PREDICTIVE MODELING FOR SUBMERGED AQUATIC VEGETATION (SAV) DECLINE DUE TO MUTE SWANS IN THE CHESAPEAKE BAY

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ABSTRACT

Mute Swans (*Cygnus olor*) have the potential to contribute to a reduction in Submerged Aquatic Vegetation (SAV) in the Chesapeake Bay, USA, owing to their high preference for SAV as a food resource, high population, year-round inhabitation of the bay, and great appetite. However, quantitative data on SAV decline due to Mute Swan herbivory along with other potential factors have not been hitherto generated for the entire bay. Based on biology and current knowledge of SAV and Mute Swans in the bay, we developed a suite of 15 *a priori* candidate models that could potentially predict SAV cover decline in the bay. Each model had Mute Swan population and/or one or more other potential environmental factors as independent variables (predictors) and SAV-percent-cover decline as the dependent variable. We generated data by measuring SAV percent cover reduction, water depth, extent of light penetration, salinity, and number of Mute Swan at 18 sites. Using these localized data, we further ranked all the candidate models through Akaike's Information Criterion (AICc) model selection. Based on the smallest value of AICc, we selected the predictive model including four predictors (water depth, extent of light penetration, salinity, and number of Mute Swans) as the most parsimonious model. It is clear that Mute Swans contribute to SAV decline, but it is not the most important factor.

INTRODUCTION

Mute Swans (*Cygnus olor*) are native to Eurasia and were introduced into North America in the late 1800s and early 1900s (Bellrose 1980, Ciaranca *et al.* 1997). Since the mid-to-late portion of the 20th century, Mute Swan populations have been rapidly expanding particularly along the Atlantic coast (Scott 2004). The portion of the Chesapeake Bay located in Maryland has greatly contributed to the expansion as the population increased at an annual rate of 23% between 1986-92 and 10% between 1993-99 resulting in the population as high as 4,000 individuals (Hindman and Harvey 2004). The phenomenal population growth of Mute Swans is harmful to Submerged Aquatic Vegetation (SAV) in the bay as it is the mainstay of their diet (Bellrose 1980). There is anecdotal information to conclude that Mute Swans impact SAV in the bay (Hindman and Harvey 2004, Perry *et al.* 2004). SAV in the Bay has been playing a vital role in providing habitat and food to numerous native organisms and performing several other ecological functions (Maryland Department of Natural Resources (DNR) 2001). It is a stressed resource since the 1960s due to several man-induced and natural factors (Hurley 1990, Naylor 2004). The increased population of Mute Swans has put additional pressure on SAV (Hindman and Harvey 2004).

Although Mute Swans are believed to contribute to the SAV decline and hamper SAV restoration activities in the Chesapeake Bay, quantitative data on reduction of SAV by Mute Swans is limited (Hindman and Harvey 2004).

Numerous other factors affect SAV growth in the bay including weather events (e.g., storm), natural population cycles, animal grazing and foraging, industrial pollutants, agricultural herbicides and general decline in water quality due to increased loadings of nutrients sediment from the surrounding watersheds (Hurley 1990). However, the relative importance of Mute Swan herbivory compared to abiotic factors is unknown. Therefore, we carried out this study with the primary objective to develop the best approximating parsimonious predictive model for SAV cover decline in the Bay using an information-theoretic approach.

STUDY AREA

We collected localized data on the eastern shore of Chesapeake Bay, Maryland (Figure 1). The bay is formed by over 150 rivers and streams and tidal waters of the Atlantic Ocean and is one of the primary waterfowl wintering areas in the Atlantic Flyway (Hindman and Stotts 1989, Meyers *et al.* 1995). The Chesapeake Bay traditionally has played a vital role in providing habitat to wintering native waterfowl, but now has been inhabited by thousands of resident exotic Mute Swans since the 1990s.

Chesapeake Bay is a 8-48-km-wide and 288-km-long shallow estuary, that lies in a north-south direction, roughly parallel to the Atlantic seacoast. The study area covered 18 sites in the mid-bay (8 in Talbot County and 10 in Dorchester County). The sites were located between 38° 25' 00" N and 38° 52' 30" N latitudes and 76° 07' 30" W and 76° 22' 30" W longitudes. SAV species in our study area were widgeon grass (*Ruppia maritime*), horned pondweed (*Zannichellia palustris*), slender pondweed (*Potamogeton pusillus*), and sago pondweed (*P. pectinatus*). Widgeon grass, which has tolerance to wide range of salinities, was wide-spread and most dominant (Tatu 2006). The population of Mute Swans was highest (total 3,286 individuals) along the eastern shore of the Chesapeake Bay (Hindman and Harvey 2004). Specifically, Dorchester (1,638 swans) and Talbot (1,023 swans) Counties in the mid-bay area supported the largest number of Mute Swans (Maryland DNR 2002, Hindman and Harvey 2004). Portions of these two counties were selected as our study sites.

METHODS

Data Collection

We established 18 study sites with SAV beds and Mute Swans (pairs/flocks) in Talbot and Dorchester Counties, Maryland, in 2003 and 2004. To assess the SAV cover decline under the influence of Mute Swan foraging at each site, we established multiple sets of treatment (exclosures) and control (open) plots in the SAV beds at each site before the on-set of the SAV growing season. Each site had three sets of 5x5 m control and treatment sampling plots. All sampling plots in a set were established in an SAV bed with uniform density level. Using a Daubenmire frame, we measured percent cover of SAV in all the sampling plots at each of the 18 sites at the end of the second consecutive season of SAV growth after the establishment of the sampling plots (Tatu 2006). Based on these measurements, we determined the difference in percent cover of SAV between 54 2-year-treatment and 54 2-year-control plots for each of the 18 sites. The percentage difference represented SAV cover decline for each site. Detailed information on exclosures and study design can be found in Tatu (2006).

We also measured environmental factors for each site. They included water depth (WD), extent of light penetration (LP), and salinity (S). Water depth was measured to the nearest 1 cm on a permanently marked pole, extent of light penetration (i.e., the ratio of Secchi depth to water depth) was measured using a Secchi disk, and salinity was measured using a YSI salinity meter. Moreover, we also estimated average Mute Swan population (SP) for each site by counting the swans fortnightly.

Model development

We considered a basic *a priori* model in which the predictors (covariates) for SAV cover decline (Y) were selected based on our current knowledge regarding SAV and Mute Swans in the bay. Its structure can simply be expressed as:

$$Y = (WD) \pm (LP) \pm S \pm SP.$$

We further translated it into statistical model in the form of linear regression model as given below:

$$Y = \beta_O - \beta_1 (WD) - \beta_2 (LP) + \beta_3 (S) + \beta_4 (SP), \text{ where}$$

Y = SAV cover decline at a site in the bay, β_0 = intercept, β_1 (WD) = slope on water depth, β_2 (LP) = slope on extent of light penetration, β_3(S) = slope on salinity, and β_4 (SP) = slope on average population of Mute Swans.

In developing the model we hypothesized that SAV-percent-cover decline (Y) had a negative linear relationship with water depth (WD) and extent of light penetration (LP), but had positive linear relationship with salinity (S) and average Mute Swan population (SP). Based on the basic model, we further developed 14 other *a priori* candidate models by considering biologically meaningful associations of the covariates (i.e., WD, LP, S, and SP) used in the basic model. As a result, we had a suite of 15 *a priori* candidate models, each having an unique structure (Table 1). In our *a priori* models, we did not include any interactions of covariates as there is typically only one model without interactions, but an infinite number of models with interactions because the interaction can be characterized by any function of the covariates (Mangel *et al.* 2001). We used an information theoretic approach to select the relatively best predictive model among the general linear models for SAV-cover-decline (Burnham and Anderson 1998). This method allows model uncertainty to be included in model evaluation and the derivation of parameter estimates (Hepp *et al.* 2005). The best approximating and competing models were identified using Akaike's Information Criterion corrected for small sample size (AIC_c) in Proc Mixed (SAS 2001), which determines AIC values based on likelihood. Model comparisons were made with ΔAIC_c, which is the difference between the AIC_c for each individual model and the lowest observed AIC_c value (Burnham and Anderson 1998). Models with $\Delta AIC_c \leq 2$ have substantial support from the data (Burnham and Anderson 1998). To evaluate support for model parameters, we summed AIC_c model weights across all models (parameter likelihood; Burnham and Anderson 1998). The AIC_c weight of a model signifies the relative likelihood that the specific model is the best of the suite of all models (Hepp *et al.* 2005). It was premised that the parameters with good support will have high summed AIC_c model weight values (near 1) due to that parameter's inclusion in most of the better models (Hepp *et al.* 2005).

RESULTS

Table 2 presents the data from the 18 sites that we used to evaluate the predictive models. Of the 15 candidate models, 8 models included swan population as one of its covariate either singly or in combination with one or more covariates. The remaining seven models did not involve the SP covariate, but we still retained them as we expected that the comparison of AIC values for such models with those involving SP might reveal the significance of swan population as a predictor for SAV decline. The best model (selected using the minimum AICc value = 127.5) contained the combined effects of water depth (WD), extent of light penetration (LP) (i.e., light penetration depth relative to total depth), salinity (S), and average Mute Swan population (SP) to predict SAV-percent-cover decline (Y) (Table 1). Thus, the most plausible model (which also was our basic model) is:

$$Y = 55.2929 - 10.7255WD - 38.3855LP + 8.1752S + 0.6477SP$$

DISCUSSION

In the selected parsimonious model, SAV-percent-cover decline (Y) had a negative linear relationship with water depth (WD) and extent of light penetration (LP), but had a positive linear relationship with salinity (S) and average Mute Swan population (SP). The model indicates that SAV decline would increase with increasing salinity (S) or average swan population (SP) at a site, and it would also increase with a decrease in depth of water (WD) or decrease in extent of light penetration (LP) at a site. An increase in SAV decline with decreasing water depth was predicted due to the possibility of greater destruction of SAV in shallower water because of its greater exposure to Mute Swan herbivory and other environmental factors (e.g., storms, strong wave action). An increase in SAV decline with increasing salinity was predicted considering that with the exception of eelgrass (*Zostera marina*), no SAV species in the bay is a true sea grass and so increasing salinity would be an adverse environmental condition for most SAV species in the bay (Hurley 1990, Short *et al.* 2001). Likewise, we predicted that SAV decline would increase with a decrease in extent of light penetration because less light penetration would decrease primary productivity of SAV.

There are no other competing models (as $\Delta AICc > 2.0$ (Burnham and Anderson 1998). The Akaike weights (Table 1) indicate that the best model selected based on minimum AICc values is very likely as well, with no other models coming close in terms of their relative likelihood. The Akaike weights for all the models in the candidate set sum to 1(Franklin *et al.* 2001). Therefore, the best model has a substantial proportion (84.3%) of the weight associated with all the models. In terms of strength of evidence, the best model is 8 times (0.843/0.108) more likely than the second-ranked model which did not involve the covariate of swan population. Moreover, the selected parsimonious model was 34 times more likely than the third-ranked model, which involved the covariate of swan population but not salinity. There was no support for the models involving only number (population) of Mute Swans as predictor variable or its association with water depth, salinity, or extent of light penetration.

We initially considered inclusion of nutrients (i.e., nitrogen and phosphorus) as one of the potential predictor variables in the basic *a priori* model, but after careful consideration about the nutrient-rich status of the bay, we did not include it. We considered that the increasing load of nutrients in water is ultimately linked with light penetration, the variable which we had already included in our basic *a priori* model. This is because excess amounts of nutrients like phosphorus and nitrogen cause rapid growth of phytoplankton, creating dense populations or blooms reducing the amount of sunlight available to SAV (Chesapeake Bay Program 2005). Measurement of extent of light penetration at 18 study sites (localities) on the eastern shore of the bay revealed that there was considerable variation in extent of light penetration from site to site. Thus, at seven sites extent of light penetration was as high as 100%, at two sites it was less than 50%, at another five sites its extent was 50% to 75%, and the remaining four sites had over 75% to less than 100% light penetration. Thus, considering variation in extent of light penetration from site to site, the relevant predictor variable (LP) might have high site-specific (i.e., locality wise) relative importance with respect to growth and survival of SAV in the bay. In Chesapeake Bay, the most important factor determining growth and survival of SAV is light (Chesapeake Bay Program 2005). In the best model selected by us, highest relative importance of the relevant predictor variable (i.e., extent of light penetration) can be judged from its highest weight (Table 1).

The other two predictor variables (water depth and salinity) also are important in determining growth and survival of SAV in the bay. This is because SAV is mainly restricted to water less than 2 m deep and different species of SAV have different salinity requirements (Hurley 1990, Chesapeake Bay Program 2004). Therefore, the most parsimonious model selected by us has appropriately included these two predictor variables. However, for the middle portion of the Bay (Talbot and Dorchester Counties), where the maximum population of Mute Swans in the bay was concentrated (Hindman and Harvey 2004), the locality-wise relative importance of these two factors might be lower as compared to that of extent of light penetration. Overall uniformity of water depth and salinity in mid-bay was the potential cause for the lower relative importance of the relevant predictor variables (i.e., WD and S). Thus, measurement of environmental factors at 18 study sites in the mid-bay portion revealed that water depth and salinity were more or less uniform among individual sites. At seven (39%) sites, water depth was 0.50 to 0.75 m, at another seven (39%)sites, the depth was over 0.75 m but less than 1 m and only four (22%) sites had 1 m (or slightly more) depth. At 15 (83%) sites, salinity was around 9-10 ppt, and the remaining 3 (17%) sites had salinity over 10 ppt. In our view, the relative importance of the salinity variable also would be low because 30 of the 34 SAV beds (88%) consisted of *R. maritima* only (Tatu 2006). The SAV beds consisting of only *R. maritima* covered about 97% of the total SAV bed area at our study sites (Tatu, in press) indicating its predominance in our study area. Because *R. maritim,* is a eury-haline species (Hurley 1990), salinity would not have a substantial impact on its growth and survival.

The relative importance of the predictor variable of the Mute Swan population (SP) might be lower than that of other predictor variables because Mute Swans are not the primary cause for SAV decline in the bay, but an additional factor (Maryland DNR 2001). Accordingly, the weight of this predictor variable was lower than that of other predictor variables in the best selected model (Table 1). Mute Swans likely cause a synergistic effect with abiotic variables, resulting in increased SAV decline in the Bay. Mute Swan control should be used along with other practices to combat SAV decline in the Chesapeake Bay.

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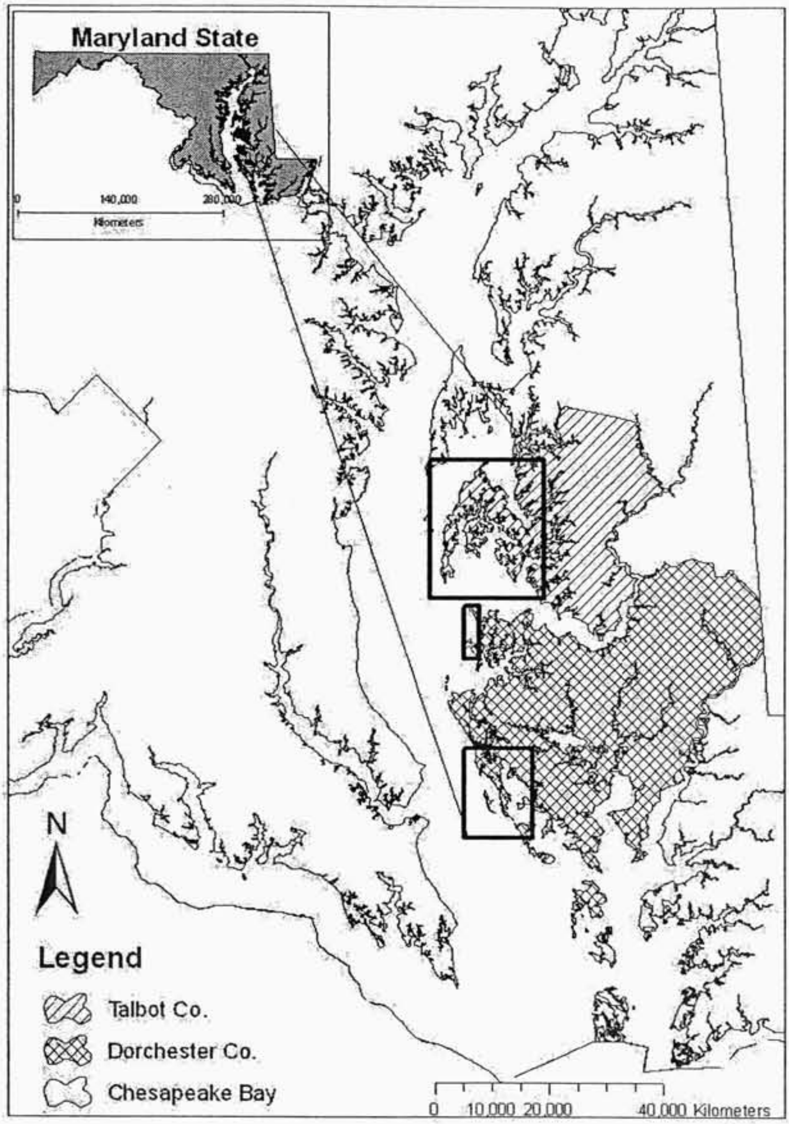

Figure 1. Portions of Talbot and Dorchester Counties, Maryland (marked) on the eastern shore of Chesapeake Bay where 18 sites for data collection were located, 2003-04.

Table 1. Ranking of 15 *a priori* candidate models relating Submerged Aquatic Vegetation cover decline to predictor variables (water depth [WD], light penetration [LP], salinity [S], and Mute Swan population [SP]) for Chesapeake Bay, Maryland, 2003-04. Models were ranked using Akaike's Information Criterion for small sample size (AICc).

Model structure	Equation	AICc	ΔAICc	K	w_i
Y = Decline in percent cover					
Y = WD ± LP ± S ± SP	55.2929 - 10.7255WD - 38.3855LP + 8.1752S + 0.6477SP	127.5	0	6	0.8430
Y = WD ± LP ± S	28.127 - 0.2264 WD - 21.0908LP + 3.3922S	131.6	4.1	5	0.1080
Y = WD ± LP ± SP	39.4587 - 5.0608WD - 27.1802LP + 0.5804SP	134.5	7.0	5	0.0250
Y = LP ± S ± SP	35.7047 - 33.6013LP + 7.5071S + 0.6303SP	136.0	8.5	5	0.0120
Y = WD ± S ± SP	40.0742 - 6.8446WD + 3.3218S + 0.5424SP	137.8	10.3	5	0.0050
Y = WD ± LP	66.1595 - 1.7946WD - 16.9337LP	137.9	10.4	4	0.0050
Y = LP± S	28.5030 - 20.9971LP + 3.3805S	140.2	12.7	4	0.0020
Y = WD ± S	76.6266 - 9.1784WD + 0.9758S	142.7	15.2	4	0
Y = LP ± SP	45.2999 - 25.2724LP + 0.5746SP	142.9	15.4	4	0
Y = WD ± SP	72.9620 - 7.1079WD + 0.5244SP	143.9	16.4	4	0
Y = S ± SP	33.8981 + 3.3724S + 0.5458SP	146.1	18.6	4	0
Y = LP	64.1566 - 17.5823LP	146.5	19.0	3	0
Y = WD	86.1549 - 9.2344WD	146.7	19.2	3	0
Y = S	68.6378 + 1.0239S	149.2	21.7	3	0
Y = SP	67.0658 + 0.5277SP	152.2	24.7	3	0

Table 2. Localized data on Mute Swan population and other environmental variables used to predict the best approximating model for Submerged Aquatic Vegetation decline using information theoretic approach (Burnham and Anderson 1998) on the Chesapeake Bay, Maryland, 2003-04.
[a] Total water depth (m).

WD[a]	*LP*[b]	*S*[c]	*SP*[d]	Y[e]
0.95	77.40	9.20	2	55.55
0.75	100.00	9.24	44	100.00
0.79	100.00	10.20	7	63.05
0.75	68.30	9.70	22	88.88
0.69	74.30	10.44	44	92.62
0.91	93.50	9.03	2	36.71
0.59	100.00	9.73	27	83.17
1.00	43.70	11.26	2	76.92
0.97	100.00	9.96	2	89.88
0.64	100.00	8.65	12	88.93
0.95	96.40	9.46	48	92.86
1.10	65.40	9.50	50	81.20
1.02	50.20	9.60	30	92.96
1.07	93.50	9.60	9	90.54
0.50	100.00	10.62	10	75.00
0.76	62.00	9.66	18	31.58
0.77	52.70	9.73	39	75.07
0.54	100.00	9.38	25	100.00

[b] Extent of light penetration= [Secchi depth/Total water depth]x100.
[c] Salinity of water (ppt).
[d] Mute Swan population.
[e] Decline in SAV percent cover due to Mute Swan herbivory, i.e. % difference in SAV cover in exclosure and open plots.