Six years of submerged plant community dynamics in a freshwater tidal wetland

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SUMMARY

1. The dynamics of a submerged plant community were studied for 6 years in a freshwater tidal wetland. The degree and nature of change at several spatial scales (quadrat, transect and overall community) was determined, and the implications for community stability were assessed.

2. A high degree of change was recorded in 1 m^2 quadrats, and this was reflected in 10 m^2 transects as well. In quadrats, mean species richness changed every year. Species richness changed in >60% of quadrats each year. Stem number changed by as many as several 100 stems per quadrat from one year to the next.

3. Richness varied more among quadrats than among transects and varied less at the community level than among either quadrats or transects. Greater stability at the spatial scale of the whole community was reflected in high scores on the Jaccard and Morasita–Horn indices and Kendall's coefficient of concordance.

4. Although most of the submerged species were perennials, persistence at the local scale was low, and 4-year persistence exceeded 50% for only one species. Change in abundance was largely independent among the species.

5. In the face of great small-scale changes, species remain in the community (and the community persists) because of high recruitment rates.

Keywords: community structure, diversity, *Elodea nuttallii*, submerged macrophytes, *Vallisneria americana*

Introduction

Quantifying temporal and spatial variation in ecological communities can provide insights into natural function and is essential to understand community stability and persistence (Bormann & Likens, 1979; Sale, 1977; Connell & Sousa, 1983; Pimm & Redfearn, 1988; Rahel, 1990). Communities of submerged aquatic plants are particularly dynamic, often because of high disturbance rates, but have rarely been studied for long enough to reveal the natural levels of variation, either across space or time (Wiegleb,

1988). Interpreting long-term changes in community structure and determining their causes can be difficult or impossible if short-term stochastic fluctuations have not been characterised.

In some cases, the study of change in aquatic plant communities has involved surveys of species richness which are compared with surveys conducted in the same water body years earlier (Lind & Cottam, 1969; Harman & Doane, 1970; Arts *et al.*, 1990). These studies have linked the loss of biological richness to increasing nutrient concentrations in the atmosphere and waters of the world, but they provide little information on short-term community change under natural conditions. Furthermore, fewer studies of riverine systems have been performed, which differ fundamentally from lentic waters (Butcher, 1933).

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Riverine communities are structured largely by the forces of flow (Breen, Rogers & Ashton, 1988; Dawson, 1988) and are more dynamic, although a limited number of studies have investigated the dynamics explicitly (Ham *et al.*, 1982; Hamel & Bhèreur, 1982; Henry, Bornette & Amoros, 1994; Bornette & Amoros, 1996; Combroux *et al.*, 2001). Recent work has suggested that the life history traits of aquatic plants can be linked to variation in their colonisation success and the relative abundance of life forms in particular locations (Abernethy & Willby, 1999; Combroux *et al.*, 2001), but additional work is needed to characterise the variation in these largely stochastic systems (Barrat-Segretain, 1996).

I studied spatial variation and dynamics of a submerged plant community in a freshwater tidal marsh over a period of 6 years. The data were used to characterise variation in the community and its dynamics and to explore the implications of spatial and temporal variation for community stability. Following Rahel (1990), stability was measured at several spatial scales of resolution. Finally, I discuss the implications of the data for modelling submerged plant communities.

Methods

The research was conducted in Whalebone Cove (41°25′N, 72°25′W), a wetland on the east side of the Connecticut River, 17 km north of its outlet into Long Island Sound, which is 50 km east of New Haven, CT, U.S.A. This 50 ha wetland is connected to the river by a narrow channel through which water enters and leaves the wetland twice daily as the tide rises and falls about 80 cm. Two small freshwater streams also feed the wetland. Water depth is <2 m at high tide in most of the wetland and exceeds 5 m nowhere. Water flows strongly (>35 cm s^{-1}) in deep, sandy channels but very slowly through most of the wetland area, where the sediments are deep, fine silt. Although tidal, Whalebone Cove is strictly a freshwater wetland.

In 1998, 10 transects, each 10 m in length, were established in areas chosen to reflect the variety of conditions in the wetland, including areas with swift running water as well as large areas of shallow, calm water. Transects were divided into 10 consecutive quadrats, each 1 m^2 in area. Each end of a transect was marked with a steel pipe sunk into the sediment

so the transect could be re-established in the same position each year. Censuses were conducted in quadrats in early July each year from 1998 to 2001. In each quadrat, rooted stems of all submerged angiosperms were identified and counted. Because many submerged plants spread clonally, the stems do not represent separate plants. However, because I counted only stems that were rooted, each stem potentially represented an independent plant or ramet. One transect could not be censused because of the early appearance of large wild rice (*Zizania aquatica* L.) in 1999, and the position of a different transect could not be identified in 2000. Only the eight transects censused every year from 1998–2001 were used to examine the degree of species-level changes among quadrats and transects. Censuses of submerged plants were conducted in different quadrats in 1996 ($n = 328$) and 1997 ($n = 272$). These 1 m^2 quadrats were arranged in eight-quadrat arrays in plots 4 m^2 and distributed around the community to reflect the range of conditions. Data obtained in these quadrats were not used in analysing change at particular locations but were used to examine the degree of change at the spatial scale of the whole community.

Quadrat censuses in each of the 6 years were conducted by snorkelling. Many studies of submerged plants are based on biomass measurements, but destructive sampling is unsuitable for long-term studies of natural change, such as those undertaken here. Furthermore, although more time-consuming, in-water surveys provide more comprehensive and accurate information on community composition (Sheldon & Boylen, 1978; Wade & Bowles, 1981; Capers, 2000). In addition to quadrat censuses, I conducted a species inventory of the wetland from May to September each year, both by snorkelling and from a canoe, to compile a complete list of submerged angiosperms present during the 6-year period.

Using the snorkelling censusing data, I calculated mean species richness in 1 m^2 quadrats and 10 m^2 transects and mean stem density in quadrats, calculating the significance of year-to-year changes for eight transects (80 quadrats) censused from 1998–2001, using repeated measures analysis of variance (Sokal & Rohlf, 1995). I also calculated the Shannon–Weaver diversity index, H', and used the method of Magurran (1988) to calculate the significance of change in the index. I measured evenness by calcu-

lating J, the observed value of the Shannon–Weaver index as a proportion of its maximum value, which, with perfect evenness, equals the natural logarithm of the number of observed species. I used D, the proportion of all stems represented by the most abundant species, as a measure of dominance.

Similarity in the community from one year to the next was determined using the Jaccard index, which is based on the presence of shared species (Jaccard index $= C/S_1 + S_2 - C$, where C is the number of species present in both the years, S_1 is the number of species in the first year and S_2 is the number of species in the second), and the Morasita–Horn index (Magurran, 1988), which also considers abundance of species, using EstimateS software (Colwell, 1997). The Morasita–Horn index, C value, is calculated as:

$$C = 2 \sum [(an_i)(bn_i)]/[(da + bd)(aN)(bN)]$$

where aN is the number of individuals of all species in year a, bN is the number of individuals in year b, an_i is the number of individuals in the ith species in year a, and bn_i is the number of individuals in the ith species in year b,

$$da = \sum an_i^2/aN^2$$

and

$$db = \sum bn_i^2/bN^2.$$

In addition to determining compositional stability, defined as the year-to-year persistence of common species (Veblen, 1992), stability in the community was assessed by calculating Kendall's coefficient of concordance, W, using rank abundance data for the most abundant 11 species over the 6-year period (Siegel, 1956). This non-parametric statistic is calculated as:

$$W = \frac{\sum (R_j - (1/2)k(n+1))^2}{(1/12)[k^2(n^3 - 1)]}$$

where R_j is the sum of the ranks of each species across the 6 years, k is the number of years being compared and n is the number of species (Siegel, 1956). The statistic ranges from 0 when there is no correspondence among the ranks to 1 when there is perfect correspondence for all years; the probability that the observed level of concordance could occur by chance is determined by calculating the statistic $k(1 - n)W$, which approximately follows a χ^2 distribution with $n-1$ degrees of freedom (Siegel, 1956). Population

variation was assessed by calculating the standard deviation of the log of population censuses (Connell & Sousa, 1983). Correlation analysis was used to explore possible relationships either among species abundance or changes in their abundance.

Persistence was determined by calculating the proportion of occupied sites where species were present in consecutive years. Two-year persistence was based on cumulative totals for all possible 2-year combinations (1998–1999, 1999–2000 and 2000–2001), and 3-year persistence was based on the proportion of sites where species were present in 1998 and remained for two consecutive years, plus the proportion of sites where species were present in 1999 and remained through 2001. Four-year persistence is the proportion of sites where species occurred each year from 1998 to 2001. Colonisation rates were calculated as the proportion of sites from which a species was absent one year but present the next, using all available 2-year periods (1998–1999, 1999–2000 and 2000–2001).

The importance of spatial scale was assessed by comparing the coefficient of variation in species richness at the spatial scale of the quadrat, transect and entire community. I investigated the degree to which change varied with area by calculating mean percentage change for species richness in quadrats, transects and the entire community.

Finally, I used ordination to assess the degree of stability in the community, using transect data from 1998 to 2001. By considering many variables simultaneously, ordination provides a way to visualise the interrelationships among species or plots in multidimensional space. I used detrended correspondence analysis (Hill & Gauch, 1980), an unconstrained ordination procedure executed with the PC-Ord for Windows software package (McCune & Mefford, 1997). Abundance data for the nine most abundant species were centred and standardised to unit variance before being used in the analysis.

Results

During the 6-year study period, 17 submerged species were recorded in Whalebone Cove (Table 1), 16 of which were present every year from 1998 to 2001. The stable composition was reflected by high community similarity scores, especially on the Jaccard index (Table 2) and Kendall's coefficient of

Table 1 Species recorded in a freshwater tidal wetland from 1996 to 2001. The total number of stems of each species recorded in 1 m² quadrats each year is shown. P indicates that a species was not recorded in quadrats but was observed in other surveys of the wetland that year. The number of quadrats censused was 328 in 1996, 272 in 1997, 100 in 1998 and 2001 and 90 in 1998 and 1999

Family	Species	1996	1997	1998	1999	2000	2001
Hydrocharitaceae							
	Elodea nuttallii (Planch.) St. John	2809	5796	2968	1070	882	1849
	Vallisneria americana Michx.	4556	4527	3404	2885	1559	1904
Potamogetonaceae							
	Potamogeton crispus L.	85	P	1	P	P	P
	P. epihydrus Raf.	P	33	110	1	P	P
	P. nodosus Poir.	87	11	51	87	260	P
	P. pectinatus L.	16	47	P	P	6	23
	P. perfoliatus L.	732	153	179	210	897	96
	P. pusillus L.	2111	660	170	203	1117	591
	P. spirillus Tuckerm.	P	62	117	156	599	483
Najadaceae							
	Najas flexilis (Willd.) Rostk. & Schmidt	39	67	45	7	6	10
	N. minor Allioni	–	5	–	–	–	–
Zannichelliaceae							
	Zannichellia palustris L.	2530	1080	41	1302	5518	306
Ceratophyllaceae							
	Ceratophyllum demersum L.	670	405	826	329	202	296
Haloragaceae							
	Myriophyllum spicatum L.	8	1	12	9	24	P
Lentibulariaceae							
	Utricularia vulgaris L.	–	2	P	P	P	P
Callitrichaceae							
	Callitriche sp.	P	P	160	18	308	279
Pontederiaceae							
	Heteranthera dubia (Jacq.) MacM.	P	–	P	P	P	P

Table 2 Similarity in the submerged plant community in a freshwater tidal wetland, as measured by the Jaccard index, above the diagonal, and the Morasita–Horn index, below the diagonal. Abundance of species in 1 m² quadrats was used to calculate the Morasita–Horn index. The Jaccard index is based on shared species in the community, and more complete information on species present each year, based on whole-wetland inventories, was used in its calculation. No change in the species recorded in the wetland occurred from 1998 to 2001

	1996	1997	1998	1999	2000	2001
1996		0.82	0.94	0.94	0.94	0.94
1997	0.85		0.88	0.88	0.88	0.88
1998	0.84	0.96		1	1	1
1999	0.93	0.83	0.86		1	1
2000	0.69	0.42	0.32	0.65		1
2001	0.9	0.95	0.95	0.86	0.44	

concordance, which was 0.743 ($\chi^2_{10} = 44.55$, $P < 0.001$). The number of species in individual transects ranged from 2 to 10 (median = 6), and the number in single quadrats varied from 0 to 8 (median = 2). Stem density in quadrats ranged from 0 to >800 stems (median = 38).

Although species composition in the community changed little, the Shannon–Weaver diversity index differed significantly between years ($P < 0.001$ all years except 2000–2001, when $P < 0.05$). The index declined from 1996 to 1997, then rose each year until 2001, reflecting gradually increasing evenness in abundance distributions (Table 3). The distribution of species richness shifted during the 6-year period. From 1996 to 1999, more than half of the quadrats had two or fewer species, and <25% had four or more

Table 3 Six-year data for the submerged plant community in Whalebone Cove, a freshwater tidal wetland on the Connecticut River. All quadrats used in community censuses were 1 m². Quadrats were arranged in 10-m transects from 1998 to 2001, and eight of these transects were used in transect-level mean richness and stem density comparisons over time. Whole-wetland inventories, conducted by snorkelling and from a small boat, were also used to determine total species richness for the community. Repeated-measures analysis of variance was used to determine significance of change over time in mean richness and stem density in quadrats and transects from 1998 to 2001, and *F* statistics of these tests (d.f. = 3 in all cases) are shown

|	1996 (*n* = 328)	1997 (*n* = 272)	1998 (*n* = 100)	1999 (*n* = 90)	2000 (*n* = 90)	2001 (*n* = 100)	*F*
Richness, community	15	16	16	16	16	16	
Richness, transect mean (SE)	–	–	5.8 (0.696)	5.56 (0.503)	7.44 (0.294)	5.1 (0.722)	5.690*
Richness, quadrat mean (SE)	2.09 (0.067)	2.13 (0.073)	2.55 (0.163)	2.44 (0.163)	3.622 (0.163)	2.88 (0.173)	18.551**
Stem abundance, quadrat total	13 643	12 849	8004	6227	11 378	5837	
Stem density, quadrat mean	41.6 (2.09)	47.2 (3.10)	80.8 (6.09)	69.7 (10.82)	126.4 (20.89)	58.4 (5.53)	11.599**
Shannon–Weaver diversity, *H'*	1.690	1.349	1.399	1.551	1.681	1.719	
Evenness, *J*	0.705	0.511	0.545	0.624	0.677	0.747	
Dominance, *D*	0.334	0.451	0.425	0.460	0.485	0.326	

*$*P \leq 0.01$, $**P \leq 0.001$.

(Fig. 1). Richness values shifted in 2000, when <40% had two or fewer species, and 40% had four or more.

The coefficient of variation is species richness was higher among quadrats than among transects in each of the 4 years for which transect data were available

(mean = 0.574 for quadrats, 0.312 for transects) and was higher among both quadrats and transects than at the community level (CV = 0.027), indicating that variability decreased as the spatial scale of sampling increased. Change in richness in quadrats from one
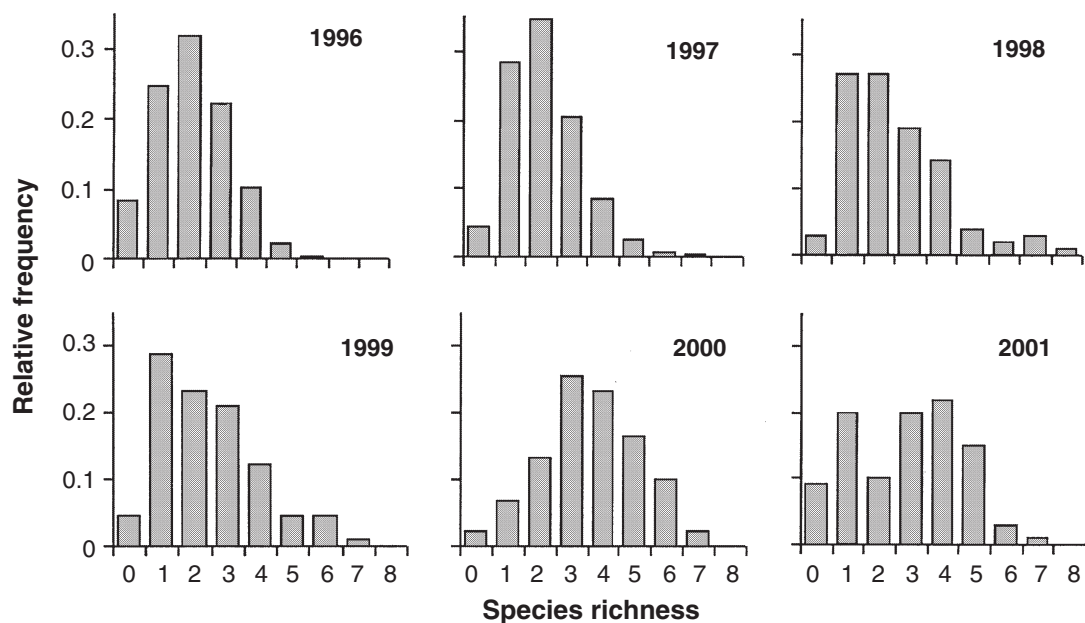
Fig. 1 The relative frequency distributions of submerged species richness in quadrats are shown for the 6 years of study in a freshwater tidal wetland. For each year, bars represent the proportion of all sampled quadrats in which the richness value was 0–8 species. From 1996 to 1999, more than half of all 1 m² quadrats had two or fewer species, but richness increased in 2000, when 78% had three or more species. The proportion with three or more species declined to 61% again in 2001, but the modal class increased to four species for the first time.
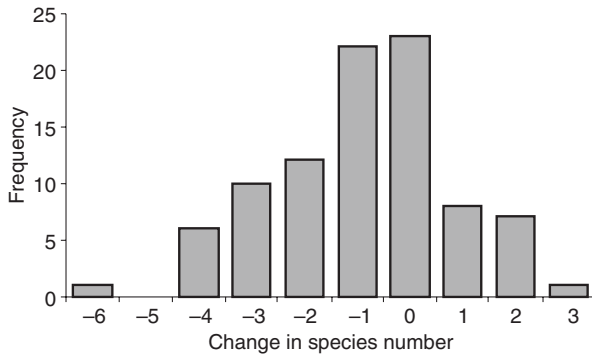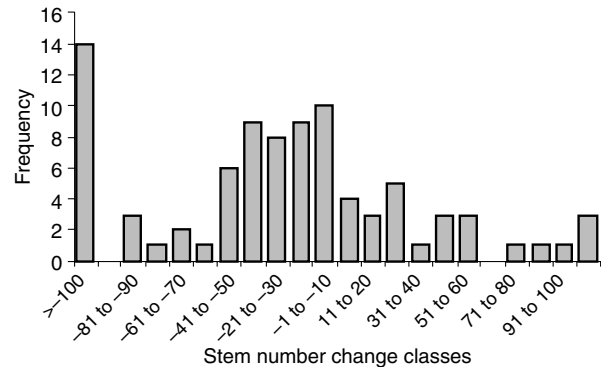
Fig. 2 Distribution of change in species richness values among submerged plant species in a freshwater tidal wetland. Shown are the number of quadrats where the number of species present increased or decreased by the indicated amount between 2000 and 2001, based on in-water censuses in 90 quadrats, each 1 m² in area.

Fig. 3 Distribution of stem abundance change values among submerged plant species in a freshwater tidal wetland. Shown are the number of quadrats where the total number of stems increased or decreased by the indicated amount from 2000 to 2001, based on in-water censuses in 90 quadrats.

year to the next also was greater than in transects (59% on average in quadrats, 43.7% in transects), and both exceeded the level of change in the community (10.3% if only quadrat data were considered and 1.3% when all information on species present was considered).

Species number and stem density commonly changed in transects and quadrats from one year to the next. No quadrat maintained the same complement of species from 1998–2001, and richness changed in >60% of all quadrats each year. Of the nine transects censused in both 2000 and 2001, seven lost species, with three losing four or more species. Among the 90 quadrats censused in both 2000 and 2001, 16 gained at least one species, 51 lost at least one species, and two had no plants in either year (Fig. 2); species richness was unchanged in 21 quadrats. Quadrats gained as many as three species and lost as many as six. Only 10 quadrats had exactly the same complement of species both years. One quadrat lost >800 stems from 2000 to 2001, although this was extreme. Among the 88 quadrats with submerged vegetation, 49 lost fewer than 100 stems, and 14 lost 100 or more; 22 quadrats gained fewer than 100 stems and three gained 100 or more (Fig. 3).

Vallisneria americana was most frequent each year, appearing in 54–76% of all quadrats. The importance of several other frequently occurring species changed from year to year: *Elodea nuttallii* occurred in 28–52% of all samples, *Ceratophyllum demersum* in 28–44% of samples and *Potamogeton pusillus* in

24–54%. *V. americana* was the most abundant species in 4 of the 6 years (and second most abundant in the other two).

The abundance of individual species often changed dramatically from one year to the next, although the standard deviation of log abundance (based on total abundance in the eight transects censused every year from 1998 to 2001) was not exceptionally high, ranging from 0.30 to 0.40 for half of the 10 most abundant species in transects (Table 4). Fluctuations in abundance were not always reflected by rearrangement of abundance and frequency ranks. Abundance of *V. americana* declined by >50% (3082 to 1532 stems) across eight transects from 1998 to

Table 4 Temporal variation in the abundance of submerged plants in a freshwater tidal wetland, measured as the SD of the logarithm of the total abundance of each species in the eight transects surveyed annually from 1998–2001. All species were recorded in the transects every year except *P. nodosus*, which was present 3 years

Species	SD
Vallisneria americana	0.160
Elodea nuttallii	0.187
Ceratophyllum demersum	0.303
Potamogeton spirillus	0.355
P. nodosus	0.361
P. pusillus	0.385
Najas flexilis	0.402
P. perfoliatus	0.417
Callitriche sp.	0.569
Zannichellia palustris	0.982

Table 5 Persistence in a submerged plant community in a freshwater tidal wetland. Shown is the proportion of 1 m^2 quadrats ($n = 80$) in which species occurred each year of 2-, 3- and 4-year periods (and the number of quadrats on which the percentage was calculated) using combined data. Two-year persistence is the total from 1998–1999, 1999–2000 and 2000–2001; 3-year persistence is based on the periods from 1998 to 2000 and from 1999 to 2001; 4-year persistence indicates species were present each year from 1998 to 2001

	2-year	3-year	4-year
Vallisneria americana	83.8 (191)	65.5 (139)	56.3 (71)
Potamogeton pusillus	74.5 (98)	53.6 (56)	45.8 (24)
P. spirillus	48.1 (79)	50 (28)	40 (15)
Ceratophyllum demersum	75 (100)	47.8 (69)	40 (40)
P. perfoliatus	57.4 (47)	48.1 (27)	38.5 (13)
Elodea nuttallii	72.8 (103)	48.1 (79)	36.5 (52)
Callitriche sp.	32.4 (34)	42.9 (14)	33.3 (9)
Zannichellia palustris	55.3 (47)	29.6 (27)	18.2 (11)
Najas flexilis	18.8 (16)	0 (12)	0 (8)
Myriophyllum spicatum	6.7 (15)	0 (11)	0 (6)
P. nodosus	52.6 (19)	40 (10)	0 (4)

Table 6 Mean recruitment rates of submerged plants in a freshwater tidal wetland for 1998–2001. Shown is the percentage of quadrats from which a species was absent one year and present the next (with the number of potential colonisation sites across the four years).

Species	Rate (N)
Potamogeton pusillus	27.7 (177)
P. spirillus	27.6 (199)
Vallisneria americana	22.5 (80)
Ceratophyllum demersum	21.1 (171)
Elodea nuttallii	19.3 (166)
Callitriche sp.	12.2 (237)
Zannichellia palustris	9.9 (232)
P. perfoliatus	8.1 (234)
Najas flexilis	3.8 (263)
Myriophyllum spicatum	3.4 (264)
P. nodosus	1.5 (262)
P. pectinatus	1.4 (277)
P. epihydrus	0 (277)

2000, although it remained one of the two most abundant species. Abundance of *E. nuttallii* declined from 2357 stems to 1070 stems in nine transects between 1998 and 1999. *Zannichellia palustris*, an annual species, increased its abundance from 30 stems in eight transects in 1998 to >5500 in 2000, although its frequency increased only from 7.8 to 25%; the species declined again in 2001, with only 209 stems in the eight censused transects at a frequency of 12.5%. Generally, frequency fluctuated less dramatically than abundance. There were exceptions, however; *P. spirillus* was recorded in 3% of all quadrats in 1997 and in 59% 4 years later.

The four most abundant species remained in >70% of quadrats from one year to the next, but only *V. americana* remained for 4 years in more than half of the quadrats it occupied in 1998 (Table 5). Six species were found each year from 1998 to 2001 in 33 to 50% of quadrats, but no other species appeared in any quadrat for four consecutive years, either through persistence or recruitment. Four species, all of them among the most abundant each year, had high recruitment rates, appearing each year in at least 20% of the quadrats from which they had been absent a year earlier (Table 6). Several less abundant species had very low rates of colonisation.

Neither abundance nor change in abundance was strongly correlated among species. Abundance was not correlated for any species pair in more than 4 of

the 6 years for which data were available: abundance of *E. nuttallii* and *C. demersum* was correlated positively in 4 years ($P < 0.001$ in all cases), abundance of *E. nuttallii* and *Callitriche* was correlated positively in 4 years ($P < 0.001$ in all cases), and abundance of *E. nuttallii* and *V. americana* was correlated negatively in 4 years ($P \leq 0.006$ in all cases). Changes in the abundance of *P. nodosus* and *Z. palustris* were correlated positively from 1998 to 1999, 1999 to 2000 and 2000 to 2001 ($P < 0.001$ in all cases) but not from 1996 to 1997, and changes in no other species pairs were correlated (at the $P \leq 0.01$ level) in more than two of the four periods.

In the ordination, only axis 1 explained a significant amount of variation in the data (18% of the total). The axis divided transects primarily according to abundance of *E. nuttallii* and *C. demersum*, which were high on axis 1, and *V. americana*, which was low (Fig. 4). Each year, transects were divided in approximately the same way, with some closer to *E. nuttallii* and some closer to *V. americana*. Most transects moved little from one year to the next; those affiliated with *E. nuttallii* remained near that species in ordination space, and those near *V. americana* remained there each year. There were two exceptions, however. Transect 6 was closely associated with *Elodea* in 1998 and 2001 but with *Vallisneria* in 1999 and 2000. The trajectory of transect 8 was the reverse, beginning and ending near *Vallisneria*, but closely associated with *Elodea* in 1999 and 2000.
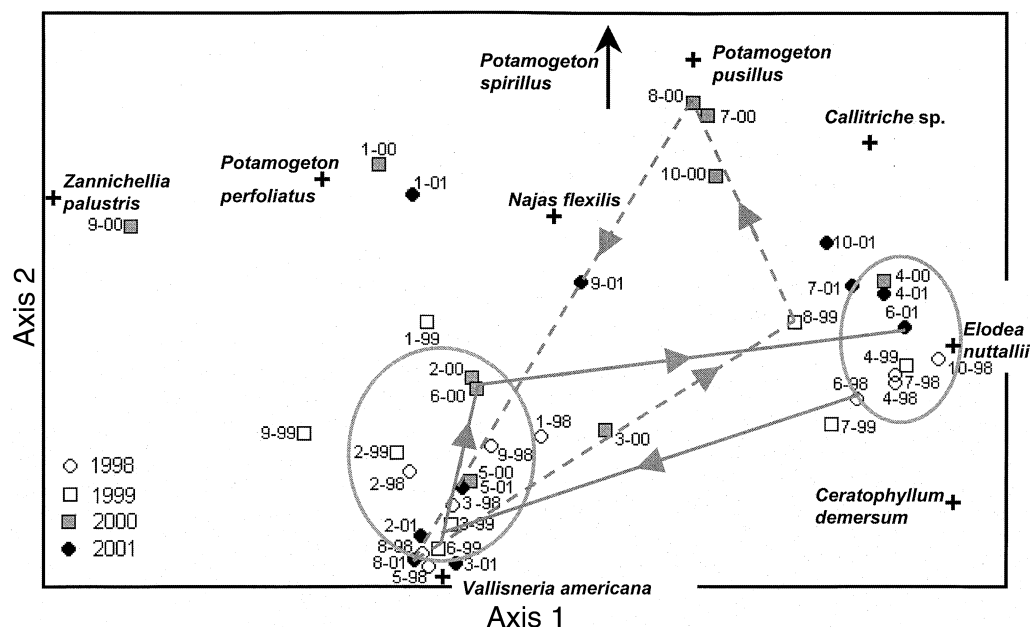
Fig. 4 Detrended correspondence analysis of 10 transects that were censused each year from 1998 to 2001. The abundance of the nine most abundant and frequently occurring species were used in the ordination, and their centroids are indicated. The positions of transects each year also are indicated; '9-00', for example, indicates the position of transect 9 in 2000. The positions of most transects changed little from one year to the next. The positions of transects 2 and 4 all 4 years, for example, lay within the ellipses shown. However, transects 6 and 8 were more variable, and their positions in ordination space changed dramatically from one year to the next. Axis 2 was shortened in the figure, and the position of *P. spirillus* was beyond the limit of the axis shown.

Discussion

The submerged plant community in Whalebone Cove had high compositional stability, based on species presence at the largest spatial scale, especially during the final 4 years of the study, when no change occurred among the 16 species present. This stability was reflected by high community similarity scores and the high Kendall's *W*. However, community-level stability was maintained in spite of constant change at the smaller spatial scales of quadrat and transect. Richness changed in >60% of quadrats every year, and species composition changed in many of the quadrats where richness did not. No quadrat had the same complement of species for four consecutive years. Species often colonised quadrats where they had not occurred before and disappeared from other quadrats. Although species composition changed little at the scale of the whole community, fluctuations in abundance were reflected in annual changes in the Shannon–Weaver diversity index. In the hierarchical scheme for persistence proposed by Rahel (1990), this community was persistent in terms of species presence but not in rank abundance or

absolute abundance. At the spatial scales of the transect and quadrat, all persistence disappeared. Both variability and change depended on spatial and temporal scales. Species richness varied more among quadrats than among transects and more among transects than in the community as a whole; richness also changed more among quadrats than among transects and more among transects than in the community.

The dependence of stability on spatial scale in the community was well-illustrated by the ordination, in which transects each year clustered around the dominant species, *V. americana* and *E. nuttallii*, indicating that organisation at the scale of the community does not change from one year to the next. Individual transects, however, changed, and two of the 10 switched from one major species to the other and then back again. That the trajectories of these transects over time were exactly opposite each other indicates that the fluctuations in species abundance were local and did not reflect larger, directional changes in the community. The independence among both species abundance values and change in abundance was confirmed by the correlation analysis, showing that

whatever determined abundance and change in abundance varied among species.

In the face of high turnover at the smallest spatial scale, the community persisted each year through recruitment at new locations. Although most species in the community were perennials, no species remained at an average of >85% of the quadrats where it occurred from one year to the next, and 4-year persistence reached 50% for only one species. On the other hand, four species colonised 20% or more of available sites every year. Presumably, colonisation rates for other species were higher than they appeared. The methods used in this study underestimate recruitment and overestimate persistence, especially for the more abundant species, because it was not possible to determine whether a species had disappeared but then recolonised any quadrat between censuses; such instances would have been recorded as persistence, but in many cases the species may have re-established, either by *in situ* recruitment or recolonisation from external sources. As one example, *Z. palustris* appeared to persist in an average of 55% of quadrats where it occurred from one year to the next but, because it is an annual species, must have regrown from seed in all of them.

Other research also has found a high degree of change in riverine communities at small spatial scales but a high degree of stability at the level of the community, at least in moderately disturbed systems. Butcher (1933) found that abundance of plants in two rivers changed constantly over a 3-year study period, with patches repeatedly colonised and later left bare. Composition of an aquatic plant community on the South River in Quebec did not change over 6 years, but *V. americana* replaced *E. canadensis* as the dominant species (Hamel & Bhèreur, 1982). Wiegleb (1988) found that, over a period of 10 years, composition of a river community in northern Germany remained nearly constant, and changes among species were independent of each other. Similar community stability was reported in a 10-year study of a frequently disturbed former channel of the River Rhône, although a less disturbed site experienced considerable change in community composition during the period (Bornette & Amoros, 1996).

At the population level, year-to-year changes were dramatic but do not appear to be unusual, based on a review by Connell & Sousa (1983) of 49 studies
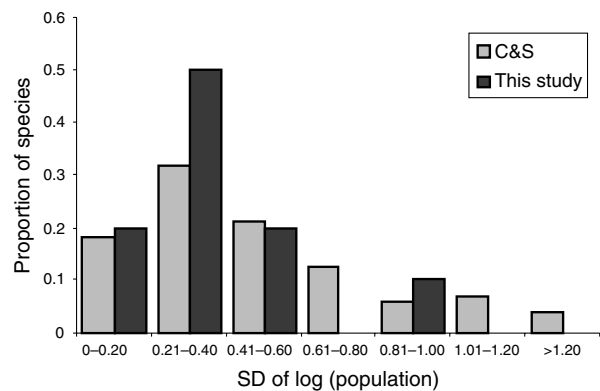

Fig. 5 The distribution of variation in 10 populations of submerged plants is compared with those reported by Connell & Sousa (1983) for 104 species, including terrestrial plants, terrestrial insects, aquatic invertebrates, parasites, birds and mammals. Populations of aquatic plants in Whalebone Cove appear to be no more variable than other species.

involving 104 species, including terrestrial plants, terrestrial insects, aquatic invertebrates, parasites, birds and mammals. Connell & Sousa (1983) reported that the standard deviation of log abundance ranged up to 1.89, but the highest recorded in Whalebone Cove was 0.98 (Table 4). The modal class of standard deviations reported by Connell & Sousa (1983) was between 0.21 and 0.40, and that was also the modal class for the aquatic plants in the present study (Fig. 5). It is significant that Connell & Sousa (1983) found no aquatic plant study that satisfied the criteria for inclusion in their review, such as quantitative population data and study duration long enough to permit at least one complete turnover in the community.

The exact cause of the high degree of species turnover and abundance fluctuations across the wetland was not the focus of this study. However, there was no evidence of interspecific interactions or successional changes, and disturbance was presumably largely responsible for the observed changes. Many submerged plant species root weakly in the sediment (*C. demersum* has no roots at all), and communities of these plants traditionally have been thought to be highly vulnerable to disturbance, especially in river systems (Barrat-Segretain, 1996; Barrat-Segretain & Amoros, 1996; Combroux *et al.*, 2001). Disturbance in aquatic plant communities is caused by flood or ice scour, wind-driven waves, ducks, mammalian herbivores, boats and other agents

(Fassett, 1957; Sculthorpe, 1967; Hutchinson, 1975; Jupp & Spence, 1977; Liddle & Scorgie, 1980; Murphy & Eaton, 1983; Wetzel, 2001), although quantitative data on the distribution of frequency, spatial extent and severity of disturbances are almost completely lacking (Sousa, 1984; Barrat-Segretain & Amoros, 1996). A further cause of small-scale disturbance in the studied wetland is the shifting of the unconsolidated sediment during the winter, which results in redistribution of many propagules (R. S. Capers, unpublished data). Although silty sediment is common in the lower reaches of many large rivers, it is unclear how widely the findings of this study may be applied elsewhere. Would submerged plant communities in open streams undergo even more dramatic small-scale changes because of stronger currents or less change because of coarser, more stable substrata? Research on the River Rhône (Henry *et al.*, 1994) found that areas of coarse substratum were more extensively disturbed by floods than fine-sediment areas removed from the main channel. Floods in coarse-substratum areas reduced species number and affected the abundance of individual species, although the community recovered quickly and community composition remained stable over 5 years (Henry *et al.*, 1994).

This and other recent work has confirmed the long-held belief that vegetative reproduction is more important than sexual reproduction for maintaining aquatic plant populations (Barrat-Segretain, 1996; Philbrick & Les, 1996; Cellot, Mouillot & Henry, 1998; Abernethy & Willby, 1999; Combroux *et al.*, 2001), and it has contributed to a growing body of evidence that life forms and life history traits vary along a disturbance gradient in riverine wetlands (Abernethy & Willby, 1999; Combroux *et al.*, 2001). Vegetative fragments appear to be most important where plants are subject to frequent flood scour, while areas exposed to both flooding and sediment emersion are more favourable for regeneration from seed and bud banks (Combroux *et al.*, 2001). In an eight-site study, Abernethy & Willby (1999) found that hydrophytes in permanently submerged, moderately disturbed wetlands were maintained by rhizomes and vegetative fragments. These areas were most similar to the wetland studied here, and populations of this community also rely primarily on vegative propagules to recolonise locations from which they have been removed by disturbance (Capers, 2003). The studied riverine plant community exists as a shifting mosaic of patches (Resh *et al.*, 1988) in which submerged plants repeatedly colonise and are locally extirpated, persisting in a dynamic equilibrium (Huston, 1979) or dynamic stability (Dawson, 1988).

Acknowledgments

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