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Role of Weather and Water Quality in Population Dynamics of Submersed Macrophytes in the Tidal Potomac River

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ABSTRACT: Weather and water-quality data from 1980 to 1989 were correlated with fluctuations in submersed macrophyte populations in the tidal Potomac River near Washington, D.C., to elucidate causal relationships and explain population dynamics. Both reaches were unvegetated in 1980 when mean growing-season Secchi depths were <0.60 m. Macrophyte resurgence in the upper tidal river in 1983 was associated with a growing-season Secchi depth of 0.86 m, total suspended solids (TSS) of 17.7 mg l^{-1}, chlorophyll *a* concentrations of 15.2 $\mu g\ l^{-1}$, significantly higher than average percent available sunshine, and significantly lower than average wind speed. From 1983 to 1989, mean seasonal Secchi depths <0.65 m were associated with decrease in plant coverage and mean seasonal Secchi depths >0.65 were associated with increases in plant coverage. Changes in mean seasonal Secchi depth were related to changes in mean seasonal TSS and chlorophyll *a* concentration; mean Secchi depths >0.65 generally occur when seasonal mean TSS is <19 mg l^{-1} and seasonal mean chlorophyll *a* concentration is ≤15 $\mu g\ l^{-1}$. Secchi depth is highly correlated with plant growth in the upper tidal river and chlorophyll *a* and TSS with plant growth in the lower tidal river. Wind speed is an important influence on plant growth in both reaches.

Introduction

Submersed macrophyte populations are highly dynamic in terms of spatial and temporal variability and species composition. Population declines and increases have been reported for the Chesapeake Bay and its tributaries including the Potomac River (Bayley et al. 1968; Orth and Moore 1984; Carter and Rybicki 1986). The historic distribution of submersed macrophytes in the tidal Potomac River further illustrates this point. Before the late 1930s plants were abundant (Cumming et al. 1916; Secretary of the Treasury 1933); between the late 1930s and 1982, virtually no macrophytes were present in the tidal river (Carter et al. 1985); and in 1983, a resurgence of macrophytes occurred (Carter and Rybicki 1986). The monoecious variety of the southeast Asian exotic *Hydrilla verticillata* (L.f.) Caspary became well established in the tidal Potomac River in 1983, following its initial discovery in 1982 (Steward et al. 1984).

The resurgence of submersed macrophytes in the tidal Potomac River in 1983 was associated with several changes in water quality during or just prior to 1983 (Carter and Rybicki 1986). These included a dramatic increase in Secchi depth from <0.55 m to >0.80 m; a change in the primary nitrogen loading from ammonia to nitrate as a result of nitrification at the Blue Plains Waste Water Treatment Facility (BPF) in Washington, D.C. (Shultz 1989); and a decrease in total suspended solids (TSS) and phosphorus loads from the BPF.

Light availability has been identified as a major control on the distribution of submersed aquatic macrophytes in the Chesapeake Bay and the tidal Potomac River (Kemp et al. 1983; Carter and Rybicki 1990; Dennison et al. 1993). Light availability at depth is affected directly by the presence of TSS and phytoplankton (chlorophyll *a*) in the water column and by epiphytes and sediment accumulations upon the leaf surface (Sand-Jensen and Sondergaard 1981; Kemp et al. 1983; Carter and Rybicki 1990). Increasing nutrient loading increases epiphytic algae and phytoplankton; increases in phytoplankton cause an increase in TSS as well. Light availability is also closely related to weather variables such as available sunshine and wind, which causes resuspension in shallow areas (Orth and Moore 1986; Bennett et al. 1986).

The purpose of this investigation was to examine the interrelations among water quality, weather, and submersed macrophyte population fluctuations from 1983 to 1989 in two reaches of the tidal

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Potomac River, thereby extending the earlier work of Carter and Rybicki (1986, 1990) toward an increased understanding of the mechanisms controlling submersed macrophyte population dynamics in tidal systems. We hypothesize that areal coverage of submersed aquatic vegetation in the tidal Potomac River is controlled by light availability, which is a function of weather and water quality. Further, we hypothesize that two of the dominant species, *Hydrilla verticillata* and *Vallisneria americana*, might be most sensitive to poor water clarity early in the growing season. This report focuses on analysis of growing-season data and data for a 6-wk period following germination of dominant species by reach.

Study Site

The tidal Potomac River extends 61 km from Chain Bridge in Washington, D.C., to Quantico, Virginia (Fig. 1). The water is fresh (salinity <0.5 mg l^{-1}) except during periods of low discharge. The average annual flow is 323 m^3 s^{-1}. The river consists of a deep channel bordered by wide shallow margins and several shallow tidal embayments such as Piscataway Creek and Gunston Cove. For the purposes of this analysis, as in previous studies (Carter and Rybicki 1990), the tidal river has been divided into two reaches: the upper tidal river from Chain Bridge to Marshall Hall, Maryland, and the lower tidal river from Marshall Hall to Quantico, Virginia (Fig. 1). The lower tidal river has a larger cross-sectional area, a smaller tidal range, and larger tributary inlets than the upper tidal river. The mean tidal range in the upper tidal river is 0.6 m to 0.9 m and in the lower tidal river 0.5 m to 0.6 m. Data were collected at three stations in the upper tidal river, and two in the lower tidal river, as shown in Fig. 1.

Species reported from the tidal Potomac River prior to the late 1930's include *Vallisneria americana* Michx., *Ceratophyllum demersum* L., *Najas flexilis* (Wild.) Rostk. and Schmidt, *Elodea canadensis* (Michx.) Planch., and *Potamogeton crispus* L. (Carter et al. 1985). Thirteen species were reported from the tidal river during 1983–1989 (Carter and Rybicki 1986; Rybicki et al. 1987, 1988; Rybicki and Schening 1990). The most widespread species from 1983 to 1989 were *Hydrilla verticillata, V. americana, Myriophyllum spicatum* L., *C. demersum,* and *Heteranthera dubia* (Jacquin) MacMillan. The dominant species currently in terms of biomass and cover are *H. verticillata, M. spicatum,* and *V. americana. H. verticillata* and *M. spicatum* are exotic species and are often considered nuisance plants because they outcompete native species.

Methods and Materials

Several datasets were used in the study, including weather data (monthly wind speed and percent available sunshine) measured at National Airport (National Oceanic and Atmospheric Administration 1970–1989); near-surface water-quality data (water temperature, Secchi depth, and TSS and chlorophyll *a* concentrations) collected by the Maryland Department of the Environment (MDE) and the District of Columbia Department of the Environment (DCE) and acquired through the Washington Metropolitan Council of Governments (Metropolitan Washington Council of Governments 1989); and near-surface water-quality and discharge data collected by the United States Geological Survey (USGS) during 1980–1989 (Blanchard and Coupe 1982; Blanchard et al. 1982; Coupe and Webb 1983; James et al. 1989).

This analysis is limited to data from the growing season (April–October) of each year of study. We have earlier reported seasonal (April–October) medians for Secchi depth, total suspended solids, and chlorophyll *a* concentration by station for the tidal Potomac River and estuary in an Environmental Protection Agency Report prepared for the Chesapeake Bay Program as part of an effort to set baywide water-quality goals and standards for restoration of submersed aquatic vegetation (Batiuk et al. 1993).

Data for this analysis came from five stations: RB, HP, and MH in the upper tidal river and IH and Q in the lower tidal river (Fig. 1). USGS samples for 1980 were collected at least twice a month at these five stations (Fig. 1). USGS TSS samples were depth-integrated. MDE began sampling at HP, MH, IH, and Q in 1983, with data collection once a month in 1983–1984 and twice a month thereafter. DC data are only for station RB, with TSS and chlorophyll *a* collected once a month from 1984 to 1986 and Secchi depth measured once a month from 1984 to 1989. In 1983, Secchi depth was measured at RB more frequently, but only those values measured near the time of the monthly MDE sampling were used for the growing-season mean.

Meteorological data were in the form of monthly means for wind speed and percent available sunshine for the period 1970–1989. Percent available sunshine is the ratio of minutes of actual sunshine to total possible minutes of sunshine from sunrise to sunset.

The USGS monitored the distribution and species composition of submersed macrophytes in the tidal Potomac River from 1979 to 1989 (Carter et al. 1985; Carter and Rybicki 1986; Rybicki et al. 1988; Rybicki and Schening 1990), reporting results to the Chesapeake Bay Program. For this report, data on areal coverage by submersed macrophytes in the upper and lower tidal river from 1984 to 1989 exclusive of 1988 were obtained

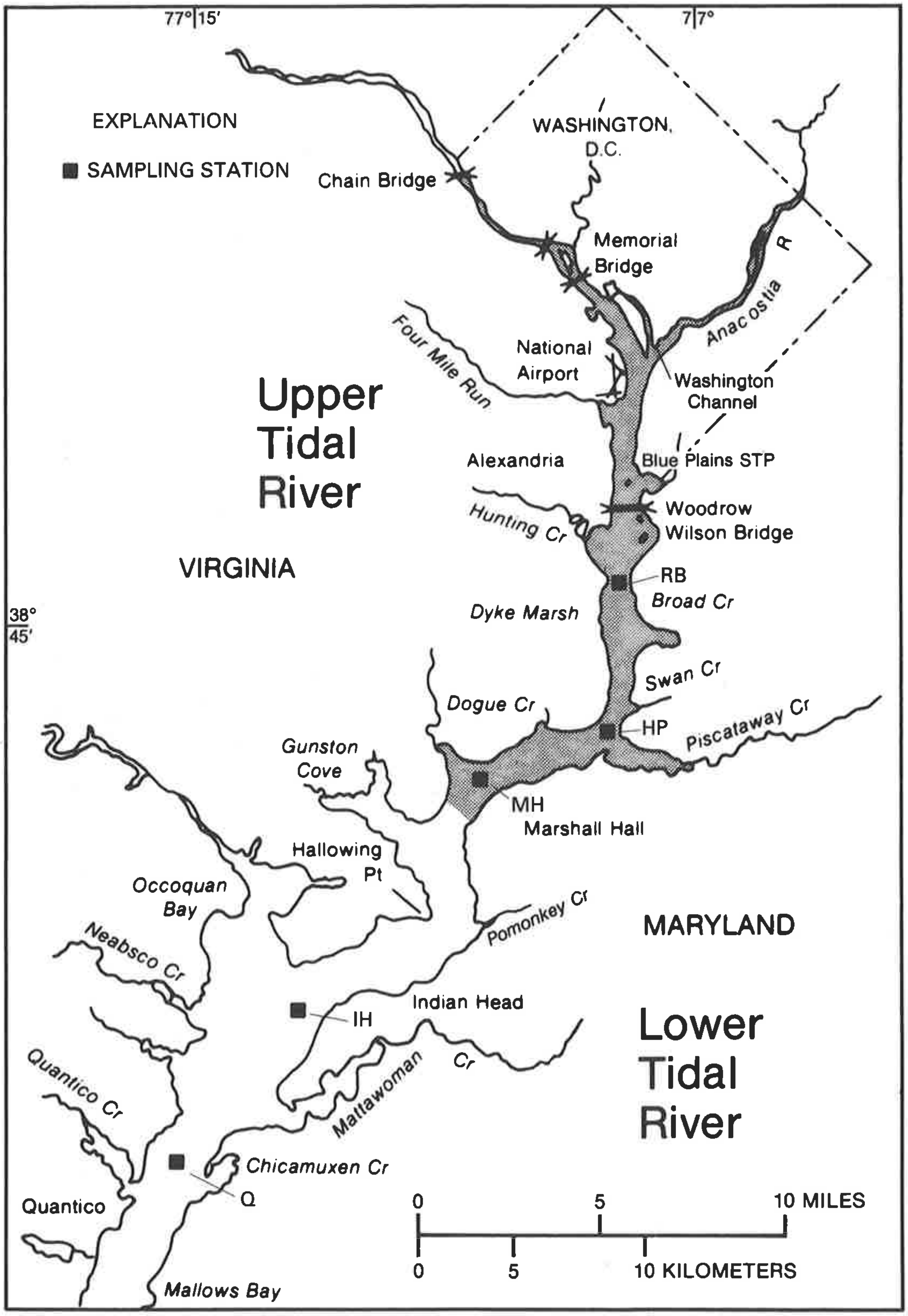

Fig. 1. Map of the upper and lower tidal Potomac River showing sampling stations.

TABLE 1. Selected growth characteristics of *Myriophyllum spicatum, Hydrilla verticillata,* and *Vallisneria americana.*

Species	Germination Temperature	Spring Growth	Growth Rate at 16°C	Growth Habit	Reproduction
Myriophyllum spicatum	12–13°C[a]	From overwintering stems and root-mass[b]	moderate[c]	Grows rapidly to surface and forms a canopy with leafless stems below and leaves concentrated at surface[b]. Canopy submerged at high tide.	Increases vegetatively. Spreads by means of rooted fragments. Seed reproduction minor.
Hydrilla verticillata	15°C[a,d]	From overwintering tuber, length (9.5–50.5 m)	slow[c]	Grows prostrate on bottom until July: forms canopy and fills water column in late July through September. Canopy submerged at high tide.	Increases vegetatively. Spreads by means of rooted large roots with tubers or turions attached. Seed reproduction not documented.
Vallisneria americana	13°C[a]	From overwintering tubers, length (5.0–15.0 m)	slow[c]	Elongates toward surface, but primary biomass is in lower two-thirds of water column at high tide.	Increases vegetatively. Spreads by movement of uprooted plants with tubers attached. Seed reproduction minor.

[a] Unpublished data: Carter and Rybicki.
[b] Smith and Barko (1990).
[c] Barko and Smart (1981).
[d] Stewart and Van (1987).

from the Chesapeake Bay Program database, which contains the results of interpretation of 1:24,000-scale aerial photographs (Orth et al. 1989). Coverage in 1983 was estimated from USGS surveys and coverage in 1988 was estimated from aerial photographs. In order to determine germination period (early growing season) Secchi depth, we examined the 1983–1989 temperature data. The growth characteristics of the three major species are presented in Table 1; at 15°C all species can be expected to germinate. We chose the sampling data when the temperature exceeded 15°C and remained higher than 15°C until the end of the summer. The germination period was defined as the 6-wk period including and immediately following that date (Table 2).

Growing-season means were calculated for Secchi depth and TSS and chlorophyll *a* concentrations for 1980 and 1983–1989. In 1984 and 1986, a few TSS concentrations for RB and HP were less than the detection limit so concentration means were estimated by the log-probability plotting method (Helsel and Cohn 1988). A 7-yr growing-season mean was calculated for each meteorological variable and the growing-season means for each of the years of interest were compared with the 7-yr means. Statistical analyses of data were done by means of the computer software SAS (SAS Institute, Inc. 1985) and MINITAB (Minitab, Inc. 1986). We examined the statistical correlation of the annual areal coverage and the annual change in areal coverage in each river reach with the relevant environmental variables, namely, germination period Secchi depth, seasonal Secchi depth, TSS, chlorophyll *a,* wind speed, percent available sunshine, average growing season discharge, April–June discharge, and May–June discharge.

TABLE 2. Time period used to calculate germination period.

Year	Germination Period
1983	May through mid June
1984	May through mid June
1985	Mid April through May
1986	Mid April through May
1987	May through mid June
1988	May through mid June
1989	June through July

Results

Macrophyte Growth

Figure 2 shows the area covered by submersed macrophytes in the upper and lower tidal rivers from 1983 to 1989. In 1983, the newly established macrophyte community consisted of a mixture of 13 species. Propagules (uprooted plants and plant fragments) washed into the upper tidal river (from above the fall line and from the small tributaries during the spring and summer) and became established in patches throughout shallow areas. The plant beds expanded rapidly, reaching a total area >1,300 ha in the upper tidal river from 1985 through 1987 and a depth at mean low water (mlw) of >2 m. *Hydrilla verticillata* dominated the macrophyte community in the upper tidal river by 1985 and comprised >70% of the area covered by 1987. The 60% decrease in areal coverage in the

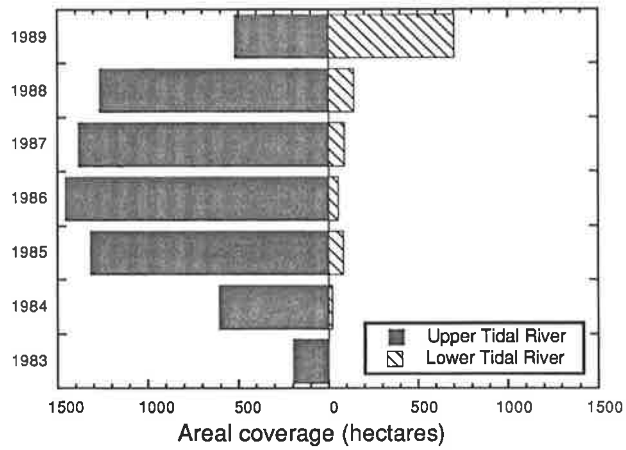

Fig. 2. Area covered by submersed aquatic macrophytes in the upper and lower tidal Potomac River, 1983–1989.

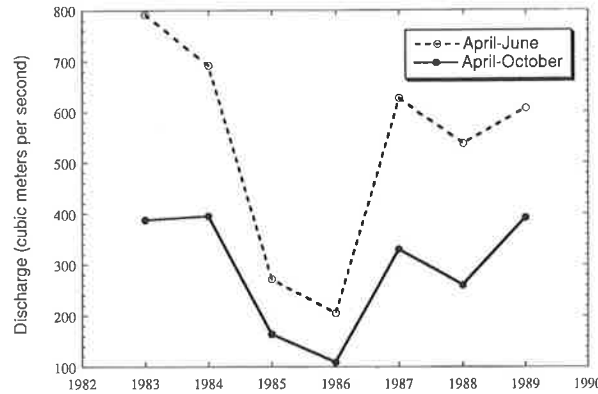

Fig. 3. Average monthly discharge of the Potomac River at Little Falls, Maryland, for April–October and April–June, 1983–1989.

upper tidal river in 1988 and 1989 was primarily the result of loss of *H. verticillata*. The remaining beds of *H. verticillata* in 1989 were primarily located in shallow water (<1 m at mlw). Virtually no macrophytes were found in the lower tidal river in 1983–1984. Small patches of submersed macrophytes became established in the lower tidal river below Marshall Hall in 1985 and 1986; *H. verticillata* did not colonize this reach until 1986. Coverage increased in 1987 and coincident with the decline in the upper tidal river in 1989, submersed macrophyte cover in the lower tidal river expanded by 350% to 807 ha, dominated by *H. verticillata.*

Average monthly river discharges for April through October and for April through June are summarized in Fig. 3. Relatively high spring discharge in 1983 caused the influx of vegetative propagules into the previously unvegetated upper tidal river from the nontidal Potomac River and tributaries in the reach. In a similar fashion, high spring discharge in 1987–1989 may have increased the influx of vegetative propagules into the lower tidal river from the well-established population in the upper tidal river.

Secchi Depth

Prior to 1983, mean growing-season Secchi depths were <0.60 m in both the upper and lower tidal river (Carter and Rybicki 1986). In 1983, the mean growing-season Secchi depth in the upper tidal river was 0.86 m, significantly higher ($p < 0.05$) than both the mean growing-season Secchi depth in 1980 for either reach and the mean growing-season Secchi depth in the lower tidal river in 1983 (0.60 m) (Fig. 4). The mean Secchi depth in the upper tidal river for June (1.40 m) was the highest monthly Secchi depth for the period of record.

From 1983 to 1989, conditions in the upper and lower tidal river gradually changed until the water clarity of the lower tidal river was significantly greater than that of the upper tidal river in 1989 (Fig. 4). Mean growing-season Secchi depths in the upper tidal river remained >0.70 m through 1985 as the plants increased in abundance, and then decreased slowly to 0.54 m by 1989. In the lower tidal river, mean growing-season Secchi depth ranged from 0.49 m to 0.66 m during 1983–1986, then increased to >0.70 m during 1987–1989, the period during which macrophyte cover increased.

The growing-season mean Secchi depth in the upper tidal river in 1989, when the *H. verticillata* cover decreased dramatically, was 0.54 m. Growing-season mean Secchi depth in the lower tidal river in 1989, where areal cover of *H. verticillata* and other macrophytes increased, was 0.76 m (significantly greater than that of the upper tidal river, $p = 0.0002$). The June 1989 mean Secchi depth in the upper tidal river (0.36 m) was the lowest June Sec-

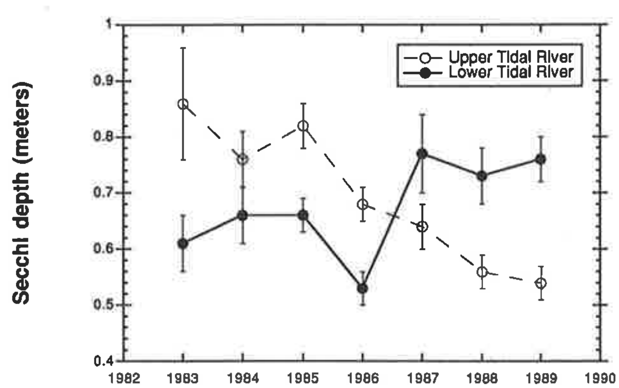

Fig. 4. Growing-season mean Secchi depth in the tidal Potomac River, 1983–1989. Bars represent 1 standard error.

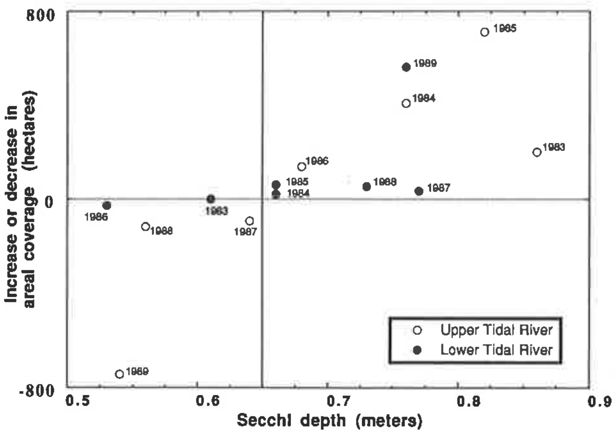

Fig. 5. Relation of increase or decrease in areal coverage from the previous year to mean growing-season Secchi depth in the tidal Potomac River, 1983–1989.

chi depth, whereas that in the lower tidal river (0.85 m) was the second highest June Secchi depth for 1983–1989 for either reach.

Mean seasonal Secchi depths >0.65 m were associated with annual areal increases in plant coverage and mean seasonal Secchi depths of <0.65 m were associated with annual declines in plant coverage (Fig. 5). Light availability during the germination period did not appear to be as good a predictor of increase or decline in plant cover as mean light availability during the active growing season (measured as seasonal Secchi depth) when considered over the entire 7-yr period. Germination period Secchi depth was 0.53 m in the lower

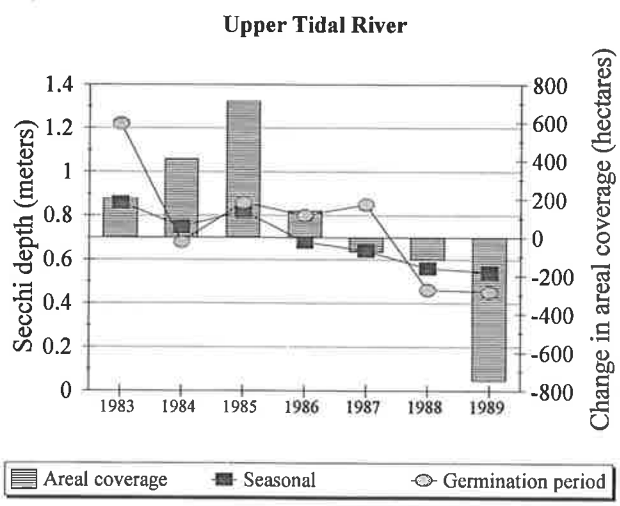

Fig. 6. Relation of mean growing season Secchi depth and germination period Secchi depth to increase or decrease in areal coverage from the previous year in the upper tidal Potomac River, 1983–1989.

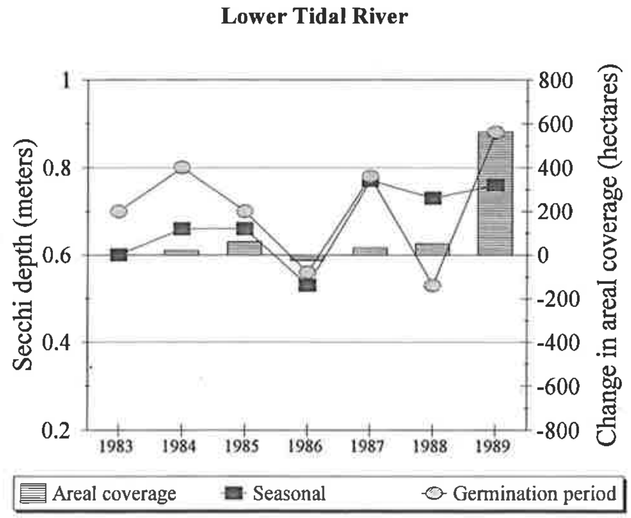

Fig. 7. Relation of mean growing season Secchi depth and germination period Secchi depth to increase or decrease in areal coverage from the previous year in the lower tidal Potomac River, 1983–1989.

tidal river in 1988 when plant cover increased (Figs. 6 and 7).

CHLOROPHYLL *a* AND TSS

Water quality improved in the river between 1980 and 1983. The mean growing-season chlorophyll *a* concentration was 23.5 $\mu g\ l^{-1}$ in 1980 and 15.2 $\mu g\ l^{-1}$ in 1983 in the upper tidal river and 43.4 $\mu g\ l^{-1}$ in 1980 and 32.8 $\mu g\ l^{-1}$ in 1983 in the lower tidal river. Mean growing-season TSS was 25 $mg\ l^{-1}$ in 1980 and 18.8 $mg\ l^{-1}$ in 1983 in the upper tidal river and 30 $mg\ l^{-1}$ in 1980 and 23 $mg\ l^{-1}$ in 1983 in the lower tidal river. This improvement continued in the lower tidal river after 1983 (Figs. 8 and 9). The decrease in mean growing-season Secchi depth in the upper tidal river from

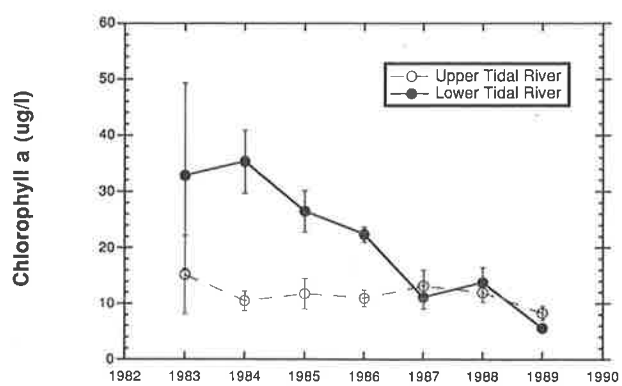

Fig. 8. Mean growing-season chlorophyll *a* concentration in the tidal Potomac River, 1983–1989. Bars represent 1 standard error.

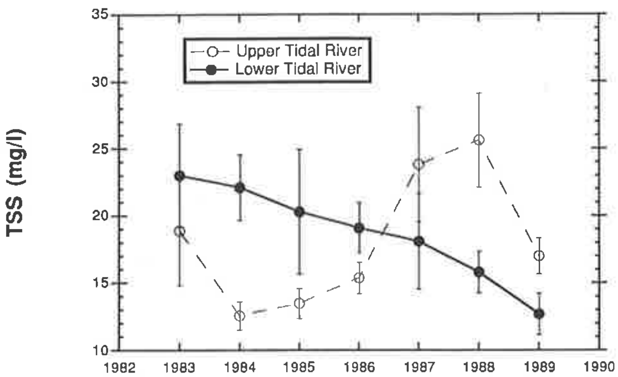

Fig. 9. Mean growing-season TSS in the tidal Potomac River, 1983–1989. Bars represent 1 standard error.

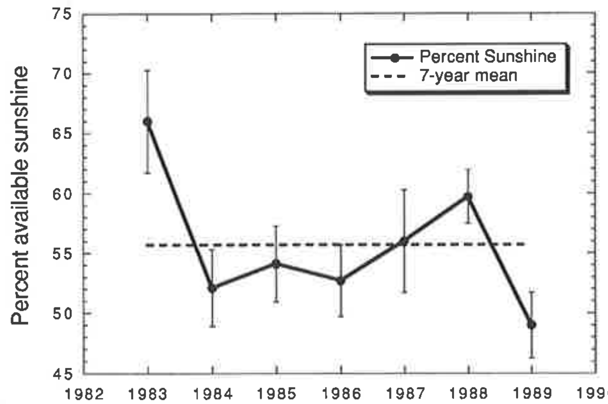

Fig. 10. Mean growing-season percent available sunshine in the tidal Potomac River, 1983–1989. Bars represent 1 standard error.

1982 to 1989 was primarily associated with an increase in mean growing-season TSS from a range of 12.0–14.4 mg l^{-1} during 1984–1986 to a range of 17.0–25.6 mg l^{-1} during 1987–1989. Mean growing-season chlorophyll *a* concentration remained <16 μg l^{-1}. The increase in mean growing-season Secchi depth in the lower tidal river during this period was associated with a gradual decrease in mean growing-season TSS concentration from a range of 20.3–23.0 mg l^{-1} in 1983–1985 to a range of 12.7–19.1 mg l^{-1} in 1986–1989, and a large decrease in mean growing-season chlorophyll *a* concentration from a range of 26.5–35.2 μg l^{-1} during 1983–1985 to a range of 7.4–13.7 μg l^{-1} during 1984–1989. In 1989, upper tidal river growing season mean TSS was 17.7 mg l^{-1} and chlorophyll *a* was 9.3 μg l^{-1}. Lower tidal river growing season mean TSS was 13.4 mg l^{-1} (significantly less than that of the upper tidal river, $p = 0.039$) and chlorophyll *a* was 6.3 μg l^{-1}. Seasonal mean Secchi depths >0.60 m were generally associated with seasonal mean TSS <19 mg l^{-1} and seasonal mean chlorophyll *a* concentrations ≤ 15 μg l^{-1}.

WEATHER

The mean growing-season available sunshine in 1983 was 66% of that possible (significantly higher than the 7-yr average of growing-season means of 56%, $p = 0.0137$) and was the highest for the 1983–1989 period (Fig. 10). Mean growing-season wind speed was 11.1 km h^{-1}, the lowest mean wind speed for the period of record and significantly lower than the 7-yr average of growing-season means (mean = 14.5 km h^{-1}, $p = 0.0009$) (Fig. 11). The June–August mean wind speed was the lowest June–August wind speed for the period of record (1970–1989). The 1989 growing season was unusually cool and cloudy. The mean growing-season wind speed was 15.8 km h^{-1} and the available sunshine was 49% (lower than the 7-yr average of growing season means of 56% and the lowest mean percent available sunshine observed during 1970–1989).

Table 3 shows the results of statistical correlation of the study variables. For $n = 7$ the Pearson correlation coefficient must be >0.75 to be statistically significant at the 0.95 level—only correlation coefficients of 0.7 or larger are shown on the table. The two reaches are very different in terms of correlated variables; Secchi depth (SEC) appears to be a more important indicator of water clarity in the upper tidal river and TSS and chlorophyll *a* (CHL) in the lower tidal river. In the upper tidal river, there is a significant (positive) correlation between change in areal coverage from the previous year (DIFF) and SEC, whereas in the lower tidal river, both areal coverage (AC) and DIFF are significantly (negatively) correlated to TSS. Wind is a factor in both the upper and lower tidal rivers; it is negatively correlated to SEC in the upper

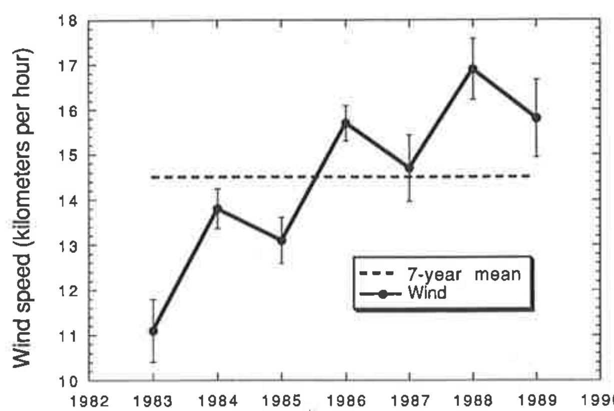

Fig. 11. Mean growing-season wind speed and 7-yr mean wind speed in tidal Potomac River, 1983–1989. Bars represent 1 standard error.

TABLE 3. Significant correlation coefficients from analysis of factors affecting growth of submersed aquatic macrophytes in the tidal Potomac River. For n = 7, Pearson correlation coefficient must be >0.75 to be statistically significant at the 0.95 level. GPS = germination period Secchi, SEC = Secchi depth, TSS = total suspended solids, CHL = chlorophyll *a* concentration, AC = areal coverage, DIFF = change in areal coverage from previous year, Q = discharge, J = June, A = April, Jl = July, O = October.

Upper Tidal River		Lower Tidal River	
Factors	Pearson Correlation Coefficient	Factors	Pearson Correlation Coefficient
CHL and sun	0.91	TSS and wind	−0.79
SEC and wind	−0.91	CHL and wind	−0.71
GPS and wind	−0.87	TSS and CHL	0.94
GPS and CHL	0.81	CHL and AC	−0.72
GPS and SEC	0.84	TSS and AC	−0.85
SEC and DIFF	0.82	TSS and DIFF	−0.77
$Q_{(A-J)}$ and AC	−0.76	AC and DIFF	0.99
$Q_{(A-O)}$ and AC	−0.80	$Q_{(Jl-O)}$ and DIFF	0.78

reach, indicating clarity drops as wind increases, but it is negatively correlated to CHL and TSS in the lower reach, indicating clarity increases as wind increases. The strong correlation of AC and DIFF in the lower tidal river may indicate that more propagules are available for population expansion. In the upper tidal river, an estimated 10% of the bottom <2 m in depth was available for expansion in 1986 as compared with an estimated 90% in the lower tidal river. The negative correlation of early spring discharge $Q_{(A-O)}$ and growing season discharge $Q_{(A-O)}$ with areal coverage in the upper tidal river may reflect the fact that higher discharges bring in higher TSS loads. The positive correlation of spring discharge with DIFF in the lower tidal river may be related to high discharges washing propagules into the reach from upstream during the active growth period. Upper tidal river CHL was correlated with available sunshine as would be expected (Bennett et al. 1986). Multiple regression analysis showed that DIFF in the upper tidal river was significantly related to SEC and wind, whereas DIFF in the lower tidal river was significantly related to AC and TSS and to TSS, wind, and $Q_{(Jl-O)}$ (Table 4). SEC in the upper tidal river was significantly correlated with TSS plus CHL, but this did not hold in the lower tidal river.

Discussion

Our analysis suggests that submersed macrophytes returned to the upper tidal river in 1983 because of improved water clarity and a fortuitous combination of weather factors that affected light availability. Greater than normal percent-available sunshine provided ample light, and the lower than average wind speed probably resulted in less sediment resuspension and turbulence. Discharge was high during April–June but generally low through the summer and, although weather conditions were condusive to large chlorophyll *a* concentrations (Bennett et al. 1986), a phytoplankton bloom in the lower tidal river (Woodward et al. 1984) spread into the upper tidal river only after the plants had become well established and reached the water surface. The reduced ammonia load from the Blue Plains Waste Water Facility (BPF) (Shultz 1989) probably delayed the onset of the phytoplankton bloom and thus contributed to the macrophyte resurgence.

The data also support the conclusion that the expansion of macrophyte populations in the upper tidal river after 1983 and the spread of macrophytes into the lower tidal river after 1985 were the result of critical light conditions as indicated by a threshold mean Secchi depth >0.65 m associated with relatively low mean growing-season TSS (<19 m l^{-1}) and chlorophyll *a* concentration (≤15 μg l^{-1}). Under these conditions, macrophytes rapidly covered all shallow areas in the mainstream and tidal embayments and *H. verticillata* outcompeted all other species. The decrease in Secchi depth in the upper tidal river toward the end of the study period appears to have been due mainly to an increase in TSS in that reach, whereas decreases in chlorophyll *a* and TSS both contributed to the increase in Secchi depth in the lower tidal river. In 1989, chlorophyll *a* peaked in June in the upper tidal river and moderate levels of TSS and chlorophyll *a* combined to produce the lowest June water clarity observed in either reach in any year. At the same time, low levels of chlorophyll *a* and TSS in the lower tidal river combined to produce the second highest June water clarity observed in either reach in any year.

TABLE 4. Significant results of multiple regression analysis of data from tidal Potomac River. GPS = germination period Secchi, SEC = Secchi depth, TSS = total suspended solids, CHL = chlorophyll *a* concentration, AC = areal coverage, DIFF = change in areal coverage from previous year, Q = discharge, Jl = July, J = June, A = April, O = October.

Upper Tidal River				Lower Tidal River			
Dependent Variable	Independent Variables	$r^2_{(adj)}$	p	Dependent Variable	Independent Variables	$r^2_{(adj)}$	p
DIFF	SEC, WIND	87.4	0.007	DIFF	TSS, WIND, $Q_{(Jl-O)}$	89.9	0.019
DIFF	SEC, WIND, $Q_{(A-J)}$	84.0	0.037	DIFF	AC, TSS	99.2	0.000
SEC	TSS, CHL	96.7	0.000				

The apparent sensitivity of *H. verticillata* to mean Secchi depths of <0.6 m in the upper tidal river in 1989 was unexpected, especially considering that the authors observed that *V. americana* and *M. spicatum* populations did not decline. This sensitivity may be the combined result of relatively high germination temperature, small overwintering propagule size, and growth habit (Table 1). Both *V. americana* and *M. spicatum* germinate at about 13°C whereas *H. verticillata* germination starts at 15°C. Growth of *V. americana* and *H. verticillata* is relatively slow at water temperatures from ~12°C to 16°C (Barko and Smart 1981; Barko et al. 1982), whereas *M. spicatum* growth is not substantially slowed at these low temperatures (Barko and Smart 1981). Tuber size positively effects shoot survival and shoot length of *H. verticillata* when tubers are germinated and held in complete darkness at 25°C and initial growth of small *H. verticillata* tubers is less than that of large tubers when grown under identical greenhouse conditions (Bowes et al. 1977; McFarland 1991). *Vallisneria americana* tubers are generally larger than those of *H. verticillata* (Table 1) and may therefore have given it a competitive edge over *H. verticillata* in the 1989 prolonged spring period of low temperature and low light availability. In the tidal Potomac River, *H. verticillata* adopts a prostrate form of growth, remaining in the lower half of the water column until July, when it forms a dense surface canopy (Carter et al. 1987). *H. verticillata, V. americana,* and *M. spicatum* grow rapidly toward the water surface into more favorable light conditions as rising water temperatures in the spring cause germination. The relationship of survival to tuber size, germination, and growth habit is tentative and needs to be substantiated by additional research into the relative distribution and size of tubers, germination requirements, and elongation potential for both species.

The Chesapeake Bay Program under the direction of the United States Environmental Protection Agency is attempting the restoration of submersed aquatic vegetation baywide by setting habitat goals for nutrients, Secchi depth, and chlorophyll *a* and TSS concentrations based on growing-season medians (Dennison et al. 1993). Our data support the use of growing-season averages to set goals. It is possible that controlling nutrient levels and chlorophyll *a* and TSS concentrations during the spring months might be sufficient to encourage regrowth in freshwater reaches of the bay as canopy-forming species such as *Hydrilla verticillata* and *M. spicatum* may be less sensitive to changes in water clarity in summer and fall than during the early growth period. However, our results show that seasonal Secchi depth is a better indicator of overall plant success than early spring Secchi depth. The influence of weather on macrophyte dynamics has important implications for the Chesapeake Bay Program goals for reestablishment of submersed aquatic macrophytes. Variation in weather can complicate attempts to increase submersed macrophyte abundance by controlling nutrients and increasing water clarity. The distribution and abundance of submersed macrophyte is controlled by numerous interacting factors, and only a few of these factors can be controlled by human activity. Steps taken to reduce nutrient and sediment loading are important to improve water clarity and reduce the likelihood of algae blooms, thus providing a habitat where submersed aquatic macrophytes are likely to thrive. However, weather and river discharge can combine to thwart the most assiduous control measures. More information on phenology (timing of germination, propagule reserves, elongation, and canopy formation), allocation of reserves, and relative growth rate of major species in the freshwater reaches of the bay under various conditions of light and temperature is needed to predict the outcome of various climate scenarios and management plans on population dynamics of submersed aquatic vegetation.

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