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RESEARCH ARTICLE

Temporal variability in potential connectivity of *Vallisneria americana* in the Chesapeake Bay

Michael W. Lloyd · Paul A. Widmeyer · Maile C. Neel

Abstract

Context Submersed aquatic vegetation (SAV) performs water quality enhancing functions that are critical to the overall health of estuaries such as the Chesapeake Bay. However, eutrophication and sedimentation have decimated the Bay's SAV population to a fraction of its historical coverage. Understanding the spatial distribution of and connectedness among patches is important for assessing the dynamics and health of the remaining SAV population.

Objectives We seek to explore the distribution of SAV patches and patterns of potential connectivity in the Chesapeake Bay through time.

Methods We assess critical distances, from complete patch isolation to connection of all patches, in a merged composite coverage map that represents the sum of all probable *Vallisneria americana* containing patches between 1984 and 2010 and in coverage maps for individual years within that timeframe for which complete survey data are available.

Results We have three key findings: First, the amount of SAV coverage in any given year is much smaller than the total recently occupied acreage. Second, the vast majority of patches of SAV that are within the tolerances of *V. americana* are ephemeral, being observed in only 1 or 2 years out of 26 years. Third, this high patch turnover results in highly variable connectivity from year to year, dependent on dispersal distance and patch arrangement.

Conclusions Most of the connectivity thresholds are beyond reasonable dispersal distances for *V. americana*. If the high turnover in habitat occupancy is due to marginal water quality, relatively small improvements could greatly increase *V. americana* growth and persistence.

Keywords Graph theory · Submersed aquatic vegetation · Fragmentation

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Introduction

Submersed aquatic vegetation (SAV) is a keystone assemblage of species found in estuarine systems. SAV beds provide food resources for migratory waterfowl (Korschgen and Green 1988) and habitat for fish and aquatic invertebrates (Rozas and Odum

1987). SAV also performs essential ecosystem services that improve water quality, such as stabilizing sediments (Madsen et al. 2001) and buffering nutrient levels (Moore 2004). In turn, the extent and vitality of SAV populations are determined by water quality; excessive sediment and nutrient levels preclude the existence of SAV. In this way, SAV both contributes to and is dependent upon the overall health of an estuary.

Historically, an estimated ∼250,000 ha of SAV was thought to cover the bottom of the Chesapeake Bay (Stevenson and Confer 1978; Dennison et al. 1993; Orth et al. 2008). By the 1970s, air photo mapping by the Virginia Institute of Marine Science (VIMS; Orth et al. 2010a) showed that SAV acreage in the Chesapeake Bay was drastically reduced to a small fraction of its historical extent, primarily due to eutrophication and increased sedimentation (Bayley et al. 1978; Orth and Moore 1983; Brush and Davis 1984; Dennison et al. 1993). As late as 2012, SAV abundance (19,503 ha) remained far below the 74,866 ha target level (U.S. Environmental Protection Agency 2010). Efforts to increase acreage and restore SAV species have resulted in annual acreages that have fluctuated around ∼30,000 ha since the early 1990s (Orth et al. 2010a).

Given the ecosystem services SAV provides, the magnitude of SAV loss has been a cause of concern (Gardner et al. 1987; Jaeger 2000; Keller and Largiader 2003; Helm et al. 2006; Prugh et al. 2008; Thrush et al. 2008). Moreover, habitat loss and fragmentation may have substantially reduced the functional connectivity of the remaining SAV patches. The degree to which patches are functionally connected depends on the interaction between the sizes of and distances among patches (Merriam 1984; Baudry and Merriam 1988; Ferrari et al. 2007) and on how individual organisms perceive, use, and move among those patches (Taylor et al. 1993, 2006; Ricketts 2001; Tischendorf and Fahrig 2001; Brooks 2003; McRae 2006). Understanding the spatial distribution of and connectedness among patches is important for assessing the dynamics and health of the remaining SAV population. While the loss of SAV habitat area has been well documented by other researchers (i.e., Bayley et al. 1978; Orth and Moore 1983; Brush and Davis 1984; Dennison et al. 1993), no research to date has investigated connectivity amongst SAV habitat. Because such information may prove useful to natural

resource managers, we seek to explore the distribution of SAV patches and patterns of connectivity in the Bay through time.

Connectivity facilitates movement both through relatively continuous large patches and among discrete patches that are close enough that propagules can move through the intervening matrix (Ferrari et al. 2007; Saura and Rubio 2010; Saura et al. 2011). For any amount of habitat on a landscape, spatial distribution strongly affects movement, which in turn can determine the amount of habitat effectively available to an organism and confer resistance and resilience to environmental perturbations. As patches are lost or reduced in size, among-patch distances can increase such that dispersal is reduced or eliminated, and colonization or recolonization of areas that are otherwise suitable habitat is prevented. Conserving, restoring, or increasing the areas of sites that contribute to connectivity can have greater ecological benefits than adding habitat area alone (Tewksbury et al. 2002).

In the absence of complete information on usage and movement, the scales at which patches become isolated can be estimated from what is known or inferred about the dispersal capabilities of individual species (e.g., Calabrese and Fagan 2004; Urban 2005). If scales of isolation coincide with distances that are likely to be important for dispersal, the movement can be assessed via more detailed behavioral and demographic research at the appropriate spatial scales. We use graph theory and associated metrics (e.g., proportion of patches in largest component, equivalent connectivity) to assess potential connectivity of *V. americana* by identifying the dispersal distances required for any observed patch distribution to be connected (Calabrese and Fagan 2004; Pascual-Hortal and Saura 2006; Zetterberg et al. 2010; Galpern et al. 2011; Saura et al. 2011).

As is the case in many natural habitats, sites supporting individual SAV species in the Chesapeake Bay were likely always patchily distributed due to species-specific limitations imposed by physiological tolerances to light (i.e., depth) and to salinity. Even in suitable habitat, SAV patches are known to be somewhat ephemeral (e.g., Rybicki and Carter 2002), becoming extirpated and later reappearing and/or changing in species composition. This indicates that SAV species may display metapopulation (*sensu* Levins 1969) or source-sink (*sensu* Pulliam 1988) dynamics. In such dynamic systems, changes in dispersal within and among patches of suitable and

occupied habitat could affect overall network persistence (Hanski 1998). This would in turn affect many ecological and evolutionary processes driven by interactions between total habitat area, extent and size of continuous habitat patches, and connectivity among discrete patches (Merriam 1984, 1991; Baudry and Merriam 1988; Fahrig and Merriam 1994; Fahrig 1997, 2003; Wiegand et al. 2005; Chetkiewicz et al. 2006; Taylor et al. 2006).

We quantify the extent and patterns of potential connectivity for probable habitat of one of the dominant SAV species, *Vallisneria americana* Michx. (Hydrocharitaceae; American wild celery). We use graph networks developed from habitat patches separated by predefined distances to document the location and extent of *V. americana* in the Chesapeake Bay of eastern North America, and we highlight the distances at which changes in connectivity of these networks exhibit threshold-like behaviors (Bunn et al. 2000; Urban and Keitt 2001). Such thresholds represent the distances at which a landscape changes from facilitating dispersal to being disconnected and thus vulnerable to disruptive ecological and evolutionary processes (e.g., drift, modified gene flow). Lack of distribution data prior to major declines precludes comparison with baseline levels of abundance or potential connectivity. Instead, we compare amounts and spatial distribution of potential habitat across individual years, and we compare individual years with the merged composite of potential habitat area documented by VIMS between 1984 and 2010.

We focus on *V. americana* because this meadow-forming species is one of the dominant and more persistently occurring SAV species in freshwater and oligohaline portions of the Bay and tributaries. These areas have suffered the largest SAV declines (Kemp et al. 1983; Moore et al. 2010) and, as a result, *V. americana* has been a target of restoration efforts for over 20 years. Although there is little specific dispersal information available for *V. amerciana*, we use information from the literature on SAV dispersal to infer a reasonable range of dispersal distances. *V. americana* disperses via seed and vegetative propagules. Gene flow also occurs via pollen dispersal. Pollination occurs when pistillate flowers, borne on the water surface, are fertilized by free-floating staminate flowers and pollen (Korschgen and Green 1988). Once released to the water column, pollen remains viable for only a few days (McFarland and Shafer 2008) and individual female flowers remain receptive for approximately 24 h (West et al. 2013), indicating little potential for movement beyond short distances. Results from a two-generation analysis of paternity indicate that, on average, pollen moves ~1–20 m depending on local currents (Lloyd et al. in prep). Pollen movement of <15 m has been documented for the ecologically similar species *Zostera marina* (Harwell and Orth 2002).

Seed dispersal in both *Vallisneria* and *Zostera* occurs by three mechanisms. First, fruits and seeds can be dispersed by waterfowl, either through ingestion or through adhesion to feathers (Santamaria and Klaassen 2002; Figuerola et al. 2003; Higgins et al. 2003), which could potentially connect populations from distant reaches of the Bay and beyond. Second, fruits can rupture while they are attached to the mother plant, releasing clusters of seeds bound in a gelatinous matrix into the water column (Korschgen and Green 1988). Once freed, seeds generally settle quickly within tens of meters from the source (Kaul 1978; Berkovića et al. 2014). Finally, entire reproductive ramets may become detached from the mother plant and float freely. Movement distances for seeds dispersed in this way are not known, but floating reproductive shoots are commonly seen in the fall and can be carried appreciable distances by currents. *Zostera marina* seeds are known to disperse between 5 m and 10 km by such rafting, and successful reestablishment is considered likely after dispersal of 1–10 km (Harwell and Orth 2002; Orth et al. 2012). We more closely examine critical distances ≤10 km because we consider dispersal of *V. americana* at those distances to be more likely based on inferences from the dispersal mechanisms described above; however, the relative frequency of dispersal by these different mechanisms is unknown. Quantifying the change in occupied area and potential connectivity across years in which surveys of SAV in the Bay were completed allows us to investigate how the scale and nature of networks has changed across time. These temporal changes in patch distribution provide insight into patch dynamics and the influence of patch dynamics on facilitating or preventing colonization or recolonization of suitable habitat.

Methods

We acquired coverage data for the distribution of SAV in tidal regions of the Chesapeake Bay from 1984 to

2010 from the Virginia Institute of Marine Science (VIMS; http://web.vims.edu/bio/sav/gis_data.html). VIMS has mapped SAV using aerial photography each year from 1971 to 2010, except for 1988, using methodology described in annual reports (e.g., Orth et al. 2010a). We converted polygon SAV coverages for each year to raster format with a cell size of 30 m. Larger cell sizes were tested, but beyond 30 m the continuity and distribution of mapped patches was inconsistent.

We obtained bathymetry data for the southeastern U.S. Atlantic coast at a scale of 3 arc-seconds from the National Geophysical Data Center coastal relief model (www.ngdc.noaa.gov) and clipped it to include only the tidal portion of the Chesapeake Bay. The bathymetry data were resampled from 84 m cells to 30 m to facilitate clipping of the SAV raster.

We used salinity data from all available georeferenced monthly water quality monitoring stations in the Chesapeake Bay and its major tributaries (range 104–430 stations per year) from the Chesapeake Bay Program's database (www.chesapeakebay.net/data_waterquality.aspx) for all years from 1984 to 2010 that had SAV coverage data available. We calculated the maximum yearly salinity at each station and used these values to interpolate a continuous salinity surface with a 30 m cell size across the Bay for each year using the geostatistical wizard kriging tool within ArcMap v10.3.1 (ESRI 2016). We used universal kriging with constant trend removal to account for the north–south directionality of salinity data within the Chesapeake Bay. Data were untransformed and fit with a Gaussian kernel function that was optimized separately for each salinity layer within the geostatistical wizard tool. Interpolated salinity surfaces from 1984 to 2010 were averaged to generate a single salinity surface.

The bathymetry and salinity data were used to clip the SAV layers to sites meeting known requirements for growth of V. americana. We used the single depth limit ≥ -5 m that represents the lower limit of prevalent growth of V. americana in low turbidity environments (Dutton and Juday 1944; Sheldon and Boylen 1977; Titus 1983). Temporal and spatial scales of water quality data were not sufficient to model the complex effects of turbidity on depth limitations of SAV growth (Hudon et al. 2000). However, because we limited our potential V. americana habitat to areas previously or currently occupied by SAV, growth

limitations due to turbidity and depth were *de facto* incorporated.

Each annual SAV raster was clipped using the average salinity data over 1984–2010. Competitive ability and growth of V. americana decline when salinity is >8 ppt (Doering et al. 2001; Cho and Poirrier 2005; Boustany et al. 2010) and growth is minimal at ≥ 15 ppt (Twilley and Barko 1990; Doering et al. 2001; French and Moore 2003; Boustany et al. 2010). We explored four salinity cutoff levels: 8, 10, 12, and 15 ppt. In our analysis, coverages resulting from 10 ppt cutoffs yielded distributions that coincided with many confirmed V. americana occurrences without including sites in which the species has never been documented (Moore et al. 2000). We therefore used the maximum salinity limit of 10 ppt to provide a generous but realistic distribution of V. americana. The resulting coverage maps represent patches of SAV that are within the environmental limits of the species, but only a subset have been confirmed through ground truthing. Thus, we certainly overestimate the actual extent of the species, but we do so in the same manner for all data sets. We consider this the best-case scenario for the distribution and abundance of V. americana and a reasonable basis for assessing maximum potential connectivity.

To determine the full extent of potential V. americana habitat within the Bay that had been recently occupied, we merged the separately clipped annual rasters from 1984 to 2010 into one composite coverage map. Using information provided in the VIMS annual reports for all years, we determined which flight lines within USGS quadrangles were completely surveyed, partially surveyed, or not surveyed. Each 30 m cell in the composite coverage was coded for the number of times SAV occurred in that cell and the number of times the quadrangle containing that cell was surveyed. Using these cell occurrence and survey frequency data, we calculated the average and maximum number of years that individual composite patches occurred across all survey years. This provides insight into the persistence of patches through time. We used simple linear regression to compare the sizes of patches by average age for only those patches present in the composite coverage for all 26 survey years in R v3.2.2 (R Development Core Team 2008).

Additionally, to assess changes through time and to compare habitat extent and potential connectivity

within these years to what had been occupied at any time between 1984 and 2010, we individually examined 9 years for which all flight lines were flown, yielding complete survey data: 1998, 2000, 2002, 2004, 2006, 2007, 2008, 2009, 2010.

Landscape analysis

For all ten data sets (1 composite and 9 individual years), we calculated the area of each patch and of all patches combined with Fragstats v3.4 (McGarigal et al. 2002). We measured potential connectivity using standard graph theoretic statistics based on the number of *nodes* (patches) that lay within a range of critical distance thresholds, from complete patch isolation to connection of all patches and thus were connected into *components* (patch groupings at a critical distance thresholds) by edges (links among patches).

Discrete patches for each data set were defined in ArcMap v10.3.1 using an eight-neighbor rule. Text representations of all rasters were extracted and subsequently submitted to GenGraph (Urban 2003) to create node files. We used the PopGenReport v2.2 (Adamack and Gruber 2014) package in R v3.2.2 to calculate pairwise over-water distances between patches, because pollen dispersal and most seed dispersal are limited to the water column (Harwell and Orth 2002; Kendrick et al. 2012). Even waterfowl, which could disperse across land, tend to follow waterways during localized and long-distance flight (Hochbaum 1955). Friction layers were constructed for each year by assigning a dispersal cost of 1 to water, a cost of 0 to occupied habitat, and no-data (i.e., no dispersal) to land. Calculating distance in this way provides measures that are analogous to edge-to-edge distances between patches across water. Graph edges are shown in figures as straight lines from patch centroids for graphical convenience.

Node and distance files for all coverage maps were submitted to the program Conefor Sensinode v2.6 (Saura and Torné 2009) to evaluate networks at critical distance thresholds in 100 m increments ranging from 100 m to the distance at which all nodes were connected by edges into a single component. We examined distances ≤10 km more closely, as this distance represents the upper limit we consider likely for dispersal among patches. At each critical distance, we calculated the number of components, proportion

of all patches in the largest component, and the integral index of connectivity (*IIC*) (Saura and Pascual-Hortal 2007). The metric *IIC* is a binary model, which treats two patches as connected if an area-weighted link is below a threshold distance. *IIC* incorporates not only distance but also the size of patches, thus avoiding the result of increased connectivity with increases in patch number regardless of total patch area. *IIC* is a fraction with total landscape area in the denominator, which in this study results in minute values; therefore we used a standardized form of the numerator (*IIC*num). *IIC*num is defined as $\sum_{i=1}^{n}\sum_{j=1}^{n}\left(\frac{a_i \cdot a_j}{1 + nl_{ij}}\right)$, where a_i and a_j are the areas of patches i and j and nl_{ij} is the shortest number of edges required to link patches i and j (Saura and Pascual-Hortal 2007). *IIC*num is considered a habitat availability index because it integrates interpatch connectivity with habitat area (Pascual-Hortal and Saura 2006). As with *IIC, IIC*num is maximal for one large, contiguous patch and declines as patch size decreases and patches become numerous and more distant from one another. For any particular landscape, *IIC*num reaches a maximum when all patches are directly connected to one another.

*IIC*num is difficult to compare across different landscapes due to the integration of area and distance. To facilitate comparisons across landscapes, we used and present a form of *IIC*num that represents equivalent connectivity (*EC*). *EC*(*IIC*) (the square root of *IIC*num) is interpreted as the size of a single habitat patch that would provide the same *IIC* value as the actual habitat pattern (Saura et al. 2011), and therefore it can be compared across landscapes. *EC*(*IIC*) will equal the total habitat area in a landscape when all habitat is within a single patch.

For each critical distance threshold, we calculated *EC*(IIC) and also compared proportional differences in *EC*(IIC) (*dEC*(IIC)) as a function of proportional differences in habitat area (*dA*) to provide insight into the degree to which differences in habitat amount yields changes in connectivity. Comparing EC and area in this way provides an assessment of the impact of changing habitat area on overall connectivity (Saura et al. 2011). When *dEC*(IIC) > *dA*, the additional habitat area makes substantial contributions to connectivity (Saura et al. 2011). Conversely, when *dEC*(IIC) < *dA*, the additional habitat represents isolated patches that make little contribution to increased

habitat connectivity beyond the additional area (Saura et al. [2011](#)). Finally, when $dEC(IIC) = dA$, the additional habitat area is adjacent to or contiguous with the original habitat area and corresponds to a neutral area gain in connectivity (Saura et al. [2011](#)).

We calculated the difference between $dEC(IIC)$ and dA in two ways. First, to examine changes in potential connectivity through time, we compared each sequential pair of years for which survey data were complete by calculating $dEC(IIC)$ as the absolute value of $\left(\frac{EC(IIC)_{year_1} - EC(IIC)_{year_0}}{EC(IIC)_{year_0}}\right)$ and dA as the absolute value of $\left(\frac{Area_{year_1} - Area_{year_0}}{Area_{year_0}}\right)$ (Saura et al. [2011](#)). Then, we calculated the difference between the values ($dEC(IIC) - dA$). Second, we compared potential habitat connectivity within individual years to that of the composite coverage. This comparison was accomplished by calculating $dEC(IIC)$ as the absolute value of $\left(\frac{EC(IIC)_{composite} - EC(IIC)_{year}}{EC(IIC)_{year}}\right)$, then calculating the corresponding proportion of change dA (Saura et al. [2011](#)), and afterward calculating the difference between the values ($dEC(IIC) - dA$).

Results

The total amount of SAV acreage occupied between 1984 and 2010 is 76,836 ha, an amount much greater than is found in individual years. We estimate that 25,204 ha of this total constitutes potential *V. americana* habitat, based on appropriate salinity and depth. This acreage is distributed across 2138 patches that range in size from 0.09 to 4834.35 ha (median = 0.27 ha; Table [1](#)).

Forty-six percent of patches in the composite coverage (n = 997) occur in only a single survey. These patches are located in quadrangles that were surveyed an average of 18.56 years out of 26 possible. An additional 776 patches are present in 2–5 years, and the quadrangles in which these patches are located were surveyed an average of 17.57 years. Only 30 patches are documented to have been in place for over 20 years, and all of these patches greatly increased in extent during that time. Patches existing for more than 20 years are found in quadrangles that were surveyed an average of 25.4 years. In the composite coverage, average patch occurrence for each individual patch is the average of the number of times each cell within a patch was occupied. The mean average patch occurrence is 2.09 years (median = 1.5 years), and the maximum average patch occurrence for an individual patch is 12.1 years. Unfortunately, patch occupancy and survey coverage are confounded due to unequal survey effort across quadrangles and years. The quadrangles containing patches that potentially contained *V. americana* were surveyed an average of 18.33 years (median = 16 years) out of 26 possible years (range 5–26 years). There are 207 patches contained within quadrangles with complete survey coverage. For these patches, there is a positive linear relationship between average patch age and patch size (Fig. [1](#); $r^2 = 0.3346$, F(1, 104.6), $\beta = 12.373$, $p < 0.005$).

In the composite coverage, we identify three critical distance thresholds at which there are rapid changes in potential connectivity as measured by $EC(IIC)$ (Fig. [2](#)a): 17, 139.1, and 210.4 km. Increases in $EC(IIC)$ between 0.1 and ~ 17 km indicate that many patches are separated by distances within this range and that small changes in distance have large effects on whether or not they are connected into components. At a critical distance of 17 km, the proportion of patches contained in the largest component is 0.30 (Fig. [2](#)b). At these shorter distances, components form eight general areas that correspond to patches in the northern and central Bay and graph networks within the following seven rivers: Chester, Patuxent, Potomac, Rappahannock, Pamunkey, Mattaponi, and James (Fig. [3](#)). At ≥17 km, $EC(IIC)$ connectivity increases are minimal, because most patches are joined into one or a few components within each area.

A second critical distance threshold occurs at 139.1 km. The small but abrupt increase in $EC(IIC)$ in the composite coverage at this distance results from the north-central component joining with the Patuxent and Potomac Rivers into one component. The third threshold in $EC(IIC)$ occurs at a critical distance of 210.4 km and corresponds to the joining of the component above with components in the tributaries in the southern part of the Bay (Table [1](#)).

At the 10 km critical distance, there are single components in each of five rivers (Chester, Patuxent, Rappahannock, Pamunkey, and Mattaponi) and multiple components in the Potomac and James Rivers (Fig. [3](#)). At this critical distance, the patches in the

Table 1 Landscape characteristics of potential *Vallisneria americana* habitat: number of patches, area, average patch area, critical distance required to yield seven main components, maximum critical distance required to connect all patches across the 9 years with complete flight line coverage and the composite coverage

Year	Number of patches	Total area (ha)	Avg. patch size (ha)	Distance to seven components (km)	Max. critical distance (km)
1998	1251	7064	5.65	17.3	242.9
2000	1262	9529	7.55	24.8[a]	242.4
2002	1079	7973	7.39	15.7	251.4
2004	1292	10,992	8.51	46.4/22.3[b]	235.8
2006	1717	10,662	6.21	34.1/14.8[b]	245.7
2007	2018	13,072	6.48	41.7/14.6[b]	245.7
2008	2164	14,802	6.84	18.1	237.3
2009	2077	14,938	7.19	13.5	237.3
2010	2150	13,883	6.46	14.9	237.8
Composite	2138	25,204	11.79	33.3/16.9[b]	210.4

[a] In the year 2000 there were only six main components due to lack of patches in the Mattaponi

[b] Larger of the two numbers is the critical distance required to completely connect the Potomac River. Smaller of the two numbers is the critical distance required to form 8 main components with the Potomac River and Wicomico tributaries being disconnected
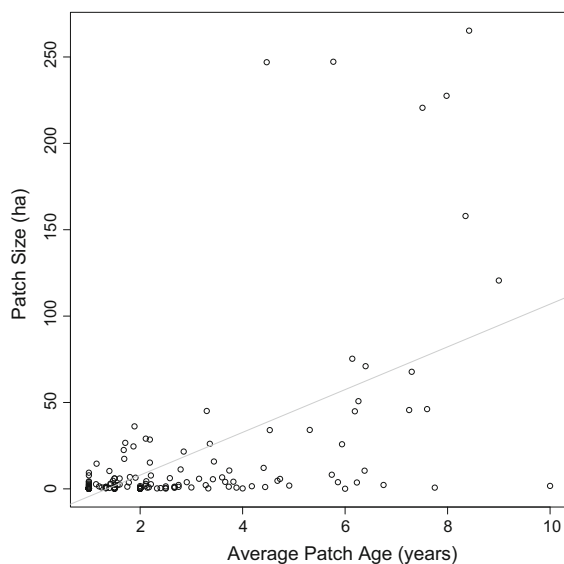
Fig. 1 Patch size (ha) against average patch age for 207 patches within quadrangles with complete survey coverage. $r^2 = 0.3346$, $F(1, 104.6)$, $\beta = 12.373$, $p < 0.005$

north central Bay form two isolated components on the northeastern shore and central western shore (Fig. 3). A critical distance of 33.3 km is required to form single components in each of these regions, but single components form in all regions except the Potomac at a critical distance of 16.9 km.

Years with complete survey data (1998, 2000, 2002, 2004, 2006, 2007, 2008, 2009, 2010)

individually support between 28 and 60 % of the total recently occupied potential *V. americana* habitat (Table 1). The number of patches per component generally increases through time (Table 2). The general shapes of the *EC(IIC)* curves for individual years are similar to that observed in the composite coverage; however, the distances at which connectivity thresholds are reached differ (Fig. 2a).

Within individual years, patches are united into single components at critical distances ranging from 235.8 to 251.4 km, exceeding the distances required in the composite coverage by 12.1–19.5 %. The same main components seen in the composite coverage are fully formed at distances between 13.5 and 46.4 km (Table 1), and at a critical distance of 17 km the proportion of total patches in individuals years contained within the largest component ranges from 0.26 to 0.55 (Fig. 2b). Due to the presence of patches within the Wicomico tributary of the Potomac River, additional distance is required to fully connect that river for the 2004, 2006, and 2007 coverages (Table 1). For the year 2000, no SAV patches are mapped on the Mattaponi River, so only six major components are formed within the entire Bay, and this occurs at a critical distance of 24.8 km.

The values of *dEC(IIC)* in relation to *dA* vary slightly across critical distances and pairs of years (Fig. 4a). Paired years in which area increases (1998–2000, 2002–2004, 2006–2007, 2007–2008,
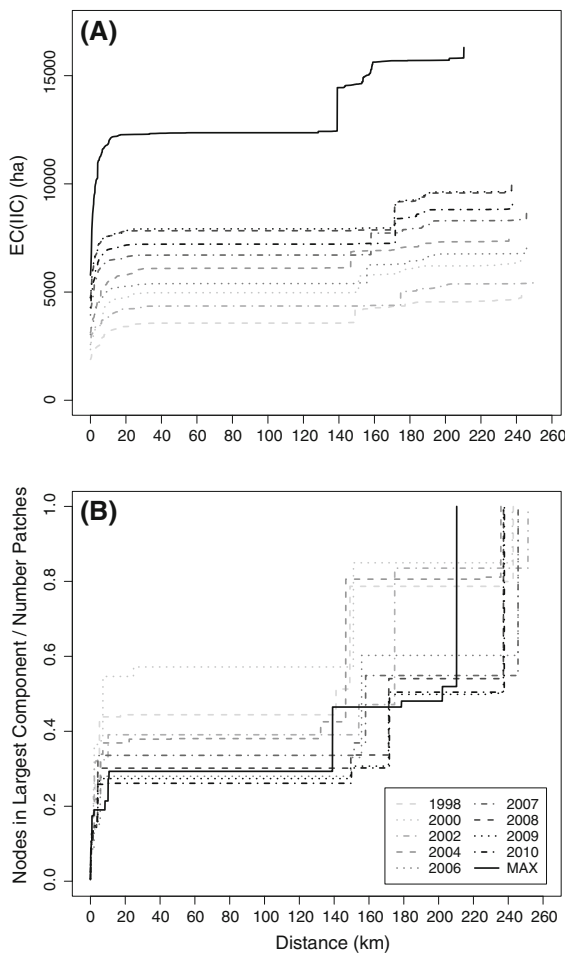
Fig. 2 a Equivalent connectivity ($EC(IIC)$) for each critical distance (km) and coverage map. **b** Proportion of total patches in the largest component for each critical distance (km) and coverage map

2008–2009) versus decreases (2000–2002, 2004–2006, 2009–2010) yield no consistent directional effect on potential connectivity. This is most evident at critical distances below 8 km, where the addition or subtraction of habitat area across all years could either enhance or have little impact on connectivity (Fig. 4b). Beyond the 8 km critical distance, the change in area influences connectivity, except in the 2000–2002 and 2008–2009 paired years. Between the years 2000 and 2002, ~150 km are required before changes in habitat area positively affect connectivity. Between 2008 and 2009, little or no connectivity change is observed across all critical distances, likely

due to habitat area only increasing by 136 ha between the 2 years.

When comparing coverages from individual years with complete survey data to the composite coverage, the values of $dEC(IIC)$ in relation to dA vary widely across critical distances and years (Fig. 5a). Below ~1.5 km, the composite coverage has similar potential connectivity to all individual years, as $dEC(IIC)$ is always smaller than dA. Between 1.5 and ~8 km, the additional area in the composite coverage increases overall connectivity relative to the 1998, 2000, and 2004 coverages (i.e., $dEC(IIC) > dA$); $dEC(IIC) \approx dA$ over these critical distances for the 2006 coverage (Fig. 5b). Above 8 km, $dEC(IIC)$ is less than dA for all years except for 1998, where the difference is not negative until ~20 km. At a distance of 139.1 km, there is an abrupt change in all years that corresponds to the point at which the north-central Bay component joins with the Patuxent/Potomac component. Between 140 and 210 km, values fluctuate around zero as a function of the connectedness of components within individual years. Within each year, as river and regional components are connected to each other, the gains in potential connectivity over area in the composite coverage are lost. Beyond 210.4 km, when a single component forms in the composite coverage, values again become positive, indicating that $dEC(IIC)$ is mostly greater than dA and that the additional area in the composite coverage results in greater potential connectivity than is present in individual years.

Discussion

Our analysis of patch distributions and potential connectivity yields three striking results. First, the amount of SAV coverage in any given year is much smaller than the total recently occupied acreage. Second, relately, the vast majority of patches of SAV that are within the tolerances of *V. americana* are ephemeral, being observed in only 1 or 2 years. Third, this high patch turnover results in highly variable potential connectivity from year to year, dependent on dispersal distance and patch arrangement.

Although the overall amount of total SAV in the Chesapeake Bay increased between 1984 and 1993, it
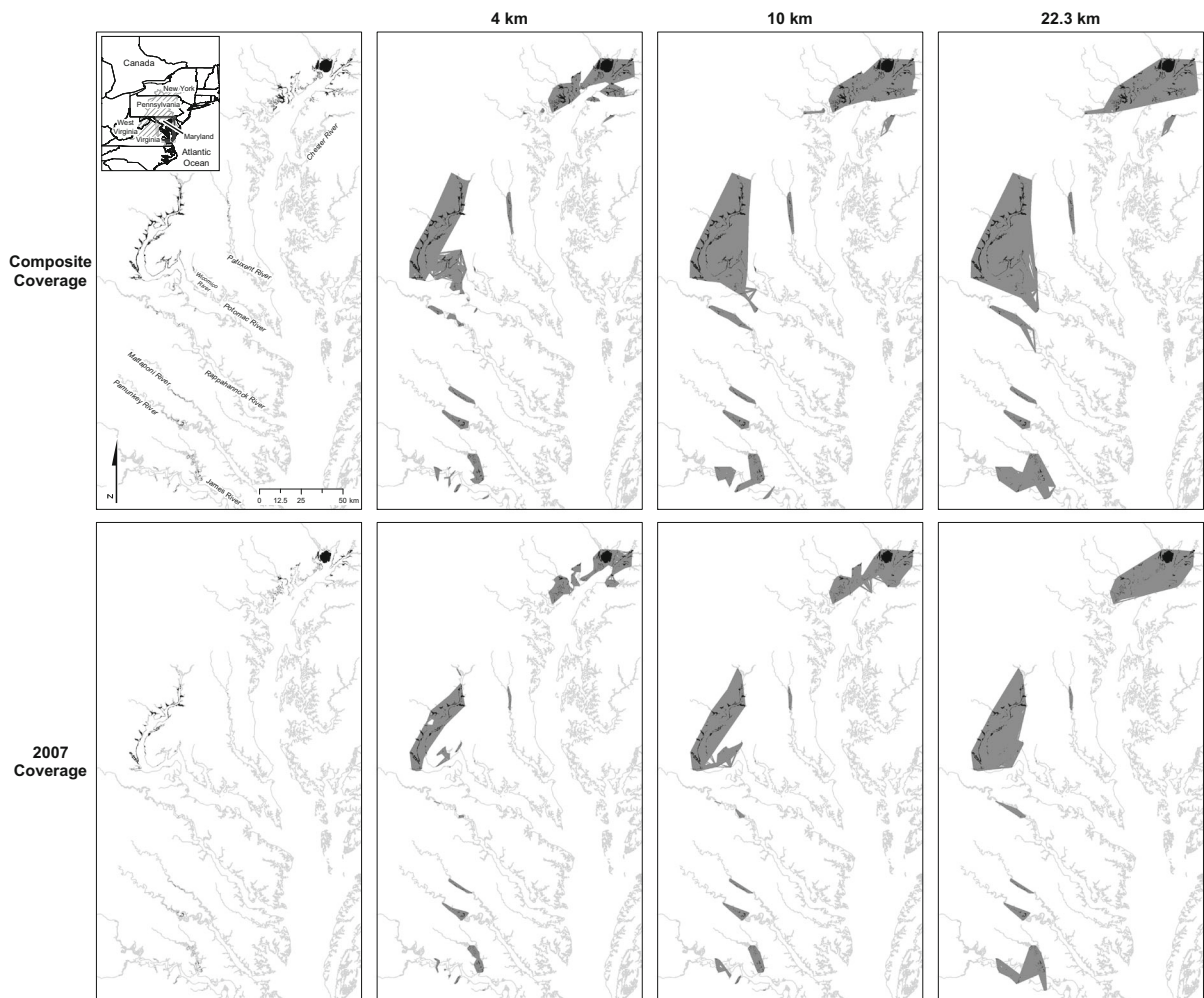
Fig. 3 Distribution of potential patches of *Vallisneria americana* within the Chesapeake Bay for the composite and 2007 coverages. The 2007 coverage map was selected as a representative of the years with complete survey coverage.

Connectivity among patches (edges) at critical distances of 4.0, 10.0 and 25.5 km are presented. Map projected in NAD 1983 UTM zone 18 N

has since fluctuated around 30,000 ha each year (Orth et al. 2010a). Lack of further increase may be due to poor water quality continuing to create unsuitable habitat conditions. However, we calculated the sum of SAV acreage occupied between 1984 and 2010 to be 76,836 ha. Thus, even under compromised environmental conditions, a large area of the Bay has historically supported SAV, although the full extent of this potential habitat is not realized in any 1 year. Even within the 25,204 ha that potentially contain *V. americana* based on salinity and depth, individual years have supported only 28–60 % of the acreage occupied in all years combined. The

significant positive linear relationship between patch age and patch size suggests that larger patches are more resilient to turnover; however, large size does not guarantee long-term persistence (Fig. 1). The inter-annual variation in extent and coverage could result from conditions fluctuating from suitable to unsuitable (e.g., salinity, temperature, turbidity; Carter et al. 1994; Rybicki and Landwehr 2007). Alternatively, conditions in the ephemeral locations may be marginal, capable of supporting annual species or tolerable for short time periods but incapable of supporting long-term persistence of perennial species. Further study of the relationship between

Table 2 Number of components, mean number of patches per component with standard deviation for each coverage map at 4, 10 and 22.3 km critical distances

Year	Components	Mean patches per component	SD
4 km crit. dist.			
1998	24	52.17	79.76
2000	25	50.52	95.20
2002	26	41.54	73.51
2004	25	51.72	80.91
2006	25	68.72	75.61
2007	21	96.14	114.38
2008	18	120.28	120.59
2009	23	90.35	108.02
2010	20	107.55	111.72
Composite	27	79.22	104.30
10 km crit. dist.			
1998	10	125.20	184.74
2000	11	114.82	207.64
2002	13	83.08	109.28
2004	15	86.20	133.93
2006	11	156.18	145.99
2007	12	168.25	196.14
2008	10	216.50	207.93
2009	9	230.89	180.20
2010	9	239.00	178.89
Composite	13	164.54	146.47
22.3 km crit. dist.			
1998	7	178.86	206.48
2000	7	180.43	245.59
2002	7	154.29	179.78
2004	8	161.63	199.43
2006	8	214.75	202.37
2007	8	252.38	242.00
2008	7	309.29	231.57
2009	7	296.86	210.51
2010	7	307.29	183.38
Composite	8	267.38	202.49

environmental variability and patch persistence and turnover is needed, both for fully understanding the factors that are limiting broader distribution of *V. americana* and for developing strategies to increase extent and connectivity.

The discrepancy between individual year coverages and total potential habitat (i.e., the composite coverage) has implications for long-term persistence of *V.*

americana in the Bay. The fact that the average patch occurrence in the composite coverage is 2 years shows that the majority of patches are short-lived. Locations that are within appropriate environmental tolerances (as indicated by occupancy) in a given year act as a shifting mosaic within the larger area of suitable habitat. This pattern indicates that the network is potentially functioning as a classically defined metapopulation (Levins 1969). However, given that a few patches are consistently present and many patches are present only one or a few years, source-sink dynamics may also be involved (Pulliam 1988), with persistent patches providing propagules for colonization and recolonization. Turnover could be exaggerated in two ways: First, it is possible that small patches remain present but are not detectable in aerial photographs or were lost in our raster conversion, and thus patches are more persistent than the record indicates. Second, clipping SAV coverages using the threshold in the interpolated salinity surface could cause different pixels to be included or excluded from the resulting surface in a way that might exaggerate turnover at the edges. On the other hand, much of the area considered to contain *V. americana* is actually occupied by invasive species such as Hydrilla (*Hydrilla verticillata*) and Eurasian water milfoil (*Myriophyllum spicatum*), suggesting that our results may be overly optimistic with regard to the actual distribution of *V. americana*.

We are unsurprised to find turnover in patch occupancy because substantial yearly changes in the local and regional distribution of submersed aquatic species are common (Cristofor et al. 2003; Demars and Harper 2005; Lirman et al. 2008), reflecting the dynamic nature of aquatic environments (van der Nat et al. 2003; Orth et al. 2010b; Santos et al. 2011; O'hare et al. 2012). Nonetheless, the magnitude of turnover and the number of patches persisting for less than 2 years is surprising. In addition to outright patch turnover, annual changes include increasing or decreasing size of persisting patches, coalescing of patches, breaking apart of single patches into multiple patches, and colonizing of new areas that subsequently persist. Changes will negatively affect colonization or recolonization ability if distances among occupied sites and other unoccupied, suitable sites increase beyond what is reasonable for dispersal of seed or vegetative propagules. The relative role of environmental conditions versus inability to reach
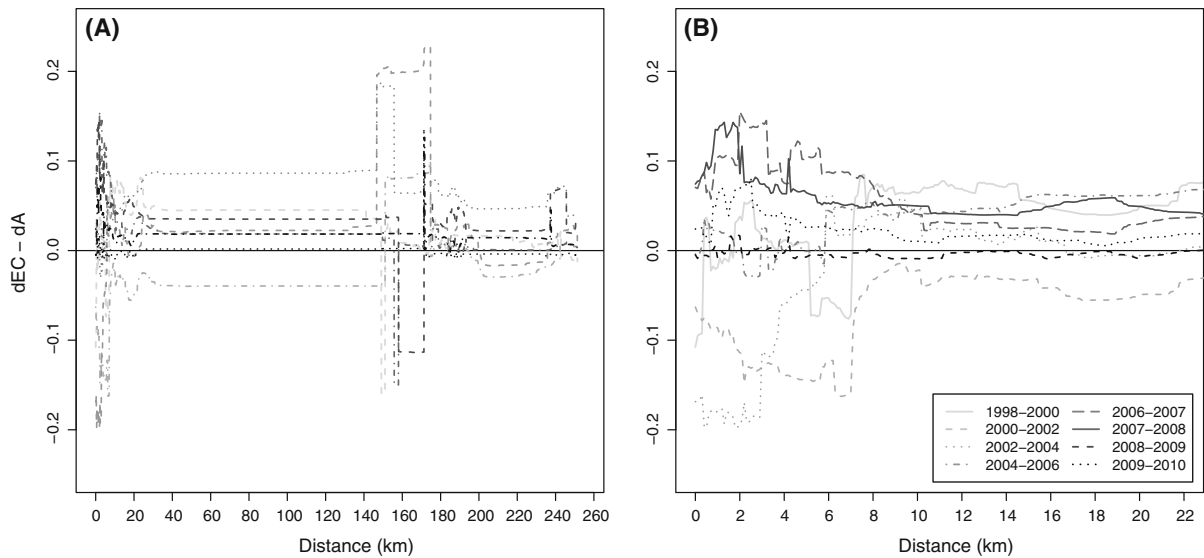
Fig. 4 a Difference in dEC(*IIC*) and dA for each pair of subsequent years across all critical distances. b Difference in dEC(*IIC*) and dA for each pair of subsequent years from 0 to 22 km. When dEC(*IIC*) > dA, the additional habitat area contributes additional connectivity (Saura et al. 2011). Conversely, when dEC(IIC) < dA the additional habitat represents

isolated patches and makes only a modest contribution to increased habitat connectivity (Saura et al. 2011). Finally, when dEC(IIC) = dA the additional habitat area is adjacent to, or overlapping the original habitat area and corresponds to a neutral area gain in connectivity (Saura et al. 2011)
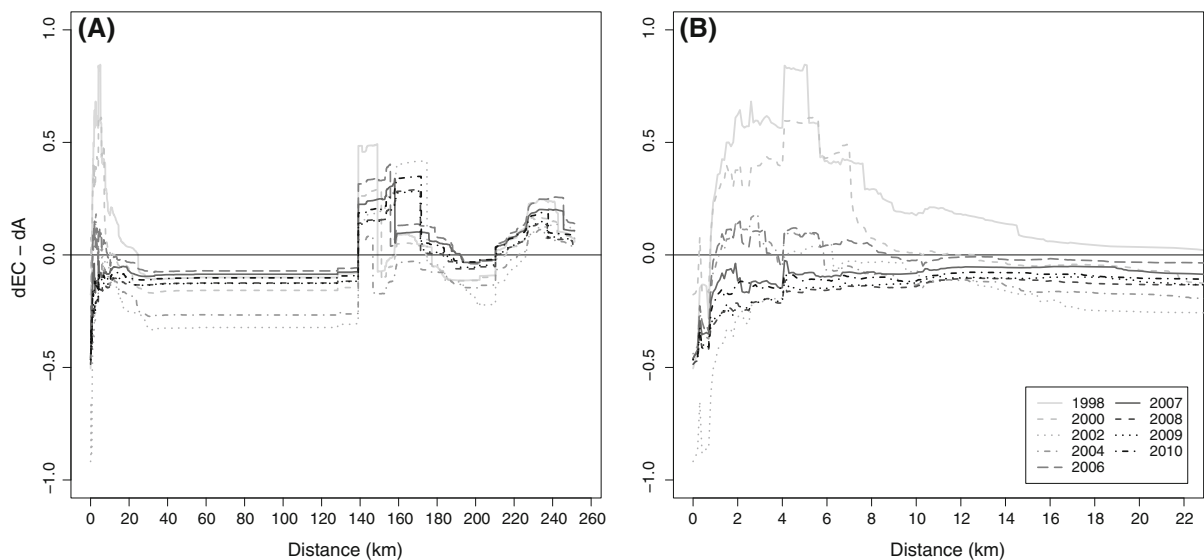

Fig. 5 a Difference in dEC(IIC) and dA for each year compared with the composite coverage across all critical distances. b Difference in dEC(IIC) and dA for each year compared with the composite coverage from 0 to 22 km. When dEC(IIC) > dA, the additional habitat area in the composite coverage has generally been connected to previously existing habitat areas (Saura et al. 2011). Conversely, when

dEC(IIC) < dA the additional habitat represents isolated patches and makes only a modest contribution to increased habitat connectivity (Saura et al. 2011). Finally, when dEC(IIC) = dA the additional habitat area is adjacent to, or overlapping the original habitat area and corresponds to a neutral area gain in connectivity (Saura et al. 2011)

suitable habitat requires further investigation that is beyond the scope of this investigation. Here we explore only the degree to which potential connectivity changes temporally and therefore might affect functional connectivity.

Although Bay-wide potential connectivity within individual years provides a benchmark for distribution of *V. americana* habitat, it is unreasonable to expect that pollen, seed, or vegetative propagules commonly disperse across the distances required to connect all patches (235.8–251.4 km). Even if all recently occupied habitat was occupied simultaneously, the maximum distance at which all patches are connected (210.4 km) is not within the realm of regular dispersal. In fact, only dispersal of seed by waterfowl has a reasonable potential to span those distances, and there is no evidence for judging how commonly such dispersal occurs. At critical distances most relevant to dispersal, based on SAV in general and the similar species *Z. marina* (<10 km for seed; Harwell and Orth 2002; Kendrick et al. 2012; Orth et al. 2012), we find a high degree of connectivity among patches within river drainages in the northern and central regions of the Bay. At the 10 km critical distance, between 26 and 55 % of patches were captured within the largest component of the graph network. At this scale, the majority of patches are connected into single components within river drainages or regions; however, the James and Potomac rivers require additional distance to be fully connected (Fig. 3). Pollen dispersal is most likely limited to localized areas within patches at typical dispersal distances [15 m in *Zostera* and 1–20 m in *Vallisneria*; (Harwell and Orth 2002); Lloyd et al. in prep].

Using *dEC(IIC)* to directly compare data sets with different amounts of habitat, we find that changes in area between sequential years does not necessarily strongly affect connectivity beyond within-patch connectivity that results from increased acreage alone. Pairs in which area increases (e.g., 1998–2000, 2002–2004) versus decreases (e.g., 2000–2002, 2009–2010) yield no consistent directional effect on connectivity. Rather, spatial arrangement of habitat following addition or subtraction of habitat area drives the metric values. In cases where habitat increases but is similarly distributed (e.g., from 2006 to 2007), there are only small additional gains to connectivity, as connectivity at shorter distances within regions and at longer distances among regions is largely unaffected

by the fluctuations in patch area. Examining the relationship between *dEC(IIC)* and *dA* provides an assessment of connectivity through time that is difficult to obtain with other connectivity metrics.

The benefits to connectivity of having all potential habitat occupied differ according to the critical distance. Below 1.5 km, the additional area in the composite coverage does not increase overall connectivity (Fig. 5b), indicating that the additional patches gained in the composite coverage are isolated and contribute minimally to connectivity. Between 1.5 and ~8 km, the added area in the composite coverage has an effect on connectivity in those years when habitat amounts are relatively low (1998 and 2000) and when habitat is more evenly distributed across the landscape (2004). In years in which a larger amount of habitat exists and in which it is aggregated into more discrete, isolated components (e.g., 2002, 2007–2010), the additional area in the composite coverage does not enhance connectivity at these distances. It is not until beyond 139 km that additional habitat area enhances connectivity, as it is at this distance that the composite coverage is largely connected within a few components.

Examining *V. americana* coverage data within a single year fails to capture the dynamic and ephemeral nature of this community in the Chesapeake Bay. By looking at 26 years of available data, we find that more patches and locations have been occupied recently than would be apparent based on yearly acreages alone. We also find high patch turnover from year to year. This turnover may be due to lack of persistence of marginal habitats resulting from compromised water quality. If so, then small reductions in turbidity and nutrient levels could yield more extensive and consistently suitable conditions that could support increased growth of *V. americana* (Rybicki and Carter 2002). However, such small reductions will depend on overall improvement in water quality of the watershed, which is beyond the scope of what individual resource managers can achieve. While we did not analyze data from 2011 to 2015, it is promising that total SAV coverage in the Chesapeake Bay has nearly doubled since 2012, reaching a record high of 37,077 ha in 2015 (Orth et al. 2016). It remains to be seen if the increase will continue. We show that if all sites that have been occupied in the recent past were occupied in a single year, the total amount of SAV coverage would be sufficient to exceed the 2010 restoration goal of

74,866 ha by nearly 1970 ha. Areas suitable for *V. americana* represent ∼33 % of this acreage and if it were completely occupied, the occupancy would represent up to ∼360 % of what we find in individual years. This increased acreage would greatly enhance probabilities of SAV persistence and their continued ecosystem service benefits.

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