment, were not significantly correlated with relative abundance in the submerged plant community (Table 6; rank correlation $r = 0.414$, $P = 0.308$ for 2000, and $r = 0.317$, $P = 0.406$ for 2001).

In the seed bank samples, seedlings began to emerge 12 days after sediment samples were moved into the greenhouse. With the exception of two *Lindernia dubia* plants, all seedlings had emerged by July 18. Seedlings germinated in 68% of the seed bank samples and were produced by eight identified species (Table 3), of which three are annuals: *Lindernia dubia*, *N. flexilis*, and *N. gracillima*. Only three of the species were emergent or mud flat plants, but these produced 59% of the seedlings, compared with 28% produced by the five submerged species. The number of seedlings in individual samples ranged from 1 to 17. Nine seedlings died before they could be identified. Because of the low number of seedlings that emerged, little can be said with confidence about the frequency with which individual species are represented in the seed bank or about the mean density of their seeds. The mean seedling density pooled over all species (mean \pm standard error) was $280 \pm 76 \text{ m}^{-2}$. Mean seedling

Table 3
Seed bank sampling results

	<i>n</i>	Frequency (%)
<i>Lindernia dubia</i>	38	30
<i>Elodea nuttallii</i>	7	15
<i>Potamogeton pusillus</i>	6	15
<i>Vallisneria americana</i>	3	8
<i>Najas flexilis</i>	2	5
<i>N. gracillima</i>	1	3
<i>Sagittaria latifolia</i>	1	3
<i>Typha latifolia</i>	1	3
Unidentified	9	15

Shown are the number of seedlings of each species that appeared and the frequency of each species in 40 seed bank samples covering in total 2355 cm² of wetland sediment. The samples were obtained in early spring and maintained in a greenhouse through one growing season.

density for submerged species was $115 \pm 24 \text{ m}^{-2}$. No submerged species appeared in more than 15% of the samples (Table 3), and only four of the 16 submerged species known to exist in the community appeared in the seed bank. One additional species, *N. gracillima*, has never been observed there.

Netting produced 3489 propagules, representing 15 species of submerged plants. Almost all of the propagules were whole plants or fragments capable of establishing whole plants. In addition, many fragments of *P. spirillus* and *Z. palustris* bore fruits, as did smaller numbers of *P. pusillus* fragments. Many of the plant fragments were small—pieces of rhizome 2–3 cm long, including winter buds from *E. nuttallii* and *C. demersum*. Some fragments were large, including many shoots of *C. demersum* more than 1 m long. *V. americana* does not produce winter buds or generate large numbers of vegetative fragments, but the surface net captured many free-floating rosettes of the species. Although counted as a single propagule, more than one-third of these *V. americana* propagules represented rosettes attached by stolons to at least one other rosette. A total of 144 *Vallisneria* propagules were recorded, but these included 257 rosettes, each of which could establish a separate plant.

The nets intercepted an area equal to 1.85% of the channel at high tide and 3.03% at low. However, observations in the water indicated that propagule movement was limited to the surface of the water and the very deepest part of the channel, where the bottom was nearly level over a distance of 12 m. A net placed on the slope of the channel collected no propagules during an entire incoming tide. Submerged plants grow on the slope, slowing the current and likely intercepting most propagules moving through the vegetation, whereas the flat bottom of the channel was free of plants. Therefore, I estimated the total number of propagules moving into and out of the wetland on the basis of an assumption that propagules captured in the surface net represented 1/29 of the total surface load in the channel, which was 29 m wide at high tide, and that the bottom net captured 1/12 of the total number of propagules moving along the bottom. This probably underestimated the true number of propagules moving through the channel, but it seemed better to present a minimum estimate of propagule density. Some 4000–5000 propagules were estimated to enter the community

Table 4

Mean number of propagules of each species estimated to enter and leave the community during each 6 h rising ($n = 9$) and falling ($n = 11$) tide, based on collections in two nets

	Rising	Falling
<i>Elodea nuttallii</i>	1823 ± 230	2075 ± 409
<i>Ceratophyllum demersum</i>	1522 ± 500	676 ± 205
<i>Potamogeton pusillus</i>	437 ± 56	250 ± 121
<i>Vallisneria americana</i>	425 ± 217	124 ± 33
<i>Zannichellia palustris</i>	353 ± 71	48 ± 18
<i>P. spirillus</i>	275 ± 66	233 ± 55
<i>P. perfoliatus</i>	106 ± 20	41 ± 17
<i>Callitriche</i> sp.	50 ± 26	132 ± 64
<i>Najas flexilis</i>	43 ± 15	65 ± 24
<i>Myriophyllum spicatum</i>	35 ± 17	12 ± 6
<i>N. gracillima</i>	30 ± 14	19 ± 10
<i>P. crispus</i>	17 ± 11	13 ± 8
<i>P. epiphydrus</i>	3 ± 3	0
<i>P. nodosus</i>	3 ± 3	3 ± 3
<i>Utricularia vulgaris</i>	3 ± 3	0
Unknown	16 ± 13	29 ± 15
Total	5141 ± 822	3718 ± 685

One net collected 1/12 of the propagules moving along the bottom of a channel entering the community, and the second net collected 1/29 of the propagules in the top 40 cm of the water. All kinds of propagules were combined in calculating the totals for each species, although the nets would not have captured free-floating seeds.

with each rising tide, with an approximately equal number leaving on each falling tide. Estimates by species are listed in Table 4.

The number of propagules collected in nets varied greatly among species, and the differences were found to be significant in an analysis limited to the nine most abundant species (Table 5). *E. nuttallii* and *C. demersum* were far more abundant than all other species. The number of propagules collected in the surface net represented 75% of the total, and the mean number captured during each tide (131 ± 74) was significantly greater than that in the

Table 5

Repeated measures analysis of propagule netting results, including the nine species most abundantly represented in the propagule stream

Source	<i>F</i>	d.f.	<i>P</i>
Species	7.80	11	<0.0001
Net	147.64	1	<0.0001
Tide	1.91	1	0.1835
Day	1.15	1	0.2955
Species × Net	8.42	11	<0.0001
Species × Tide	4.49	11	<0.0001
Species × Day	4.05	11	<0.0001
Net × Tide	20.66	1	<0.0001

Net position (surface or bottom), Tide (rising or falling) and Species were entered as factors. The square-root transformed number of propagules of each species collected in a net during a single rising or falling tide was entered as the response variable. Only significant interactions remain in the model.

Table 6
Mean abundance (± 1 S.E.) of submerged plants

	2000	2001
<i>Vallisneria americana</i>	2.46 \pm 1.14	19.04 \pm 3.08
<i>Elodea nuttallii</i>	17.43 \pm 2.93	18.49 \pm 3.50
<i>Potamogeton pusillus</i>	2.79 \pm 1.27	5.91 \pm 0.83
<i>P. spirillus</i>	0.37 \pm 0.16	4.83 \pm 1.21
<i>Zannichellia palustris</i>	–	3.06 \pm 0.85
<i>Ceratophyllum demersum</i>	2.03 \pm 0.46	2.96 \pm 0.57
<i>Callitriche</i> sp.	3.87 \pm 1.61	2.79 \pm 1.25
<i>P. perfoliatus</i>	0.04 \pm 0.04	0.96 \pm 0.33
<i>P. pectinatus</i>	–	0.23 \pm 0.16
<i>Najas flexilis</i>	0.14 \pm 0.11	0.10 \pm 0.06
<i>P. nodosus</i>	0.20 \pm 0.20	–
<i>Myriophyllum spicatum</i>	0.07 \pm 0.07	–

Data were taken in 1 m^{-2} quadrats in 2000, based on 70 random samples, and in 2001, based on 100 quadrats of the same size but arranged in 10 transects distributed to capture the range of conditions in the tidal wetland. All 12 species were observed in the community each year, although not recorded in formal censuses, as were four other species: *Potamogeton crispus*, *P. epiphydrus*, *Heteranthera dubia* and *Utricularia vulgaris*.

bottom net (46 ± 34 , Table 5). The difference between the surface net and the bottom net was greater on incoming tides than outgoing tides, which was recognized as a significant interaction term. Among individual species, only *N. flexilis* was more abundant on the bottom. No difference was found in the mean number of propagules captured moving into or out of the community by the two nets (194 ± 32 on rising tides and 164 ± 26 on falling tides). Propagules of most species were more abundant on rising tides, although *E. nuttallii*, *N. flexilis*, and *Callitriche* were more abundant on falling tides (Table 4), and this resulted in a significant interaction between species and tide. The number of propagules collected each day varied greatly, and although the number generally increased toward the end of the growing season (Fig. 1), rates varied among species, producing a significant interaction (Table 5).

Spearman's rank correlation analysis indicated that the abundance of species propagules was positively correlated with the standing community as determined by community censuses in 2000, based on the 10 species recorded in both random samples and propagule nets, and in 2001, based on the nine species recorded in both quadrats and propagule nets (Table 6; $r = 0.733$, $P = 0.016$ for 2000, and $r = 0.767$, $P = 0.016$ for 2001). Similarity between the propagule stream and the mature community, based on 2000 and 2001 samples, was found to be very high (0.80 and 0.72 on the Sørensen index and 0.92 and 0.74 on the Morasita–Horn index, respectively). The same 16 submerged species were recorded in the community each year, and 14 of them were recorded in the propagule stream, producing a Sørensen score of 0.90.

4. Discussion

In the studied freshwater wetland, I found that submerged plants rely primarily on abundantly available vegetative propagules and vegetative growth to colonize newly available

habitat. For the purpose of colonization, the seed bank appears to be less important for most species, although seeds are of obvious importance in re-establishing annual species each year. Sexual reproduction complemented vegetative reproduction for *P. pusillus*, *E. nuttallii*, and *V. americana*. That these species are both most abundant in the seed bank and among the most abundant in the community each year suggests that there may be an advantage to using multiple reproductive strategies. In fact, every submerged species except the annual *N. flexilis* was found to use two colonization strategies. The species collected in propagule nets corresponded more closely with the standing community than did the seed bank (14 submerged species shared compared with 4), which supports the conclusion that vegetative reproduction is more important in colonization and community structure. The fact that colonization peaked at about the same time as drifting propagule abundance (Fig. 1) suggests that drifting propagules may be more important to community composition than vegetative propagules in the sediment, although drifting propagules may be the ultimate source of many of those in the sediment.

E. nuttallii, *C. demersum*, and *P. pusillus* existed abundantly as fragments in the sediment, producing new shoots when conditions became favorable—presumably the removal of standing vegetation and the increased availability of light. Each of these three produced new shoots from fragments in more than two-thirds of the colonization subplots. The same three species were the most abundant in propagule nets. All three have been among the most abundant submerged species in the wetland each year since 1996 (Capers, 2000, and unpublished), and all exist primarily in areas with shallow water and deep silty sediment. These areas are most vulnerable to winter ice scour (Robertson and Mann, 1984) but appear to be recolonized each year largely by regrowth from vegetative propagules produced above the sediment and released into the water. The correspondence between high propagule numbers and high abundance among these species suggests that colonization success may depend on the propagule supply and that abundance of other species in shallow-water areas of this wetland may be limited by propagule numbers.

This close relationship between propagule density and abundance is less likely to hold in deeper water. Neither seeds nor aboveground vegetative propagules of *V. americana* are likely to play much role in colonization in this wetland. The species grows widely as single plants or small patches and occurs in dense, nearly monospecific stands in areas where the water flows most strongly, producing deep channels and sandy substrate. *Vallisneria* spreads vegetatively in these areas and overwinters as tubers in the sediment (Titus and Hoover, 1993; Capers, personal observation). These areas are relatively invulnerable to ice scour, and it appears that the species is able to survive winter disturbance in other areas as well, persisting in the wetland with only occasional production of seeds to colonize new habitat. In fact, even in shallow water areas of the wetland, colonization is not uniform, and species appear to be highly sensitive to small-scale variation in conditions. *P. perfoliatus* and *V. americana* colonized in only one of three plots, which was on the side of a channel, and colonization rates for *E. nuttallii* were much lower there than in the other two plots, where the current may have been lower.

Except for *P. pusillus* and *P. spirillus*, the seven *Potamogeton* species in the standing vegetation were poorly represented in the seed bank and colonization plots. Some *Potamogeton* species, including *P. perfoliatus*, *P. nodosus*, *P. epihydrus*, and *P. pectinatus* overwinter as rhizomes, stolons, or tubers in the sediment (Yeo, 1965; Heisey and Damman, 1982;

Spencer and Anderson, 1987; Van Wijk, 1989; Wiegleb and Brux, 1991), so persistence of these species in the community may result less from recolonization than from escaping wintertime disturbance deep in the sediment.

It was surprising that *Z. palustris*, an annual that produces abundant fruit each year, was not recorded in the seed bank. Seeds of some submerged species are viable for at least 15 years (Hutchinson, 1975; Van Vierssen, 1993; DeWinton et al., 2000), although *Z. pedunculata* Reichen. and *Z. obtusifolia* Talavera have been described as having poor long-term viability (Bonis et al., 1995). Even if *Z. palustris* seeds remained viable only for a few years, a substantial seed bank would be expected in this wetland. There are several possible explanations for its absence. Most simply, it might reflect the small number of samples or small amount of sediment collected. It also is possible that the light and temperature conditions necessary for germination were not provided (Lombardi et al., 1996), or that prolonged dormancy is enforced in the *Zannichellia* seeds in this wetland. Van Vierssen (1982) found that European *Z. palustris* germinated less readily than other *Zannichellia* species but that a high proportion of seeds germinated after a 2-month period of cold stratification. One final possibility is that the species, for unknown reasons, produces no viable seed in this wetland and that the community persists because of seed entering the wetland in the propagule stream. *Zannichellia* was the only species for which the number of propagules entering the wetland was significantly greater than the number leaving it (Table 4).

Even without *Zannichellia*, annual species were more abundant than perennial species in the seed bank, as observed in previous studies (Kautsky, 1990; Westcott et al., 1997). One submerged annual that both germinated from the Whalebone Cove seed bank and was collected in propagule nets has never before been observed in the wetland. *N. gracillima* occurs in several inland ponds and lakes in Connecticut but was last collected from the Connecticut River watershed in 1901. The sediment containing the *N. gracillima* seed came from an area where a stream enters the cove, and it is likely that the seed was carried into the cove from some upstream habitat. The presence of *N. gracillima* in the seed bank and propagule nets shows that the species has ample opportunities for colonization; its absence from the community likely results from its failure to find acceptable conditions.

As observed in previous research in perennial communities, there was little correspondence between the submerged plant seed bank and the standing vegetation. Westcott et al. (1997) found in Ontario Lake marshes that, although *V. americana* and *C. demersum* were abundant in the community, they were rare in the seed bank. In an Alberta lake, only five of 12 submerged species germinated from the seed bank (Haag, 1983). Closer correspondence between the seed bank and mature plants has been found in ephemeral habitats (Grillas et al., 1993; Brock and Rogers, 1998). The overall density of seedlings emerging from the seed bank in Whalebone Cove (0–329 seedlings m^{-2} for submerged species, 0–2,797 seedlings m^{-2} for all species) was comparable to that found in some previous studies of perennial communities of submerged plants (0–2400 m^{-2} ; Haag, 1983; DeWinton and Clayton, 1996; Westcott et al., 1997). Higher values have been reported for communities dominated by annual species (4000–1.7 million, including oospores, Grillas et al., 1993, and references therein) and communities of emergent species (8286–481,000 seeds m^{-2} , Van der Valk and Davis, 1978; Leck and Simpson, 1987; Skoglund and Hytteborn, 1990; Grelsson and Nilsson, 1991).

There is increasing evidence that colonization strategies vary with abiotic conditions, not just in ephemeral habitats, where seeds ensure persistence (Grillas et al., 1993; Brock and Rogers, 1998). In more permanent riverine systems, composition of the plant community has been found to correspond not with the entire sediment propagule bank but only with vegetative propagules (Combroux et al., 2001). The authors of that study on the Rhône River concluded that the community did not depend on a single type of propagule but was maintained by the different regenerative strategies of the constituent species (Combroux et al., 2001), and they suggested that different methods of colonization represent evolutionary strategies with regard to resistance and resilience. Barrat-Segretain and Bornette (2000) also found that species differ in the ways they use vegetative fragments to colonize and that these strategies vary by season in ways that could affect community composition. Abernethy and Willby (1999) found, in two locations with perennial hydrophytes, that 37 and 53% of species in the sediment propagule bank existed in the standing community. I found an even higher proportion (93%) of species with drifting propagules existed in the community. The significant correlation and high similarity between the drifting propagule abundance and abundance of submerged species in the community also indicate their great importance in the tidal wetland studied here. Few other colonization studies have included drifting propagules, although these have confirmed their importance. Cellot et al. (1998) found 23 taxa among drifting propagules in a riverine wetland, and Harwell and Orth (2002) recently found that *Zostera marina* L. had established more than 100 km from parent populations by seeds carried on drifting shoots. More research on drifting propagules is warranted in the context of how colonization strategies vary with abiotic conditions (Rollon et al., 1998; Barrat-Segretain, 2001; Combroux et al., 2001).

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