Estuaries Vol. 23, No. 1, p. 115–127 February 2000

Analysis of the Abundance of Submersed Aquatic Vegetation Communities in the Chesapeake Bay

KENNETH A. MOORE[1]
DAVID J. WILCOX
ROBERT J. ORTH
The Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062

ABSTRACT: A procedure was developed using aboveground field biomass measurements of Chesapeake Bay submersed aquatic vegetation (SAV), yearly species identification surveys, annual photographic mapping at 1:24,000 scale, and geographic information system (GIS) analyses to determine the SAV community type, biomass, and area of each mapped SAV bed in the bay and its tidal tributaries for the period of 1985 through 1996. Using species identifications provided through over 10,000 SAV ground survey observations, the 17 most abundant SAV species found in the bay were clustered into four species associations: ZOSTERA, RUPPIA, POTAMOGETON, and FRESHWATER MIXED. Monthly aboveground biomass values were then assigned to each bed or bed section based upon monthly biomass models developed for each community. High salinity communities (ZOSTERA) were found to dominate total bay SAV aboveground biomass during winter, spring, and summer. Lower salinity communities (RUPPIA, POTAMOGETON, and FRESHWATER MIXED) dominated in the fall. In 1996, total bay SAV standing stock was nearly 22,800 metric tons at annual maximum biomass in July encompassing an area of approximately 25,670 hectares. Minimum biomass in December and January of that year was less than 5,000 metric tons. SAV annual maximum biomass increased baywide from lows of less than 15,000 metric tons in 1985 and 1986 to nearly 25,000 metric tons during the 1991 to 1993 period, while area increased from approximately 20,000 to nearly 30,000 hectares during that same period. Year-to-year comparisons of maximum annual community abundance from 1985 to 1996 indicated that regrowth of SAV in the Chesapeake Bay from 1985–1993 occurred principally in the ZOSTERA community, with 85% of the baywide increase in biomass and 71% of the increase in area occurring in that community. Maximum biomass of FRESHWATER MIXED SAV beds also increased from a low of 3,200 metric tons in 1985 to a high of 6,650 metric tons in 1993, while maximum biomass of both RUPPIA and POTAMOGETON beds fluctuated between 2,450 and 4,600 metric tons and 60 and 600 metric tons, respectively, during that same period with net declines of 7% and 43%, respectively, between 1985 and 1996. During the July period of annual, baywide, maximum SAV biomass, SAV beds in the Chesapeake Bay typically averaged approximately 0.86 metric tons of aboveground dry mass per hectare of bed area.

Introduction

Aerial photography and mapping surveys have been used in a number of regions to determine the distribution of submersed aquatic vegetation (SAV) populations and changes in these populations over time (Orth and Moore 1984; Larkum and West 1990; Coles et al. 1993; Bulthuis 1995; Ferguson and Korfmacher 1997; Robbins 1997). Aerial mapping surveys of Chesapeake Bay SAV have been conducted annually in the Chesapeake Bay and its sub-estuaries since 1985. Published in report form (e.g., Orth et al. 1997) as well as on the world wide web (http://www.vims.edu/bio/sav) these data have proven to be useful for many bay management activities. Because of the strong relationships which have been developed between the occurrence of submersed angiosperms and water quality conditions (Batiuk et al. 1992; Dennison et al. 1993), the recovery of these communities has been chosen as one the principal indicators of the success of Chesapeake Bay clean-up efforts. The baywide annual aerial surveys have therefore become a cost effective and comprehensive tool with which to assess changes in this resource. However, the various SAV communities found in the Chesapeake Bay system can respond differently to changing water quality conditions as communities may differ in their capacity to withstand periods of high turbidity, nutrient enrichment, or salinity extremes (Stevenson and Confer 1978; Carter and Rybicki 1985; Stevenson et al. 1993; Moore et al. 1996). Since it is cost prohibitive to annually survey the SAV species composition of each of the thousands of SAV beds in the bay, and there has been as yet no effective way to discriminate individual SAV beds into their dominant species or community

[1] Corresponding author; tele: 804/684-7384; fax: 804/684-7293; e-mail: moore@vims.edu.

types from high altitude aerial photography alone (Orth and Moore 1983; Zieman et al. 1989; Bulthuis 1995), a procedure was necessary to assign a classification type to each bed so that year-to-year changes in the various SAV communities could be assessed.

The aerial photographic surveys of the Chesapeake Bay shorelines provide measures of SAV bed areas which are then subsequently photointerpreted into four density classes (Orth and Moore 1983). While these category-type data provide good measures of relative abundance they do not provide sufficient information to determine SAV species biomass or standing crop. In addition, estimates of SAV abundance at various times throughout the year are not directly available since the photography is usually flown only once annually at times of estimated peak SAV aboveground biomass and these flight dates vary among the various regions of the bay. Typically, high salinity regions are photographed in the late spring or early summer and low salinity and freshwater tidal areas in the late summer.

Estimates of spatial and temporal variability of SAV biomass has become increasingly important as the capacity of researchers and managers to effectively model coastal bay ecosystems improves. Differences between measurements of SAV area coverage and actual biomass can be important. During any particular year overall bay SAV area may increase, or decrease, or remain the same from previous years, while SAV biomass may not vary linearly with change in area. A common metric such as biomass or standing crop is necessary to discriminate potential changes over both spatial or temporal intervals, especially in context of the overall bay ecosystem. In addition, calibration and validation of landscape scale, ecosystem simulation models (e.g., Boumans and Sklar 1990; Constanza et al. 1990; Cerco and Cole 1994) which are developed with an SAV component generally require information on SAV mass, not area or relative abundance.

The overall goal of this study was to determine the biomass for all areas of SAV mapped in the Chesapeake Bay over the period of 1985 through 1996 using SAV distribution and abundance information available from annual reports, biomass information available from published and unpublished studies by bay researchers, and species ground survey observations provided by researchers, trained volunteers and others in the bay community. Our specific objectives were to use previously collected survey information to develop appropriate SAV species associations which could be used to classify the SAV beds found throughout the bay into a small number of community types; to develop annual models of SAV biomass for each of these SAV community types; and to develop a procedure using geographic information system (GIS) analyses to assign the appropriate SAV community types and calculate the biomass of each SAV bed mapped in the Chesapeake Bay annually from 1985 through 1996.

Methods

Development of SAV Community Types

The identification of SAV community types was based on an analysis of SAV ground survey data published in annual SAV distribution reports from 1985 to 1996 (e.g., Orth et al. 1997). These reports document the locations of all the SAV species which have been identified by presence/absence censuses in field surveys conducted during the growing season of each of the years by researchers, government agencies, and trained individuals, including citizens groups. All eleven years of ground survey information from 1985–1996 (no aerial mapping data in 1988) were digitized into a database using ARC/INFO GIS for use in this analysis. Species information was assigned to each of the individual locations which were identified on the SAV maps in each yearly report. *Chara* sp., *Najas flexilis, Nitella* sp., *Potamogeton epihydrus, Potamogeton nodosus,* and *Trapa natans* were identified in twelve or fewer observations and therefore were not used in the determination of SAV community types. Figures 1a–n present the recorded occurrences of each of the individual species from 1985–1996.

Community types were developed from the entire ground survey database using numerical clustering analysis. Dice's coefficient of similarity (Boesch 1977) is a commonly used quantitative resemblance measure which is useful for the numerical clustering of binary (presence/absence) ground truth data such as gathered in the ground surveys (Clifford and Stevenson 1975). The greater the coefficient of similarity, the more frequently paired species or groups of species occur in the database. The overall bay SAV species spatial distributions, which are controlled in most cases by salinity tolerance (Stevenson and Confer 1978), were then used along with the results of the clustering analysis in the final assignment of individual species to specific community types.

Figure 2 presents a summary of the clustering analysis of all 11 yr of ground survey information (10,023 observations) in dendrogram form. Dice's coefficients between individual species or species groups are represented by the vertical lines. Table 1 presents a matrix of the number of observations reporting pairs of individual species as well as the number of observations reporting only a single

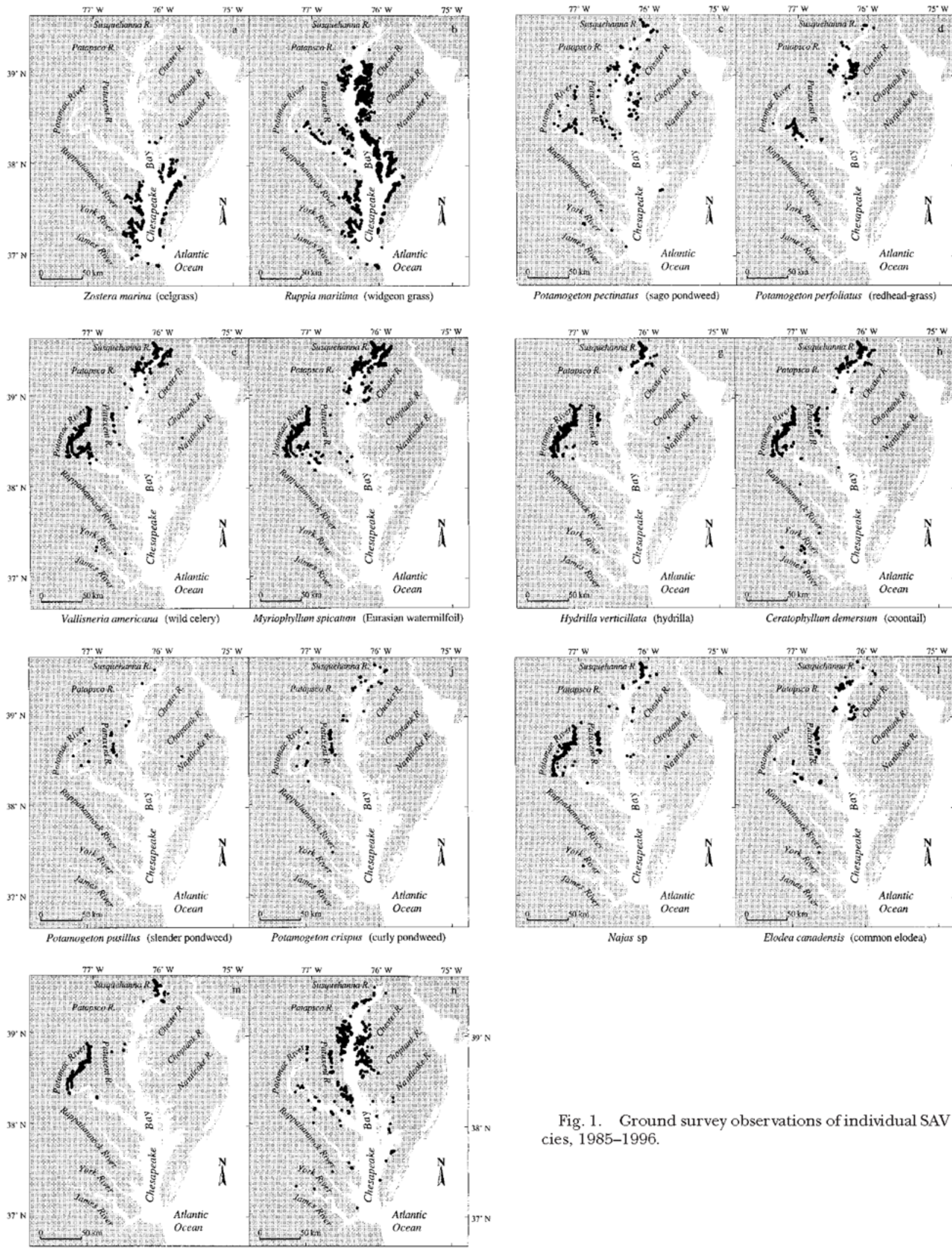

Fig. 1. Ground survey observations of individual SAV species, 1985–1996.

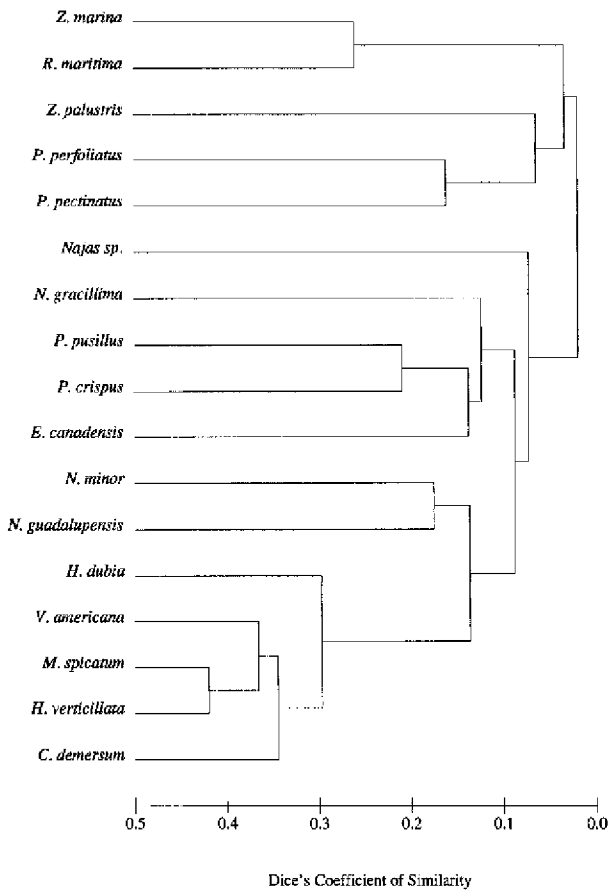

Fig. 2. Dendrogram of species association based upon all 1985–1996 ground survey information.

species. For example, *Zannichellia palustris* (Zp) was found growing with *Ruppia maritima* (Rm) 134 times and *Zostera marina* (Zm) 11 times, but in monospecific stands 874 times. *Vallisneria americana* (Va) was observed growing with *M. spicatum* (Ms) 1,201 times, in monospecific stands 209 times, but never with *Z. marina*. Although *Z. marina* and *R. maritima* are highly associated (Fig. 2), *R. maritima* is typically a minor component of polyhaline SAV beds in the lower bay, which are usually dominated by monospecific stands of *Z. marina* in all but the shallowest areas (Orth and Moore 1983; Moore et al. 1995; Table 1). *R. maritima,* however, has a wide salinity tolerance and has also been found throughout the mid-bay as well as the Patuxent, Potomac, and Rappahannock Rivers in many monospecific beds (Table 1; Fig. 1b). Based upon this additional information *Z. marina* and *R. maritima* were divided into two species groups with all beds containing *Z. marina* assigned to a ZOSTERA community type and beds containing *R. maritima,* but not *Z. marina* assigned to a RUPPIA community type.

Assignment of lower salinity species into community types was similarly determined. For example, *Z. palustris, Potamogeton pectinatus,* and *P. perfoliatus* were found throughout many of the same mid-bay regions and overlapped the distribution of *R. maritima,* although usually not at the same locations (Fig. 1b,c,d,n). *Z. palustris* can grow in monospecific beds early in the year (Haramis and Carter 1983) and may not be found in some areas by late-summer. In fact, some of the beds of *Z. palustris* which are located by ground truth surveys early in the year (Fig. 1n) do not appear on the

TABLE 1. A matrix display of the number of observations out of 10,023 total bay wide observations from 1986–1996 reporting each pair of species. The number of observations reporting a single species is reported on the diagonal. Zp—*Zannechellia palustris,* Zm—*Zostera marina,* Va—*Vallisneria americana,* Rm—*Ruppia maritima,* Ppu – *Potamogeton pusillus,* Ppf—*Potamogeton perfoliatus,* Ppc—*Potamogeton pectinatus,* Ppc—*Potamogeton crispus,* Nm—*Najas minor,* Ngu—*Najas guadalupensis,* Ngr–*Najas gracillima,* N—*Najas* sp., Ms—*Myriophyllum spicatum,* Hv—*Hydrilla verticillata,* Hd—*Heteranthera dubia,* Ec—*Elodea canadensis,* Cd—*Ceratophyllum demersum.*

	Zp	Zm	Va	Rm	Ppu	Ppf	Ppc	Pcr	Nm	Ngu	Ngr	N	Ms	Hv	Hd	Ec	Cd
Cd	54	0	532	3	23	13	40	74	155	117	43	80	981	839	371	172	88
Ec	44	0	143	25	18	62	29	60	44	44	31	11	196	40	7	41	
Hd	5	0	409	1	2	10	8	6	37	58	1	41	622	551	16		
Hv	22	0	877	0	13	3	16	25	298	118	31	66	1,453	445			
Ms	54	0	1,201	36	8	87	67	32	177	98	17	61	773				
N	6	0	61	4	4	2	5	5	1	6	1	16					
Ngr	17	0	13	0	6	0	0	17	26	19	8						
Ngu	18	0	90	0	14	3	5	22	51	7							
Nm	14	0	135	0	9	0	5	25	4								
Pcr	26	0	40	1	19	5	9	7									
Ppc	51	1	77	53	2	57	79										
Ppf	49	0	70	123	1	89											
Ppu	18	0	13	0	0												
Rm	134	699	25	2,387													
Va	34	0	209														
Zm	11	567															
Zp	874																

TABLE 2. SAV Species Associations. Species occurrence in community exceeds 10% of species observations. * Dominant Species

• ZOSTERA Community	*Zostera marina** *Ruppia maritima*
• RUPPIA Community	*Ruppia maritima** *Potamogeton perfoliatus* *Potamogeton pectinatus* *Zannichellia palustris*
• POTAMOGETON Community	*Potamogeton pectinatus** *Potamogeton perfoliatus** *Potamogeton crispus* *Elodea canadensis*
• FRESHWATER MIXED Community	*Myriophyllum spicatum** *Hydrilla verticillata** *Vallisneria americana** *Ceratophyllum demersum* *Heteranthera dubia* *Elodea canadensis* *Najas guadalupensis* *Najas gracillima* *Najas minor* *Najas* sp. *Potamogeton crispus* *Potamogeton pusillus*

aerial photography surveys of these regions in August (Orth et al. 1997). Although *Z. palustris* has been found to be associated with a variety of species it was found most commonly growing with *R. maritima* and is included in that association. Since there were few beds of SAV which consist principally of *Z. palustris* in the aerial mapping database (e.g., Orth et al. 1997) the abundance of this species may be underestimated. *P. perfoliatus* and *P. pectinatus* in contrast, have been typically found as dominants in a variety of mixed and monospecific stands (Table 1; Fig. 1c–d). Therefore, all beds reported with either *P. perfoliatus* or *P. pectinatus,* but no *Z. marina* or *R. maritima,* were assigned to a POTAMOGETON community type.

Freshwater regions of the upper bay and the upper Potomac River were vegetated with a diverse assemblage of SAV (Fig. 1e–m) which were clustered in a large group of 12 species ranging from *Najas* sp. to *Ceratophyllum demersum* (Fig. 2). Of these 12 species *Myriophyllum spicatum, Hydrilla verticillata,* and *Vallisneria americana* were the most abundant. *H. verticillata* and *M. spicatum* had the highest co-occurrence of any two species reported with over 1,450 observations reporting both species (Table 1). *V. americana* was found to co-occur with *H. verticillata* and *M. spicatum* 877 and 1,201 times, respectively. All beds not assigned to the ZOSTERA, RUPPIA, or POTAMOGETON community types were assigned to a FRESHWATER MIXED community type.

Table 2 presents the species associations for all four community types including all species where occurrence exceeded 10% of observations. Figure 3a–d display the SAV bed field observations after assignment to community type. FRESHWATER MIXED and POTAMOGETON communities dominate the upper bay and upper tributaries, while RUPPIA was found throughout much of the bay excluding most freshwater tidal regions. ZOSTERA dominates the lower bay.

Assignment of Individual SAV Beds to Community Types

Since yearly ground survey species information was not available for each individual SAV bed a procedure was developed to classify each mapped bed into a specific community type for each year of the aerial survey. In most areas of the bay and its tributaries, SAV beds which are located near one another tend to be composed of similar species. Therefore, to a certain extent, beds can be assigned to the community type of the nearest point where field survey information is available. This confidence decreases with increasing distance from a survey location. To determine the maximum distances that can be used with confidence, the distribution of field observations for 1994 and 1995 were analyzed spatially using ARC/INFO GIS software. Ground surveys for the years 1994 and 1995 were chosen because of the broad distribution and intensity (33% of all beds surveyed) of ground survey observations made during that period. On average, between 1985 and 1996, 29% of all the beds in the bay were ground surveyed each year.

First, the over-water distance between reported survey locations was computed and used to determine the percentage of observations within a particular distance of each other that share the same community type. This distance relationship can vary greatly throughout the bay due to factors such as the local salinity gradient. Therefore, the CBP segmentation scheme, an area compartmentalization of the Chesapeake Bay into subunits, which was developed based upon salinity distributions, natural geographic partitions and other natural features (see Orth et al. 1997), was used to apply this spatial analysis throughout the entire bay. Each of 44 Chesapeake Bay Program (CBP) segments was analyzed individually to estimate the maximum distance within which at least 90% of the ground survey observations within that segment were of the same community type. An example of this analysis for CBP Segment CB6 is presented in Fig. 4. In this CB6 Segment area all SAV ground survey locations surveyed in 1994 and 1995 were found to be of the same community type when they occurred within approximately 8 km of each other.

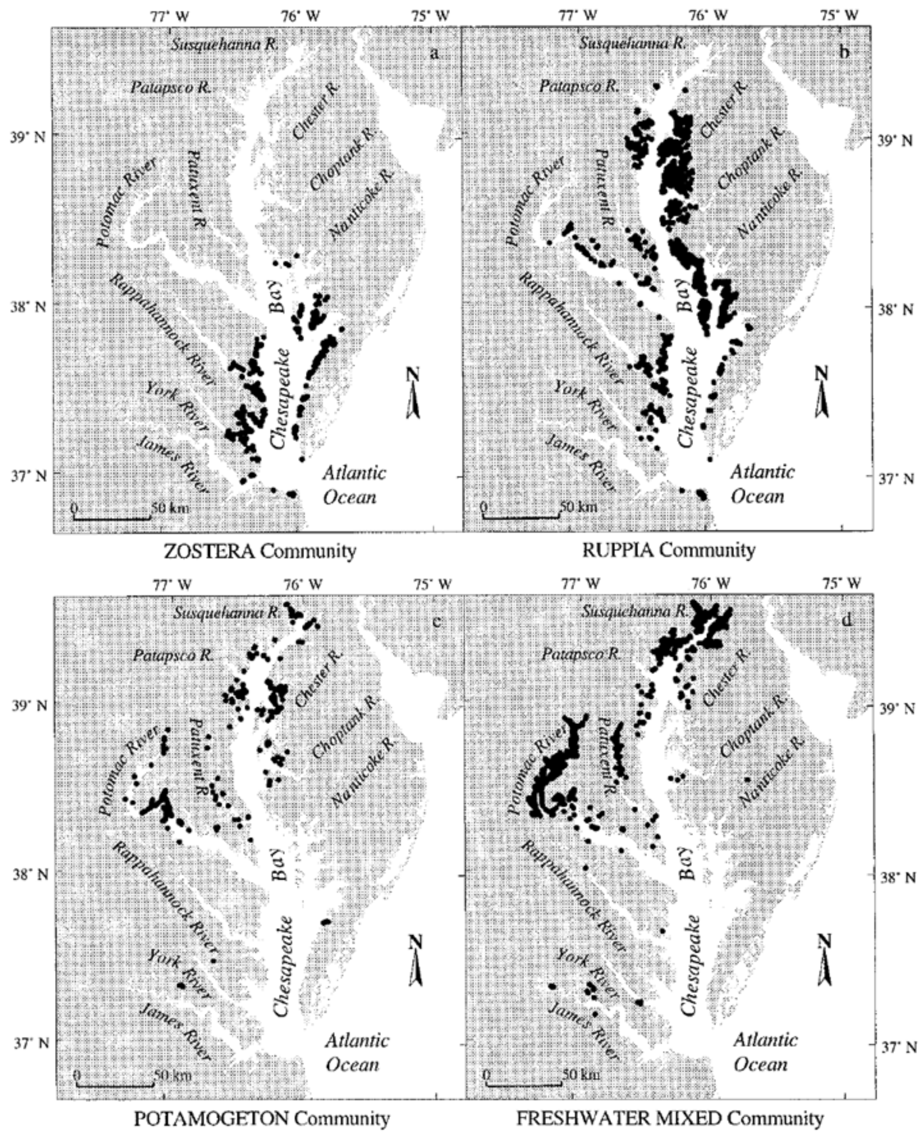

Fig. 3. Ground survey observations of SAV after assignment to community type, 1985–1996.

A 90% similarity was found up to a distance of approximately 11 km apart with a linear decrease in similarity with increasing distances up to 30 km. An increased similarity at distances beyond 30 km was likely due to comparisons between beds in separate tributaries within that segment area where salinity regimes were similar.

A step-wise procedure was used to assign a community type to each bed mapped in the annual aerial surveys from 1985 to 1996. If beds were directly surveyed in the current year they were assigned to a community type based on the species reported. If a bed was not directly surveyed in a year assignment procedures were followed in the following order until assignment could be made. Beds were assigned to the community type of the nearest field observations of the current year which were located within the 90% similarity distance computed for the CBP segment where the bed was located. Beds that were directly surveyed in the preceding year were assigned to a community type based on the species report at that time. Beds were assigned to the community type of the nearest field observations made the previous year within the 90% similarity distance computed for the CBP segment where the bed was located. Beds that were directly surveyed in the subsequent year were assigned to a community type based on the species reported. Beds were assigned to the community type of the nearest field observations made

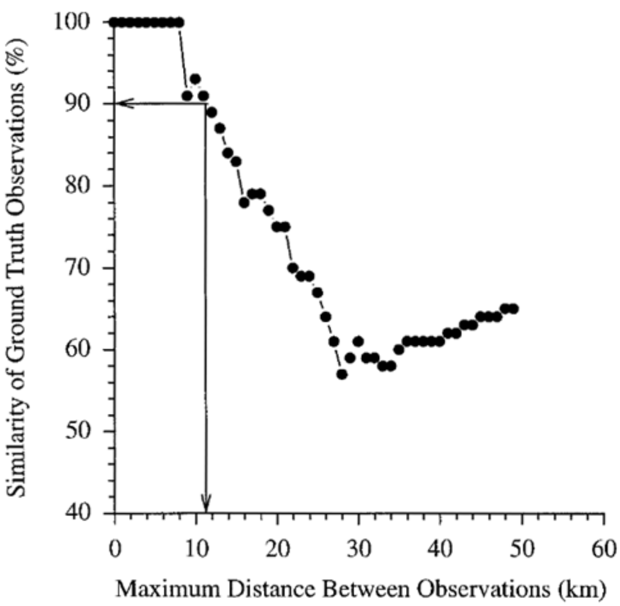

Fig. 4. Analysis of similarity of SAV species reported in ground survey observations compared to the over water distance between the observations for Chesapeake Bay Program Segment CB6. Arrows indicate distance at which pairs of individual species ground survey observations are classified in the same community type 90% of the time.

TABLE 3. Sources used in development of SAV biomass models for each community type.

FRESHWATER MIXED Community
Naylor and Kazyak 1995
Rybicki and Carter 1995
Carter et al. 1994
Carter and Rybicki unpublished data
Stevenson et al. 1993
Rybicki unpublished data
Kilgore et al. 1989
Rybicki et al. 1988
Rybicki et al. 1985
Staver 1986
Staver unpublished data
Nichols et al. 1979
POTAMOGETON Community
Stevenson et al. 1993
Lubbers et al. 1990
Nichols et al. 1979
RUPPIA Community
Moore et al. 1995
Stevenson et al. 1993
Orth and Moore 1986
Orth and Moore 1981
ZOSTERA Community
Moore et al. 1995
Orth and Moore 1986
Orth and Moore 1981

the subsequent year within the 90% similarity distance computed for the CBP segment where the bed was located. Any remaining SAV beds were individually assigned to a community type based on the spatial patterns provided by the entire ground survey data set.

Development of SAV Biomass Models for Each Community Type

Published and unpublished studies of SAV biomass from the Chesapeake Bay region (Table 3) were used to determine average monthly biomass values for the dominant species of each community type (Table 2). Only data from studies in which SAV aboveground biomass from dense monotypic stands were reported at least periodically in units of mass per area throughout the growing season were selected for use. Belowground measurements were not available for most species and therefore monthly models for this component of biomass were not attempted. Aboveground biomass values were converted from wet weight or other reported units to dry mass per unit area by first transforming each study's data to their proportion of the reported seasonal maximum of each species (cf., Nichols et al. 1979). These proportions of seasonal maxima were then applied to an overall average maximum seasonal value in units of grams dry mass m^{-2} which was calculated using the subset of studies that specifically reported results in units of dry mass per area. In those studies where field biomass sampling was not conducted monthly, values for months not sampled were estimated by linear interpolation. The mean monthly biomass values were determined by averaging the monthly values assuming equal area of each of the dominant species (Table 2) comprising a community type.

Each of the four SAV communities demonstrated a distinctive pattern of shoot biomass (Fig. 5a–d). The ZOSTERA and RUPPIA communities were found to exhibit peaks of shoot biomass in the early and late summer, respectively, and both maintained aboveground shoot biomass throughout the winter. Shoot growth for ZOSTERA from average winter minimums of 45 gdm m^{-2} was evident as early as February and rapid shoot dieback was apparent beginning in July after reaching an average maximum of 220 gdm m^{-2}, with a second short period of growth in the fall. RUPPIA did not demonstrate a significant increase in shoot biomass until June and it subsequently reached a maximum standing crop in August of approximately 100 gdm m^{-2} after which it declined to winter levels of 20–25 gdm m^{-2}. Both the POTAMOGETON and FRESHWATER MIXED communities were found to maintain no shoot biomass from December to April. Beginning at this time, however, shoot biomass of both communities rapidly increased. The

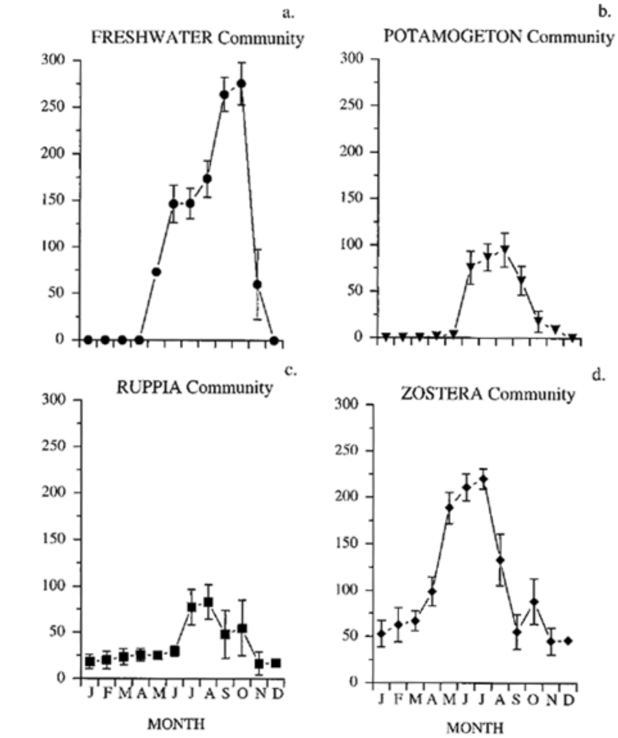

Fig. 5. Mean monthly (±SE) SAV aboveground biomass by community type.

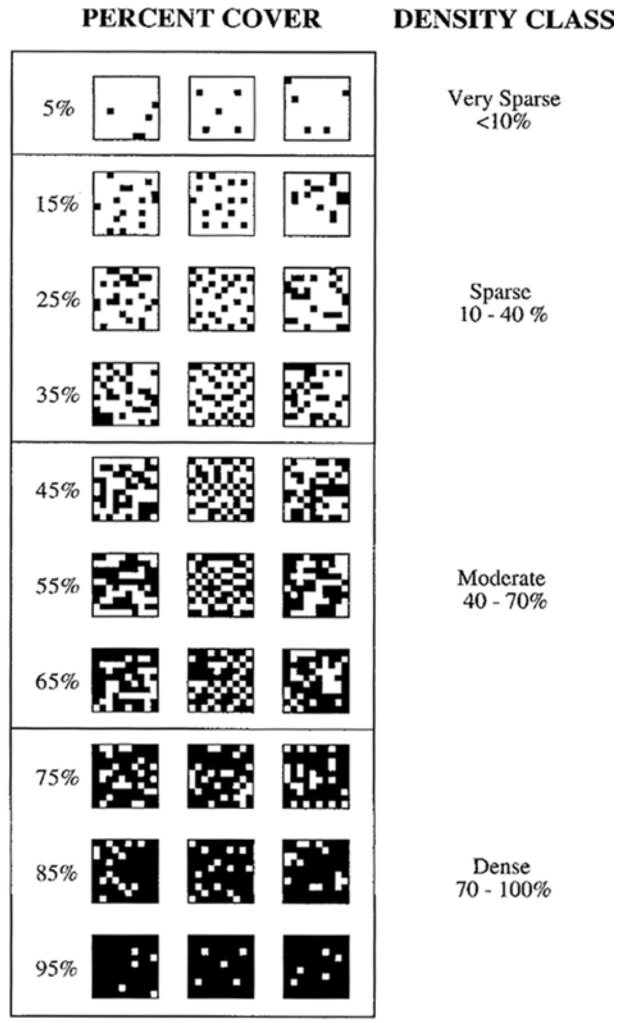

Fig. 6. Crown density scale used for estimating density of SAV beds from aerial photography. Rows of squares with black and white patterns represent three different arrangements of vegetated cover for a given percentage (Adapted from Paine 1981).

POTAMOGETON community reached a peak standing crop of 100 gdm m^{-2} or more by August with complete loss by December. In contrast, shoot biomass of the FRESHWATER MIXED community increased throughout the summer and early fall, and reached an average maximum of nearly 300 gdm m^{-2} by October. A precipitous decline of shoot material typically followed with complete loss by December.

Application of SAV Biomass to Aerial Photographic Cover Classes

Annual aerial photographic surveys of SAV coverage are summarized (e.g., Orth et al. 1997) as SAV areas which have been assigned to ranked density classes based upon photo-interpretation using a Crown Density Scale adapted from Paine (1981) (Fig. 6). It was necessary to quantify how these density classes corresponded with measurements of SAV ground survey biomass so that the aerial survey data could be used to determine SAV biomass baywide. To accomplish this task unpublished field data obtained during the summer of 1990 at 35 locations throughout the bay were used. This data consisted of point-intercept measurements obtained by divers at 10 m intervals along transects oriented perpendicular to the shore across SAV beds of different densities and species composition. Each point sample consisted of triplicate estimates of bottom cover and depth within randomly placed 0.25 m^2 sampling rings. Such measurements have been previously demonstrated to provide very good estimates of SAV density and biomass ($r^2 > 0.86$; Orth and Moore 1988). The individual ground cover transects were then separated into segments based upon the published photo-interpreted density class zones comprising each area in 1990 (Orth et al. 1991).

Figure 7 illustrates the relationship between field ground cover measurements and the photo-interpreted density classes for all transect segments. The relationship was linear and significant ($p < 0.001$); however, the aerial photo-interpretation tended to underestimate ground cover at lower

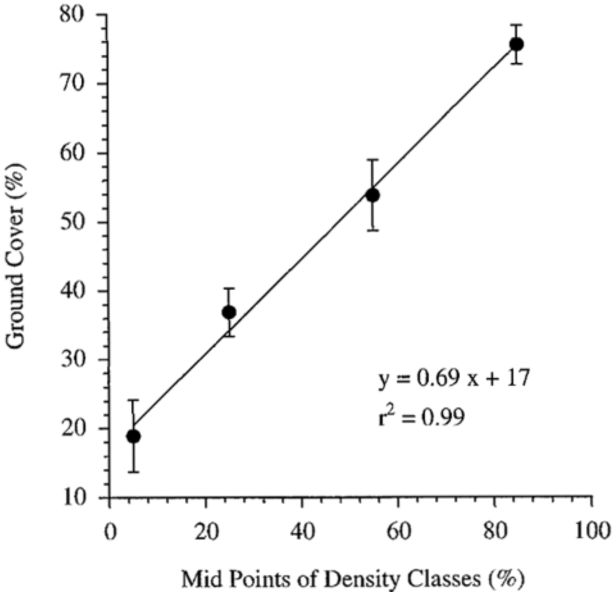

Fig. 7. Comparison of SAV aerial density classification categories to SAV groundcover measurements.

SAV densities and overestimate at higher densities. No consistent effects of community type or depths of SAV growth on the relationship between ground cover and density class assignments could be determined. Therefore, density class to ground cover conversion was applied consistently across all SAV beds.

Calculation of Monthly SAV Bed Biomass

Monthly aboveground biomass for each individual SAV bed, or bed segment where a bed had been photointerpreted into subunits of different density class, was calculated by the following formula:

$$\text{Monthly Biomass} = Mb * Cc * Ba$$

Where Mb = model monthly biomass for assigned community type (gdm m^{-2}), Cc = photo-interpreted density class to ground cover conversion, and Ba = bed area (m^2).

Results

Results of the monthly shoot biomass calculations for all SAV beds from 1985 through 1996 is summarized in Fig. 8. During this period SAV maximum summer biomass increased baywide from lows of 15,000 metric tons in 1985 and 1986 to highest levels of nearly 25,000 metric tons during 1991 through 1993. The high salinity ZOSTERA community dominated total bay SAV biomass during the winter, spring and summer. Lower salinity communities (RUPPIA, POTAMOGETON, and FRESHWATER MIXED) dominated in the fall. At peak biomass in July, total bay system standing stock of SAV was approximately 22,800 metric tons in 1996. Minimum standing stock in December and January of that year was less than 5,000 metric tons.

Year-to-year comparisons of annual bay-wide

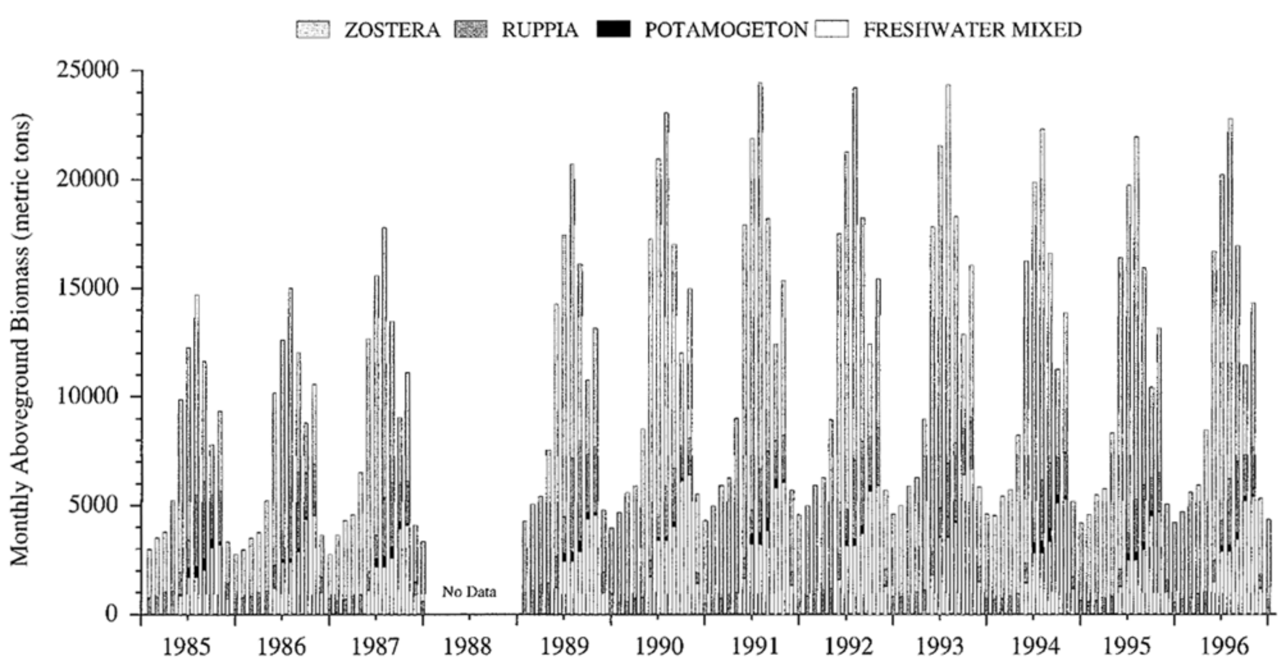

Fig. 8. Total monthly Chesapeake Bay SAV aboveground biomass by community type.

TABLE 4. Baywide annual maximum SAV community total biomass (metric tons), total area (hectares), and mean biomass (tons/hectare). Month when maximum occurred.

	ZOSTERA (Jul)			RUPPIA (Aug)			POTAMOGETON (Aug)			FRESHWATER MIXED (Oct)			TOTAL BAY SAV (Jul)		
Year	Total Biomass (t)	Total Area (ha)	Mean Biomass (t/ha)	Total Biomass (t)	Total Area (ha)	Mean Biomass (t/ha)	Total Biomass (t)	Total Area (ha)	Mean Biomass (t/ha)	Total Biomass (t)	Total Area (ha)	Mean Biomass (t/ha)	Total Biomass (t)	Total Area (ha)	Mean Biomass (t/ha)
1985	9,228	7,877	1.17	3,501	7,552	0.46	581	1,197	0.49	3,203	3,248	0.99	14,716	19,873	0.74
1986	9,182	7,749	1.18	3,486	6,900	0.51	185	384	0.48	4,529	4,154	1.09	14,995	19,187	0.78
1987	12,439	9,705	1.28	2,897	5,902	0.49	546	2,357	0.23	4,079	2,154	1.89	17,797	20,118	0.88
1988	no mapping data for 1988														
1989	13,540	10,084	1.34	4,610	9,040	0.51	497	2,126	0.23	4,546	2,901	1.57	20,694	24,152	0.86
1990	17,190	13,406	1.28	2,451	5,523	0.44	224	475	0.47	6,385	4,887	1.31	23,060	24,292	0.95
1991	17,814	13,565	1.31	3,091	6,531	0.47	600	947	0.63	6,040	4,582	1.32	24,442	25,625	0.95
1992	17,140	14,049	1.22	3,886	9,253	0.42	357	802	0.45	5,892	4,462	1.32	24,206	28,566	0.85
1993	17,385	14,827	1.17	3,611	9,803	0.37	61	162	0.38	6,647	4,795	1.39	24,323	29,587	0.82
1994	16,153	13,347	1.21	2,990	7,420	0.40	609	995	0.61	5,291	4,723	1.12	22,298	26,484	0.84
1995	16,673	13,477	1.24	2,602	6,267	0.42	393	650	0.60	4,683	3,857	1.21	21,936	24,252	0.90
1996	16,605	13,385	1.24	3,272	7,300	0.45	334	564	0.59	5,412	4,444	1.22	22,783	25,669	0.89

maximum community aboveground biomass and bed areas from 1985 to 1996 (Table 4) indicate that regrowth of SAV in the Chesapeake Bay has occurred principally in the ZOSTERA community. Rapid growth of ZOSTERA beds occurred between 1986 and 1991 with peak biomass increasing from approximately 9,200 to 17,800 metric tons, or a nearly 94% increase, during that five year period, but declining to 16,600 metric tons by 1996. Area similarly increased from approximately 7,750 hectares to over 14,800 hectares by 1993 and declined to 13,390 by 1996. Throughout the 12 yr study period the overall biomass of the ZOSTERA community remained consistent with an average of 1.24 metric tons per hectare and a coefficient of variation (CV) of 5%.

Baywide annual maximum biomass of FRESHWATER MIXED SAV beds also increased from a minimum of approximately 3,200 metric tons in 1985 to a maximum of 6,650 metric tons in 1993, nearly a 108% increase over eight years (Table 4). Year-to-year changes were quite large with a 40% increase in biomass between 1989 and 1990 alone. Mean biomass ranged from a low of 0.99 metric tons per hectare in 1985 to a high of 1.89 just two years later in 1987 with an average of 1.31 over the study period. This increase in baywide biomass from 1985 to 1987 was associated with marked decline in total community area suggesting that much of the decline occurred in the lower density beds.

Baywide biomass of RUPPIA and POTAMOGETON beds fluctuated between 2,600 and 4,600 metric tons and 60 and 600 metric tons, respectively, during the study period with net declines in peak biomass of 7% and 43%, respectively, between 1985 and 1996 (Table 4). Baywide mean biomass of 0.45 and 0.47 metric tons per hectare during the study period were quite similar for the RUPPIA and POTAMOGETON communities respectively, although year-to-year variability was larger for POTAMOGETON (30% versus 19% CV). Some of this large variability was related to a large decrease in POTAMOGETON biomass which occurred during the 1987 to 1989 period, due in part to a large increase in the area of low density beds.

In spite of year-to-year variability in the baywide annual maximum biomass of the individual SAV community types (16% CV), the combined annual maximum biomass of Chesapeake Bay SAV was quite consistent from year-to-year (8% CV) and averaged approximately 0.86 metric tons per hectare (Table 4). This consistency was due, in large part, to the more constant annual maximum biomass of the ZOSTERA community that dominated the baywide SAV communities and averaged approximately 70% of the total bay annual maximum biomass throughout the 1985–1996 study period.

Discussion

In this study, aerial photography, ground survey observations, and biomass data from a variety of sources are integrated by GIS analysis to provide a summary of the changing SAV community abundance in the Chesapeake Bay over a 12 yr period. These results demonstrate how new information and insights can be developed for a complex system based upon existing data. Although only a summary of the results of this application of GIS techniques are presented here, the direct availability of this type of information through mechanisms such as the world wide web are providing for a variety of applications ranging from ecosystem modeling to management. The emerging applications of geographic information systems and remote sensing to aquatic botany (Ferguson and Korfmacher 1997; Lehmann and Lachavanne 1997; Robbins 1997) can provide for comprehensive analysis of population level changes with greatly increased accuracy over traditional manual, ground survey techniques.

The annual biomass models presented here, since they are based directly upon published and unpublished measurements of SAV biomass for the region, reflect quite well the average annual patterns of aboveground biomass which have been observed in these communities locally (e.g., Orth and Moore 1986; Stevenson et al. 1993), as well as worldwide (e.g., Sand-Jensen 1975; Pulich 1985). However, they are by definition average models of biomass which have been adjusted by annual measurements of aerial coverage and density obtained by photography taken during annual periods of peak abundance for each community. During any particular year SAV seasonal abundances may be greater or less than model averages depending in part upon seasonal climatic or other conditions (Carter and Rybicki 1986; Carter et al. 1994). For example, we have noted that after particularly hot summers the aboveground biomass of ZOSTERA beds may dieback more than usual and the fall biomass in some areas may be less than average (Orth and Moore 1986). However, the predicted assessments of interannual and intra-annual changes in SAV community biomass presented here provide us with the best available measures of system spatial and temporal variability.

The results of this study (Table 4) demonstrate that in the period following the declines of SAV in the Chesapeake Bay and its tributaries which occurred from the early 1970s to the early 1980s (Haramis and Carter 1983; Orth and Moore 1983), there has been a nearly 66% increase in total bay SAV biomass from 1985 to 1991 followed by an extended period of little or no change (1991–1996). Similarly, total bay SAV area increased approximately 49% from 1985 to 1993. One major tributary, the Potomac, experienced a resurgence in freshwater SAV species beginning during the 1980s (Carter and Rybicki 1986; Carter et al. 1994) which was initiated by the spread of *H. verticillata.* Due in large part to this regrowth, the annual maximum biomass of the FRESHWATER MIXED community was observed to increase approximately 69% baywide over the 12 yr study period reported here. However, most of overall bay increase in total bay SAV abundance (85% of the 9,607 metric ton increase in annual maximum biomass and 71% of the 9,714 hectare increase in area) during this period occurred in the ZOSTERA community. The recovery in these communities may be due to a widespread improvement in habitat conditions (Dennison et al. 1993) necessary for growth, or may simply be a recovery from the effects of a very large environmental stress of Hurricane Agnes in 1972 which was associated with the initial decline (Orth and Moore 1983) with no real improvement in habitat quality since the 1970s. This storm produced rainfall and runoff rates which were several times greater than those expected for return period frequency of 100 years and resulted in hydrological, geological, biological and water quality effects which might only occur at 100 to 200 yr intervals (CRC 1975). In contrast to the ZOSTERA and FRESHWATER MIXED communities, the RUPPIA and POTAMOGETON communities have not experienced a resurgence in abundance in most areas of the bay and its tributaries and, although there have been some localized increases (Orth et al. 1997) annual maximum biomass has declined 7% and 43%, respectively, since the mid 1980s. This suggests that habitat conditions necessary for SAV regrowth of these species in most mesohaline regions (Stevenson et al. 1993) remain poor, or alternatively some other factors may be limiting regrowth there.

Although there has been regrowth of some SAV communities, with the most recent total bay abundances reported here ranging between 25,000 to 30,000 hectares, SAV in the Chesapeake Bay system still represent only a fraction of the 250,000 hectares of bottom, 2 m or less in depth, which at one time may have been capable of supporting SAV (Orth et al. 1994). The enormous potential for primary and secondary production (Fredette et al. 1990) which could have been supported by this 10-fold or greater abundance in SAV, especially in the mesohaline and freshwater regions of the system, underscores the tremendous state change in the bay ecosystem which current conditions represent.

Acknowledgments

Special thanks to Judith Nowak, Jennifer Whiting and Leah Nagey for their efforts in assembling and organizing the ground survey information from a multitude of sources. Also, our thanks to Britt-Anne Anderson for her assistance in compilation of the SAV biomass information and digitization of the ground truth survey data. Funding for this research was provided by a grant from the United States Environmental Protection Agency, Chesapeake Bay Program Office, Annapolis, Maryland. This is contribution 2285 from the Virginia Institute of Marine Science, School of Marine Science, College of William and Mary.

Literature Cited

Batiuk, R. A., R. J. Orth, K. A. Moore, W. C. Dennison, J. C. Stevenson, L. Staver, V. Carter, N. Rybicki, R. E. Hickman, S. Kollar, S. Bieber, P. Heasly, and P. Bergstrom. 1992. Submerged aquatic vegetation habitat requirements and restoration targets: A technical synthesis. CBP/TRS 83/92. U.S. Environmental Protection Agency, Annapolis, Maryland.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. United States Environmental Protection Agency Ecological Research Series. EPA-600/3–77–033. Corvallis, Oregon.

Boumans, R. M. J. and F. H. Sklar. 1990. A polygon-based spatial (PBS) model for simulating landscape change. *Landscape Ecology* 4:83–97.

BULTHUIS, D. A. 1995. Distribution of seagrasses in a North Puget Sound estuary: Padilla Bay, Washington. *Aquatic Botany* 50: 99–105.

CARTER, V. AND N. B. RYBICKI. 1985. The effects of grazers and light penetration on the survival of transplants of *Vallisneria americana* Michx in the tidal Potomac River, Maryland. *Aquatic Botany* 23:197–213.

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

CARTER, V., N. B. RYBICKI, J. M. LANDWEHR, AND M. TURTORA. 1994. Role of weather and water quality on population dynamics of submersed macrophytes in the tidal Potomac River. *Estuaries* 17:417–426.

CERCO, C. AND T. COLE. 1994. Three-dimensional eutrophication model of Chesapeake Bay. *Journal of Environmental Engineering* 119:1006–1025.

CHESAPEAKE RESEARCH CONSORTIUM (CRC). 1975. The effects of tropical storm Agnes on the Chesapeake Bay estuarine system. CRC Publication No. 54. The Johns Hopkins University Press, Baltimore, Maryland.

CLIFFORD, H. T. AND W. STEVENSON. 1975. An Introduction to Numerical Classification. Academic Press, New York.

COLES, R. G., W. J. L. LONG, R. A. WATSON, AND K. J. DERBYSHIRE. 1993. Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns harbour, a tropical estuary, Northern Queensland, Australia. *Australian Journal of Marine and Freshwater Research* 44:193–210.

COSTANZA, R., F. H. SKLAR, AND M. L. WHITE. 1990. Modeling coastal landscape dynamics. *BioScience* 40:91–107.

DENNISON, W. C., R. J. ORTH, K. A. MOORE, J. C. STEVENSON, V. CARTER, S. KOLLAR, P. BERGSTROM, AND R. BATIUK. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience* 43:86–94.

FERGUSON, R. L. AND K. KORFMACHER. 1997. Remote sensing and GIS analysis of seagrass meadows in North Carolina, USA. *Aquatic Botany* 58:241–258.

FREDETTE, T. J., R. J. DIAZ, J. VAN MONTFRANS, AND R. J. ORTH. 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in lower Chesapeake Bay. *Estuaries* 13:431–440.

HARAMIS, G. M. AND V. CARTER. 1983. Distribution of submersed aquatic macrophytes in the tidal Potomac River. *Aquatic Botany* 15:65–79.

KILGORE, K. J., R. P. MORGAN, II, AND N. B. RYBICKI. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. *North American Journal of Fisheries Management* 9:101–111.

LARKUM, A. W. D. AND R. J. WEST. 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. *Aquatic Botany* 37: 55–70.

LEHMANN, A. AND J.-B. LACHAVANNE. 1997. Geographic information systems and remote sensing in aquatic botany. *Aquatic Botany* 58:195–207.

LUBBERS, L., W. R. BOYNTON, AND W. M. KEMP. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* 65:1–14.

MOORE, K. A., J. L. GOODMAN, J. C. STEVENSON, L. MURRAY, AND K. SUNDBERG. 1995. Chesapeake Bay nutrients, light, and SAV: Relationships between water quality and SAV growth in field and mesocosm studies. Final Report. U.S. Environmental Protection Agency, Chesapeake Bay Program. Annapolis, Maryland.

MOORE, K. A., H. A. NECKLES, AND R. J. ORTH. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Sereries* 142:247–259.

NAYLOR, P. AND M. KAZYAK. 1995. Quantitative characterization of submerged aquatic vegetation species in tidal freshwater reaches of the Patuxent River drainage basin. Final Report, Maryland Department of the Environment. Annapolis, Maryland.

NICHOLS, L., R. R. ANDERSON, W. C. BANTA, E. J. FORMAN, AND S. H. BOUTWELL. 1979. Evaluation of the effects of the thermal discharge on the submerged aquatic vegetation and associated fauna in the vicinity of the C.P. Crane Generating Station. Final Report. Maryland Department of Natural Resources, Annapolis, Maryland.

ORTH, R. J., R. A. BATIUK, AND J. F. NOWAK. 1994. Trends in the distribution and abundance of habitat quality of submerged aquatic vegetation in Chesapeake Bay and its tidal tributaries: 1971 to 1991. U.S. Environmental Protection Agency, Chesapeake Bay Program Office. CBP/TRS 137/95. Annapolis, Maryland.

ORTH, R. J. AND K. A. MOORE. 1981. The biology and propagation of *Zostera marina*, eelgrass, in the Chesapeake Bay. Special Report 265 in Applied Marine Science and Ocean Engineering. Virginia Institute of Marine Science. Gloucester Point, Virginia.

ORTH, R. J. AND K. A. MOORE. 1983. An unprecedented decline in submerged aquatic vegetation (Chesapeake Bay). *Science* 22:51–53.

ORTH, R. J. AND K. A. MOORE. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: An historical perspective. *Estuaries* 7:531–540.

ORTH, R. J. AND K. A. MOORE. 1986. Seasonal and year-to-year variations in the growth of *Zostera marina* L. (eelgrass) in the lower Chesapeake Bay. *Aquatic Botany* 24:335–341.

ORTH, R. J. AND K. A. MOORE. 1988. Distribution of *Zostera marina* and *Ruppia maritima* sensu lato along depth gradients in the Lower Chesapeake Bay, U.S.A. *Aquatic Botany* 32:291–305.

ORTH, R. J., J. F. NOWAK, G. F. ANDERSON, AND J. R. WHITING. 1997. Distribution of submerged aquatic vegetation in the Chesapeake Bay and tributaries and Chincoteague Bay—1996. Final Report. U.S. Environmental Protection Agency, Chesapeake Bay Program Office. Annapolis, Maryland.

ORTH, R. J., J. NOWAK, A. FRISCH, K. KILEY, AND J. WHITING. 1991. Distribution of submerged aquatic vegetation in the Chesapeake Bay and tributaries and Chincoteague Bay—1990. Final Report. U.S. Environmental Protection Agency, Chesapeake Bay Program Office. Annapolis, Maryland.

PAINE, D. P. 1981. Aerial Photography and Image Interpretation for Resource Management. John Wiley & Sons, Inc. New York.

PULICH, W. M. 1985. Seasonal growth dynamics of *Ruppia maritima* L.s.l. and *Halodule wrightii* aschers. in southern Texas and evaluation of sediment fertility status. *Aquatic Botany* 23:53–66.

ROBBINS, B. D. 1997. Quantifying temporal change in seagrass areal coverage: The use of GIS and low resolution aerial photography. *Aquatic Botany* 58:259–267.

RYBICKI, N. B., R. T. ANDERSON, AND V. CARTER. 1988. Data on the distribution and abundance of submersed aquatic vegetation in the tidal Potomac River and transition zone of the Potomac estuary, Maryland, Virginia, and the District of Columbia, 1987. U.S. Geological Survey Open-File Report 88–307.

RYBICKI, N. B. AND V. CARTER. 1995. Revegetation and propagule transport in the tidal Potomac River, p. 201–218. *In* Proceedings, 29th Annual Meeting Aquatic Plant Control Program. U.S. Corps of Engineers, Vicksburg, Mississippi.

RYBICKI, N. B., V. CARTER, R. T. ANDERSON, AND T. J. TROMBLEY. 1985. *Hydrilla verticillata* in the tidal Potomac River, Maryland, Virginia, and the District of Columbia, 1983 and 1984: U.S. Geological Survey Open-File Report 85–77.

Sand-Jensen, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Ophelia* 14:185–201.

Staver, L. W. 1986. Competitive interactions of submerged aquatic vegetation under varying nutrient and salinity conditions. M.S. Thesis, University of Maryland, College Park, Maryland.

Stevenson, J. C. and N. M. Confer. 1978. Summary of available information on Chesapeake Bay vegetation. U.S. Fisheries and Wildlife Service Report. FWS/OBS-78/66. Annapolis, Maryland.

Stevenson, J. C., L. Staver, and K. W. Staver. 1993. Water quality associated with survival of submerged aquatic vegetation along an estuarine gradient. *Estuaries* 16:346–361.

Zieman, J. C., J. W. Fourqurean, and R. L. Iverson. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292–311.

Sources of Unpublished Materials

Carter, V. unpublished data. U.S. Geological Survey, 430 National Center, Reston, Virginia 22092.

Rybicki, N. unpublished data. U.S. Geological Survey, 430 National Center, Reston, Virginia 22092.

Staver, L. unpublished data. Center for Environmental and Estuarine Studies, University of Maryland, Horn Point Laboratory, P. O. Box 775, Cambridge, Maryland 21613.

Received for consideration, December 22 1998
Accepted for publication, August 17, 1999