Limnol. Oceanogr., 52(3), 2007, 1195–1207
© 2007, by the American Society of Limnology and Oceanography, Inc.

Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality

Nancy B. Rybicki[1] *and Jurate M. Landwehr*
United States Geological Survey, 430 National Center, Reston, Virginia 20192

Abstract

We assessed species-specific coverage (km^2) of a submerged aquatic vegetation (SAV) community in the fresh and upper oligohaline Potomac Estuary from 1985 to 2001 using a method combining field observations of species-proportional coverage data with congruent remotely sensed coverage and density (percent canopy cover) data. Biomass (estimated by density-weighted coverage) of individual species was calculated. Under improving water quality conditions, exotic SAV species did not displace native SAV; rather, the percent of natives increased over time. While coverage-based diversity did fluctuate and increased, richness-based community turnover rates were not significantly different from zero. SAV diversity was negatively related to nitrogen concentration. Differences in functional traits, such as reproductive potential, between the dominant native and exotic species may explain some interannual patterns in SAV. Biomass of native, as well as exotic, SAV species varied with factors affecting water column light attenuation. We also show a positive response by a higher trophic level, waterfowl, to SAV communities dominated by exotic SAV from 1959 to 2001.

Submerged vascular macrophytes, commonly referred to as submerged aquatic vegetation (SAV) in the Chesapeake Bay, provide necessary habitat and/or food for invertebrates, fish, and waterfowl (Rozas and Odum 1988; Perry and Deller 1996), but the quality of this habitat is threatened by the stress of diminishing water quality and invasion by exotic species. Despite the global prevalence of these stressors on SAV (Litav and Agame 1976; Phillips et al. 1978; Kozhova and Izhboldina 1993), there is a lack of long-term and quantitative data with which to characterize the behavior of a SAV community subject both to such stresses and to restorative efforts to improve water quality.

The tidal Potomac River and Potomac Estuary are part of the Chesapeake Bay watershed (Fig. 1), and large public expenditures have been made to protect its living resources, including SAV. Several episodes of high SAV abundance in the upper tidal Potomac River have been documented. A dense community of SAV reported in 1916 (*Potamogeton crispus* L. [curly pondweed] and other *Potamogeton* spp., *Ceratophyllum demersum* L. [coontail], and *Vallisneria americana* Michaux [wild celery]) remained abundant until the late 1930s, but disappeared by 1952 as wastewater contributions increased (Carter et al. 1985). From the 1950s to the 1970s, algal blooms became massive and persistent. The exotic species *Myriophyllum spicatum* L. (milfoil) proliferated from 1958 until it disappeared abruptly after 1965 (Stevenson and Confer 1978). For more than a decade, the upper tidal Potomac was devoid of SAV. Following upgrades to sewage treatment plants, including enhanced phosphorus removal, SAV returned after 1982 (Carter and Rybicki 1986). Its resurgence was attributed to the decreased frequency of algal blooms and greater water clarity, as well as to favorable flow and weather conditions (Carter et al. 1994). Among the 12 species observed was a monoecious biotype of *Hydrilla verticillata* (L. f.) Royle (hydrilla), an aggressive exotic that was newly reported in the tidal Potomac River. Between 1985 and 1998, point and nonpoint source loadings of total nitrogen (TN) were reduced; TN concentration in effluent from the Blue Plains Wastewater Treatment Plant (Fig. 1), the major plant serving Washington, D.C., and vicinity, was reduced by half, to 7.5 mg L^{-1} (Butt and Brown 2000). SAV, including *H. verticillata*, continues to be present, while exhibiting considerable interannual variation in coverage.

Rapid expansion of exotics in an ecosystem threatens its stability by the possible displacement of native SAV species (Madsen et al. 1991; Knapton and Petrie 1999), particularly if the exotic SAV has low value as a food and habitat source for waterfowl (Dick et al. 2004). These negative effects of exotic species on native species of SAV and on waterfowl are sometimes used as support for regional aquatic weed-eradication programs. However, food studies indicate that some exotics (*H. verticillata* and *M. spicatum*) are consumed readily by waterfowl (Johnson and Montalbano 1984; Perry and Deller 1996). Furthermore, some exotic and native species of SAV can provide food resources throughout the year, not just during the summer growing season. Some waterfowl feed on the benthic invertebrates that are abundant in sediments of SAV beds, and many birds feed directly on below-ground buds and tubers, which persist and are consumed by birds through the winter (Perry and Deller 1996). Although most above-ground SAV biomass senesces by December in temperate

[1] Corresponding author (nrybicki@usgs.gov).

Acknowledgments

We appreciate the technical assistance of J. T. Reel and A. V. Lombana and the constructive comments from R. C. Jones, George Mason University, and the anonymous reviewers whose suggestions improved this manuscript.

We are grateful for support from the United States Geological Survey (USGS) National Research Program; Chesapeake Bay Program; Virginia Institute of Marine Sciences; United States Army Corps of Engineers (Baltimore, Maryland); the Metropolitan Washington Council of Government's Aquatic Plant Management Program; and the Washington D.C. Fisheries Division.

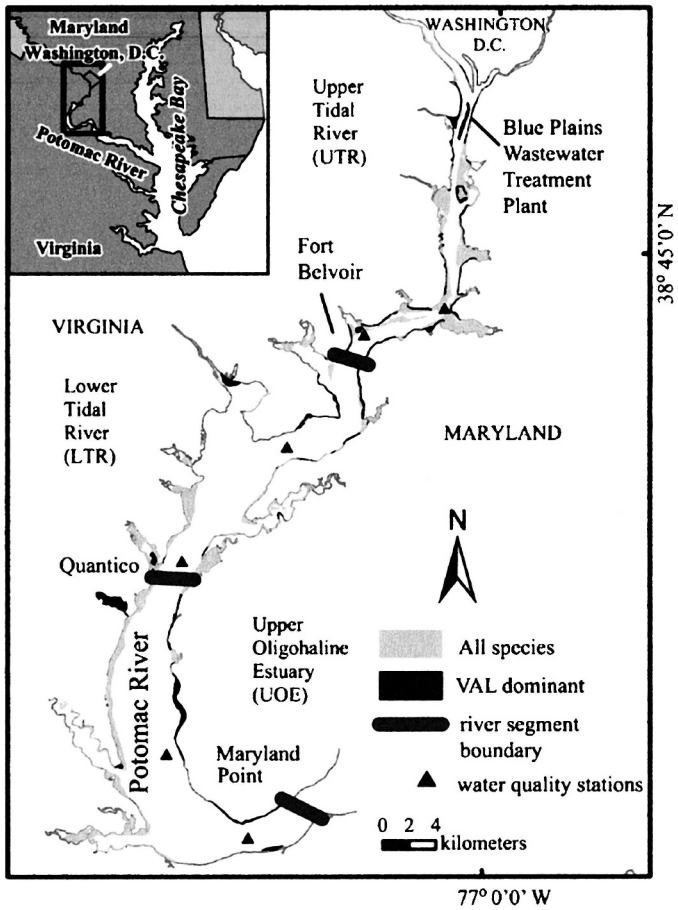

Fig. 1. Study area showing submerged aquatic vegetation (SAV) coverage combined for all years of the study and water quality stations in the three river segments of the tidal Potomac River and Estuary. Top of map is the northern boundary of the study area and VAL is *Vallisneria americana*.

regions, some live shoots remain standing, and others form floating mats containing dormant buds that wash up onto the intertidal zone and are available for winter waterfowl.

In this work we make use of annual field observations to develop a multiple-year quantitative data set with which to document the species composition of the SAV community in an estuary subject to the invasion of exotic SAV species during a period of improving water quality. We examine relations between SAV species, diversity, richness, and water quality. We then test the null hypotheses that exotics displace natives, that diversity and abundance are responsive to water quality change, that diversity and spatial or temporal turnover rates vary with biomass production, and that this primary producer community dominated by exotics is detrimental overall to a higher trophic community, waterfowl. We focus on two exotic SAV species, *H. verticillata* and *M. spicatum*, and one native species, *V. americana*. Not only are they the most prominent species in this study, but also they show two different types of functional traits, based on the terminology of Grime (1979), Murphy et al. (1990), and Suding et al. (2005). Relative to one another, *H. verticillata* and *M. spicatum* have acquisitive survival strategy traits (i.e., competitive and exploitative), while *V. americana*'s survival traits are more conservative (i.e., stress tolerant) (Murphy et al. 1990; Madsen et al. 1991). Significant covariation between species biomass and water quality conditions that help identify differences and similarities between individual species as well as between exotic and native species will be discussed. Relevant results will be placed in context with ecosystem restoration efforts, aquatic plant management, and current concepts about species diversity and richness.

Methods

Study area—The study was conducted in the tidal Potomac River, the second largest tributary in the Chesapeake Bay watershed (Fig. 1). The study area extended 40 km from Washington, D.C., to Maryland Point along a salinity gradient from freshwater to oligohaline water. The average annual river discharge at the Little Falls streamflow gauging station was 322 $m^3 s^{-1}$ for the period of record, 1930–2001. Tides are semidiurnal and range between 0.9 and 0.3 m at the uppermost and lowermost river segments, respectively (Cronin 1971). Within the study area, the channel is narrow and deep, but flanked by wide shoals. The tidal river is turbid (Secchi depth < 1.0 m), so that the potential SAV habitat is largely confined to areas that are <2 m deep at mean low tide.

The reach from Washington, D.C., to Quantico, Virginia, is termed the freshwater tidal Potomac River (average surface salinity < 0.5). This reach has been further divided for this and previous studies into the upper tidal river (UTR) and lower tidal river (LTR) segments (Fig. 1) based on differences in SAV distribution and water clarity between the two segments (Carter and Rybicki 1986; Carter et al. 1994). The UTR receives effluent (16.2 $m^3 s^{-1}$) from the Blue Plains Wastewater Treatment Plant (Fig. 1), and during low river flows, effluent constitutes a substantial portion of the total discharge. The third river segment is the upper oligohaline estuary (UOE; Fig. 1), in which freshwater mixes with salt water, and mean surface salinity ranges from 0.5 to 5.

SAV data—Species coverage in each river segment from 1985 to 2001 was quantified based on concurrent information obtained through two independent programs. First, SAV beds were identified from annual aerial photographs, and the total surface area of these photo-interpreted (PI) beds was determined (e.g., Orth et al. 1986 and subsequent years). Second, SAV beds were identified annually by direct field observation, and the proportion of the field bed's surface area occupied by any specific SAV species was determined (Rybicki 2000). Both field and photo observations were made at the end of the growing season (August–October), when most freshwater species have reached their maximum annual standing crop (Orth et al. 1986).

Aerial photos, acquired under specific guidelines (maximum biomass season of SAV, low tidal stage, low turbidity, etc.) to allow for optimal photography of SAV, are an efficient and widely used technique to analyze the distribution and abundance of SAV (Orth and Moore

1983). Such black-and-white aerial photographs (1 : 24,000 scale) of the Chesapeake Bay have been acquired annually by the Virginia Institute of Marine Sciences (VIMS). These photographs were used to identify areas with SAV present at a level detectable by this technique. The imagery of the vegetation is transferred to the standard United States Geological Survey (USGS), 1 : 24,000 scale topographic quadrangle (quad) maps that provide land features in significant detail to insure the photographs and base maps are properly aligned (Orth and Moore 1983). Surface area of PI beds is termed coverage, whereas the percent of this coverage overlain by SAV canopy is termed SAV density (percent canopy cover). Each individual PI bed was classified by VIMS into one of four SAV density classes: class 1 indicates that plants within the bed are very sparse, with canopy cover of <10%; class 2 indicates canopy cover of 10–40%; class 3 indicates canopy cover of 40–70%; and class 4 indicates canopy cover of >70%. Each PI bed was assigned an identity code and was digitized to determine its coverage (area).

In September 1988, black-and-white imagery (1 : 24,000) was not available from VIMS, but color aerial photographs (1 : 12,000 scale) were acquired by the Washington Metropolitan Council of Governments for their Aquatic Plant Management Program employing the same protocol as that used by VIMS. USGS workers determined SAV coverage for each river segment by overlaying the color photos with a transparent, ruled grid and counting vegetated cells. Percent canopy cover was mainly >70%, and therefore, all beds in 1988 were designated as class 4 density. Again, in 2001, complete aerial photographic coverage of the study area was not available from VIMS. That year, perimeters for each bed were sketched from field observation onto USGS 1 : 24,000 scale quad maps. SAV measured at ≤1 m below the surface was visible from a boat, and direct field observations were used to draw the perimeters of each bed. Bed location was referenced to depth contours and other map features and then digitized using geographical information software. Bed density class was assigned on the basis of field observations of each bed.

Species composition cannot be determined from aerial photos and requires field observations. In the first year of this study (1985), field observations were only made in the UTR; however, as *H. verticillata* spread downstream, field observations were initiated in 1986 in the LTR and in 1990 in the UOE. As *H. verticillata* became established (>0.5 km^2) in a river segment, direct field observations of vegetated areas and shoals (<2.0-m depth contour) were made annually from a shallow draft boat. Observations were made during the season of maximum biomass of SAV and within ~2.5 h of the low tidal stage so that the SAV was generally clearly visible from a boat. Additional raking of the sediment with a metal rake was used to establish presence and species composition of deeper plants or understory plants or to verify absence of vegetation on shoals in which SAV was not visible. Plants growing at depths greater than 2 m may be difficult to see, and abundance of understory and linear leaved species may be underestimated by the raking technique. Proportional canopy coverage of each species in a SAV bed was estimated primarily from visual observation of the SAV canopy.

Isolated or contiguous beds of substantially different composition were differentiated from one another on the field map, and the beds (and their species associations) were termed "field beds." As in 2001, field bed locations were recorded each year in the field on 1 : 24,000 scale maps. Absence of vegetation on shoals was also noted on the quad maps. In the laboratory, the field bed data were entered in a spreadsheet, and each (of 12) USGS 1 : 24,000 scale quad map that was annotated with field bed locations was cross referenced with the corresponding map showing the location of the PI beds digitized by VIMS. That is, based on a spreadsheet listing all PI beds by quad, each field bed and the field bed's species composition attributes were assigned to the corresponding PI bed by one USGS staff member, and correspondence of overlap and assignment to the correct PI bed was verified by a second staff member for each field bed assignment. In some cases the relationship between field beds and PI beds was one to one, and in other cases there was more than one field bed observation (species association) within a single PI bed. In a few cases, a field bed was observed where no PI bed was delineated because the bed area was below the aerial detection limit of ~5 m^2; in these cases the species data and coverage of the bed were dismissed from the data set. The maps of field beds, including the species data, are provided to the VIMS, and a list of species for each observation is shown in annual reports (for example, Orth et al. 1986).

Annual information was cumulated by river segment, so that the areal coverage (km^2) of a species v in river segment L is $AS_{vL} = \sum_{j=1}^{NB_L} a_j \left[\sum_{i=1}^{n_j} f_i\, p_{vi}/100\right]$ where NB_L is the number of PI beds in a river segment L, j is a specific PI bed, a_j is the area (km^2) of the j-th PI bed, n_j is the total number of field beds mapped within the j-th PI bed, i is a specific field bed identified to lie within the j-th PI bed, p_{vi} is the field-determined percent coverage by species v in the field bed i, and f_i is the estimated fraction of the j-th PI bed area encompassed by field bed i, such that the f_i are positive values and sum to 1. Estimates of f_i were obtained by visual comparison of maps of PI and field beds. The cumulative species coverage in river segment L is $CAS_L = \sum_{v=1}^{M_L} AS_{vL}$, where M_L represents richness (the number of observed species in river segment L), so that the percent coverage by each species is $P_{vL} = 100\, AS_{vL}/CAS_L$. The SAV diversity in river segment L is defined using percent coverage as an areal analogue to the Shannon–Weiner diversity, namely, $DIV_L = -\sum_{v=1}^{M_L} (P_{vL}/100) \ln (P_{vL}/100)$.

To estimate a more realistic coverage and one that represents SAV biomass (used here to indicate peak biomass), we derived a density-weighted coverage using-the density class attribute for each PI bed. Based on field observations (Moore et al. 2000; Rybicki 2000) for bed density of classes 1, 2, 3, and 4, we assigned a fractional canopy cover conversion coefficient, C_j, of 0.05, 0.25, 0.55, and 0.85, respectively. The biomass (km^2) of species v in river segment L is calculated as

Table 1. Submerged aquatic vegetation community characteristics and seasonal (April to October) median values of water quality for three river segments in the upper tidal Potomac River and Estuary.*

Year	Cumulative coverage (km²)	Richness	Diversity	Exotic (%)	Cumulative biomass (km²)	Chl *a* (μg L⁻¹)	TSS (mg L⁻¹)	TN (mg L⁻¹)	TP (mg L⁻¹)
Upper tidal river									
1985	12.8821	9	1.44	73.8	8.5616	7.98	14.5	n.d.	0.07
1986	14.1392	7	0.75	91.4	9.9544	7.35	15.0	2.60	0.06
1987	14.4783	6	0.77	90.5	11.8608	8.37	14.0	2.54	0.08
1990	5.4839	8	0.30	96.7	3.3712	8.52	18.0	2.60	0.08
1993	3.3856	8	1.35	59.4	2.3168	12.71	19.5	2.60	0.08
1994	3.9203	7	0.66	85.4	2.7275	18.44	17.0	2.42	0.08
1995	4.0340	7	0.76	83.2	3.0766	19.94	20.0	2.39	0.09
1996	2.6690	8	0.92	80.5	1.1481	8.65	23.0	2.19	0.08
1997	3.6273	7	0.75	81.3	2.4501	20.50	20.5	2.01	0.07
2001	13.1418	8	1.62	59.2	10.1710	12.33	10.3	1.81	0.07
Lower tidal river									
1986	0.3167	6	0.39	99.8	0.0323	12.79	17.5	1.95	0.09
1987	0.9401	6	0.81	93.5	0.6115	7.73	14.0	2.20	0.06
1990	9.9873	7	0.55	93.6	7.7484	4.38	17.0	2.40	0.07
1993	7.4403	6	0.95	88.3	5.9176	4.98	15.5	2.05	0.08
1994	4.4729	6	0.89	89.5	3.1667	12.96	19.3	1.84	0.09
1995	1.6617	6	0.93	82.2	1.2707	17.57	22.0	1.79	0.08
1996	4.5439	7	0.89	74.7	3.0392	11.04	27.5	2.04	0.09
1997	3.1649	9	0.93	78.2	2.4478	25.08	26.3	1.51	0.08
2001	6.8383	7	1.08	76.7	5.0761	15.05	12.6	1.40	0.07
Upper oligohaline estuary									
1990	8.4887	7	0.87	89.4	5.9062	3.42	21.0	1.60	0.09
1993	6.9283	7	1.36	69.3	5.6636	4.02	19.3	1.27	0.10
1994	6.2143	9	0.85	90.0	5.1402	4.86	21.0	1.48	0.09
1995	6.2891	7	1.30	79.8	5.0479	6.15	20.8	1.50	0.09
1996	5.3015	7	1.14	84.0	3.9130	8.83	30.5	1.90	0.10
1997	5.6792	6	1.23	87.5	4.3620	11.85	25.3	0.75	0.08
2001	12.4682	7	1.52	64.1	8.4105	3.67	14.2	1.09	0.09

Cumulative coverage (CAS) and cumulative biomass (CRAS) include only the vegetated areas with species data available. Biomass is density-weighted coverage (km²).

* Chl *a*, chlorophyll *a*; TSS, total suspended sediment; TN, total nitrogen; TP, total phosphorus; n.d., no data.

$RASvL = \sum_{j=1}^{NB_L} C_j\, a_j \left[\sum_{i=1}^{n_j} f_i\, p_{vi}/100\right]$, where C_j is the fractional canopy cover conversion coefficient assigned to the *j*-th PI bed and the other terms are as defined above, and the cumulative biomass of all species is $CRAS_L = \sum_{v=1}^{M_L} RAS_{vL}$.

Water quality data—During the growing season (April–October), the Maryland Department of Natural Resources takes water samples biweekly at two mid-channel stations in each of the three river segments (Fig. 1). The data are reported in the Chesapeake Bay Program water quality database (www.chesapeakebay.net, October 2002; also *see* Rybicki [2000] for field and analytical methods). Annual growing season water quality conditions were represented by the median seasonal concentration of TN, total phosphorus (TP), chlorophyll *a* (Chl *a*), and total suspended sediment (TSS; Table 1). No TN data were available for 1985.

Waterfowl and SAV—National Audubon Society Christmas Bird Count Surveys provide an indicator of avian population change (Pranty 2002). We examined waterfowl (31 species of coot, swans, ducks, and geese) abundance during the winter from 1959 to 2001; data were extracted from the National Audubon Society Christmas Bird Count Surveys conducted in and near Washington, D.C., in two survey areas that encompass ~40 km of the study-area shoreline (Kain 1999; www.audubon.org/bird/cbc, accessed May 2005). The 60th to 102nd Christmas Bird Counts correspond to the 1959 to 2001 SAV growing season. Volunteers count all birds observed during a single day within 2 weeks of 25 December in two sample areas, one in the UTR (Washington, D.C., survey) and one in the LTR (Fort Belvoir, Virginia, survey). The cumulated annual results, reported as waterfowl counts per observer hour, were compared with the combined SAV coverage in the UTR and LTR from 1959 to 2001 (Stevenson and Confer 1978; Orth and Moore 1984; Landwehr et al. 1999). SAV biomass (closely correlated with SAV coverage) was not considered because SAV bed density data were not available for 1959 to 1983.

Statistical analysis—For all statistical methods used herein, results were considered significant if probabilities were ≤ 0.05. Pearson correlation analyses were used to

Table 2. Twelve species of submerged aquatic vegetation found in the three river segments of the tidal Potomac River and Estuary, 1985–2001.

Family (common name)	Species (common name)	Abbreviation
Ceratophyllaceae (coontail)	*Ceratophyllum demersum* L. (coontail)	CER
Haloragaceae (water milfoil)	*Myriophyllum spicatum* L. (Eurasian water-milfoil)	MYR*
Hydrocharitaceae (frogbit or tape-grass)	*Hydrilla verticillata* (L. f.) Royle (water thyme or Hydrilla)	HYD*
	Vallisneria americana Michaux (American wild celery)	VAL
Najadaceae (water nymph)	*Najas guadalupensis* (Sprengel) Magnus (Southern naiad)	NG
	Najas minor Allioni (brittle water nymph)	NM*
Pontederiaceae (pickerelweed)	*Heteranthera dubia* (Jacquin) MacMillan (water stargrass)	HET
Potamogetonaceae (pondweed)	*Potamogeton crispus* L. (curly pondweed)	PCR*
	Potamogeton perfoliatus L. (redhead grass)	PPF
	Potamogeton pusillus L. (slender pondweed)	PPU
	Stuckenia pectinata (L.) Boerner (formerly *Potamogeton pectinatus* L.) (sago pondweed)	SPC
Zannichelliaceae (Horned pondweed)	*Zannichellia palustris* L. (horned pondweed)	ZP

* Exotic species.

assess significant time trends with SAV diversity, SAV richness, the percent coverage and biomass by species of SAV, water quality, and waterfowl counts. Regression analyses were used to model significant relationships between SAV biomass and water quality variables and to determine rates of change if time trends were significant. Only significant regression and correlation results are reported. For significant regressions, and for significant time trends where a rate was reported, r^2 is calculated as a measure of the variance explained by the model. SAV biomass (in real units and natural log-transformed units) was used in all statistical analyses except those with waterfowl, in which case SAV coverage was the variable examined. Biomass in the current year was compared to that in the previous year to determine persistence, which is an indicator of ecosystem resilience or a carryover effect as afforded by overwintering propagules (e.g., tubers, rootstocks, seeds). Species richness–based turnover rate, β_{sim}, was computed according to the definition of Koleff and Gaston (2002). Turnover rates were computed within the single regions UTR, LTR, and UOE; within the double regions UTR+LTR, LTR+UOE, and UTR+UOE; or within the entire region UTR+LTR+UOE and between 1-yr, 3-yr, and 4-yr periods, and we determined if spatial or temporal turnover rates varied with SAV biomass.

Linear regression was used to develop predictive models for the entire study area for eight dependent variables: richness, diversity, biomass of each of the three most prevalent species (*H. verticillata*, *M. spicatum,* and *V. americana*), biomass of the exotic (four species) and native (eight species) groups of species, and the cumulative species biomass. We evaluated the variation of these variables with relation to one another, to the previous year's biomass, and to water quality variables.

Regression analysis was used to examine the relationship between fluctuations in total waterfowl abundance and SAV coverage in the UTR and LTR from 1982 to 2001. Because responses may not be linear but rather may reflect threshold effects, bird counts were compared among time periods, where the time period was determined by SAV abundance. We considered two situations separately: first, contrasting the two time periods: (1) 1959–1982, pre–*H. verticillata* and (2) 1982–2001, post–*H. verticillata*; and second, comparing the three periods: (1) 1959–1966, when *M. spicatum* was present and disappeared; (2) 1966–1982, when no SAV was present; and (3) 1982–2001, when a more diverse community of SAV reemerged. In addition to total waterfowl abundance, waterfowl species abundance was summarized by period. Counts of the most abundant waterfowl species (those eight species ranked as most abundant in all three periods and that had counts h^{-1} of greater than two) were compared using Kruskal–Wallis and the Tukey nonparametric multiple comparison test.

Results

SAV coverage patterns—Between 1985 and 2001, concurrent PI and field bed data were available for 10, 9, and 7 yr in the UTR, LTR, and UOE, respectively (Table 1). During those years when concurrent data were collected, PI beds in some subtributaries were not visited, but species data were available for >90% of the SAV coverage in the majority of the areas (Rybicki 2000). Rarely were SAV beds incorrectly photo-interpreted. The number of false PI beds (no vegetation found in field survey) was determined each year and compared to the total number of PI beds. There were zero false beds in six of the study years, and no more than 3% of the PI beds in a given year were observed to have no vegetation (Rybicki 2000).

Twelve SAV species were identified (http://plants.usda.gov [2005]; Crow and Hellquist 2000), four of which are exotic (http://invasions.si.edu/nemesis/chesapeake.html [2002]); Table 2). The 12 species are common members of the freshwater community in North American estuarine, lake, and river systems (Moore et al. 2000). All species present were tolerant of salinities of 0 to 3 or greater. *H. verticillata*, *V. americana*, and *M. spicatum* were prominent during most years in all river segments (Table 3). Five other species were also present in each of the segments, and four

Table 3. Percent coverage of each species of submerged aquatic vegetation (abbreviations as in Table 2) in the three river segments of the tidal Potomac River and Estuary.

Year	HYD* (%)	MYR* (%)	NM* (%)	PCR* (%)	VAL (%)	CER (%)	HET (%)	NG (%)	SPC (%)	ZP (%)	PPU (%)	PPF (%)
Upper tidal river												
1985	36.82	36.97	trace	0	6.71	5.05	10.56	3.82	0.06	0.02	0	0
1986	79.86	11.42	0.11	0	2.03	3.06	2.97	0.54	0	0	0	0
1987	75.83	14.56	0.06	0	7.88	0.65	1.02	0	0	0	0	0
1990	93.29	3.39	0.06	0	3.12	0.05	0.08	0.01	Trace	0	0	0
1993	44.79	14.54	0.01	0.01	26.53	2.09	11.48	0	0.57	0	0	0
1994	80.92	3.79	0.66	0	13.50	0.49	0.64	Trace	0	0	0	0
1995	77.66	4.65	0.88	0	14.50	0.98	1.30	0	0.03	0	0	0
1996	69.36	9.64	1.50	0	18.10	1.20	0.19	Trace	Trace	0	0	0
1997	76.44	0.81	4.04	0	17.18	1.22	0.23	0	0.07	0	0	0
2001	43.67	11.98	3.51	Trace	13.61	15.58	4.19	7.45	0	0	0	0
Lower tidal river												
1986	12.09	87.68	0	Trace	0.09	Trace	0.14	0	0	0	0	0
1987	73.39	19.83	0.30	0	3.00	1.53	1.94	0	0	0	0	0
1990	87.00	5.88	0.68	0	4.62	0.58	1.18	0.05	0	0	0	0
1993	69.23	17.98	1.11	0	8.75	2.19	0.74	0	0	0	0	0
1994	64.94	24.47	0.13	0	9.86	0.56	0.05	0	0	0	0	0
1995	69.65	4.17	8.36	0	17.14	0.69	0	Trace	0	0	0	0
1996	66.55	3.36	4.81	0	25.01	0.26	Trace	0.02	0	0	0	0
1997	67.61	0.45	10.13	0	19.60	2.18	0.01	Trace	Trace	0	0.01	0
2001	63.47	3.13	10.06	0	19.83	3.07	0.42	Trace	0	0	0	0
Upper oligohaline estuary												
1990	71.81	17.18	0.41	0	8.65	0.47	0.66	0.83	0	0	0	0
1993	45.58	22.67	1.05	0	21.02	0.85	7.85	0.98	0	0	0	0
1994	67.14	22.89	0.01	0	9.67	0.05	0.17	0.01	0.03	0	0	0.03
1995	51.86	19.27	8.70	0	16.57	3.31	0.06	0.25	0	0	0	0
1996	57.01	22.63	4.37	0	14.69	0.80	0.20	0.29	0	0	0	0
1997	51.79	18.17	17.56	0	12.28	0.19	0.01	0	0	0	0	0
2001	39.58	11.77	12.72	0	26.02	7.83	1.40	0.69	0	0	0	0

Trace is <0.01% and no sighting is indicated by 0%.
* Exotic species.

species were frequently absent and always represented <0.1% of the total coverage. Only the exotics *H. verticillata* and *M. spicatum* were, however, dominant (>40% of the species coverage), and dominance of *M. spicatum* occurred only in the LTR in 1986, when the SAV coverage and biomass were low (Table 1). Toward the end of the study, the exotic, *Najas minor,* increased from a trace amount to 4% or more in all river segments. Over the study period in all three segments, the initial peak in biomass of SAV and *H. verticillata* occurred in a downstream progression, consistent with downstream colonization and propagule dispersal (Fig. 2). After the initial peak, no consistent pattern was apparent.

Although the coverage of exotic species was always >59% (Table 1), it decreased (and that of native species increased) significantly at the rate of 1.3% per year (r^2 = 0.32) from 1985 to 2001. No such simple linear relationship was seen for *H. verticillata,* but the coverage of *V. americana* (Table 3) increased at the rate of 1.20% per year (r^2 = 0.55). During this study, none of the native species ever dominated a river segment, but the map of cumulative (1985–2001) SAV coverage shows that *V. americana* dominated certain locations that were generally along the main stem of the estuary (Fig. 1). Few locations in the tributaries were ever dominated by *V. americana*.

Diversity increased significantly (r = +0.46) during the course of the study and was highest in 2001 in all three river segments (Table 1). The largest diversity value, 1.62, occurred in the UTR. In comparison, if each of the eight species present in each segment had equal coverage, the computed diversity would be 1.95. Richness in each segment ranged from six to nine species (Table 1) with no observed time trend, despite an increase in percent coverage of native species. Turnover rates, β_{sim}, were not significantly different from zero, whether among 1-yr, 3-yr, or 4-yr periods within the single regions UTR, LTR, and UOE; within the double regions UTR+LTR, LTR+UOE, and UTR+UOE; or within the entire study region UTR+LTR+UOE.

Water quality and biomass trends with time—During the study, seasonal median values for the concentration of TN, TP, Chl *a*, and TSS ranged from 0.75 to 2.6 mg L^{-1}, 0.06 to 0.10 mg L^{-1}, 3 to 25 μg L^{-1}, and 10 to 28 mg L^{-1}, respectively. Only one of the four water quality variables

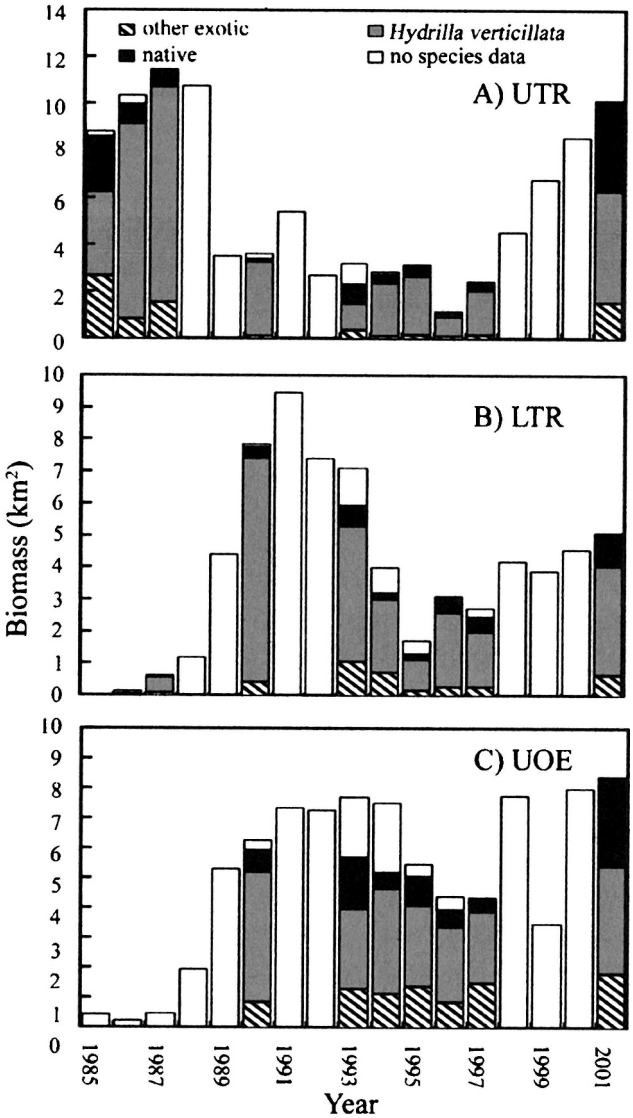

Fig. 2. Annual biomass (density-weighted coverage, RAS and CRAS) of submerged aquatic vegetation (SAV) community, native species, *Hydrilla verticillata*, other exotic species, and biomass of SAV with no species data for three river segments, (A) UTR, (B) LTR, and (C) UOE.

showed a trend with time: the seasonal median TN concentration decreased significantly over the course of the study over all segments ($n = 25$, $r = -0.56$). The biomass of two SAV species was positively correlated with time: *V. americana* ($n = 26$, $r = +0.48$) and *N. minor* ($n = 26$, $r = +0.66$).

Relations among SAV biomass, water quality, diversity, and turnover rate—The significant relationships among species (Table 4) were used to identify differences and similarities between exotic and native species and to determine the impact of individual species on cumulative biomass (Table 1). Variation in biomass of the exotics explained more of the cumulative biomass than did that of the natives. Nonetheless, the biomass of exotics and natives was positively correlated, and for no two species were biomasses negatively correlated. In addition, since none of the turnover rates were significantly different from zero, there was no relationship between biomass and either temporal or spatial turnover rates.

The variation in the cumulative biomass in a given year was largely explained by the previous year's biomass (Fig. 3A). That is, the cumulative biomass is highly autocorrelated. A similar relationship held for the two exotic species, *H. verticillata* and *M. spicatum*, but no significant autocorrelation was seen for *V. americana*.

In addition to determining relationships among species, we identified the significant trends between species biomass or diversity and water quality conditions (Table 4). During the study period, cumulative species biomass, as well as biomass of the exotic group and its largest component, *H. verticillata*, all varied inversely with Chl *a* and TSS concentration. *M. spicatum* biomass also varied inversely with Chl *a* concentrations. As a group, natives varied inversely with TSS, but *V. americana*, the largest component of the group, did not. Variation in seasonal TN concentration was found to explain 25% of the variation in the biomass of *V. americana,* the dominant native. No significant relationship was found between TN concentration and any exotic. Richness had no significant linear relationship with biomass of any of the three most prevalent species (*H. verticillata*, *M. spicatum,* and *V. americana*), biomass of the exotic (four species) and native (eight species) groups of species, the cumulative species biomass, nor did it have a significant linear relationship with any water quality measure. Diversity varied positively with the biomass of the single most prominent native species (*V. americana*; Fig. 3B), the native species group, and *M. spicatum,* but not with *H. verticillata* (Table 4). In addition, diversity varied inversely with TN (Fig. 3C) such that, within the range of 0.8 to 2.6 mg L^{-1}, a decrease of the seasonal median TN concentration by 1 mg L^{-1} corresponded to an increase in diversity of 0.4. A significant relationship was seen between diversity and (natural log of) cumulative biomass (Table 4; Fig. 3D), although the significance of the relationship was dependent upon one observation (1986, LTR), so that this ecosystem response should not be considered confirmed. No significant linear relationship was found between any SAV community measure and the seasonal median TP.

Waterfowl—The time series of winter waterfowl counts show several significant changes over the period of study (Fig. 4). An abrupt change is observed following the appearance of *H. verticillata* and the reemergence of SAV in 1983. From 1959 to 1982, the total counts decreased significantly at the rate of 1.5 birds lost per observer hour per year ($n = 24$, $r^2 = 0.40$). In contrast, the counts increased significantly from 1982 to 2001, at the rate of 5.9 birds gained per observer hour per year ($n = 20$, $r^2 = 0.50$). We can further subdivide the period as follows: (1) 1959–1966, when *M. spicatum* was present and the average annual count (±standard error [SE]) was 44.3 ± 7.0; (2) 1966–1982, when no SAV was present and the average count per observer hour was 19.5 ± 1.4; and (3) 1982–2001, when a more diverse but mostly exotic community of SAV

Table 4. Significant (probability ≤ 0.05) regression relationships (sample size is n, explained variance is r^2) found among cumulative biomass of all species (CRAS), biomass of a species or a species group (RAS), water quality variables, and diversity in three river segments of the tidal Potomac River and Estuary, 1985–2001.

Dependent variable	Explanatory variable	n	r^2	Slope estimate	Intercept estimate
CRAS	CRAS in the previous year	15	0.79*	1.02	−0.138
RAS (*Hydrilla verticillata*)	RAS (*H. verticillata*) in the previous year	15	0.58*	0.983	0.314
RAS (*Myriophyllum spicatum*)	RAS (*M. spicatum*) in the previous year	15	0.42*	0.450	0.163
CRAS	RAS (exotic species)	26	0.93*	1.17	0.186
CRAS	RAS (*H. verticillata*)	26	0.81*	1.27	0.764
CRAS	RAS (*M. spicatum*)	26	0.53*	3.65	2.55
CRAS	RAS (native species)	26	0.46	2.27	2.84
CRAS	RAS (*Vallisneria americana*)	26	0.29*	3.68	2.84
RAS (*M. spicatum*)	RAS (*H. verticillata*)	26	0.24*	0.137	0.173
RAS (*V. americana*)	RAS (*M. spicatum*)	26	0.16	0.296	0.340
RAS (native species)	RAS (exotic species)	26	0.21	0.167	0.186
CRAS	Chlorophyll *a*	26	0.21	−0.246	7.39
CRAS	Total suspended sediment	26	0.24	−0.329	10.94
RAS (exotic species)	Chlorophyll *a*	26	0.22	−0.207	6.13
RAS (exotic species)	Total suspended sediment	26	0.17	−0.229	8.23
RAS (*H. verticillata*)	Chlorophyll *a*	26	0.16	−0.152	4.78
RAS (*H. verticillata*)	Total suspended sediment	26	0.16	−0.190	6.72
RAS (*M. spicatum*)	Chlorophyll *a*	26	0.27*	−0.055	1.20
RAS (native species)	Total suspended sediment	26	0.24	−0.100	2.72
RAS (*V. americana*)	Total nitrogen	25	0.25*	−0.469	1.42
Diversity	Natural log of CRAS	26	0.19	0.123	0.815
Diversity	RAS (native species)	26	0.58*	0.271	0.735
Diversity	RAS (*V. americana*)	26	0.46*	0.487	0.710
Diversity	RAS (*M. spicatum*)	26	0.28*	0.280	0.793
Diversity	Total nitrogen	25	0.32*	−0.365	1.64

* Indicates probability ≤ 0.01. *Note*: Biomass is density-weighted coverage (km^2).

reemerged with the greatest SAV coverage of the three periods and the average bird count per observer hour was 82.2 ± 11.1 (Table 5). The Kruskal–Wallis and the Tukey nonparametric multiple comparison tests confirmed that these counts were significantly different and that waterfowl counts were greater when SAV coverage was greater. Furthermore, during the subperiods 1959–1966 and 1966–1982, there was no significant time trend, indicating that

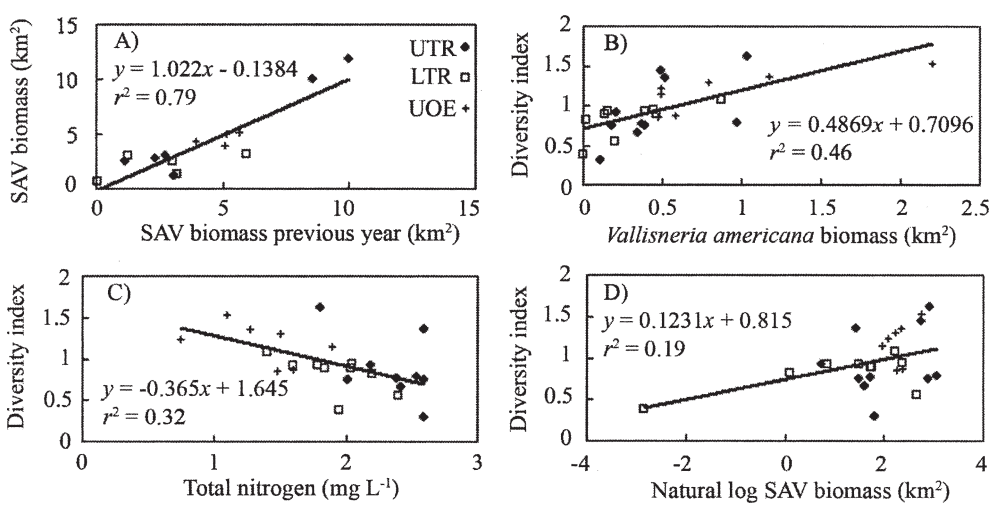

Fig. 3. Relationships among submerged aquatic vegetation (SAV) biomass (density-weighted coverage), diversity, and other variables. (A) SAV biomass and SAV biomass the previous year, (B) diversity and *Vallisneria americana* biomass, (C) diversity and total nitrogen, and (D) diversity and SAV biomass for three river segments (UTR, LTR, and UOE) in the tidal Potomac River and Estuary, 1985–2001.

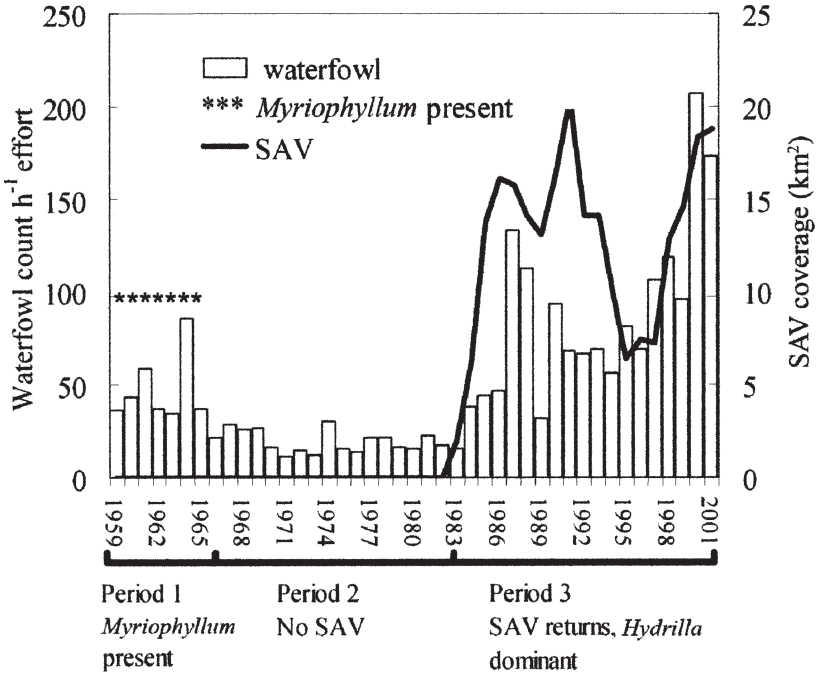

Fig. 4. Waterfowl counts from National Audubon Society Christmas Bird Count Surveys (bar) and submerged aquatic vegetation (SAV) coverage summed for the upper and lower tidal river segments (line) for three time periods. *Myriophyllum spicatum* was present, but SAV coverage was unknown for 1959–1965.

these subperiods were two stable periods, with more waterfowl before than after the disappearance of *M. spicatum*. Finally, we constructed SAV diversity index values for the two river segments combined (UTR + LTR) for the 10 common years on the basis of the cumulative coverage of all species (Table 1) and the percent coverage of each species for UTR and LTR for each year (Table 3). No significant linear relationship was found between diversity of SAV and waterfowl counts.

The Kruskal–Wallis and the Tukey nonparametric multiple comparison tests of the counts of the eight most prevalent types of waterfowl indicated that six of the eight were significantly greater in period 3, when SAV was present in fall and overwintering propagules were available in winter, than in period 2, when no SAV was present (Fig. 5). Among the eight prevalent taxa of waterfowl, the six taxa of waterfowl that increased significantly in period 3 are known to consume SAV, while the two other species are known to feed on mollusks or fish. Of the 35 types of waterfowl (31 were individual species and four were genus groups that observers could not differentiate by species) present from 1982 to 2001, 30 showed increased mean counts from period 2 to period 3. Indeed, 29 of the 35 had more than doubled the counts, and 17 of the 35 had increased by greater than a 10-fold measure (Table 5). Swans are notable for their high consumption of SAV tubers and shoots (Allin and Husband 2003). Though swans were not among the most prevalent species in this study, the average abundance of *Cygnus olor* (Mute Swan, an exotic species) more than doubled, and the abundance of *Cygnus columbianus* (Tundra Swan) increased more than 10-fold from period 2 to period 3.

Discussion

The spread of aggressive exotic macrophytes has been documented worldwide (Kozkova and Izhboldina 1993; Hofstra et al. 1999), but only rarely has changing community species composition been monitored with water quality over an extended period. In this work we test current hypotheses about diversity and about native and exotic species relationships in our assessment of species diversity, turnover rates, and by-species biomass of SAV in the tidal freshwater and oligohaline Potomac River from 1985 to 2001. In addition, we compared the abundance of a higher trophic community, waterfowl, to coverage of SAV in three time periods: periods when exotic SAV coverage was high (1982–2001) and low (1959–1966) and when all SAV coverage had disappeared (1966–1982) in the tidal freshwater Potomac River.

Though we observe some differences between their responses to environmental variables, as will be discussed below, when cumulated as a group, the biomass values of exotics and natives were positively correlated, and no two species' biomasses were negatively correlated. Our findings are consistent with those of previous studies indicating that native and invading species sometimes do increase together (Kennedy et al. 2002) and that factors known to favor exotic species can also promote native species (Levine et al. 2002). Relationships between exotics and natives are more likely to be inhibiting when the study scale is reduced from a landscape (region) to a neighborhood (local) level, at which scale direct competition dominates interactions (Stohlgren et al. 1999; Kennedy et al. 2002; Levine et al.

Table 5. Mean waterfowl counts for three time periods in order of period 3 abundance.

Genus and species	Common name	Mean species count 1959–1966, period 1 (count h^{-1})	Mean species count 1966–1982, period 2 (count h^{-1})	Mean species count 1982–2001, period 3 (count h^{-1})
Branta canadensis	Canada goose	1.8313	1.6289	20.0909
Aythya affinis	Lesser scaup	6.6131	1.7085	15.2110
	scaup sp.	1.2290	0.1878	10.5552
Anas platyrhynchos	Mallard	0.6232	3.0786	9.2777
Oxyura jamaicensis	Ruddy duck	23.1835	7.3925	5.5424
Anas rubripes	American black duck	1.0417	1.6594	4.1295
Aythya valisineria	Canvasback	1.1825	1.1114	4.0786
Fulica americana	American coot	0.4297	0.1701	2.6587
Mergus merganser	Common merganser	0.4031	1.2285	2.2880
Bucephala albeola	Bufflehead	0.6624	0.3475	1.5046
Cygnus columbianus	Tundra swan	0.0014	0.0106	1.2030
Aythya collaris	Ring-necked duck	0.5585	0.0959	0.8970
Anas strepera	Gadwall	0.0038	0.0291	0.8027
Aythya marila	Greater scaup	4.5292	0.1395	0.6910
Anas crecca	American green-winged teal	0.3289	0.1241	0.7865
Anas americana	American wigeon	0.0091	0.0219	0.5511
Lophodytes cucullatus	Hooded merganser	0.0007	0.0444	0.5144
Anas acuta	Northern pintail	1.5353	0.2115	0.3741
Aix sponsa	Wood duck	0.0028	0.0471	0.2826
Anas clypeata	Northern shoveler	0.0117	0.0067	0.1971
Mergus serrator	Red-breasted merganser	0.0407	0.0527	0.1713
	merganser sp.	0.0000	0.0000	0.1411
Chen caerulescens	Snow goose	0.0000	0.0040	0.0754
Aythya americana	Redhead	0.0637	0.1259	0.0613
Bucephala clangula	Common goldeneye	0.0194	0.0643	0.0590
Melanitta fusca	White-winged scoter	0.0000	0.0010	0.0176
Gavia immer	Common loon	0.0054	0.0064	0.0146
	scoter sp.	0.0000	0.0056	0.0107
Melanitta perspicillata	Surf scoter	0.0000	0.0028	0.0088
Gavia stellata	Red-throated loon	0.0000	0.0003	0.0075
Cygnus olor	Mute swan	0.0000	0.0014	0.0059
Anas discors	Blue-winged teal	0.0000	0.0000	0.0044
Clangula hyemalis	Long-tailed duck (oldsquaw)	0.0000	0.0000	0.0036
Melanitta nigra	Black scoter	0.0000	0.0100	0.0005
	Mallard/Gadwall hybrid	0.0000	0.0000	0.0002
Total mean (±SE) for waterfowl (count h^{-1})*		44.3±7	19.5±1.4	82.2±11.1

Of the 35 types of waterfowl present, 31 were individual species and 4 were genus groups that observers could not differentiate by species.
* SE, standard error.

2002), or in small, isolated systems in which the area of interaction is confined (Parker et al. 1999).

Consistent with findings for terrestrial systems (Suding et al. 2005) and for lentic systems (James et al. 2005), a significant inverse relationship was observed between TN and SAV diversity in this system. During this study, growing-season TN concentration decreased in all three river segments; in contrast, we found no significant relationship between seasonal TP and SAV diversity or any other variable we examined. However, we note that phosphorus reduction at the major wastewater treatment plant on the Potomac was realized in the 1970s and early 1980s (Carter and Rybicki 1986) and that median seasonal TP changed little during our study period. It has recently been suggested that phosphorus loads may be rising in this system (Langland et al. 2004). This may pose a future concern, not only because of the effect of high nutrient loads on phytoplankton, water clarity, and SAV dynamics (Phillips et al. 1978), but also because of the significant role phosphorus enrichment appears to play in plant species loss (Wassen et al. 2005).

In contrast to this study, patterns with richness and biomass are well documented in the literature. Scientists have found that in terrestrial systems, plant richness varies positively with plant abundance (for example, Loreau et al. 2001; Rajaniemi 2003) or quadratically (rising then falling) as biomass increases (Chalcraft et al. 2004). In a study of 73 Danish lakes, SAV richness was found to vary positively with size of colonized areas (Vestergaard and Sand-Jensen 2002). However, we found no relationship between richness and SAV biomass. Similarly, turnover rates—compared over both different spatial and temporal scales—were found not to be significantly different from zero, with no relationship to the variation in SAV biomass in this study. Perhaps we did not observe this effect in the Potomac River because of the relatively small range of

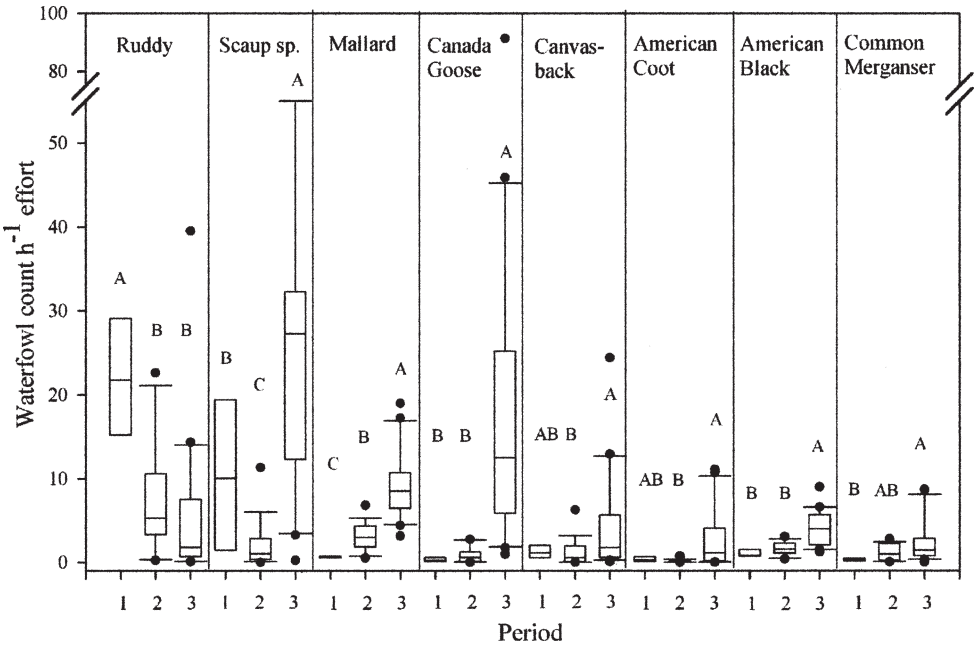

Fig. 5. Waterfowl counts for the most abundant species from National Audubon Society Christmas Bird Counts for three time periods. Boxes show median and upper and lower quartile (circles are outliers), and for each species, boxes with different single letters are significantly different and boxes with AB designation indicate those counts were not significantly different from either of the other periods (significant if $p < 0.05$). Period 1 = 1959–1966; Period 2 = 1966–1982; Period 3 = 1982–2001.

SAV species richness (six to nine species) or because of the regional scale of this study. Koleff and Gaston (2002) also found no relationship between spatial turnover and regional species richness at the regional scale in a terrestrial system, but they did observe a negative relationship between turnover and local species richness at a smaller scale.

The biomass of both exotic and native species increased with decreasing median growing season suspended matter concentrations at the regional scale of this study (Table 4). At the local scale, the spread of prolific exotics may alter the local habitat by slowing water velocity, increasing removal (settling) of particulates, and stabilizing sediment, reducing sediment resuspension, thus clarifying turbid water (Rybicki et al. 1997; Van Nes et al. 2002), which facilitates the spread of natives. If so, in this unconfined system, the spread of exotics has led to expanding SAV coverage by providing an ecosystem function, namely, bed scale water clarification. Efforts to control exotics without concurrent restoration of natives with similar functions can negatively affect those ecosystem benefits that both natives and exotics provide (Stromberg 1998).

Differences in reproductive potential between the dominant native and exotic species may explain some interannual patterns in SAV. Biomass of each of the two prominent exotics, *H. verticillata* and *M. spicatum*, was highly autocorrelated: that is, biomass in the previous year was the best predictor of biomass in the present year (Table 4). Since these were often the dominant species, their variation drives that of the cumulative SAV biomass (Fig. 3A). Although SAV reproduce from seeds, numerous species in this community also produce overwintering storage organs (Rybicki et al. 2001) that receive energy from the previous year's production and carry it over to the next year (Van Nes et al. 2002). In fact, *V. americana* and *H. verticillata* sprout from tubers in spring, and even in complete darkness they can elongate several decimeters toward the surface, where light is less attenuated and is more likely to provide adequate energy for continued growth (Rybicki and Carter 2002). The stored energy can ameliorate the effects of interannual variation in suspended matter and turbidity. No significant autocorrelation was found for the native species, in particular, for *V. americana*. The density of tubers of *V. americana* ($\leq$36 tubers m^{-2}) was approximately one half that of *H. verticillata* ($\leq$75 tubers m^{-2}) in the Potomac River (Rybicki et al. 2001). Therefore, we suggest that the ability to reproduce greater numbers of overwintering propagules provides the exotic species with a stronger carryover effect under the conditions in this study.

With respect to the question of how exotics in this system have affected ecosystem function in their apparent value to waterfowl, we found that most waterfowl species appeared to benefit from the *H. verticillata*–dominated resurgence of SAV after 1982 (Table 5). Though waterfowl are known to consume tubers, and *H. verticillata* tubers filled the gizzard of one duck (*Anas platyrhynchos* [Mallard]) shot by a hunter in the study area in the 1980s (Carter pers. comm.), no winter food habit data are available for waterfowl in this study. However, Scaup species (Fig. 5), particularly *Athya affinis* (Table 5), were abundant from 1982 to 2001 and seem suited to benefit from an expansion of *H. verticillata*.

This species dives and consumes tubers (Knapton and Petrie 1999), and during migration in the southern United States they were observed to equally utilize ponds planted with either *H. verticillata* or native SAV species (Dick et al. 2004).

While waterfowl trends reflect factors besides SAV coverage, such as hunting pressure, disease, and breeding ground conditions, positive relationships between waterfowl and SAV have been well documented (Noordhuis et al. 2002). However, grazing by waterfowl, particularly by large species such as swans, can diminish both the shoot biomass in fall (Allin and Husband 2003) and the density of the perennial organs in winter (Sponberg and Lodge 2005). Though our study does not indicate that waterfowl are negatively affecting the current SAV diversity, modeling results indicate that there is a critical biomass of tubers below which some vegetation will not reestablish itself in turbid waters because the density of vegetation is too low to initiate the positive feedback mechanism between the vegetation and water clarity (Van Nes et al. 2002). Further research on waterfowl populations and food habits and the critical SAV tuber biomass needed for reestablishment of SAV species is needed to better determine if the changing diversity of SAV is significantly mediated at the consumer level in this region.

In this study, we found that the native populations were not displaced even though the SAV community was dominated by exotics, nor was ecosystem function with respect to waterfowl communities degraded; indeed, it was enhanced. To our knowledge, this research represents the only long-term, quantitative study of SAV biodiversity following the colonization of an exotic species in an estuarine ecosystem in which millions of dollars were spent annually (Butt and Brown 2000) to reduce nutrient input. Our approach can be used in any ecological assessment requiring analysis of congruent field and remotely sensed spatial coverage data. Our findings support current management strategies to improve water clarity and reduce nutrient concentrations to enhance SAV coverage, thereby increasing waterfowl habitat, with the additional benefit of protecting biodiversity of the SAV community. Numerous mechanisms, such as harvesting, herbicides, and triploid grass carp, are currently used to control nuisance exotic SAV species once they have become established. We suggest that an integrated aquatic plant management program that considers nutrient reduction as an additional tool could protect the beneficial aspects of SAV coverage and encourage diversity. More such studies on SAV coverage and diversity along nutrient gradients and at different scales will improve our understanding of the processes driving species interactions and will improve our ability to determine the consequences of management decisions about exotic species and eutrophication.

References

Allin, C. C., and T. P. Husband. 2003. Mute swan (*Cygnus olor*) impact on submerged aquatic vegetation and macroinvertebrates in a Rhode Island coastal pond. Northeast. Nat. **10:** 305–318.

Butt, A. J., and B. L. Brown. 2000. The cost of nutrient reduction: A case study of Chesapeake Bay. Coast. Manag. **28:** 175–185.

Carter, V., J. E. Paschal, Jr., and N. Bartow. 1985. Distribution and abundance of submersed aquatic vegetation in the tidal Potomac River and Estuary, Maryland and Virginia, May 1978 to November 1981. United States Geological Survey Water-Supply Paper 2234A.

———, and N. B. Rybicki. 1986. Resurgence of submersed aquatic macrophytes in the tidal Potomac River, Maryland, Virginia and the District of Columbia. Estuaries **9:** 368–375.

———, ———, J. M. Landwehr, and M. Turtora. 1994. Role of weather and water quality in population dynamics of submersed macrophytes in the tidal Potomac River. Estuaries **17:** 417–426.

Chalcraft, R. D., J. W. Williams, M. D. Smith, and M. R. Willig. 2004. Scale dependence in the species-richness-biomass relationship: The role of species turnover. Ecology **85:** 2701–2708.

Cronin, W. B. 1971. Volumetric, areal and tidal statistics of the Chesapeake Bay Estuary and its tributaries. Special Report 20, Reference 71-2. The Johns Hopkins University Chesapeake Bay Institute.

Crow, G. E., and C. B. Hellquist. 2000. Aquatic and wetland plants of Northeastern North America. Univ. of Wisconsin Press.

Dick, G. O., J. K. Smith, and R. M. Smart. 2004. Migratory waterfowl habitat selection in relation to aquatic vegetation. ERDC/TN APCRP-EA-09. United States Army Engineer Research and Development Center.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley.

Hofstra, D. E., J. Clayton, J. D. Green, and M. Auger. 1999. Competitive performance of *Hydrilla verticillata* in New Zealand. Aquat. Bot. **63:** 305–324.

James, C., J. Fisher, V. Russell, S. Collings, and B. Moss. 2005. Nitrate availability and hydrophyte species richness in shallow lakes. Freshw. Biol. **50:** 1049–1063.

Johnson, F. A., and F. Montalbano, III. 1984. Selection of plant communities by wintering waterfowl on Lake Okeechobee, Florida. J. Wildl. Manag. **1:** 174–178.

Kain, T. 1999. Virginia Christmas Bird Counts: 1998–99. Raven **70:** 53.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature **417:** 636–638.

Knapton, R. W., and S. A. Petrie. 1999. Changes in distribution and abundance of submerged aquatic macrophytes in the Inner Bay at Long Point, Lake Erie: Implications for foraging waterfowl. J. Gt. Lakes Res. **25:** 783–798.

Koleff, P., and K. J. Gaston. 2002. The relationships between local and regional species richness and spatial turnover. Glob. Ecol. Biogeogr. **11:** 363–375.

Kozhova, O. M., and L. A. Izhboldina. 1993. Spread of *Elodea canadensis* in Lake Baikal. Hydrobiologia **259:** 203–211.

Landwehr, J. M., J. T. Reel, N. B. Rybicki, H. A. Ruhl, and V. Carter. 1999. Chesapeake Bay habitat criteria scores and the distribution and abundance of submersed aquatic vegetation in the tidal Potomac River and Potomac Estuary, 1983–1997. United States Geological Survey Open-File Report 99-219.

Langland, M. J., S. W. Phillips, J. P. Raffensperger, and D. L. Moyer. 2004. Changes in streamflow and water quality in selected nontidal sites in the Chesapeake Bay Basin, 1985–2003. United States Geological Survey Scientific Investigation Report 2004-5259.

Levine, J. M., T. A. Kennedy, and S. Naeem. 2002. Neighborhood scale effects of species diversity, p. 114–124. *In* M. Loreau, S. Naeem and P. Inchausti [eds.], Biodiversity and ecosystem functioning. Oxford Univ. Press.

Litav, M., and M. Agami. 1976. Relationship between water pollution and the flora of two coastal rivers of Israel. Aquat. Bot. **2:** 23–41.

Loreau, M., and others. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science **294:** 804–808.

Madsen, J. M., C. F. Hartleb, and C. W. Boylen. 1991. Photosynthetic characteristics of *Myriophyllum spicatum* and six submersed aquatic macrophyte species native to Lake George, New York. Freshw. Biol. **26:** 233–240.

Moore, K. A., D. J. Wilcox, and R. J. Orth. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. Estuaries **23:** 115–127..

Murphy, K. J., B. Rorslett, and I. Springue. 1990. Strategy analysis of submersed lake macrophytes communities: An international example. Aquat. Bot. **36:** 303–323.

Noordhuis, R., D. T. van der Molen, and M. S. van den Berg. 2002. Response of herbivorous water-birds to the return of *Chara* in Lake Veluwemeer, The Netherlands. Aquat. Bot. **72:** 349–367.

Orth, R. K., and K. A. Moore. 1983. Submerged aquatic plants: Techniques for analyzing their distribution and abundance. Mar. Technol. Soc. J. **17:** 38–52.

———, and ———. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: An historical perspective. Estuaries **7:** 531–540.

———, and others. 1986. Distribution of submerged aquatic vegetation in the Chesapeake Bay and tributaries—1985. United States Environmental Protection Agency, Chesapeake Bay Program Office.

Parker, I. M., and others. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biol. Invasions **1:** 3–19.

Perry, M. C., and A. S. Deller. 1996. Review of factors affecting the distribution and abundance of waterfowl in shallow-water habitats of Chesapeake Bay. Estuaries **19:** 272–278.

Phillips, G. L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophic freshwaters. Aquat. Bot. **4:** 103–126.

Pranty, B. 2002. The use of Christmas bird count data to monitor populations of exotic birds. American Birds. The 102nd Christmas Bird Count: 24–28.

Rajaniemi, T. K. 2003. Explaining biomass-diversity relationships in plants. Oikos **101:** 449–457.

Rozas, L. P., and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: Testing the roles of food and refuge. Oceologia **77:** 101–106.

Rybicki, N. B. 2000. Relationships between environmental variables and submersed aquatic vegetation in the Potomac River, 1985–1997. Ph.D. thesis, George Mason Univ.

———, and V. Carter. 2002. Light and temperature effects on the growth of *Vallisneria americana* L. and *Hydrilla verticillata* (L.f.) Royle. J. Aquat. Plant Manag. **40:** 92–99.

———, H. L. Jenter, V. Carter, R. A. Baltzer, and M. Turtora. 1997. Observations of tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. Limnol. Oceanogr. **42:** 307–317.

———, D. G. McFarland, H. A. Ruhl, J. T. Reel, and J. W. Barko. 2001. Investigations of the availability and survival of submersed aquatic vegetation propagules in the Tidal Potomac River. Estuaries **24:** 407–424.

Sponberg, A. F., and D. M. Lodge. 2005. Seasonal belowground herbivory and density refuge from waterfowl herbivory for *Vallisneria americana*. Ecology **86:** 2127–2134.

Stevenson, J. C., and N. M. Confer. 1978. Summary of available information on Chesapeake Bay submerged vegetation. United States Fish and Wildlife Service Report FWS/OBS-78/66.

Stohlgren, T. J., and others. 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. **69:** 25–46.

Stromberg, J. 1998. Functional equivalency of saltcedar (*Tamarix chinensis*) and freemont cottonwood (*Populus fremonth*) along a free-flowing river. Wetlands **18:** 675–686.

Suding, K. N., and others. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc. Natl. Acad. Sci. USA **12:** 4387–4392.

Van Nes, E. H., M. Scheffer, M. S. van den Berg, and H. Coops. 2002. Dominance of charophytes in eutrophic shallow lakes—when should we expect it to be an alternative stable state? Aquat. Bot. **72:** 275–296.

Vestergaard, O., and K. Sand-Jensen. 2002. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency and lake area. Can. J. Fish. Aquat. Sci. **57:** 2022–2031.

Wassen, M. J., H. O. Venterink, E. D. Lapshina, and F. Tanneberger. 2005. Endangered plants persist under phosphorus limitation. Nature **437:** 547–550.

Received: 18 April 2006
Accepted: 20 November 2006
Amended: 27 December 2006