ASSESSING POTENTIAL ECOLOGICAL EFFECTS OF MUTE SWAN (*CYGNUS OLOR*) EXPANSION IN NORTHEASTERN NORTH AMERICA

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INTRODUCTION

Mute swan (*Cygnus olor*) management and proposed future management in North America have been controversial. Conservation controversies can benefit from an impartial and transparent evaluation of available scientific evidence, including its gaps and uncertainties (Redpath et al. 2013). Conservation practice is often guided by myth rather than evidence (Sutherland et al. 2004), or by evidence drawn from flawed studies (e.g., Allen et al. 2013). This paper reviews what we know of mute swan ecology relative to its potential effects in northeastern North America, to assess the scientific underpinnings of proposed management goals and methods.

In this review we draw extensively on ecological studies of mute swan in both its native and introduced ranges, in order to evaluate claims of this large aquatic herbivore’s impacts on aquatic vegetation (including food resources for other waterfowl), and its competitive or agonistic (aggressive) behavior toward other species (and potential displacement of nesting waterbirds). These claims have formed the basis of management plans in many U.S. states. We summarize relevant aspects of mute swan biology and ecology, including habitat use, seasonal flocking, territoriality, and diet. We also examine the larger context of aquatic vegetation dynamics, including the roles of a demanding and changeable physical environment, herbivory, and anthropogenic stressors in the maintenance or decline of these communities. To assess the potential effects of mute swans on natural communities and organisms of conservation concern, we rely as much as possible on robust experimental and observational studies. Where case studies or single observations are discussed, we identify them as such. We discuss potential interactions between mute swans and other expanding native and nonnative species, and touch on ecosystem processes that could be affected by swans. We outline possible effects of swans on humans, identify important unanswered questions, discuss factors that limit mute swan populations, and review the effectiveness of different management actions and potential barriers to successful management.

Hudsonia is not supporting or opposing mute swan management in general, or any particular management proposal or plan. We are examining the scientific evidence and analysis that are cited to support swan management in many states.

HISTORY

Mute swans are considered native to parts of north and central Eurasia, although a long history of semi-domestication has made distinctions between their natural and introduced range difficult (Scott 1972). Swans have played an important role in mythology and art around the world, and the “brilliant creatures” of W.B. Yeats continue to be valued for their beauty. They have also been harvested extensively for meat and skins. Historically, swans of all species (including mute swans) were hunted at any time of year, and sometimes rounded up and killed by the hundreds when flightless during molt. However, the mute swan is unique in its semi-domestication (i.e., with a history of being bred and raised in captivity but genetically indistinguishable from wild birds) from very early times. In England, mute swan ownership was a mark of social standing denoted by marking adult birds; any unmarked swans were (and still are) property of the Crown. Mute swan was prized for its meat, often serving as the centerpiece of a banquet, and also as an ornament on estates (Scott 1972). Populations in many European countries were very small or extirpated by the early 1900s. European populations have greatly increased in abundance since the 1930s (Scott 1972) and have both expanded in range and increased in abundance since the 1970s (Weiloch 1991), more than doubling between the late 1980s and early 2000s (Gayet et al. 2014). This growth may be due to some combination of the swan's protected status (in many countries dating from the early–mid-20th century), wetland eutrophication (increased fertility), warmer winters, the creation of new habitat, and increased winter food availability due to the intensification of agriculture and human handouts (Gayet et al. 2014). Mute swans have shown great plasticity in migration distance, location of breeding, molting, and wintering areas, territoriality, and use of food resources, which has apparently enabled them to expand into areas with warmer winters (where they tend to become less migratory) and into agricultural and urban landscapes (where they depend to a variable degree on crops and human handouts for winter food).

The eastern U.S. population probably originated from multiple introductions to four areas: Dutchess County, New York; the southern shore of Long Island, Suffolk County, New York; the eastern shore of New Jersey (Monmouth and Ocean counties); and Boston—during the first three decades of the twentieth century (Ciaranca et al. 1997; Teale 2011). The swans were originally imported from Europe to decorate estates; their wings were generally clipped to prohibit escape. They were first documented breeding in the wild in the 1920s in New York (Teale 2011) and in the 1940s-1960s in other eastern states (Ciaranca et al. 1997). The U.S. eastern seaboard population grew from approximately 6,000 in 1986 to 14,000 in 2002, then declined to 9,000 in 2011 due to management. Naturalized and expanding populations have also been established along the Great Lakes, in the Pacific Northwest, and in Australia, New Zealand, South Africa, and Japan (Ciaranca et al. 1997).

POPULATION IN THE NORTHEAST

Regional growth rates in the Atlantic Flyway between 1986 and 1999 ranged from 43% in New England (mostly in Massachusetts, Rhode Island, and Connecticut) to 62% in the upper Mid-Atlantic states (mostly in New York, New Jersey, and Pennsylvania) to 1271% in the Chesapeake Bay Region (Maryland and Virginia; Costanzo et al. 2015). At more local scales, mute swan populations may double every five years in the initial growth phase after establishment, but then population growth slows after 25-30 years due to density dependence (Ellis & Elphick 2007). Mute swans have been actively but not consistently managed (through egg addling and/ or culling or relocating adult birds) in several Atlantic Flyway states: Maryland, Delaware, Rhode Island, New York, and Vermont (State of Rhode Island 2006). Surveys in 2008 and 2011 recorded approximately 2,600-2,900 swans in New England (mostly in Rhode Island, Connecticut, and Massachusetts), 2,800-3,900 in New York and New Jersey, and approximately 3,000 in Ontario, mostly along the Lower Great Lakes (Meyer et al. 2012; Costanzo et al. 2015). Chesapeake Bay had over 4,400 swans in 1999 but management reduced survey results to approximately 300 by 2011 (Costanzo et al. 2015).

In the Northeast, mute swans occur at the highest densities along coastal and Great Lakes shorelines and estuaries, but are increasingly common inland in freshwater ponds, rivers, and wetlands (State of Rhode Island 2006; Swift et al. 2013; Costanzo et al. 2015), a trend also noted in Ontario (Meyer et al. 2012) and Sweden (Berglund et al. 1963). At some coastal locations in Rhode Island, Connecticut, New York, and adjacent areas, nesting mute swans may have reached the local carrying capacity (Ellis & Elphick 2007; Swift et al. 2013). Breeding Bird Atlas data show a substantial expansion in distribution inland in New York between 1985 and 2005 (Swift et al. 2013).

SEASONAL HABITAT USE, FLOCKING, AND TERRITORIALITY

Habitat requirements of mute swans are similar year-round, and ideally consist of open, shallow water (20-45 cm deep) with abundant aquatic macrophytes, especially submergent plants and macroalgae (also referred to as submerged aquatic vegetation [SAV]). They may be found in a variety of saline to freshwater, natural or constructed, estuaries, wetlands, rivers, lakes, and ponds that have these characteristics (Ciaranca et al. 1997), and they are more likely to be found near urban land cover (Weaver et al. 2012). Mute swans are either year-round residents or short-distance migrants, and their behavior and habitat use depend on swan age and breeding status as well as season and habitat condition. Understanding the (often complex) linked consequences of these factors is prerequisite for understanding the swans' potential effects on habitats and other species. Breeding territories and both summer and winter flocking sites may be in the same or adjacent areas, or be separated by dozens to hundreds of kilometers.

Breeding pairs establish territories in late winter or early spring. Territory size and spacing vary widely depending on habitat quality and swan density. The area of defended territory generally corresponds to the area the pair uses, and can vary from, e.g., 0.2 to 4.8 ha (based on two North American and several European studies; Ciaranca et al. 1997 [one hectare = 2.47 acres]). They also occasionally nest in colonies (nests spaced 10-30 m apart) on coastal islands (Scott 1972; Ciaranca et al. 1997). Territory size calculated as the spacing between nests varies even more: mean areas of 4.5, 500, and 2,000 ha in three sites with suitable habitat in their native range (Scott 1972); minimum areas of 0.8 and 1.9 ha in Rhode Island; and a mean area of 3.9 ha in Michigan (Ciaranca et al. 1997). Pairs often defend their territories, primarily by using threat displays to chase away other birds, but occasionally attacking with wings or bill. Males are generally more aggressive than females, and levels of aggression vary greatly by individual or pair. The pair will usually remain on the territory until food is depleted or water freezes.

Meanwhile, nonbreeding swans—including juveniles, first-year birds, and a large proportion of adults (e.g., 71% of adults were nonbreeders in one U.K. population; Watola et al. 2003)—congregate in flocks of up to hundreds of birds in areas with abundant food and open water. Molting occurs during summer, so flocks must have access to sufficient SAV during this flightless period. Juveniles generally leave their natal territory in September and join this flock. Flocks may remain in the same area, or move to different areas in late autumn. Mated pairs often leave their territories and join the winter flock in October-December, but they may remain on territories if there is sufficient food. Winter flocks are often more concentrated than summer flocks (Ciaranca et al. 1997). From 550 sightings of 131 banded mute swans in New York, most swans in the Long Island and Lake Ontario populations were sedentary year-round, but about half of Hudson River swans were sighted > 50 km away from their banding location; many moved south into New Jersey to avoid winter weather (Swift et al. 2013). GPS telemetry data from 13 additional swans supported this pattern: Long Island swans moved < 20 m along the coastline, whereas Hudson River swans migrated south to coastal New Jersey in one out of two winters (Swift et al. 2013). Swans banded in Rhode Island generally stayed within a stretch of coastline approximately 120 km long, although flocks were sometimes sighted in Long Island, New York. Most individual swans travelled less than 60 km. In this population, summer and winter flocks often congregated in different areas (Willey & Halla 1972).

DIET

In general, the diet of mute swans consists almost entirely of aquatic macrophytes (including the incidental consumption of attached invertebrates). Submergent aquatic vegetation (SAV), including both vascular plants and algae, is the most highly preferred food, and within this category mute swans generally do not strongly prefer one species over another (although at times preference for one or more species changes plant community composition; Berglund et al. 1963; Ciaranca et al. 1997; Gayet et al. 2011b). For example, Great Lakes mute swans (n = 132) most commonly consumed above-ground parts of pondweed spp. (mainly *Potamogeton zosteriformis*, *P. pusillus*, and *P. richardsonii*), common waterweed (*Elodea canadensis*), coontail (*Ceratophyllum demersum*), muskgrass *(Chara vulgaris)*, slender naiad (*Najas flexilis*), wild rice (*Zizania palustris*), and water-celery (*Vallisneria americana*); they ate roots, rhizomes, tubers, and seeds of these species less frequently, and invertebrates infrequently (Bailey et al. 2008). In mesohaline waters they may rely heavily on widgeon-grass (*Ruppia maritima*), eelgrass (*Zostera marina*), or sea lettuce (*Ulva lactuca*, an alga), among other species (O'Brien & Askins 1985; Allin & Husband 2003; Perry et al. 2004). Belowground plant parts were eaten more frequently in autumn, winter, and spring (Bailey et al. 2008). Significant plasticity in diet, especially during winter, has been recorded at different sites. In parts of the U.K., pastures and croplands are grazed during winter and spring, making up a significant portion of the diet (Wood et al. 2013b). Mute swans have been observed opportunistically consuming dying or decaying fish, earthworms, crustaceans, snails, frogs, tadpoles, and aquatic insect adults and larvae. They greatly benefit from bread and other human handouts; these can make up the bulk of the winter diet (Ciaranca et al. 1997). Flocks sometimes depend upon waste grain from mills, or refuse from fishing fleets (Scott 1972). At a reservoir in Poland, a mute swan flock was observed feeding primarily on zebra mussels (*Dreissena polymorpha)* after this introduced bivalve became extremely abundant. Winter and summer flocks increased greatly in size in the decade after zebra mussels became abundant (Wlodarczyk & Janiszewski 2014).

ECOLOGICAL CONTEXT: SAV AND HERBIVORY

To better understand the ecological role and potential ecological impacts of mute swans, it is helpful to locate the species within the context of its community. The beds of submergent aquatic vegetation (SAV) on which mute swans depend occur in brackish to saltwater marshes, estuaries, and bays as well as freshwater lakes, ponds, and rivers (Ciaranca et al. 1997). In all these contexts SAV provides habitat and food for a suite of macroinvertebrates, fish, and other organisms. SAV beds are often key nursery habitats for fish and shellfish, and key foraging grounds for waterfowl and other birds. Herbivorous, invertebrate-feeding, and fish-feeding waterfowl abundance varied with SAV cover in a freshwater lake in Sweden (Hansson et al. 2010).

Submergent aquatic vegetation (SAV) dynamics. Aquatic macrophytes include both annual and perennial species, with different tolerances for water salinity, depth, turbulence, and substrate, and different strategies for reproduction (seed dispersal and different types of vegetative reproduction). These communities are naturally dynamic systems, responding to their dynamic environment with alterations in plant community composition and cycles of decline and recovery. Responses vary by species and assemblage, even within the same water body, and are not well-understood (Patrick et al. 2017). As bottom sediments shift with storms or floods, or as water turbidity or currents change, SAV beds may disappear in one place and become established in another. The combination of fluctuating water levels, freezing, and ice breakup can destroy SAV beds (Berglund et al. 1963). Unvegetated substrates are then more prone to erosion by waves or currents, and these shifting sediments are difficult to colonize except by certain species. Calm backwaters allow the accumulation of fine sediments and development of dense SAV beds. In a study of many sites in Sweden over five years, negative changes in SAV were attributed to ice erosion, wave erosion, drying out, and shoreline displacement; positive changes due to colonization also occurred (Berglund et al. 1963).

Lakes—and in many cases rivers, estuaries, ponds, and their associated wetlands—can generally be described as existing in one of two stable states: one is a clear water state, dominated by SAV; the other is a turbid water state dominated by phytoplankton, floating-leaved or floating plants, or allochthonous inputs of organic matter. While either state can exist under a range of nutrient conditions, the latter (turbid state) generally occurs in response to nutrient additions, especially in nontidal water bodies. This is a “bottom-up” effect, as nutrient additions allow plankton to proliferate, creating turbid conditions. In the turbid water state, light availability for SAV is limited by the phytoplankton and sediment suspended in the water, and also by the periphyton (algae, etc.) growing on the macrophyte’s leaf surfaces. As an example, Tatu et al. (2007b) found that the most important variable in predicting Chesapeake Bay SAV decline was light penetration, along with water depth and salinity. SAV decline is a common effect of eutrophication in salt and fresh waters, and such effects tend to be exacerbated by warming associated with climate change (Short et al. 2016). “Top-down” effects can also alter the system, via different pathways. Fish control macroinvertebrates such as snails that graze on the periphyton; other fish consume zooplankton which control phytoplankton (Phillips et al. 2016). As an example, after phytoplankton-consuming zebra mussels invaded the Hudson River estuary, water clarity increased along with SAV and its associated fish and invertebrates, while phytoplankton, zooplankton, and the native bivalves and fish that depend on them declined (Strayer 2010).

SAV and herbivory. Aquatic herbivory is another top-down effect important in regulating the abundance and diversity of producers and consumers in aquatic systems. Median annual removal of freshwater and marine SAV biomass is 48-60% (compared to 4-8% annual removal of terrestrial plants by herbivory; Bakker et al. 2016a). Grazed vegetation may respond by compensatory growth, overcompensation (a common feature of terrestrial grasslands, where grazing promotes growth), or undercompensation (when depleted plant resources slow recovery, or the population is destroyed entirely). Meta-analysis of aquatic herbivory points to compensatory growth of SAV at moderate levels of herbivory, but undercompensation at higher levels (Wood et al. 2017).

Herbivores of aquatic vegetation include insects, mollusks, echinoderms, fish, birds, reptiles, and mammals. Overall, birds appear to have a weaker effect on SAV abundance than fish, echinoderms, or mollusks (Wood et al. 2017), which makes sense given their greater mobility and more facultative use of aquatic vegetation (Bakker et al. 2016a). In general, declines in SAV appear to be greater when the plant/s are native and the herbivore/s are nonnative (compared to other combinations) and when the species richness of herbivores is low (Wood et al. 2017). Large herbivores (>10 kg) that consume aquatic vegetation, including swans—as well as moose, elk, beavers, sea turtles, dugongs, manatees, and hippopotamuses—constitute a special case for several reasons. Large herbivores have a greater per capita impact; they tend to be more mobile so can graze vegetation down to a threshold level and then move elsewhere; and their plant preferences can have a large effect on SAV composition, either increasing or decreasing plant evenness (Bakker et al. 2016b).

SAV and waterfowl. Many waterfowl depend, to a greater or lesser extent, on SAV beds and the invertebrates and fish that inhabit them. Some species depend on these resources during the breeding season in the Northeast, such as pied-billed grebes, American black ducks, mallards, and Canada geese. During autumn, winter, and spring, large flocks of migrating and overwintering ducks, geese, and swans depend on the belowground parts of perennial aquatic plants (as well as seeds, invertebrates, and other foods). Many factors influence the effects of herbivorous waterfowl on aquatic plants, including the density of waterfowl at a site, the mass and dietary preferences of individual waterfowl species (Wood et al. 2012a), the growth strategies of the different plant species, the season during which herbivory takes place relative to the plant growth cycle, the underlying nutrient level of the aquatic habitat, the periphyton load on the aquatic plants, shading from overhanging deciduous trees, and water temperature (Wood et al. 2012b). For instance, in fishponds in France, SAV beds were grazed to disappearance only when initial cover was low, mute swans were abundant, and grazing occurred early in the season (Gayet 2012). However, the most obvious effects on cover occurred with late summer grazing, when plants had less compensatory ability (growth rate is highest in late spring; Gayet 2012). Vegetation either compensated or over-compensated for autumn consumption of pondweed tubers by migratory flocks of tundra swans (Nolet 2004). In contrast, early summer grazing of leaves and stems by waterfowl (mute swan, gadwall, mallard, and Eurasian coot) decreased sago pondweed (*Stuckenia pectinata*) tuber biomass in the autumn (Hidding et al. 2009; Gyemesi et al. 2011), resulting in time-lagged resource competition between summer and winter SAV herbivores.

Foraging theory predicts a "giving-up density" of a food resource below which foraging is too inefficient; this has been found for tundra swans in the Netherlands (Nolet et al. 2006) and mute swans in a shallow river in the U.K. (O'Hare et al. 2007), as well as for various other waterfowl (e.g., Sponberg & Lodge 2005). The actual giving-up density of aboveground or belowground biomass of SAV appears to vary according to herbivore, water depth, plant species, site, and other factors (Nolet et al. 2006, Hagy & Kaminski 2015), and sometimes waterfowl continue to forage in severely depleted areas (Tatu et al. 2007a; Hagy & Kaminski 2015). Nevertheless, the existence of such threshholds may limit overgrazing, as flocks tend to move when density is low enough. Giving-up densities may be higher for swans than for ducks (Gyemesi et al. 2012), although this needs to be tested on swans and ducks using the same sites. Given sites may be utilized to different degrees by migrating waterfowl in different years, depending on SAV density, water level, and ice cover, aiding recovery in underused years (LaMontagne et al. 2003; Nolet & Gyemesi 2013).

Decadal scale changes in SAV and waterfowl populations. Seagrasses and other SAV have increasingly suffered catastrophic declines in recent decades, driven by multiple stressors. These include increases in water temperature, sea level, and the frequency and intensity of storms; local and regional declines in water quality including loading of nutrients, sediments, and contaminants; invasive species; aquaculture and commercial shellfishing; hardened shorelines (e.g., riprap) and filling for development; and motorized watercraft use (Orth et al. 2006; Casey et al. 2014; Patrick et al. 2017). Excess nutrients and sediments are the most common causes of declines (Orth et al. 2006). Invasive species can have negative or positive effects on SAV. For instance, the nonnative water chestnut (*Trapa natans*) with its dense, floating leaves can shade out and replace beds of water-celery and other SAV in the Hudson River estuary (Hummel & Kiviat 2004). However, in Chesapeake Bay, abundance of the nonnative hydrilla (*Hydrilla verticillata*) is positively related to SAV bed recovery (Patrick et al. 2017).

Chesapeake Bay SAV suffered notorious declines between 1955 and 2006. During the same period, overwintering flocks of redheads moved from Chesapeake Bay to North Carolina, and the diet of Chesapeake redheads shifted from 99% to 67% SAV (Perry et al. 2007). Diet shifts also occurred in more omnivorous Chesapeake Bay ducks, with invertebrates making up a greater and SAV a lesser part of their diet compared to the 1950s. Perry et al. (2007) point out that in addition to food resources, winter duck abundance may be negatively affected by shoreline development, motorized watercraft use, and disease, among other factors. Some native geese and swans have experienced large population increases in the Atlantic flyway in recent decades (discussed in “Interactions with other Overabundant or Invasive Species,” below).

EFFECTS OF MUTE SWAN GRAZING ON SAV

Because of their large size, specialization on aquatic macrophytes, and feeding habitats, mute swans can have a large effect on SAV biomass in areas where they graze in high numbers. However, the effects of mute swans on SAV are not clear-cut, and may be overstated by relying on some studies with methodological problems, generalizing the results of case studies, or accepting authors’ inferences that are only loosely based on their results. For example, one study looked at the habitat use of five mute swans in Chesapeake Bay. They found that swans spent 47% of their time in SAV beds, 32% in open water, 13% at the shoreline, and 8% in uplands. From this they inferred an impact on SAV and recommended control (Sousa et al. 2008); this study was cited in the Atlantic Flyway Management Plan (Costanzo et al. 2015).

In projecting potential impacts of mute swan populations in northeastern North America, the most (and most often-cited) quantitative evidence comes from exclosure experiments in which SAV biomass (or cover, density, or height) was measured in areas where swans had access compared to areas where they were excluded. However, in reporting and summarizing the results of such studies, all studies tend to be treated equally, when in fact they vary greatly in the extent to which results can be generalized to other locations or time scales. Several frequently-cited sources on SAV impacts we propose should be de-emphasized for the following reasons: Cobb & Harlan (1980), Perry et al. (2004), and Swift et al. (2013) were not peer-reviewed, had very small sample sizes, and methods (except in Swift et al. 2013) were not described in enough detail to evaluate results. The remaining North American exclosure experiments also vary in their applicability. Region, habitat type, number of sites sampled (1-18), number of exclosure and control plot pairs per site (1-6), and the time period examined (1-4 growing seasons) are all critical factors in interpreting results. The patterns and intensity of grazing by free-ranging herbivores are beyond the control of the experimenter (Duncan 1992, p.174). Swans may or may not graze in the control plots, making an adequate sample size even more important.

Exclosures have been used for many years to study the effects of herbivory on vegetation (e.g., Daubenmire 1940). Exclosure area (6-25 m^2) and design varied among mute swan studies. They were constructed in shallow tidal and nontidal waters, and used corner posts with either wire or plastic mesh or strings forming the sides. The exclosure fence either extended down to water level to exclude waterfowl but not aquatic herbivores (Conover & Kania 1994, Tatu et al. 2007a), or was raised 0.5 m above water level (or had large enough mesh) to allow smaller waterfowl access to the swan exclosures (Gayet et al. 2011b; Stafford et al. 2012).

Some waterbirds and other animals smaller than mute swans (e.g., muskrat, Canada goose, ducks, snapping turtle, common carp) may be able to swim or dive under the exclosure sides, and graze within the exclosure, but some species or individuals might be reluctant to do so, thus confounding swan grazing with the grazing by other species. Although some papers reported observations of other species feeding within exclosures, the intensity of this grazing was not compared between exclosures and controls. If the exclosure reduced the frequency or intensity of use by these other herbivores, the effects of swan grazing would be overstated. Alternatively, other herbivores could increase their pressure on exclosed plots due to reduced competition (Duncan 1992, p.174). Also, herbivory effects may be different when herbivore species graze singly or in various combinations. Mesh exclosure sides will alter the microclimate within the exclosure by decreasing air movement and potentially raising air temperature, which could increase SAV biomass and productivity. Mesh sides, or even strings, could cause the deposition of airborne materials into the exclosure (see Daubenmire 1940), potentially increasing nutrient levels and benefitting SAV. Stakes or posts supporting the corners of an exclosure are likely to attract birds that perch on such exposed substrates (e.g., cormorants, herons, gulls, crows, red-winged blackbird), and bird excreta could have a fertilizing effect (or possibly an inhibitory effect) on plants within the exclosure. Most studies sampled biomass in the centers of exclosures to avoid this or other edge effects, but edge effects could influence SAV throughout the exclosure as a result of water movement and diffusion. We do not know if these effects occurred in the studies cited, but they were mostly not controlled for. Small actions (or their absence) could have large effects on SAV in small exclosures.

Examples of North American mute swan grazing studies.

At a single Rhode Island mesohaline coastal pond, with six pairs of exclosure and control plots and approximately 2.3-4.1 swans/ha, July and August (but not June) SAV biomass (*Ruppia maritima*, *Stuckenia pectinatus*, *Chara* sp. most abundant) was lower in grazed versus exclosure plots (Allin & Husband 2003). However, there was no cumulative decline over the four-year study period, and biomass varied from -95% to +17% in grazed plots (compared to exclosures) depending on the year. Swan effects on SAV biomass also varied according to the substrate and water depth, with greatest biomass reductions in shallow water and sandy (compared to silty or flooded marsh vegetation) substrate (Allin & Husband 2003).

In 12 Connecticut freshwater ponds, each with a single breeding pair of swans (0.07-1 swan/ha), and two pairs of control and exclosure plots in each pond, no difference in SAV (*Stuckenia* sp., *Nymphaea odorata*, *Elodea canadensis* most abundant) biomass was found after one or two growing seasons (Conover & Kania 1994); however, the study was conducted over five years (different ponds in each year) and the sample size precluded analysis of interannual variation.

At two Illinois freshwater wetlands with an estimated density of 0.1 swan/ha, and nine pairs of exclosure and control plots in each, there was no difference in aboveground SAV (dominated by *Myriophyllum spicatum*, with many other species) biomass at the end of the second growing season, but mean belowground biomass was 34% less in grazed plots than exclosures (Stafford et al. 2012). Two potential methodological problems may have influenced their results: Control plots were selected a posteriori with an element of subjectivity (“located randomly within 10 m of the exclosure where vegetation structure and composition were visibly similar”). In their statistical analysis, influence of site was not considered (the two sites were pooled).

At 18 sites in the mesohaline mid-Chesapeake Bay, with a mean density of approximately 3.6-4.2 swans/ha, and three pairs of exclosure and control plots per site, SAV (almost entirely *Ruppia maritima*) cover, density, and height decreased over two years. Cover decreased 41% in grazed plots vs. exclosures after one growing season and 79% (total) after two growing seasons. Sites with shallow water and flocks (vs. nesting pairs) experienced the greatest SAV reductions, in some cases a 100% reduction in cover. Flocks tended to use shallow areas, while nesting pairs often used deeper water areas (Tatu et al. 2007a).

Exclosure and comparative herbivory studies of mute swans in their native range can also be instructive, although an introduced species may behave and affect the ecosystem differently in its introduced range. Mute swan is different from many introduced species in that it has experienced population growth within its native range and expansion into adjacent or historically occupied areas in recent decades. Although it is considered native in the U.K., mute swan increased 59% between 1960 and 2000, leading to concerns about ecological impacts (O’Hare et al. 2007). In a shallow chalk river in the U.K. with very high swan densities (approximately 29 swans/ha) and unique water chemistry and vegetation (dominated by *Ranunculus penicillatus pseudofluitans*), grazed stretches (n = 3) of the river had 49% less aboveground biomass than ungrazed stretches (n = 3) in early summer (O’Hare et al. 2007); grazed and ungrazed reaches had similar environmental conditions. In addition, because the swans preferentially ate stem tips and leaves, the grazed plants had reduced flowering. In eastern France a form of aquaculture is practiced in which moderate-sized, shallow fishponds are periodically drained and cultivated; mute swans first nested in this region in the 1970s and the population grew to approximately 1,000 individuals over the following 30 years (Gayet et al. 2011b). An exclosure study conducted in 24 ponds (mean = 15.8 ha, most with nesting pairs and a mean density of 0.13 swans/ha, but also two flocking sites) over two growing seasons yielded conflicting results (Gayet et al. 2011b). SAV absence was predicted by grazing, swan length of stay, and their interaction, although total disappearance of vegetation cover only happened when initial cover was low. Grazing also modestly (10-18%) but significantly reduced cover, diversity, and evenness of plants. However, SAV biomass at the end of the second growing season was not affected by grazing or swan stay (Gayet et al. 2011b).

Results from these studies suggest that mute swan flocks can greatly reduce SAV cover or biomass under certain conditions in the short term (1-2 years); under other conditions there is no effect. Swan density over time at a particular site is critical in determining grazing effects; this was demonstrated in France, where higher swan days/ha predicted disappearance of SAV beds. Low densities of swans (1 swan/ha or less) do not appear to reduce aboveground SAV biomass in freshwater ponds and wetlands (Conover & Kania 1994; Stafford et al. 2012), but belowground biomass may be affected at these densities (Stafford et al. 2012). Higher densities of swans (approximately 2-4 swans/ha or greater) can greatly reduce or sometimes eliminate SAV cover or aboveground biomass in mesohaline wetlands (Allin & Husband 2003; Tatu et al. 2007a), although effects appear to be highly dependent on factors such as water depth, substrate, the presence of flocks vs. nesting pairs, and annual variation in weather or other factors. Nesting pairs may have no effect (Conover & Kania 1994) or a substantial effect on SAV cover (Tatu et al. 2007a; although significantly less than flocks). The most severe effects were found in Chesapeake Bay, which had much milder winters than the other sites; this site also had tidal action and the most monodominant submergent plant (*Ruppia maritima*), among other differences. However, in a model describing causes of SAV decline in the Chesapeake (using data from Tatu et al. 2007a), lower light penetration (a consequence of eutrophication) and higher water depth and salinity explained more of the variation than a larger swan population (Tatu et al. 2007b). Chesapeake Bay SAV had significant epiphyll growth (small organisms attached to plants), reducing light availability an additional 20-60% over water turbidity alone (Batiuk et al. 2000). Evidence suggests that the effects of herbivory on SAV become more detrimental as shading (due to eutrophication) increases, which could help explain differences in SAV responses to mute swan herbivory (Hidding et al. 2016). Also, different aquatic vascular plant and charophyte (stonewort, a group of large algae) species are likely to be affected differently by swan grazing (Mathiesson 1973, Sandsten & Klaassen 2008).

Importantly, longer-term effects of mute swan grazing have not been investigated. The longest-duration study, four years, did not show a cumulative decline at a single site. A five-year observational study of SAV across many bays in coastal Sweden found both negative and positive changes, and concluded that wave erosion and other sediment factors caused observed declines, rather than the large flocks of mute swans (Berglund et al. 1963). It would be helpful to find out the mean “giving-up density” of SAV for mute swan, the recovery time from that density, how species composition of the SAV beds affects swan use or impacts, and how winter herbivory by migrating or overwintering flocks of waterfowl affects SAV beds. In an exclosure experiment in Lake Erie during autumn migration, tundra swans, Canada geese, and ducks grazed sites down to threshold levels of above- and belowground biomass (which did not differ between areas grazed by ducks only versus all waterfowl) and then moved foraging activities to agricultural fields or deeper water (Badzinski et al. 2006). At times, swans remove all aboveground parts of aquatic macrophytes. Will such areas regenerate from underground organs or be recolonized, and what is the time frame for those processes? Belowground biomass was only addressed in one of these studies, although it is important for SAV recovery the following year. In an exclosure experiment in Argentina, constant grazing by modest numbers of black-necked swans and coots over one month reduced aboveground but increased belowground biomass (total biomass remained the same; Bortolus et al. 1998). In milder climates, swans are more likely to stay at the same site year-round, exacerbating the pressure on SAV. Short-distance migration or movements between wetlands may be more likely where winters are colder, possibly lessening the effect on SAV at any one site.

EFFECTS OF MUTE SWAN GRAZING ON OTHER WATERFOWL

Commensal feeding. Mute swans feed by dabbling, dipping, and upending while using their feet for paddling or raking the bottom. Plants are torn off, or less commonly uprooted (although some sources report substantial uprooting of plants). Mute swan grazing has been described as “exceedingly wasteful” (Gilham 1956), because a large proportion of torn or uprooted plant parts are uneaten. However, this extra plant material is used to feed cygnets (Gayet et al. 2016), and is also often eaten by other waterfowl. Foraging tundra and whooper swans were commonly (41-51%) attended by commensal associates, including Eurasian wigeon, pochard, mallard, and Eurasian coot in Sweden (Källander 2005). Foraging tundra swans in Canada were commonly attended by canvasback, redhead, gadwall, American wigeon, and lesser scaup, which competed for the closest position to the swan (Bailey & Batt 1974). In the only experimental study examining the benefits of commensal association with a swan, pochards foraging next to tundra swans doubled their food intake rate, while the swan’s intake rate was unaffected (Gyemesi et al. 2012). Mute swans may be attended by commensal feeding associates less often than these other swans (less than 3% of mute swans in the Swedish study were attended), perhaps due to less frequent foot paddling and uprooting of vegetation while foraging (Källander 2005). However, mute swan feeding techniques may change seasonally with changes in diet (Bailey et al. 2008), and mute swan-other waterfowl aggregation values have been found to change throughout the breeding season (Gayet et al. 2016). Possibly in some locations or seasons, mute swans significantly benefit other waterfowl via commensal foraging. Fragmentation or uprooting of SAV also creates propagules for colonizing or recolonizing other habitats.

Niche partitioning. In a feeding behavior study in a Connecticut estuary, mute swan feeding behavior (more neck plunging) and location (distance from shore) differed significantly from that of other herbivorous waterfowl during autumn and spring. These differences, along with a lack of aggressive interactions, implied a lack of competition for food either due to niche partitioning (dividing up the resources) or a lack of food limitation (O’Brien & Askins 1985).

Food limitation. Mute swan, as a large and predominantly herbivorous species, consumes a substantial quantity of vegetation (and may pull up more than it consumes, as described above). The amount of vegetation (wet weight) eaten by captive adult mute swans averaged 3.7-4.0 kg/day (during molting in Sweden; Mathiasson 1973); and 3.8 kg/day (in Rhode Island; Ciaranca et al. 1997). Other waterfowl that consume SAV during migration or over winter in the Northeast include tundra swan, canvasback, redhead, gadwall, and others (Bailey et al. 2008; Craves & Susko 2010). Migratory and winter flocks are often large, and generally consume seeds and belowground parts of SAV. There has been substantial speculation, often stated as fact, that the consumption of SAV by mute swans leads to food limitation for other waterfowl that depend on this vegetation (e.g., Costanzo et al. 2015). Research to date indicates that 1) Widespread SAV decline at a site may cause declines in numbers and/or diet shifts in some species of waterfowl overwintering at that site (Perry et al. 2007); 2) At some sites, and under certain conditions, mute swans may cause declines in SAV cover or biomass within one or two growing seasons (Allin & Husband 2003; Tatu et al. 2007a; Stafford et al. 2012); and 3) In some SAV species, summer grazing of aboveground vegetation can reduce belowground biomass in autumn (e.g., Gyemesi et al. 2011). Summer grazing by mute swans therefore has at least the potential to diminish SAV resources enough to affect other waterfowl. Herbivory can affect macroinvertebrate abundance as well. O'Hare et al. (2007) estimated that with the mass of SAV consumed daily by a mute swan, incidental consumption of invertebrates was approximately equal to the invertebrate mass consumed daily by a trout. However, those submergent aquatic species least palatable to waterfowl (such as *Elodea*) appear to support a higher mass and diversity of invertebrates than preferred food plants (Krull 1970). In any case, no observational or experimental evidence to date has found that grazing by mute swans results in food limitation for any other species. The question might be explored by comparing body condition of overwintering waterfowl in areas with and without heavy mute swan summer grazing pressure. Finally, it is important to emphasize that in highly mobile species (such as birds) that depend on a patchy, shifting resource (such as SAV), conditions at one or a few sites are insufficient to understand the status of the species and resources overall.

EFFECTS OF TERRITORIAL AGONISTIC BEHAVIOR ON OTHER WATERFOWL

Mute swans may actively defend their territories, at any time during the year, against other mute swans, other waterfowl, other waterbirds, mammalian predators, other mammals, humans, and even inanimate objects. Most agonistic behavior is expressed through threat displays, and most is directed toward other mute swans. A number of single observations document the occurrence of overtly aggressive behavior toward other species, such as chasing, wing-beating, and biting, and these examples often dominate the discussion (Kania & Smith 1986, personal communications cited in Allin et al. 1987 and Ciaranca 1997). Observations by Stone and Marsters (1970) are frequently cited as evidence of mute swans killing other waterfowl, although these were captive birds at high densities in confined conditions. Unpublished data cited in VDGIF (2012) indicate killing of mallard ducklings and Canada goose goslings. These sources document the presence but not the prevalence of such behavior. In most quantitative behavioral studies or other sizeable studies where such behavior was noted, overtly aggressive interactions were uncommon. In 36 freshwater ponds with breeding mute swan territories in France, aggressive interactions occurred at a rate of 0.11/h (Gayet et al. 2011a). In a large, standardized census across the U.K., only 2% of census forms reported aggression toward other birds (Eltringham 1963). In a seven-year study of nesting success (3-10 nests/year), no "serious attacks on other waterfowl" were observed (Reese 1975). During 375 short behavioral observation periods of mute swan and ducks in a Connecticut estuary during autumn and spring, no aggressive encounters were recorded (O'Brien & Askins 1985). During 144 h of observation in the Chesapeake Bay during spring and summer, at all times of day, the only interspecific agonistic interactions observed were chasing away a great blue heron, and hissing at humans (Tatu 2006). Higher levels of interspecific agonistic behavior were observed in New York and Connecticut studies. During 26 h (54 observation periods at 33 locations in NY), 39 chases or attacks were made: most against Canada goose and a few against mallard and egret (a rate of 1.5/h; Swift et al. 2013). These encounters rarely made the other bird leave the waterbody. At 15 freshwater ponds in Connecticut, over 6 years and with a total of 800 hours of behavioral observations on 15 male and 15 female swans, a total of 460 agonistic interactions with other species was observed, including 174 with humans (but this total included threat displays of raised wings). Male swans had a rate of agonistic interactions of 0.79/h and females 0.35/h (Conover & Kania 1994).

Rate of agonistic behavior is less important than knowing whether swans exclude other birds from their territories, discourage or actively disrupt nesting attempts by other birds, or deny other birds access to food or nesting areas. In shallow fishponds in France, other waterfowl were actually more likely to be found in ponds that had a nesting pair of swans, so there was no evidence of exclusion at the among-pond level (Gayet et al. 2011a). At the within-pond level in this system, a spatial point pattern analysis indicated that swans and other waterbirds were located in the same general areas within ponds; swans did not create deserted areas around their nests, but centers of waterbird activity were offset from nests, indicating some interaction or different microhabitat preference (Gayet et al. 2016). In freshwater ponds in Connecticut, there was no difference in locations of other waterfowl relative to swans versus a random point in the pond (Conover & Kania 1994). In the large U.K. census, "Many reports were received of ducks nesting peacefully and successfully within a few feet of a swan's nest" (Eltringham 1963). With the exception of Gayet et al. (2011a), studies such as these cannot estimate any displacement or exclusion of waterfowl or their nesting attempts from the general areas used by swans (e.g., waterfowl that saw swans on a pond and kept flying to a pond without swans), but they do indicate that where mute swans and other waterfowl coexist during the breeding season, there is little evidence of exclusion or nest disruption.

On the other hand, several single observations support at least the possibility of exclusion of other nesting or feeding waterfowl. In three cases a mute swan pair prevented nesting or interfered with nesting Canada geese, and in one case a swan pair caused a pair of mallards to desert their nest twice in one season (Kania & Smith 1986; Ciaranca 1990). On two occasions flocks of Canada geese were chased from feeding areas by a pair of swans (Ciaranca 1990). In a six-year study of mute swans in Rhode Island, other waterfowl sometimes nested within a few meters of a swan nest, but only on large ponds with greater numbers of waterfowl; Willey and Halla (1972) suggested that swans may exclude breeding waterfowl from small ponds. They also suggested that swans could have a larger effect on nesting waterfowl in freshwater sites than coastal marsh sites because comparatively few waterfowl nest in coastal marshes. However, in 15 freshwater ponds with nesting mute swans in Connecticut (2-30 ha), nesting occurred by mallards at 12 sites, by Canada goose at 7 sites, and by American black duck at one site. Over the 6-year study, the authors observed no nesting failures caused by swans, despite the relatively high rates of threat displays and other interspecific agonistic interactions (Conover & Kania 1994). Breeding season censuses of waterfowl in years before and after swans establish territories could help investigate the displacement question. Measuring stress hormones or other condition indicators, and nest productivity, of other birds nesting in the vicinity of mute swans would help determine whether these species were stressed by swan presence even if they did not leave the pond or abandon the nest.

EFFECTS ON OTHER SPECIES OF CONSERVATION CONCERN

Trumpeter swan was historically native to eastern North America, but the population was extirpated over 200 years ago. In the 1980s, a reintroduction program was started in Ontario, and the first records of breeding trumpeter swans in New York occurred in 1996 (most likely from escaped captive birds; Carroll & Swift 2000). Over 1,000 trumpeters were counted in Ontario in 2015 (Lumsden 2016). The Ontario population of trumpeters overwinters in ice-free open water areas from Lake Ontario south and east across parts of New York and the mid-Atlantic states, where the swans consume aquatic vegetation and human handouts (Lumsden 2013). The Mississippi and Atlantic Flyways flocks have increased 23.5% annually from 1980–2015 to a total of over 26,000 birds in 2015 (USFWS 2017a), but they are still uncommon in the Northeast in winter and listed as S1 (rare) by the New York Natural Heritage Program for breeding. As populations of both species expand, mute swan may compete with trumpeter swan for nesting territories and food resources (potentially in both the breeding and nonbreeding seasons). Trumpeter swans consume leaves and stems of submerged aquatic macrophytes as do mute swans, but they also rely much more heavily on tubers and other belowground parts of aquatic plants, as well as emergent parts and seeds of wetland plants (Scott 1972). Where trumpeter and mute swans are now competing for nesting territories in Ontario, there is some evidence that trumpeters may be more aggressive and can drive mute swans away from nest sites (Lumsden 2016). In three instances, trumpeter pairs attacked and evicted mute pairs from a nesting territory, and in two instances a male trumpeter attacked a male mute and won the encounter. At a park where both species were competing for human handouts in winter and spring, trumpeters pecked mutes 22 to 55 times more often than the reverse (Lumsden 2016).

Tundra swan, also native to North America, breeds in the arctic and migrates and overwinters in large flocks. The eastern population of tundra swans averaged 2% annual growth between 2008 and 2017 (USFWS 2017b). Most of this population overwinters in North Carolina and the Chesapeake Bay (Wilkins et al. 2010). Here their diet includes leaves and underground parts of SAV, grasses and sedges, and a substantial component of mollusks (Scott 1972). Tundra swans regularly migrate through New York and surrounding states, and a few individuals or groups overwinter in the Northeast, at least in some years. The potential exists for mute swan summer grazing to reduce SAV resources at migratory stopover sites for tundra swan and other herbivorous or omnivorous waterfowl, although this would depend on total SAV production and consumption at such sites, for which we have no estimates. Also, the dietary breadth of tundra swan and other omnivores may lessen any competition for SAV.

Two sizeable nesting colonies of black skimmer (Special Concern in New York), least tern, and common tern (both Threatened in New York) in Maryland were abandoned due to use by large flocks of molting mute swans (Therres & Brinker 2004). These colonies, located on small sandbar or oyster shell islands, supported between two and 247 pairs of nesting least terns in 1985-87, and one of them supported 13 pairs of nesting black skimmers in 1985. In subsequent years, large mute swan flocks congregated on these islands to molt—which coincided with the nesting season for terns and skimmers. Although the seabirds nested, no eggs or surviving young were documented, probably due to extensive trampling by the swans. The colonies were abandoned by 1993. After the size of the mute swan flock was reduced (from about 600 to about 100 birds), the seabirds began nesting again, at much lower numbers than previously (Therres & Brinker 2004).

Black terns have experienced significant regional declines since the 1960s (Matteson et al. 2012); causes are thought to be low adult and juvenile survival related to wetland loss (Shuford 1999), wetland degradation, and possibly mortality during migration or on their South American wintering grounds (Matteson et al. 2012). Decline and abandonment of one nesting area along Lake Ontario in New York was noted around 2001 (from 16-30 pairs in 1991-1998 to none in 2004-2010). Mute swans began nesting in the same general area in the mid-1990s. As these species nest in similar habitats, there is potential for a negative effect of swan presence on black tern nesting success (Swift et al. 2013), but no connection has been found.

Other species of regional, state, or national conservation concern occur in the tidal and freshwater wetlands favored by mute swans (Kiviat & Stevens 2001), but since most of these species are neither consumed by mute swan nor competitors for food it is unlikely the swans would pose any threat. If SAV beds decline in quality or extent, submergent plants of conservation concern, such as spiny coontail (*Ceratophyllum echinatum*), American waterwort (*Elatine americana*), and Hudson River water-nymph (*Najas muenscheri*); the fish species that use submergent plant beds as nursery areas; fishes and turtles that forage in the beds as juveniles or adults; and other organisms dependent on SAV could be affected, but we still do not know whether mute swan grazing can cause such declines.

INTERACTIONS WITH OTHER OVERABUNDANT OR INVASIVE SPECIES

As mute swan expands its range into aquatic habitats of northeastern North America, it is important to remember that it is only one of many recently arrived or expanded species in the region. A few of these that are abundant and influential enough in aquatic habitats to be considered ecosystem engineers (along with mute swan) are discussed here. We know some of the effects these species have on natural communities and ecosystem processes, but almost nothing about how they interact with or influence each other.

Canada goose (*Branta canadensis*) is a species native to eastern North America, but prior to the 1940s only the migratory population occurred in this region, and it was present only in the non-breeding season. Introductions of genetically and behaviorally distinct nonmigratory populations from the Midwest resulted in a large Atlantic flyway population of approximately 1.1 million individuals by 2011 (AFC 2011). This population may be contributing to the decline of the migratory population. The potential impacts on humans and nature are similar for Canada goose and mute swan, as they are both large, herbivorous waterfowl that use similar habitats and congregate in large flocks. Stated conflicts between Canada geese and humans include property damage due to feces and grazing, disease transmission (including coliform bacteria) to humans and livestock, aircraft collisions, aggressive behavior toward humans, traffic hazards, and crop damage (AFC 2011). Potential ecological impacts of a large Canada goose population include sediment and nutrient additions in wetlands and waterbodies, lower dissolved oxygen in water (AFC 2011), declines in wild rice and overall wetland plant diversity due to grazing, and impediments to wetland restoration projects, also due to grazing (Swarth and Kiviat 2009). However, the threats posed by Canada geese in management discussions are offset by their perceived positive values, stemming from their current and historical use as a gamebird. (The Atlantic Flyway management plan for Canada goose has a “Positive values and use” section that is absent in the mute swan plan.) Their gamebird status has also allowed management via changes in hunting seasons and bag limits, and even capture and processing of geese in problem areas for donation to food bank programs. Canada goose and mute swan may be in competition for SAV and nesting sites to some extent, although Canada goose depends more on terrestrial grazing in the northeastern states. Mute swans have more frequent agonistic interactions with Canada geese than with other species (Conover & Kania 1994; Swift et al. 2013).

The Eurasian zebra mussel occurs at high densities in the Great Lakes and Hudson River, and is rapidly expanding in distribution. Because this bivalve can have a profound effect on water clarity and aquatic macrophyte beds, and has been used as a primary food source by mute swans, there are interesting implications for both top-down and bottom-up interactions among zebra mussels, SAV, mute swans, and other consumers, which have been wholly unexplored.

The Old World subspecies of common reed (*Phragmites australis australis*) is often a major component of wetland or shoreline habitats used by mute swan in both North America and Europe. It is not a food plant for mute swan, but can be an important part of nesting habitat. Nests are constructed of emergent vegetation, including reed, and are sometimes built within a stand of emergent vegetation (Ciaranca et al. 1997). It is unknown how reed presence or reed management during wetland restoration projects affects mute swan abundance or nesting. Similarly, mute swan use or avoidance of abundant nonnative aquatic plants, such as water chestnut, has not been studied.

Despite the importance of SAV to food webs, dense SAV in freshwater ponds and lakes is often considered a nuisance by lowering “recreational and aesthetic” values (State of Connecticut 2014), or an ecological problem when introduced plants—including certain watermilfoil species (*Myriophyllum* spp.) and curly-leaved pondweed (*Potamogeton crispus*)—outcompete native species (Hussner et al. 2017). Control options for nuisance aquatic vegetation include chemical applications, mechanical removal, and the introduction of sterile grass carp (*Ctenopharyngodon idella*), among others (State of Connecticut 2014). Some nonnative, generalist herbivores have been effective at controlling nonnative invasive aquatic plants in other parts of the world (Hussner et al. 2017); potential for this has not been investigated for mute swan. Only one study in North America has examined mute swan diet in detail (Bailey et al. 2008).

EFFECTS ON ECOSYSTEM PROCESSES

Although ecosystem-level effects of mute swans have not been studied, as a large, aquatic herbivore this species has the potential to profoundly change ecosystem processes. Sustained grazing by large herbivores may increase the nitrogen content of aquatic plants, improving forage quality for all herbivores. Depending on density, large herbivores can increase or decrease the productivity of SAV beds, affecting carbon and nitrogen cycling (Bakker et al. 2016b). Swans are unlikely to significantly increase nitrogen in riverine or coastal systems (Berglund et al. 1963; O’Hare et al. 2007), or habitats which already experience large anthropogenic inputs. They can create turbid conditions, decrease sediment stability, or alter microbial processes by mobilizing sediment. Tundra swan has been found to reduce methane emissions: as it forages for sago pondweed, the bioturbation decreases methane production through direct and indirect means (Bodelier et al. 2006). Large aquatic herbivores are often agents of long-distance dispersal for aquatic plants and small animals. Large-scale movements of herbivores can create cycles of aquatic ecosystem collapse and recovery, or sometimes collapse with no recovery. Overall, large aquatic herbivores have suffered precipitous global declines in the last two centuries, with unknown consequences for these large-scale patterns (Bakker et al. 2016b).

SUMMARY OF POTENTIAL EFFECTS

Ecological effects. Mute swan is a highly adaptable species – it has expanded greatly in recent decades, both in Europe and in North America, with the potential for continued expansion in both distribution and density. Native North American swans, although in general less adaptable, are also rapidly expanding in distribution and abundance, and will likely become competitors for breeding (trumpeter) and migratory stopover and overwintering resources (trumpeter and tundra) in the Northeast. Resident Canada geese have also dramatically increased in density, and may be competing with mute swans for food or nest sites. Mute swans are territorial, and warn off other mute swans and other species with threatening postures and chasing. They do not routinely attack or kill other species, although they occasionally do this in defense of their nesting territory; most attacks in the U.S. are directed against Canada geese. They do not routinely exclude other foraging or nesting waterfowl or other waterbirds from their territories, although there are examples of this occurring. Waterbirds—including rare least tern and black skimmer—that nest on small, sandbar islands have locally suffered nest loss and abandoned nesting colonies due to summer flocks of mute swans. Other than isolated accounts (for mallards and Canada geese), there is no evidence to support significant nesting disruption of marsh-nesting birds (including black terns) by mute swans.

Exclosure experiments demonstrate mute swans' ability to reduce aboveground biomass of SAV, sometimes drastically, in estuarine aquatic habitats—over one or two years—when swans occur in flocks or sometimes pairs. In freshwater habitats, either no effect or smaller SAV reductions have been measured. (However, many exclosure studies have methodological flaws because herbivores other than mute swans are also excluded, and the abiotic effects of exclosures on the aerial and aquatic environments are not controlled.) It may be that summer swan grazing reduces overall SAV resources for migrating or overwintering waterfowl but this has not been demonstrated. SAV is adapted to dynamic environmental conditions and high natural levels of herbivory. With a patchy, shifting resource (such as SAV) and highly mobile consumers (such as swans and other waterfowl), questions of resource use must be addressed at larger spatial and temporal scales. In climates where mute swans are resident year-round, they are likely to have a greater impact on SAV. In the Northeast, winters cold enough for persistent ice cover result in starvation or short-distance migration for many mute swans, potentially lessening their effect on SAV. Mute swan shows significant dietary overlap with some other waterfowl. We do not know how much niche partitioning occurs between foraging swans and other herbivores during summer or winter, or whether other waterfowl benefit commensally from associating with foraging mute swans; both have been suggested based on research results. SAV is stressed by nutrient additions (eutrophication), more frequent storms, saltwater incursions, dredging, use of motorized watercraft, hardened shorelines, and other interrelated stressors, which may exacerbate the effects of herbivory. Considering the large shifts underway in climate, other abundant nonnative species (such as water chestnut, zebra mussel), and land use and wastewater impacts of humans, "… it probably will make sense to manage alien species and other stressors as a group of closely linked problems, rather than as separate problems" (Strayer 2010).

Effects on humans. Ecological considerations aside, most management actions are taken when an invasive species directly affects humans. Mute swan territorial defense directed against humans can prevent the use of shores and waterways for recreation. This has led to complaints in many counties in New York (NYSDEC 2017). Mute swan attacks on children, adults, elderly adults, and dogs, as well as fatal attacks on domestic waterfowl, have been reported in Rhode Island and Connecticut (State of Rhode Island 2006). In one instance, a man drowned when his boat was overturned in a mute swan attack ("Who, What, Why: How Dangerous Are Swans?" 4/17/2012; http://www.bbc.com/news/magazine-17736292; Accessed 9/21/2017). Farmers have reported mute swan damage to cranberry bogs in New Jersey and Massachusetts (State of Rhode Island 2006). In Europe, mute swans sometimes graze croplands or pastures in winter or spring, resulting in economic losses (Wood et al. 2013a). Because of their large size, mute swans pose an aviation hazard in the event of collision with an aircraft; three such collisions have been reported from JFK Airport in New York despite active management of swans on the airport property (NYSDEC 2017). Swans (as well as geese) can raise fecal coliform levels in waterbodies where they congregate in large flocks (Hussong et al. 1979). Mute swans are possible vectors for avian influenza in North America (along with other wild birds), although the high prevalence of H5N1 antibodies in mute swans probably means the chance of spreading "bird flu" to poultry is low (Kistler et al. 2015).

MANAGEMENT CONSIDERATIONS

Unanswered questions. Despite research done thus far, important questions remain about the effects of mute swan on the habitats and species where they are currently established, and the potential effects of mute swan expansion. Longer-term and larger-scale research into regional SAV dynamics and mute swan herbivory is needed to assess potential impacts in the Northeast. Specific research directions that could help clarify herbivory effects include assessing the giving-up density of SAV for mute swan grazing; exploring factors that influence SAV recovery; measuring belowground biomass, and incorporating analysis of other stressors such as nutrient levels in herbivory studies; gathering more detailed information on mute swan diet in different habitats; and investigating species-specific effects of herbivory on different plants (including nonnative, invasive species and species of conservation concern). We do not know whether mute swan grazing limits food resources for migrating or overwintering waterfowl, but this question could be addressed, at least for overwintering flocks, by comparing habitat use and body condition in areas with and without heavy mute swan summer grazing pressure. Long-term bird count data (e.g., Mid-winter Waterfowl Inventory, Christmas Bird Count, and annual counts at specific sites [e.g., McKinney et al. 2015] or focusing on single species) could also be assessed for northeastern sites at or near mute swan population carrying capacity. What other factors affect waterfowl flocks in the nonbreeding season? Most waterfowl are considered gamebirds and can be legally hunted during specific times in the autumn or winter (determined by state). Declines in scoters and long-tailed duck in Chesapeake Bay may be related to a lack of sanctuaries (especially open water sanctuaries) where diving ducks are protected from hunting and other recreational activity (Perry et al. 2007). Studies of foraging behavior and diet could determine how well swans and other waterfowl partition resources, and whether other waterfowl benefit from feeding near swans. Do mute swan nesting pairs or flocks limit nesting opportunities or reproductive output of other waterfowl or waterbirds? Species-specific studies of nesting success in relation to mute swan presence and other factors (including habitat quality and nest predators) may best address this question. Annual survey data may also be informative (e.g., Waterfowl Breeding Population and Habitat Survey, North American Breeding Bird Survey, and state Breeding Bird Atlases). Abundance estimates do not address nesting success, but assessment of post-breeding population sizes may in many cases serve as a time-lagged measure of breeding success (Rönkä et al. 2011).

What are the factors controlling population increases and carrying capacity of different habitats in the Northeast? Rates of expansion and natural population controls differ by area (Ciaranca et al. 1997). Regional growth rates in the absence of substantial management were highest in the Southeast, intermediate in the mid-Atlantic, and lowest (although still over 3% annually) in New England (Costanzo et al. 2015), although this variation may be partly caused by density dependent population regulation in northern areas with a longer history of mute swan residence (Ellis & Elphick 2007). In Finland, where mute swan was introduced in the 1930s, the number of fledglings produced per pair of swans decreased as the density of nesting pairs increased (Nummi & Saari 2003). Winter starvation is a primary cause of mortality, as is cygnet exposure to cold, rainy weather in spring (Ciaranca et al. 1997). Mute swan mortality is reputedly higher in colder climates; two studies found decreased annual or lifetime reproduction with more severe winter weather (Birkhead et al. 1983; Bacon & Andersen-Herild 1989). Several diseases cause significant mute swan mortality in some populations, including *Clostridium botulinum*, *Aspergillus*, and *Sphaeridiotrema globulus* (Ciaranca et al. 1997), and it would be helpful to know their effects in the Northeast. Rates of mortality from predators (mainly affecting eggs and cygnets), nest failures due to flooding, and collisions with overhead wires or structures (Willey & Halla 1972; Ciaranca et al. 1997) are likely to vary regionally as well. How will competition with expanding populations of resident Canada geese and nesting trumpeter swans affect mute swan populations?

Exclosure methodology is a key element in the scientific evidence underpinning the conclusions that mute swan populations require management. We have identified several potential problems with exclosure techniques used to examine mute swan effects on SAV. Grazing by other herbivores is likely affected within exclosures, regardless of exclosure design. Mesh sides may alter the microclimate within exclosures enough to affect SAV growth; and nutrients could be enriched within exclosures by perching birds or deposition of airborne materials. If present, most of these effects would tend to magnify differences between grazed areas and exclosures, overstating the effects of swan herbivory on SAV.

Barriers to management success. Mute swan populations have been managed using lethal control (culling adult birds via shooting or euthanasia) or “non-lethal” nest destruction, often accomplished by addling (oiling or shaking) eggs, which kills the developing embryos. Population modeling can help determine the efficacy of any proposed management action. Models have shown that nest destruction alone is often insufficient for achieving large population reductions or maintaining populations at a target level (Ellis & Elphick 2007; Wood et al. 2013b). Immigration from nearby, unmanaged areas may more than offset local population reductions. As an empirical example, Rhode Island addled eggs in approximately 80% of nests over a 26-year period, but immigration from neighboring states contributed to a substantial population growth rate during that time (State of Rhode Island 2006). Several northeastern states and Canada do not have management programs and could be sources of emigrants to states with ongoing management. Additionally, populations in some coastal habitats of New York, Connecticut, and Rhode Island (and possibly elsewhere) have become more stable and reproductive rates may be density dependent. Wherever this is the case, removing nests or individuals will tend to increase reproductive rates, necessitating a greater control effort (Ellis & Elphick 2007). Culling adult birds is predicted to be the most efficient control measure, and achieving the desired population reduction over a shorter time period (compared to a longer time period) would necessitate killing far fewer total birds (Ellis & Elphick 2007). However, whichever methods are used, control efforts aimed at long-established populations are unlikely to be successful without an intensive, sustained effort that for some agencies may be impossible due to limited personnel or financial resources.

Another facet of the problem is whether mute swan population reductions, if realized, will have the desired beneficial outcomes. Direct conflicts between territorial swans and humans should decline in proportion to swan numbers. For problems caused by resident Canada geese as well as mute swans, such as fecal coliform contamination and aviation hazards, we do not know what effect reduction of either species would have on total hazard levels without knowing whether these two species affect each other's population sizes, and how their bacterial outputs differ. For protection of rare waterbird nesting habitat, swan presence and density in the habitats used by those species (e.g., sandbar islands) are more important than the regional swan population size. The protection of SAV beds and maintenance of the waterfowl and other species that depend on them is a much more complicated issue, as touched on in the "Ecological Context" section above. Seasonal SAV biomass reductions can be caused by mute swan grazing, but relationships to SAV declines (of more than two years) or any measure of waterfowl exclusion or decreased reproduction, fitness, or survival have not been identified. On the other hand, known threats to long-term SAV survival and health are numerous and include nutrient and sediment inputs (e.g., from urban and residential wastewater, agricultural practices), shellfish harvesting, and motorized watercraft, in addition to invasive plant and animal species. Conservation and restoration of SAV depends foremost on achieving improvements in water quality and land use practices at the watershed level that result in decreased nutrient and sediment inputs (Orth et al. 2006). Maintaining naturally vegetated riparian areas, preserving wetlands, managing agricultural runoff, improving urban stormwater management, and updating septic and sewer systems are a few of the measures crucial for protecting estuaries, rivers, and lakes from eutrophication (Carpenter et al. 1998; WRI 2009), and policies promoting such measures may be of greater value to SAV health than management of mute swans.

In conclusion, our analysis of the scientific literature on mute swan ecology and environmental impacts indicates that some of the negative impacts imputed to mute swans are unsubstantiated or anecdotal, whereas others may be of management concern. There are methodological problems, insufficient hard data, and a lack of distinction between short-lived and long-term impacts associated with some of the research that has been used to justify control programs. There are also legitimate questions as to the efficacy of control measures practiced or proposed, and the capability of agencies to mount efforts that are intensive enough, cover large enough (e.g., interstate) regions, and can be sustained long enough to accomplish goals of population reduction.

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