Research Article

Mute Swans' Impact on Submerged Aquatic Vegetation in Chesapeake Bay

KETAN S. TATU, *Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, WV 26506, USA*

JAMES T. ANDERSON,[1] *Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, WV 26506, USA*

LARRY J. HINDMAN, *Maryland Department of Natural Resources, 828B Airpax Road, Wildlife and Heritage Service, Cambridge, MD 21613, USA*

GEORGE SEIDEL, *Department of Statistics, West Virginia University, P.O. Box 6330, Morgantown, WV 26506, USA*

ABSTRACT Mute swans (*Cygnus olor*) are poorly studied despite their potential to impact submerged aquatic vegetation (SAV). We measured vegetation characteristics (i.e., percent cover, shoot density, and canopy ht) of SAV beds in controls (unfenced), 2-year exclosures, and 1-year exclosures at 18 sites in the Chesapeake Bay, Maryland, USA, to quantify the impact of herbivory by mute swans on SAV during 2003 and 2004. Mute swan herbivory had a substantial adverse impact on percent cover, shoot density, and canopy height of SAV. At the end of the study mean percent cover, shoot density, and canopy height in the controls were lower by 79%, 76%, and 40%, respectively, as compared to those in 2-year exclosures. During 2004, percent cover, shoot density, and canopy height increased by 26%, 15%, and 22%, respectively, between early and late seasons of SAV growth in exclosures, but they decreased by 36%, 41%, and 18%, respectively, in the controls. Paired mute swans predominantly occupied 6 of 7 moderate-depth sites (0.76–0.99 m), and these sites experienced less (i.e., 32–75%) SAV reduction. All ($n = 7$) shallow water sites (0.50–0.75 m) were predominantly occupied by mute swan flocks, and percent cover reduction of SAV was as high as 75–100% at these sites. Mute swan flocks also predominantly occupied 3 of the 5 deep-water sites (≥ 1 m) and 1 of 7 moderate-depth sites, wherein we recorded considerable (i.e., 77–93%) SAV reduction. Thus, considering that flocks are more detrimental to SAV as compared to paired mute swans, we recommend that initial emphasis primarily be placed on controlling mute swans in flocks and secondarily on pairs. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1431–1439; 2007)

DOI: 10.2193/2006-130

Grazing by waterfowl can substantially reduce plant biomass and also the future reproductive potential of those plants (Mitchell and Wass 1996). Therefore, interactions between geese or swans and aquatic macrophytes have become a recent focus in studies of macrophyte dynamics (Lodge 1991, Mitchell and Wass 1996, Clevering and van Gulik 1997, Esselink et al. 1997, Perrow et al. 1997) and in studies of habitat use by waterfowl (Mitchell and Perrow 1998, Corti and Schlatter 2002, Santamaria and Rodriguez-gironés 2002, La Montagne et al. 2003, Nolet 2004). However, studies on herbivory by geese and swans in North America have mainly emphasized native birds (e.g., snow geese [*Chen caerulescens*], Canada geese [*Branta canadensis*], brants [*B. bernicla*], and trumpeter swans [*Cygnus buccinator*]; Conover and Mesier 1996, Herzog and Sedinger 2003, La Montagne et al. 2003, Person et al. 2003, Sherfy and Kirkpatrik 2003). Similar studies on exotic herbivorous waterfowl are limited, not only because most exotic bird species in North America are poorly studied (Temple 1992) but also because there are few exotic waterfowl species in North America.

One such exotic species is the mute swan (*Cygnus olor*; Conover and Kania 1994). Mute swans are native to Eurasia (Ciaranca et al. 1997) and since their introduction into the United States in the late 1800s they have increased to over 14,000 birds in the Atlantic Flyway (Atlantic Flyway Council 2003). This exotic species is considered feral and invasive (Allin and Husband 2003, Hindman and Harvey

2004). Established populations breed along the northeastern Atlantic Coast, in the Great Lakes region, and in the Pacific Northwest (Ciaranca et al. 1997). Chesapeake Bay in Maryland, USA, has been a stronghold of mute swans in the Atlantic Flyway since the 1990s. Mute swans have undergone phenomenal population growth in the Chesapeake Bay, where their numbers increased from 5 individuals in 1962 to about 4,000 individuals in 1999 (Hindman and Harvey 2004).

As an exotic, feral species, mute swan's impacts on native ecosystems and species are of concern (Ciaranca et al. 1997). One of the concerns is aggressive interaction (i.e., attacking, injuring, or killing) between territorial pairs of mute swans and native waterbirds (Hindman and Harvey 2004). More-over, disturbance of nesting colonies of native waterbirds by flocks of nonbreeding swans also constitutes a matter of concern (Therres and Brinker 2004). However, a more serious problem may be their impact on submerged aquatic vegetation (SAV). Large flocks of unsuccessful breeding and nonbreeding swans concentrate in shallow areas of the Chesapeake Bay to molt flight feathers. During this period, these flocks are capable of removing great quantities of SAV (Allin and Husband 2003). Mute swans can dislodge SAV by paddling and raking the substrate, and additional SAV that is not eaten is destroyed and uprooted (Owen and Kear 1972, Birkhead and Perrins 1986, Hindman and Harvey 2004). Sometimes this is done to provide food for cygnets. At high densities, mute swans can overgraze an area, causing a substantial decline in SAV at the local level (Cobb and

[1] E-mail: jander25@wvu.edu

Harlin 1980, Hindman and Harvey 2004, Mountford 2004).

Submerged aquatic vegetation is a key component of the Chesapeake Bay ecosystem and it provides a major food source for a number of native waterfowl like redheads (*Aythya americana*) and canvasbacks (*A. valisineria*), mammals like muskrats (*Ondatra zibethicus*) and beavers (*Castor canadensis*), and a variety of fish and invertebrates (Allin 1981, Hurley 1990, Ciaranca et al. 1997, Naylor 2004, Perry et al. 2004). Despite the potential of this invasive swan to impose adverse impacts on SAV, quantitative data on reduction of aquatic macrophytes by mute swans are limited (Hindman and Harvey 2004).

Our research was designed to answer 3 questions: 1) Does herbivory by mute swans result in reduced percent cover, density, and height of SAV? 2) Does the impact of mute swan herbivory vary according to depth of water? and 3) Does the impact of the herbivory vary according to social status (pair vs. flock) of mute swans? Our primary hypothesis was that mute swans, owing to their predominantly herbivorous diet and destructive foraging methods, could cause significant reduction in SAV. We also believed that flocks would be more destructive than pairs due to the larger number of birds in unpaired flocks and because birds in flocks would have an unsecured food supply and, thus, greater intraspecific competition for SAV. Our objectives were to evaluate the impacts of territorial pairs and nonbreeding flocks of mute swans on SAV shoot density, percent cover, and height and to evaluate the influence of water depth on mute swan herbivory.

STUDY AREA

We conducted our study on the eastern shore of Chesapeake Bay, Maryland between 2003 and 2004. The Bay was formed by >150 rivers and streams and tidal waters of the Atlantic Ocean. It was one of the primary waterfowl wintering areas in the Atlantic Flyway, supporting 40% of the wintering waterfowl in the Flyway (Hindman and Stotts 1989, Meyers et al. 1995).

Chesapeake Bay was an 8–48-km-wide and 288-km-long shallow estuary situated in a north–south direction, roughly parallel to the Atlantic seacoast and was mainly covered with clay–silt sediments (Lippson 1973, Meyers et al. 1995). Our study area covered 18 sites in the mid-bay (8 in Talbot County and 10 in Dorchester County; Fig. 1) that were located between 38°25′00″N and 38°52′30″N latitude and 76°07′30″W and 76°22′30″W longitude. It had mesohaline water with salinity ranging from 5–18 parts per thousand (Lippson 1973, Hurley 1990, Maryland Department of Natural Resources [DNR] 2005*a*) and was endowed with SAV beds (Orth et al. 2001, Maryland DNR 2005*a*) and mute swan flocks and pairs. Widgeon grass (*Ruppia maritima*), a species of SAV having a wide tolerance to salinities, was abundant, whereas the species having less tolerance to high salinity (i.e., horned pondweed [*Zannichellia palustris*], slender pondweed [*Potamogeton pusillus*],
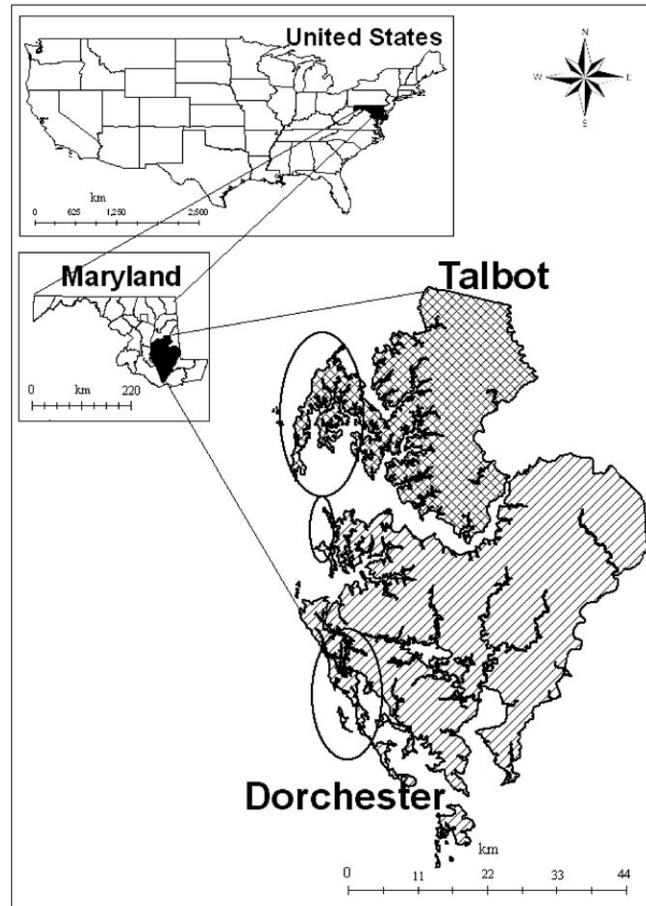

Figure 1. Portions of Talbot and Dorchester Counties, Maryland, USA, (marked with ovals) on the eastern shore of Chesapeake Bay, wherein the sites ($n = 18$) for the mute swan submerged aquatic vegetation exclosures were located, 2003 and 2004.

and sago pondweed [*Stuckenia pectinatus*]) were uncommon (Hurley 1990, Orth et al. 2003).

Although the Chesapeake Bay had traditionally played a vital role in providing habitat to wintering native waterfowl, it was inhabited by thousands of resident mute swans since the 1990s, specifically in Dorchester (1,638 swans) and Talbot (1,023 swans) counties. Mute swans were the predominant waterfowl, especially between May and September, when SAV was growing.

METHODS

Exclosure Experiment

In May 2003, at the onset of spring SAV growth, we delineated 3 sets of 3 5 × 5-m study plots at each of the 18 study sites. Because SAV density varied, we qualitatively judged areas of equal SAV density levels and placed each set of 3 plots in the areas of relatively equal density levels. Water level was usually shallow enough (i.e., $\bar{x} = 0.7$ m) for us to judge the relative density by randomly laying 1-m² quadrats in SAV beds and inspecting SAV growth inside them with our eyes and hands. However, we also employed snorkeling at deeper water sites ($n = 4$) if high tide occurred at the time of exclosure establishment. Each set of 3 plots contained one control (i.e., no exclusion of swans), one 2-
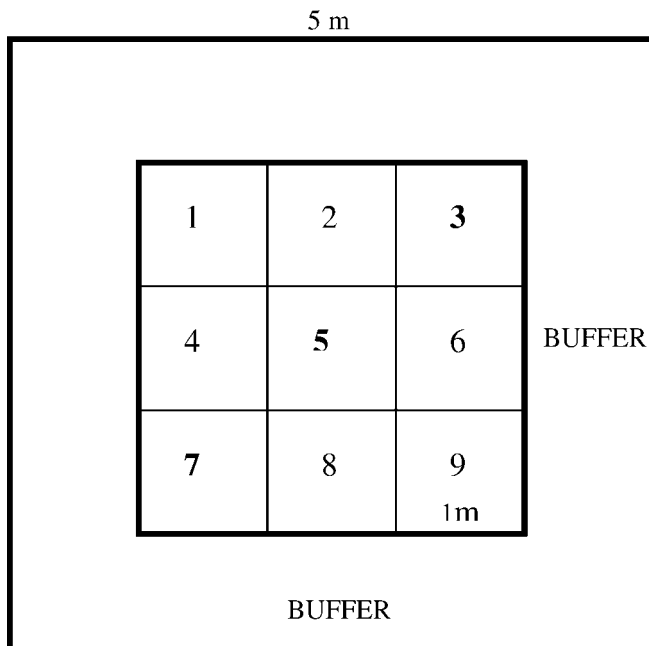
Figure 2. Lay out of sampling subplots (1 × 1 m) in a sampling plot (5 × 5 m) with core subplots marked with numbers ranging from 1 through 9 and diagonally located subplots (3, 5, 7) marked in bold fonts used for submerged aquatic vegetation measurement, Chesapeake Bay, Maryland, USA, 2003 and 2004.

year exclosure (i.e., swans excluded from May to Aug 2003 and 2004), and one 1-year exclosure (i.e., swans excluded from May to Aug 2004). Therefore, at each study site, there were 9 plots (i.e., 3 controls, 3 2-yr exclosures, and 3 1-yr exclosures). We set the distance between each type of sampling plot at 10–25 m to ensure that all the plots were in the same SAV bed, had similar relative density, and had the same water depth.

We wanted to exclude mute swans from our treatment plots but still allow access by other organisms (e.g., fish, invertebrates, turtles, cow-nose rays [*Rhinoptera bonasus*]) that might consume or destroy SAV in our treatment plots. We constructed plots this way to avoid an ambiguity whether a significant fencing effect was due solely to the mute swans or also due to the activities of nontarget species. We wanted to prevent submergence of the fence in water due to the tidal action in the Bay to prevent mute swans from entering the exclosures under all tidal conditions and to avoid accumulation of floating material (e.g., uprooted SAV) that might shade SAV within the exclosures and influence its growth. To address these 2 challenges, we designed exclosures comprised of 4 3.3-m-long metal poles (2.54 cm diam) that we erected in the bottom mud at 4 corners of the 5 × 5-m treatment plot. We put 2 cylindrical buoys (28 × 15 cm) one above the other along each pole of all treatment plots that would freely slide along the pole with changes in tide level. By winding a bright scarlet colored nylon twine having 2-mm diameter around each buoy on all 4 corner poles, we prepared a 2-strand fence for each treatment plot that moved up and down with the tides. We left a gap of 30–45 cm between the lower twine and

water surface, which was sufficient to allow access by underwater aquatic life into the exclosures (i.e., we observed cow-nose rays, fish, crabs, and turtles in the exclosures). Moreover, the sliding action of the buoys (with nylon twines around them) along the corner poles prevented submergence of the nylon twines during high tide, as at least the upper twine always remained above the water surface. We also tied 2 strands of nylon twine at the top of 2 diagonally opposite corner poles, making an 'X' configuration at the top of each exclosure. This helped in eliminating any possibility of swans or other waterfowl flying into the exclosure. During our field work in 2003 and 2004, we never saw mute swans or any other waterfowl inside our exclosures, though we often saw cow-nose rays in them. Thus, we believe the fencing was sufficient to create an effective barrier against mute swan entry into our treatment plots.

SAV Sampling

We identified submerged macrophytes using Hurley (1990) and an on-line Bay grass guide (Maryland DNR 2005*b*). We maintained a site-wise record of species and preserved voucher specimens.

We carried out measurements of SAV during the late season of SAV growth in 2003 in 162 sampling plots (i.e., 54 2-yr exclosures, 54 1-yr exclosures, and 54 control plots). In 2004, we measured SAV once during the early season (mid-May to early Jun) and once again in late season (Aug) of SAV growth. At each plot, we obtained percent cover, shoot density, and canopy height of SAV. To conduct SAV measurements, we further partitioned each 5 × 5-m plot into 1 × 1-m subplots for SAV sampling. Thus, each exclosure or open plot had 25 subplots of 1 × 1-m size. We sampled SAV in 3 diagonally arranged subplots in a northeast–southwest fashion (Fig. 2). We followed the diagonal configuration for SAV sampling at all the sites to avoid field-based bias in selecting the subplots for SAV sampling. Moreover, by keeping the subplots in the center of the exclosures, we eliminated any effects of mute swans feeding in the exclosures from the outside or the effects of droppings (i.e., nutrients) from other birds potentially perching on the poles or twines.

In each subplot, we laid a 0.1-m^2 quadrat (0.2 m × 0.5 m) on 4 sides and the center to get an average value of SAV percent cover for the subplot. We later determined the average value for an entire sampling plot by averaging SAV cover values for the 3 diagonal subplots. We estimated the amount of cover by judging the proportion of SAV cover inside the quadrat with our hands and through visual assessment when practical because we had to conduct percent cover estimation at the surface of the bottom mud that was up to 1 m below the surface of water that was often turbid. For judging percent cover of SAV, we divided the quadrat into 4 quarters with the help of twines. To increase the accuracy of SAV percent cover judgment in water, we further sub-divided each of these 4 sections with a twine to represent 12.5% of the quadrat area and we also sub-divided a few of them to represent 6.25% of the total area. We assigned the estimated cover into 1 of 6 cover classes

(Daubenmire 1959; Table 1). We used the mid-point of each class in analysis.

We measured and recorded density of SAV by species in each sampling plot by laying a 1 × 1-m quadrat (each divided into 0.1 × 0.1-m squares) in each of the 3 1 × 1-m subplots. We counted the number of shoots of SAV in each subplot in 25–50 randomly selected 0.1 × 0.1-m squares. If there was not significant variation in the number of individuals encountered from square to square, we projected density estimates (shoots/m²) for the entire 1-m² frame. We counted them in ≥75–100 squares, if we encountered significant variation in the number of individuals from each square.

We measured leaf height of SAV for each species using a ruler to the nearest 5 mm. To measure canopy height, we grabbed a large handful of rooted plants in randomly selected 0.1 × 0.1-m squares (Durate and Kirkman 2001). By extending leaves to their maximum height, we measured height up to the top of the bundle from the base with a ruler.

We measured the maximum water depth at each study site during high tide on the day of SAV measurements. We measured the depth to the nearest 1 cm on a permanently marked pole and categorized sites as shallow (i.e., 0.5–0.75 m), moderate (i.e., 0.76–0.99 m), or deep (i.e., ≥1 m) water.

Waterbird Sampling

We recorded presence or absence of pairs and flocks along with the numbers of mute swans and other waterbirds every 2 weeks at each site during the SAV growing season ([May to Aug] 2003, 2004). We conducted the counts during 3 time periods (i.e., 0600–1100 hr, 1200–1500 hr, and 1600–1900 hr). We counted waterbirds by species in a 6–7-ha area at each site. We chose this size area because it was twice the area encompassing all 3 sets of sampling plots; sampling plots were placed to cover an average territory size (i.e., 3–3.5 ha) of mute swans in the Bay (Ciaranca et al. 1997, Hindman and Harvey 2004).

Statistical Analysis

We conducted analysis of variance (ANOVA; fixed-effects model) using General Linear Models in SAS version 8 (SAS Institute, Inc., Cary, NC) to assess the effects of mute swan herbivory on SAV during the early and late seasons of SAV growth among the 3 treatments in 2004. Our experimental design consisted of a split-plot randomized block design with a hierarchical ordering of sampling plots within sets within sites, with the treatments allocated to the plots (i.e., experimental units). Thus, for our assessment of the treatment effects, combination of sites ($n = 18$) × site-wise sets of sampling plots ($n = 3$) acted as blocks ($n = 54$). As each set at a site had 3 sampling plots in our design, we had many experimental units ($n = 162$) in which we measured dependent variables (i.e., SAV characteristics). We measured the dependent variables twice (i.e., once in early growing season and again in late growing season) in all the experimental units and, therefore, a treatment × time interaction term was involved in the statistical analysis. It

Table 1. The Daubenmire cover classes used to assess extent of substrate covered by submerged aquatic vegetation in the Chesapeake Bay, Maryland, USA, 2003 and 2004.

Cover class	Range of cover (%)	Midpoint of class (%)
1	>0–5	2.5
2	6–25	15.0
3	26–50	37.5
4	51–75	62.5
5	76–95	85.0
6	96–100	97.5

further resulted in the number of observations that were double the number of experimental units. We used percent cover, shoot density, and canopy height as dependent variables indicating SAV status, and we quantified SAV status using least square means of these 3 variables. We used contrast statements to compare means from 2-year exclosures to means from controls, means from 2-year exclosures to means from 1-year exclosures, and means from 1-year exclosures to means from controls. Significance for all statistical inferences was $P \leq 0.05$.

We used ANOVA to test for differences in percent cover, shoot density, and canopy height among shallow-, moderate-, and deep-water areas. We also assessed the effect of social status (pair and flock) on these variables using a simple randomized design. The ANOVA used a 2-factor model with social status and site-wise (and not exclosure-wise) average water depth (categories as explained above) as treatments.

RESULTS

Descriptive Results

At the end of our exclosure experiment percent cover, density, and height of SAV were 79%, 76%, and 40% less, respectively, in the sampling plots that remained exposed to swan herbivory for 2 consecutive growing seasons of SAV than those kept protected from swans for the same time period. Widgeon grass was the only SAV species sampled at 13 of the 18 (72%) sampling sites. We encountered a horned pondweed–widgeon grass association at 5 study sites (i.e., Claiborne Harbor, Punch Point, Osprey Point, Middle Point Road, and Haven on the Bay; see Tatu [2006] for a complete list of sites). Overall, 94% of the total percent cover in our sampling plots was widgeon grass and only 6% was horned pondweed.

Submerged Aquatic Vegetation Cover, Density, and Height

Mean percent cover of SAV in controls during the late sampling period in 2004 (Table 2) was 79% less than that in 2-year exclosures ($F_{1,159} = 98.99$, $P < 0.001$) and 69% less than that in 1-year ($F_{1,159} = 22.90$, $P < 0.001$). One-year exclosures had 41% less cover as compared to that inside the 2-year exclosures ($F_{1,159} = 26.66$, $P < 0.001$).

Percent cover of SAV in 2-year exclosures increased by 26.4% from the early to late SAV growing season during 2004 ($F_{1,159} = 5.06$, $P = 0.026$; Fig. 3). Unlike in 2-year

Table 2. Submerged aquatic vegetation characteristics in the sampling plots at study sites ($n = 18$) in Chesapeake Bay, Maryland, USA, where we studied the effects of excluding mute swans, May 2003–Aug 2004.

	Sampling plot[a]					
	2-yr exclosure		1-yr exclosure		2-yr open (control)	
Parameter	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
% cover	43.3A	8.1	25.6B	6.5	9.2C	2.5
Density (shoots/m²)	254.9A	47.8	140.1B	33.3	59.7C	21.5
Canopy ht (cm)	10.8A	0.5	9.5B	0.6	6.5C	0.5

[a] The same letters in a row indicate no significant difference in means ($P > 0.05$).

exclosures, the extent of SAV decreased in controls by 35% from the early to late season in 2004 ($F_{1,159} = 2.21$, $P = 0.136$; Fig. 3).

Mean shoot density of SAV in the controls (Table 2) was 76% less than that in 2-year exclosures ($F_{1,159} = 83.85$, $P < 0.001$) and 57% less than that in 1-year exclosures ($F_{1,159} = 14.21$, $P < 0.001$). The 1-year exclosures had 45% less SAV density as compared to that inside the 2-year exclosures ($F_{1,159} = 29.03$, $P < 0.001$).

Shoot density of SAV increased by 15% in the 2-year exclosures ($F_{1,159} = 5.06$, $P = 0.026$) between the early and late measurements of SAV in 2004. Contrastingly, in the control plots SAV shoot density decreased by 41% ($F_{1,159} = 2.21$, $P = 0.140$; Fig. 3).

Mean canopy height of SAV in controls (Table 2) was 40% less than that in 2-year exclosures ($F_{1,159} = 88.56$, $P < 0.001$) and 32% less than that in 1-year exclosure plots ($F_{1,159} = 41.92$, $P < 0.001$). Moreover, 1-year exclosures had 12% less SAV cover as compared to that inside the 2-year exclosures ($F_{1,159} = 8.62$, $P = 0.004$).

Canopy height of SAV in 2-year exclosures increased by 21.7% between the early and late growing seasons of SAV in 2004 ($F_{1,159} = 17.50$, $P < 0.001$). Contrastingly, in the control plots, it decreased by 17.6% during the same time period ($F_{1,159} = 8.93$, $P = 0.003$; Fig. 3).

Effect of Social Status and Water Depth on SAV Reduction

The water depth class × social status category interaction was significant ($F_{1,13} = 3.71$, $P = 0.039$). Mute swan flocks predominantly occupied 3 of the 5 deeper water sites (depth ≥ 1 m), 1 of 7 moderate-depth sites (0.76–0.99 m), and all ($n = 7$) shallower water sites; the other sets had more swans in pairs than flocks (Table 3). Consequently, SAV percent cover reduction at these shallow-water sites was high (i.e., 90%; SE = 3.40), ranging from 75% (Tar Bay area) to 100% (Wades Point and Bay Shore areas; Table 3). There were no significant differences in SAV reduction between deep and moderate-depth and shallower water sites occupied by flocks ($F_{1,13} = 0.06$, $P = 0.806$). Thus, we found that flocks caused considerable SAV reduction at moderate-depth (93%; SE = 0.00) and deeper water (83%; SE = 4.16) sites, too (i.e., 77% [Hill Point Cove] to 93% [Osprey Point]). We found a significant difference in SAV

reduction between deeper versus moderate-depth sites occupied by pairs ($F_{1,13} = 5.35$, $P = 0.038$). The moderate-depth sites, which were predominantly occupied by paired mute swans, had experienced less (52%; SE = 8.11) SAV reduction (i.e., 32% [Todd's Point] to 75% [Twin's Point]), whereas the deeper water sites had experienced more (92%; SE = 4.50) SAV reduction (i.e., 90% [Hooper's Island Road Point] and 93% [Punch Point]).

Other Waterbirds

We recorded 15 species of waterbirds that shared sites with mute swans at our study sites; 13 were carnivorous (Table 4). The remaining 2 species, mallard (*Anas platyrhynchos*) and Canada goose (*Branta canadensis*), were omnivorous (Bellrose 1986) and herbivorous (Baldassarre and Bolen 1994), respectively. They occurred in low numbers (i.e., mallard: 1.19, SE = 0.68; Canada goose: 0.90, SE = 0.47; Table 4) as compared to that of mute swans (25.00, SE = 1.31) in our study area.

DISCUSSION

Mute swan herbivory had a negative impact on the vegetative characteristics of submerged macrophyte beds in the Chesapeake Bay, Maryland. The percent cover, shoot density, and canopy height of SAV were proportional to the period (i.e., 1-yr vs. 2-yr) for which the SAV was exposed to the herbivory. Mute swans consume SAV in the Bay throughout the year due to their year-round stay on the Bay (Ciaranca et al. 1997). Therefore, controls provided the longest exposure of SAV to mute swan herbivory leading to the lowest values of SAV parameters, 2-year exclosures facilitated the shortest exposure of SAV to herbivory leading to the highest values of the parameters, and 1-year exclusion of the swans resulted in exposure of SAV to herbivory for an intermediate time period leading to the intermediate values of vegetation characteristics of SAV.

Our data suggests that mute swans alone were responsible for the lower values of SAV characteristic in the controls as compared to those in the exclosures. This is because our exclosure design did not exclude grazing by nontarget organisms except other waterbird species. Moreover, 13 of 15 other waterbird species that shared the experimental sites with mute swans did not have the potential to cause SAV decline because they were carnivorous. Two species of waterfowl (i.e., mallard [an omnivore] and Canada goose [an herbivore]) that fed on SAV occurred in low numbers, leaving little possibility of substantial SAV consumption by waterfowl other than mute swans.

Waterfowl significantly reduce submerged and emergent macrophytes during the growing season (Smith and Odum 1981, Corti and Schlatter 2002) and mute swans are no exception (Clevering and van Gulik 1997, Allin and Husband 2003). In tidal areas of the southwest part of the Netherlands, mute swan grazing for 3 consecutive growing seasons resulted in the complete disappearance of an emergent aquatic macrophyte (i.e., common club-rush [*Scirpus lacustris*]; Clevering and van Gulik 1997). Mute
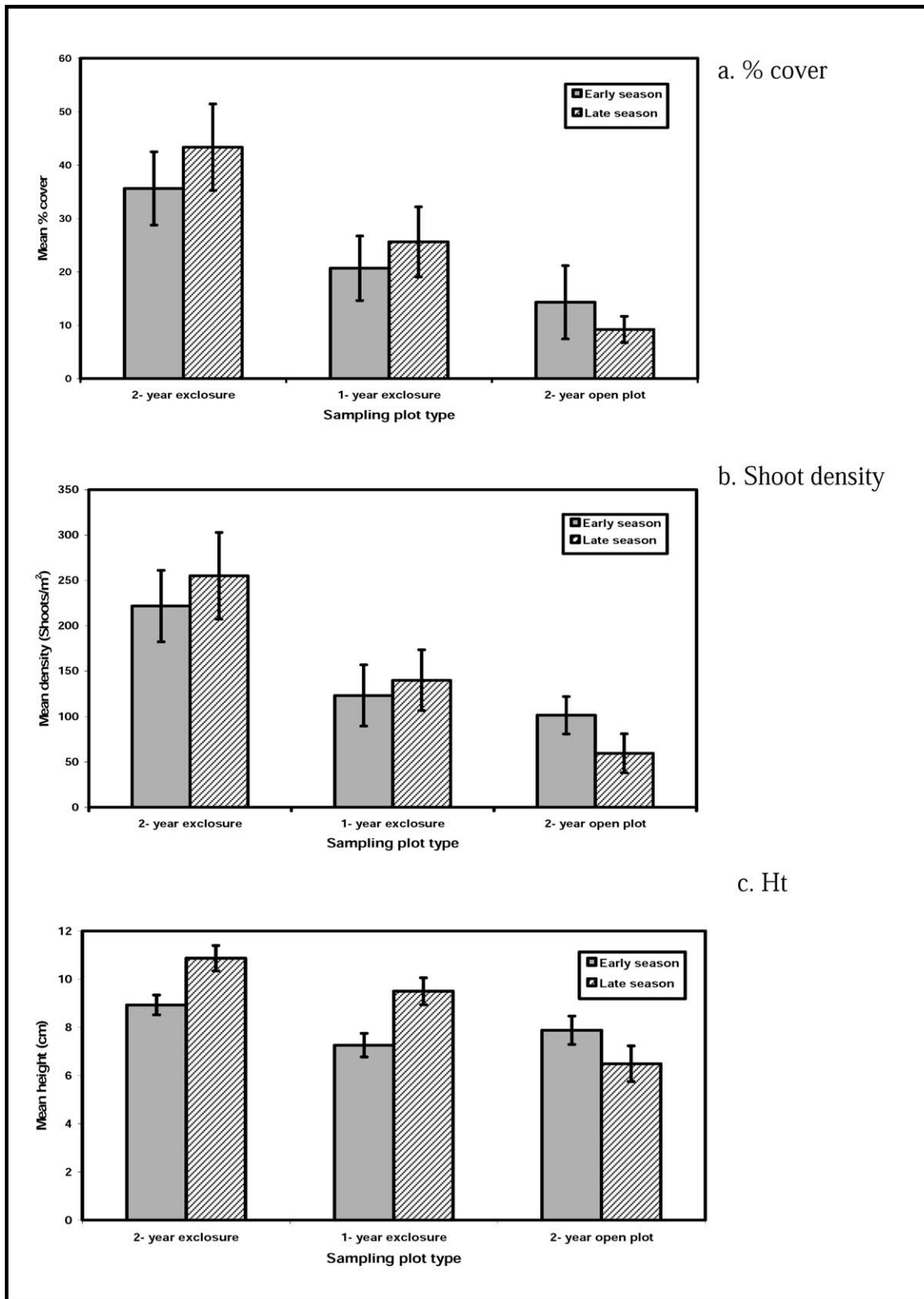
Figure 3. Submerged aquatic vegetation percent cover (a), shoot density (b), and height (c) in the mute swan exclosure and control sampling plots from early to late growing season (2004) in the Chesapeake Bay, Maryland, USA.

swans, along with mallards and Eurasian coots (*Fulica atra*), severely affected sago pondweed abundance at shallow sheltered sites adjacent to Asko island, in the northern Baltic Sea (Idestam-Almquist 1998). A mute swan exclosure

study in coastal ponds of Rhode Island, USA, documented considerable (i.e., 95%) reduction in SAV biomass in control (open) plots as compared to that in the treatment plots (exclosures) at the end of 2 years (Allin and Husband

Table 3. Water depth (m) classes, mute swan social status categories, and percent cover reduction of submerged aquatic vegetation (SAV) due to herbivory at study sites ($n = 18$), Chesapeake Bay, Maryland, USA, May 2003–August 2004.

Study site	Water depth	Depth class[a]	Social status	SAV reduction[b] %	SAV reduction[b] Intensity
Audubon Sanctuary	0.95	M	Pair	55	Moderate
Bay Shore Road	0.75	S	Flock	100	Substantial
Brannock Bay	0.79	M	Pair	63	Moderate
Claiborn Harbor	0.75	S	Flock	89	Substantial
Covey Point Farm	0.69	S	Flock	93	Substantial
Church Neck Road	0.91	M	Pair	36	Low
Haven on Bay	0.59	S	Flock	83	Substantial
Hill Point Cove	1.00	D	Flock	77	Substantial
Hooper Island Road	1.00	D	Pair	90	Substantial
Middle Point Road	0.64	S	Flock	89	Substantial
Osprey Point	0.95	M	Flock	93	Substantial
Partridge Lane	1.10	D	Flock	81	Substantial
Punch Pont Road	1.02	D	Pair	93	Substantial
Ragged Point	1.07	D	Flock	91	Substantial
Tar Bay	0.50	S	Flock	75	Moderate
Todd's Point Road	0.76	M	Pair	32	Low
Twins Point Road	0.77	M	Pair	75	Moderate
Wades Point Road	0.54	S	Flock	100	Substantial

[a] D: deep-water sites (i.e., depth ≥1 m), M: moderate-depth sites (0.76–0.99 m), S: shallow-water sites (0.5–0.75 m).
[b] Substantial: $\bar{x}$ % cover in 2-yr exclosures is >75% higher than that in control plots; Moderate: $\bar{x}$ % cover in 2-yr exclosures is 51–75% higher than that in control plots; Low: $\bar{x}$ % cover in 2-yr exclosures is 26–50% higher than that in control plots.

2003). Though we measured different SAV parameters (i.e., % cover, shoot density, and canopy ht instead of SAV biomass), we, too, revealed lower values of those parameters in the controls, indicating SAV decline.

An important finding of our study is that the extent of localized reduction in SAV cover by mute swan herbivory was influenced by water depth and mute swan social status. In shallower water SAV cover was reduced by as much as 100%. Such an excessive reduction occurred because shallow-water sites were predominantly occupied by flocks of mute swans rather than breeding pairs. Unlike shallow-

water sites, moderate-depth (0.5–0.75 m) and deeper water (≥1 m) sites were not predominantly occupied by the flocks, and yet, mute swans in the flocks reduced SAV cover up to 93% at such sites. An adult mute swan can reach SAV under water ≤1.07 m and can consume 1.8–3.6 kg wet weight of plant material each day (Willey and Halla 1972, Owen and Cadbury 1975, Fenwick 1983). Our findings that flocks were responsible for considerable SAV reduction in shallower water and that they also caused substantial SAV reduction in moderate-depth and deeper water sites suggest a serious SAV problem caused by mute swan flocks. The flocks, especially larger ones, are more detrimental to SAV beds than pairs (Cobb and Harlin 1980, Tatu 2006), because they can overgraze shallow-water areas (Hindman and Harvey 2004).

In our study, cover reduction of SAV by paired mute swans was typically lower than that by the flocks. Thus, at 5 of the 7 sites occupied by paired mute swans, SAV cover reduction was as low as 32–75% as compared to 75–100% reduction by the flocks. All of these sites were moderate-depth sites. At 2 deep-water sites occupied by pairs, SAV reduction was as high as 90–93%. Greater SAV reduction at deep-water sites compared to that at moderate-depth sites was probably due to better SAV recovery at moderate-depth sites compared to that at the deep-water sites. The extent of light penetration that was measured using a Secchi disk at the moderate-depth sites was higher (i.e., 83%) than that at deep-water sites (i.e., 53%). This, in turn, might have resulted in better SAV recovery and lesser net reduction in SAV cover at moderate-depth sites.

Allin and Husband (2003) suggested that the rate of SAV reduction by mute swan herbivory was related to water depth. They revealed that mute swans reduced biomass by as much as 95% during 1991–1992 when the water levels were relatively shallow (i.e., <0.5 m). They further noted that there was a decrease in the amount of biomass removed during the remaining period of the study, when water depth increased by 50%. Though Allin and Husband (2003)

Table 4. Waterbird species sharing study sites ($n = 18$) with mute swans during exclosure study on the Chesapeake Bay, Maryland, USA, May 2003–August 2004.

Species Common name	Species Scientific name	Count at study sites $\bar{x}$	Count at study sites SE	Feeding niche	Potential to share submerged aquatic vegetation with mute swans
Mallard	*Anas platyrhynchos*	1.19	0.68	Omnivore	Yes
Canada goose	*Branta canadensis*	0.90	0.47	Herbivore	Yes
Mute swan	*Cygnus olor*	25.00	1.31	Herbivore	Yes
Double-crested cormorant	*Phalacrocorax auritus*	0.03	0.02	Carnivore	No
Brown pelican	*Pelecanus occidentalis*	0.02	0.01	Carnivore	No
Herring gull	*Larus argentatus*	0.13	0.05	Carnivore	No
Great black-backed gull	*Larus marinus*	0.03	0.02	Carnivore	No
Laughing gull	*Larus atricilla*	0.06	0.03	Carnivore	No
Forster's tern	*Sterna forsteri*	0.05	0.03	Carnivore	No
Common tern	*Sterna hirundo*	0.14	0.06	Carnivore	No
Least tern	*Sterna antillarum*	0.04	0.02	Carnivore	No
Great blue heron	*Ardea herodias*	0.16	0.04	Carnivore	No
Great egret	*Ardea alba*	0.05	0.01	Carnivore	No
Snowy egret	*Egretta thula*	0.08	0.03	Carnivore	No
Green heron	*Butorides virescen*	0.05	0.02	Carnivore	No
Willet	*Catoptrophorus semipalmatus*	0.02	0.001	Carnivore	No

suggested that shallower water led to greater SAV reduction due to mute swan herbivory, they did not assess the influence of social status (i.e., pair vs. flock) on extent of SAV reduction in shallow water.

MANAGEMENT IMPLICATIONS

Our exclosure experiment showed that mute swan herbivory leads to considerable reduction in cover, shoot density, and canopy height of SAV. Thus, it has provided evidence that SAV under-compensates in response to mute swan herbivory. An important consequence of under-compensation of SAV may be the risk to SAV restoration activities that are being conducted by Maryland DNR and some nongovernmental organizations in the Bay. Therefore, we recommend that mute swan populations be reduced in the Chesapeake Bay, Maryland and that SAV restoration efforts take into consideration the local swan population. Our study also showed that flocks, unlike pairs of mute swans, can cause up to 100% SAV cover reduction in shallower water. Considering that flocks are more detrimental to SAV as compared to paired mute swans, emphasis should primarily be placed on reducing mute swan flocks and secondarily on pairs.

ACKNOWLEDGMENTS

LITERATURE CITED

Allin, C. C. 1981. Mute swans in the Atlantic Flyway. Proceedings of the International Waterfowl Symposium 4:149–154.

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

Atlantic Flyway Council. 2003. Atlantic Flyway mute swan Management Plan 2003–2013. Atlantic Flyway Council, Laurel, Maryland, USA.

Baldassarre, G. A., and E. G. Bolen. 1994. Waterfowl ecology and management. John Wiley & Sons, New York, New York, USA.

Bellrose, F. C. 1986. Ducks, geese and swans of North America. Stackpole, Harrisburg, Pennsylvania, USA.

Birkhead, M. E., and C. M. Perrins. 1986. The mute swan. Croom Helm, London, United Kingdom.

Ciaranca, M. A., C. C. Allin, and G. S. Jones. 1997. Mute swan (*Cygnus olor*). Account 273 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Clevering, O. A., and M. G. van Gulik. 1997. Restoration of *Scirpus lacustris* and *Scirpus maritimus* stands in a former tidal area. Aquatic Botany 55:229–246.

Cobb, J. S., and M. M. Harlin. 1980. Mute swan (*Cygnus olor*) feeding and territoriality affects diversity and density of rooted aquatic vegetation. American Zoologist 20:882.

Conover, M. R., and G. S. Kania. 1994. Impact of interspecific aggression and herbivory by mute swans on native waterfowl and aquatic vegetation in New England. Auk 111:744–748.

Conover, M. R., and T. A. Mesier. 1996. Feeding preferences and changes in mass of Canada geese grazing endophyte-infected tall fescue. Condor 38:859–862.

Corti, P., and R. P. Schlatter. 2002. Feeding ecology of the black-necked swan *Cygnus melancoryphus* in two wetlands of Southern Chile. Studies on Neotropical Fauna and Environment 37:9–14.

Daubenmire, R. F. 1959. A canopy coverage method of vegetation analysis. Northwest Science 35:43–64.

Durate, C. M., and K. Kirkman. 2001. Methods for the measurement of sea grass abundance and depth distribution. Pages 141–153 *in* F. T. Short and R. G. Coles, editors. Global sea grass research methods. Elsevier, Amsterdam, The Netherlands.

Esselink, P., G. J. F. Helder, B. A. Aerts, and K. Gerdes. 1997. The impact of grubbing by greylag geese (*Anser anser*) on the vegetation dynamics of a tidal marsh. Aquatic Botany 55:261–279.

Fenwick, G. H. 1983. Feeding behavior of waterfowl in relation to changing food resources in Chesapeake Bay. Dissertation, Johns Hopkins University, Baltimore, Maryland, USA.

Herzog, M. P., and J. S. Sedinger. 2003. Dynamics of foraging behavior associated with variation in habitat and forage availability in captive black brant (*Branta bernicla nigricans*) goslings in Alaska. Auk 121:210–223.

Hindman, L. J., and W. F. Harvey. 2004. Status and Management of mute swans in Maryland. Pages 11–17 *in* M. C. Perry, editor. Mute swans and their Chesapeake Bay habitats: proceedings of a symposium: U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR-2004-0005, Reston, Virginia, USA.

Hindman, L. J., and V. D. Stotts. 1989. Chesapeake Bay and North Carolina Sounds. Pages 27–55 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, USA.

Hurley, L. M. 1990. Field guide to the submerged aquatic vegetation of Chesapeake Bay. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Idestam-Almquist, J. 1998. Waterfowl herbivory on *Potamogeton pectinatus* in the Baltic Sea. Oikos 81:323–328.

LaMontagne, J. M., L. J. Jackson, and R. M. R. Barclay. 2003. Compensatory growth responses of Potamogeton pectinatus to foraging by migrating trumpeter swans in spring stop over areas. Aquatic Botany 76:235–244.

Lippson, A. J. 1973. The Chesapeake Bay in Maryland: an atlas of natural resources. Johns Hopkins University Press, Baltimore, Maryland, USA.

Lodge, D. M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41:95–224.

Maryland Department of Natural Resources [Maryland DNR]. 2005*a*. Recent water and habitat conditions in Maryland's Chesapeake Bay and Coastal Bays. <http://mddnr.chesapeakebay.net/eyesonthebay/index.cfm>. Accessed 3 Feb 2007.

Maryland Department of Natural Resources [Maryland DNR]. 2005*b*. Bay grasses identification key. <http://www.dnr.state.md.us/bay/sav/key/>. Accessed 3 Feb 2007.

Meyers, E., R. Fischman, and A. Marsh. 1995. Maryland Chesapeake Bay critical areas program: wetland protection and future growth. Pages 189–201 *in* D. R. Porter and D. A. Salvesen, editors. Collaborative planning for wetlands and wildlife—issues and examples. Island Press, Washington, D.C., USA.

Mitchell, S. F., and M. R. Perrow. 1998. Interaction between grazing birds and macrophytes. Pages 175–196 *in* E. Jeppesen, M. Sondergaard, and K. Christoffersen, editors. The structuring role of submerged macrophytes in lakes. Springer, Berlin, Germany.

Mitchell, S. F., and R. T. Wass. 1996. Grazing by black swans (*Cygnus atratus* Latham), physical factors, and the growth and loss of aquatic vegetation in a shallow lake. Aquatic Botany 55:205–215.

Mountford, K. 2004. Mute swan testimony: some dialog about swans and humankind through history. Pages 2–6 *in* M. C. Perry, editor. Mute swans and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR-2004-0005, Reston, Virginia, USA.

Naylor, M. 2004. Potential impacts of mute swans to SAV in Chesapeake Bay. Pages 36–37 in M. C. Perry, editor. Mute swans and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR-2004-0005, Reston, Virginia, USA.

Nolet, B. A. 2004. Overcompensation and grazing optimization in a swan–pondweed system? Freshwater Biology 49:1391–1399.

Orth, R. J., D. J. Wilcox, L. S. Negey, J. R. Whiting, and J. R. Fishman. 2001. 2000 distribution of submerged aquatic vegetation in the Chesapeake Bay and Coastal Bay. Virginia Institute of Marine Science (VIMS) Special Scientific Report no. 142. Final report to U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland, USA.

Orth, R. J., D. J. Wilcox, L. S. Negey, J. R. Whiting, and J. R. Fishman. 2003. 2002 distribution of submerged aquatic vegetation in the Chesapeake Bay and Coastal Bay. Virginia Institute of Marine Science (VIMS) Special Scientific Report no. 144. Final report to U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland, USA.

Owen, M., and C. J. Cadbury. 1975. The ecology and mortality of mute swans at the Ouses Washes, England. Wildfowl 25:31–42.

Owen, M., and J. Kear. 1972. Food and feeding habits. Pages 58–77 in P. Scott, editor. The swans. Houghton Mifflin, Boston, Massachusetts, USA.

Perrow, M. R., J. H. Schutten, J. R. Howes, T. Holzer, F. J. Madgwick, and A. J. D. Jowitt. 1997. Interaction between coot (Fulica atra) and submerged macrophytes: the role of birds in the restoration process. Hydrobiologia 342/343:241–255.

Perry, M. C., P. C. Osenton, and E. J. R. Lhones. 2004. Food habits of mute swans in Chesapeake Bay. Pages 31–36 in M. C. Perry, editor. Mute swans and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR-2004-0005, Reston, Virginia, USA.

Person, B. T., M. P. Herzog, and R. W. Ruess. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592.

Santamaria, L., and M. A. Rodriguez-gironés. 2002. Hiding from swans: optimal burial depth of sago pondweed tubers foraged by Bewick's Swans. Journal of Ecology 90:303–315.

Sherfy, M. H., and R. L. Kirkpatrik. 2003. Invertebrate response to snow goose herbivory on moist-soil vegetation. Wetlands 23:236–249.

Smith, T. J., and W. E. Odum. 1981. The effect of grazing by snow geese on coastal salt marshes. Ecology 62:98–106.

Tatu, K. S. 2006. An assessment of impacts of mute swans (Cygnus olor) on submerged aquatic vegetation (SAV) in Chesapeake Bay, Maryland. Dissertation, West Virginia University, Morgantown, USA.

Temple, S. A. 1992. Exotic birds: a growing problem with no easy solution. Auk 109:395–397.

Therres, G., and D. Brinker. 2004. Mute swan interaction with other birds in Chesapeake Bay. Pages 43–46 in M. C. Perry, editor. Mute swans and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR-2004-0005, Reston, Virginia, USA.

Willey, C. H., and B. F. Halla. 1972. Mute swans of Rhode Island. Rhode Island Department of Natural Resources Division of Fish and Wildlife, Wildlife Pamphlet 8, Wakefield, USA.

Associate Editor: Barker.