SEASONAL BELOWGROUND HERBIVORY AND A DENSITY REFUGE FROM WATERFOWL HERBIVORY FOR *VALLISNERIA AMERICANA*

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Abstract. Studies of aquatic food webs rarely address the role of migratory waterfowl, even though they are ubiquitous and many are omnivorous. Several species of waterfowl consume belowground plant tubers during winter, yet the impact of such herbivory on future plant abundance is mostly unknown. To test the impact of wintering waterfowl on submerged vegetation, we installed waterfowl exclosures ($N = 5$) and reference plots ($N = 5$) open to grazing in Lake Mattamuskeet, North Carolina, USA, where *Vallisneria americana* (water celery, or tapegrass) dominated the plant community. Over the three-year study period, we sampled above- and belowground plant standing stock every 2–3 mo. Reference plots had a lower density (number per square meter) of *Vallisneria* tubers than ungrazed exclosures (repeated-measures ANOVA treatment $P = 0.038$, time × treatment $P = 0.025$). Percentage loss of tubers in reference plots was positively related to the density of tubers at the onset of winter ($R^2 = 0.294$, $P = 0.026$). Despite significant reduction of tubers during winter, no detectable carryover effects of waterfowl exclosure on *Vallisneria* aboveground biomass occurred in subsequent growing seasons (rmANOVA treatment $P = 0.342$, time × treatment $P = 0.539$). Our study detected a threshold tuber density below which waterfowl herbivory on *Vallisneria* did not occur. Therefore, our results suggest that limits on waterfowl foraging efficiency provide a refuge for aquatic plants subject to intense, seasonal predation.

Key words: Canvasbacks; herbivory; Mattamuskeet National Wildlife Refuge; Najas guadalupensis; *North Carolina; tubers; Tundra Swans;* Vallisneria americana; *waterfowl; wild celery; wintering habitat.*

INTRODUCTION

Herbivory on vascular plants and macroalgae is considered an important structuring force in a variety of terrestrial (Herms and Mattson 1992, Rosenthal and Berenbaum 1992) and marine (Gaines and Lubchenco 1982, Hay 1991) ecosystems, but its role in freshwater ecosystems is debated (Lodge 1991, Newman 1991). Recent cross-ecosystem comparisons, though, suggest that the impact of herbivores on aboveground plant standing crop is high and ecologically important in all three ecosystem types (Lodge et al. 1998). However, important uncertainties remain about the relative importance of different herbivorous taxa and about the importance of herbivory on belowground plant parts relative to the better studied impact on aboveground tissues. Research on the impacts of herbivorous waterfowl could help to clarify both issues.

Aquatic birds are rarely considered in studies of aquatic food webs (Comin and Herrera-Silveira 2000), despite the fact that they are relatively ubiquitous and consume nearly every taxonomic group in aquatic ecosystems, including phytoplankton (flamingos, *Phoenicopterus* spp.), zooplankton (Northern Shovelers, *Anas clyptea*), aquatic insects (dabbling ducks, *Anas* spp.), mollusks (diving ducks, *Aythya* spp.), fish (Double-crested Cormorants, *Phalacrocorax auritius*), amphibians (wading birds, such as Great Blue Heron, *Ardea herodius*), and vascular plants (seeds, tubers, and foliage; most waterfowl). The few published experimental studies of waterfowl herbivory indicate that waterfowl typically reduce aboveground vascular plant standing stock by more than 50% (Lodge et al. 1998).

The potential for depletion of aquatic plant populations via consumption of belowground standing stock is even higher, and is at its peak in winter, when aboveground tissue is senescent and plants are present only as tubers or seeds in the sediment. Waterfowl are also gregarious on southern wintering grounds, with many species consuming these belowground seeds and tubers of aquatic plants. Because of the high reproductive potential of winter tubers, the impact of herbivory on winter tubers could affect the plant population long after herbivory has ceased. Although studies of underground herbivory are rare (Andersen 1987, Blossey and Hunt-Joshi 2003), exclosure studies confirm that consumption of seeds or belowground vegetative structures can have negative impacts on vegetation long after the cessation of consumption. For example, negative impacts of granivory persisted for three years after the exclusion of rodents (Howe and Brown 2001), and the impact of tuber consumption persisted five years after the exclusion of Snow Geese (Handa et al.
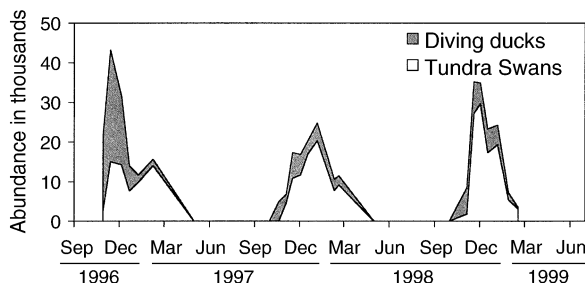
Fig. 1. Abundance of Tundra Swans and diving ducks at Lake Mattamuskeet, North Carolina, USA, as determined by aerial surveys every two weeks (data are courtesy of the U.S. Fish and Wildlife Service).

2002). Therefore, even though the presence of waterfowl is temporary, and relatively small amounts of biomass may be consumed, migratory waterfowl could have a lasting impact on vascular plants.

Despite these plausible inferences that waterfowl herbivory on belowground tissue may affect the long-term stability of macrophyte populations (Lodge 1991, Sondergaard et al. 1996, Perrow et al. 1997, Mitchell and Perrow 1998), few studies have quantified the impacts of winter tuber consumption by waterfowl on the plant populations in the following growing season (e.g., Anderson and Low 1976, Tubbs and Tubbs 1983, Idestam-Almquist 1998, LaMontagne et al. 2003). To quantify the impact of wintering waterfowl on tuber abundance and subsequent growing-season standing stock of *Vallisneria americana*, we established a winter exclosure study at Lake Mattamuskeet, North Carolina, USA. We measured above- and belowground biomass of aquatic vegetation in plots open to grazing vs. winter-only exclosures for three years.

Methods

Site description

We set up the exclosure study in Lake Mattamuskeet, located on the eastern coast of North Carolina (35°30′ N, 76°11′ W), USA. Surface area of the natural lake is 170 km^2 (maximum water depth 1.2 m), with another 10 km^2 of neighboring marsh impoundments managed for use by wildlife. Our study area reflected typical characteristics of open-water habitats at Lake Mattamuskeet, where *Vallisneria americana* (wild celery) accounted for 90% of aboveground vegetation biomass at the onset of the experiment. Other species present included *Najas guadalupensis* (southern naiad) and *Potamogeton perfoliatus* (redhead grass). Loosely packed organic material comprised the top 10 cm of sediments, and deeper sediments consisted of highly compacted clays.

A diverse assemblage of >100 000 waterfowl, including tuber-consuming Tundra Swans and diving ducks, overwinter at Lake Mattamuskeet each year from October to March, with peak use occurring in November and December (Fig. 1). The dominant species at our experimental site were Canvasback (*Aythya valisineria*), Tundra Swan (*Cygnus columbianus*), American Coot (*Fulica americana*), Ruddy Duck (*Oxyura jamaicensis*), American Wigeon (*Anas americana*), and Pied-billed Grebe (*Podilymbus podiceps*). Individuals of each of these species were observed foraging in reference plots during the study period (scans every two weeks by refuge personnel during winters 1 and 3, and twice-weekly 30-min observations by researchers during the second winter of the study). As with the vegetation community, the waterfowl assemblage was typical for open-water habitats of Lake Mattamuskeet. Because the waterfowl moved among areas of the lake throughout the winter, we believe that the impact at this site was representative of the impact of waterfowl on submerged vegetation in nearshore areas of the lake as a whole.

During 23–26 September 1996, we installed five exclosures and cageless reference pairs at the site. Each exclosure and cageless reference consisted of 5.76 m^2 (2.4 × 2.4 m). At the beginning of the experiment, water depth where exclosures and reference plots were installed ranged from 0.89 to 0.93 m. Plots were placed randomly, with exclosures and references interspersed, and ~25–35 m between plots. We constructed exclosures by attaching garden fencing (25-cm^2 rectangular openings) to corner posts. Exclosure tops stood ~0.2 m above water level and were covered with fencing. Fencing went all the way to the lake bottom in order to prevent entry by diving ducks. PVC posts that extended 0.8 m above the lake bottom marked cageless reference plots at each corner. We removed fencing from exclosures in the growing season (March–September) to allow entry by any other herbivorous organisms and to minimize any exclosure effects. Because waterfowl (principally Tundra Swans and diving ducks) are the only known tuber consumers present at Lake Mattamuskeet, and exclosures are open to herbivory during the summer when aboveground foliage is present, our study isolates the impact of tuber consumption by wintering waterfowl.

Our observations throughout the duration of the experiment suggest only minimal cage artifacts: some accumulation of organic debris at the water surface in the fall during periods of heavy aquatic plant senescence. Wave action swept away this senescent plant matter within a few weeks. Because this plant buildup on the outside of cage walls occurred during the nongrowing season when plants were only present as dormant seeds or tubers buried in the sediment surface, it should not have influenced the growth of aquatic vegetation. For the same reason, we do not believe that shading during the winter (when exclosures were in place) would have any impacts on the variables that we measured.

Because avian communities can significantly increase nutrient loading in aquatic systems (Powell et al. 1991, Fourqurean et al. 1995), we observed whether

birds perched on exclosures. At no time during the study did we observe waterfowl perched on the exclosures. This was probably because the posts and wire mesh that we used did not provide an appropriate platform for web-footed birds. On occasion, terns perched on exclosure posts. However, we did not observe any fouling of the exclosure posts, which would have occurred if significant perching were occuring. During years of low water level (1997 and early 1998), terns also occasionally perched on the PVC posts marking our reference plots. Thus, there is no reason to believe that nutrient loading due to birds would be any higher in our exclosures than in references.

We destructively sampled above- and belowground vegetation biomass every 2–3 months in exclosures and reference plots, beginning in September 1996. Within each plot, we established non-sampling zones to avoid edge effects and provide pathways for researchers. Non-sampling zones consisted of a 0.3 m wide band around the entire perimeter of each plot, plus a 0.3-m north–south band through the center of each plot. We took no samples or observations from these non-sampling zones. A grid of 120 imaginary cells (sampling locations) of size 0.15 × 0.15 m subdivided the remaining plot area for sampling vegetation. On each sampling date, we randomly chose three grid cells for sampling for each plot. Preliminary sampling with greater sample sizes demonstrated that a sample size of three was adequate to provide an accurate estimate of above- and belowground vegetation biomass. No cell was cored more than once during the course of the study.

In each cell, all aboveground vegetation within a 0.1 × 0.1 m quadrat was carefully removed by hand and saved for processing. Next, a PVC coring device (0.10 m in diameter) was placed where the vegetation had been removed and was driven into the sediments to a depth of 0.15 m. Cores taken prior to the setup of exclosures indicated that most, if not all, belowground biomass occurred in the top 0.15 m. We sampled only aboveground biomass on one sampling date, but sampled both above- and belowground biomass on the remaining 13 sampling dates. We rinsed the contents of each core through a 1 mm diameter mesh sieve. Aboveground material was rinsed carefully to remove any attached sediment or invertebrates. Aboveground vegetation and vegetative material from the cores were refrigerated until further processing. Above- and belowground plant material was sorted by species. Belowground parts were further divided into tubers and root/rhizome material. All plant material was then dried at 60°C and weighed.

We averaged the data from the three samples within each plot and conducted repeated-measures analysis of variance (rmANOVA) on the averages. For tuber density, we used data from sampling dates when tubers were present (tubers are absent during summer). For aboveground vegetation, we used data from the nine sampling dates during the growing season (June–October).

We also conducted a separate experiment to examine density-dependent winter mortality of tubers in the absence of herbivory. This experiment allowed us to measure mortality from sources other than herbivores more precisely than we could by using the exclosure data. We collected tubers of *Vallisneria americana* from the lake in November 1998 and transplanted them back into the lake at seven densities (including controls with no tubers; $N = 3$ replicates for each density). The tubers were planted in 30 cm long sections of 15 cm diameter PVC tubing. The bottom of the tube was covered with 0.1-mm mesh and was packed with 20 cm of pre-sieved lake sediment. We placed tubers in the container and added another 10 cm of sediment in the PVC tube, simulating a 10-cm burial depth for tubers, which is the common burial depth of tubers at Lake Mattamuskeet. The tube was then placed into the lake bottom so that the sediment surface of the container was level with that of the surrounding lake bottom. All transplant tubes were placed inside a single exclosure (independent of the herbivory study). We carefully removed the containers in April 1999 and counted the number of sprouts, live tubers (characterized by a firm texture and white appearance), and rotting tubers (limp texture and black appearance).

Data on percentage tuber loss were analyzed using standard regression techniques (SYSTAT Version 9.0). We removed extreme outliers, using SYSTAT's criterion of a studentized residual less than 2. By this criterion, we removed one reference and one exclosure plot (studentized residuals of −8.408 and −8.730, respectively). In general, variance in percentage loss of tubers was very high at low tuber densities because of spatial and temporal variance.

RESULTS

Impact of herbivory on vegetation

Herbivory by wintering waterfowl caused a decline in density of *Vallisneria* tubers in reference plots relative to exclosures (treatment $P = 0.038$, time × treatment interaction $P = 0.025$; Fig. 2). Given the significant time × treatment interaction, we conducted separate ANOVAs to identify years in which significant effects were present. There was a significant 60% reduction in tuber abundance in the first winter (ANOVA, $P = 0.016$), but no significant effects of herbivory in the second and third winters.

Our independent winter mortality experiment showed that non-herbivory mortality was density independent ($R^2 = 0.000$, $P = 0.563$), with an average mortality of 24% (Fig. 3). Therefore, to examine the loss of tubers due to herbivory as a function of density, we corrected the tuber loss in our reference plots by assuming that, on average, 24% of initial tuber density was lost from causes other than herbivory. Subsequent
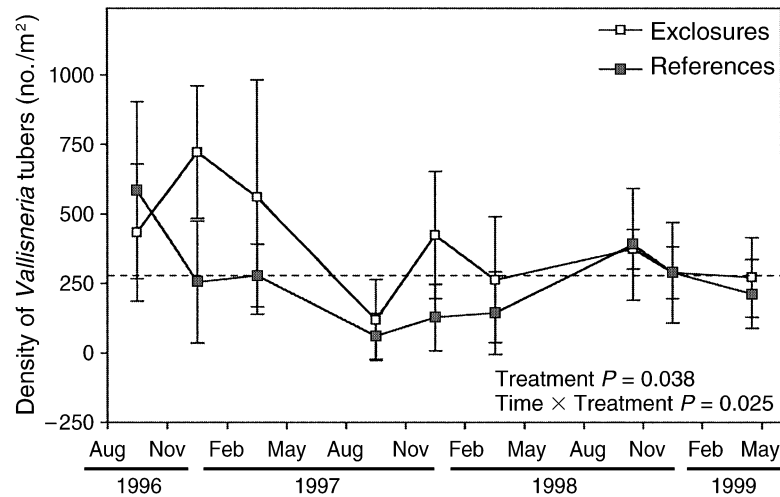
FIG. 2. Density of *Vallisneria americana* tubers over time in exclosures and reference plots. Error bars represent 95% confidence intervals. The dashed line indicates the minimum tuber density required for foraging by Canvasbacks at Lake Mattamuskeet (Lovvorn 1994). Significance values for factors treatment and time × treatment in a repeated-measures ANOVA are given.

regression analysis of percentage tuber loss confirmed that waterfowl impact was strongly dependent on initial tuber abundance. Regardless of year, loss of tubers due to herbivory during the winter was positively related to initial (September) tuber density in reference plots ($R^2 = 0.294$, $P = 0.026$), but not in exclosures ($R^2 = 0.007$, $P = 0.798$). No loss of tubers occurred in references below a density of ~234 tubers/m^2 (Fig. 3).

Despite the loss of *Vallisneria* tubers during the winter, no corresponding effects of waterfowl exclosure on aboveground biomass existed during subsequent growing seasons (treatment $P = 0.342$, time × treatment P = 0.539; Fig. 4A). Due to extreme drought conditions, peak standing stock of *Vallisneria* declined by ~80% in both reference plots and exclosures between September 1996 and September 1997, and did not recover to more than ~15% of 1996 standing stock levels for the remainder of the study period (Fig. 4A). There was no relationship between peak aboveground biomass and the tuber density at the beginning of the growing season ($N = 30$, $R^2 = 0.003$, $P = 0.987$). At the same time that *Vallisneria* biomass declined, biomass of *Najas guadalupensis* increased dramatically from September 1996 to September 1997 and 1998 (Fig. 4B). As
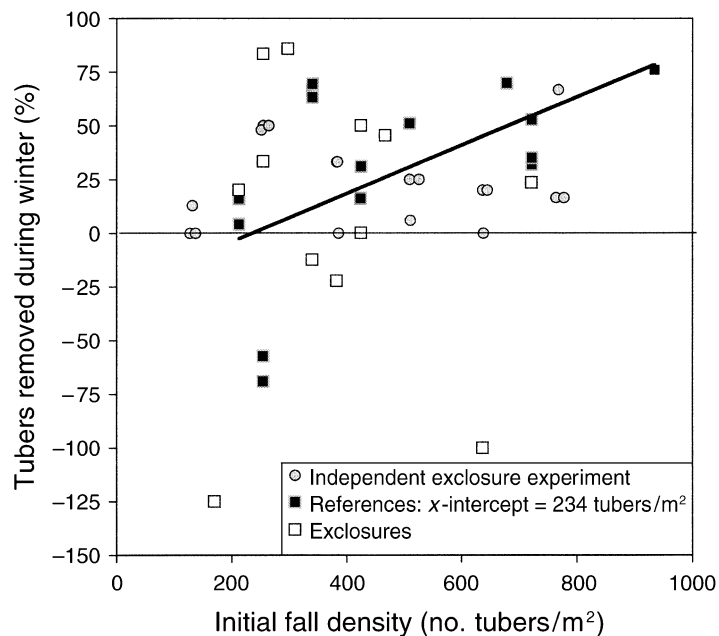
FIG. 3. Percentage mortality of *Vallisneria* tubers during the winter for exclosures (open squares; $R^2 = 0.007$, $P = 0.798$), references (black squares shown with solid regression line; $R^2 = 0.294$, $P = 0.026$), and in an independent exclosure winter mortality experiment (gray circles; $R^2 = 0.000$, $P = 0.563$) as a function of tuber density at the beginning (September) of the wintering period. A horizontal index line at zero is provided to identify the x-intercept of the reference treatment (the foraging threshold). Non-herbivory winter mortality was estimated from the independent exclosure experiment.
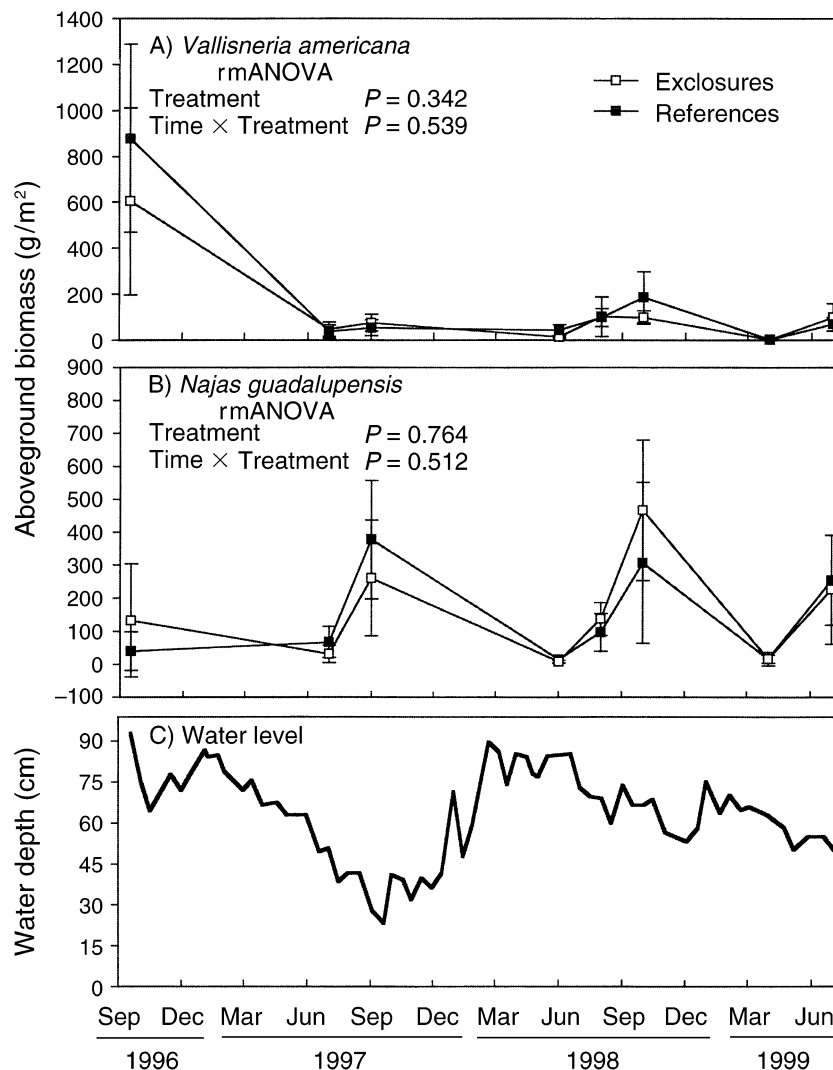
FIG. 4. Aboveground biomass of (A) *Vallisneria americana* and (B) *Najas guadalupensis* over time in exclosures and reference plots. (C) Water level at the study site.

with *Vallisneria*, waterfowl exclosure had no significant effect on aboveground standing stock of *Najas* (treatment $P = 0.764$, time × treatment $P = 0.512$; Fig. 4B). The overall decline in *Vallisneria* biomass and increase in *Najas* corresponded with a drought-induced change in water depth from 0.8 m in 1996 to only 0.2 m in the summer of 1997 (Fig. 4C).

DISCUSSION

Herbivory by wintering waterfowl, primarily Tundra Swans and diving ducks, resulted in reduced tuber density in grazed reference plots relative to exclosures (Fig. 2). The impact of herbivory on tuber densities varied highly between years of the study, however, and depended upon the initial density of tubers available to wintering waterfowl. In a previous study conducted at Lake Mattamuskeet, Lovvorn (1994) found that it was not energetically profitable for Canvasbacks to for-

age for *Vallisneria* tubers below densities of ~200–260 tubers/m², depending on the month. The patterns of depletion for the three years of our study are consistent with Lovvorn's findings. In the first year, average tuber density at the onset of winter (586 tubers/m²) was far above the threshold for profitable foraging, and there was a 60% depletion of tubers that reduced abundance close to Lovvorn's threshold (278 tubers/m²; Fig. 2A). In the second winter, the average initial tuber density, 60 tubers/m², was below the foraging threshold, and we saw no evidence of depletion by waterfowl (Fig. 2A, B). In the third year, the average tuber density was slightly above Lovvorn's threshold (390 tubers/m²), but again we saw no evidence of significant herbivory.

Examination of the loss of tubers and initial tuber densities in individual reference plots also supports the existence of a foraging threshold; no loss of tubers

occurred below 234 tubers/m² (Fig. 3). Reference plots with initial tuber densities above the threshold value of 234 tubers/m² showed a loss of tubers. In addition, loss of tubers due to herbivory was density dependent above the threshold (Fig. 3; reference plots $P = 0.026$). In contrast, both the exclosures and our separate field experiment showed that non-herbivory mortality of tubers during the winter was density independent, with an average of 24% mortality in our controlled mortality experiment (Fig. 3; $R^2 = 0.000$, $P = 0.563$). Lovvorn (1994) found a similar loss rate (21%) of tubers in *Vallisneria* patches at Lake Mattamuskeet that were below the profitable foraging threshold and therefore not subject to herbivory. Because non-herbivory mortality of tubers is independent of density, the pattern in our grazed references is due to density-dependent feeding by waterfowl.

Similarly, foraging thresholds have been found for other species of waterfowl feeding on belowground tubers of aquatic plants. Bewick's Swans (*Cygnus columbianus bewickii*) no longer foraged on *Potamogeton pectinatus* tubers once the density dropped below a threshold value (Beekman et al. 1991). Giving-up densities (measured in grams per square meter) for Tundra Swans feeding on belowground tubers of *Potamogeton pectinatus* in shallow clay sediments in a Netherlands lake (Nolet et al. 2001) fell in the range of biomass densities equivalent to the 260 *Vallisneria* tubers/m² calculated by Lovvorn for Canvasbacks in similar sediment at Lake Mattamuskeet.

Density-dependent tuber herbivory above the threshold is consistent with a type III functional response (Holling 1959), as are results of some previous experiments on tuber-feeding waterfowl. For example, in captive feeding trials, Takekawa (1987) found that Canvasbacks foraging on *Vallisneria* tubers exhibit a type III functional response. Field studies have also shown that waterfowl feed in a density-dependent manner (Sondergaard et al. 1996, Idestam-Almquist 1998).

Although they are relatively few in number, the existing rigorous studies of tuber-consuming waterfowl suggest that waterfowl are energetically incapable of totally eliminating belowground tubers of submerged aquatic plants. This trend is consistent across several species of waterfowl and aquatic plants, and is consistent with the stabilizing effect of foraging thresholds for terrestrial systems (Mitchell and Brown 1990). A recent model confirmed that the foraging threshold for tuber-consuming swans provides a refuge for tubers and has a stabilizing effect on the plant population (Jonzén et al. 2002). Because so little is known about belowground herbivory (and, in particular, the presence of belowground foraging thresholds) in terrestrial systems (Andersen 1987, Blossey and Hunt-Joshi 2003), it is not clear how widely applicable our findings for belowground herbivory are to other habitats. However, with regard to aboveground herbivory, the type III functional response is generally considered to have a stabilizing effect on terrestrial plant populations (Crawley 1997).

Impacts of tuber herbivory on aboveground standing stock

Despite the significant impact of waterfowl herbivory on tuber density in winter, aboveground biomass of *Vallisneria* did not differ between grazed and ungrazed plots in the subsequent growing season (Fig. 4A). Our results are very similar to those for migrating Trumpeter Swans (*Cygnus buccinator*), which reduced belowground biomass of *Potamogeton pectinatus* by 24%, but had no impact on aboveground biomass in the following growing season (LaMontagne et al. 2003). The insensitivity of aboveground standing stock to springtime tuber density indicates that other factors (either abiotic or competition) play a bigger role in determining aboveground standing stock during the growing season. Our ability to test this theory directly with our field data was confounded by the large, negative effects of a drought and subsequent influx of salt water from Pamlico Sound on *Vallisneria* in the summer of 1997.

Other experiments, however, suggest that production of fewer, but larger, plants in grazed areas may explain the lack of effect of tuber consumption on aboveground biomass in the following growing season. LaMontagne et al. (2003) found that areas that had been grazed in the previous year produced 57% fewer shoots of *Potamogeton pectinatus* than ungrazed areas ($P = 0.067$), but found no difference in total biomass. Similarly, in separate experiments designed to test the impact of springtime tuber density on growing-season dynamics of *Vallisneria*, the number of rosettes produced was highly, positively correlated with initial tuber density ($R^2 = 0.695$, $P < 0.001$), but rosette size was negatively related ($R^2 = 0.198$, $P = 0.014$; A. F. Sponberg and D. M. Lodge, *unpublished manuscript*). In both studies, it appears that intraspecific competition resulted in more, but smaller, rosettes (or shoots, in the case of *P. pectinatus*), hence negating the impact of tuber herbivory on total aboveground biomass. This result is similar to those of many previous experiments with terrestrial plants, showing the impact of intraspecific competition in regulating plant biomass (Watkinson 1997, Firbank and Watkinson 1990). Thus, consumption of tubers by waterfowl may be compensatory in regard to production of aboveground biomass in the following season.

At the same time that *Vallisneria* abundance declined drastically, *Najas guadalupensis* increased 2.7-fold (Fig. 4B). This same trend has been noted at Lake Mattamuskeet in previous drought years (J. Stanton, *personal observation*). As with *Vallisneria*, there was no impact of waterfowl exclosure on *Najas* aboveground biomass. Dabbling ducks foraged on *Najas* at this site in the fall, but they were consuming already senescing foliage. We would not expect an impact on *Najas* aboveground biomass in the next year, because

Najas reproduces exclusively by seed and the waterfowl community at our site consisted mostly of tuber consumers. Although seed consumption by dabbling ducks can have significant impacts on the next season's standing stock (A. F. Sponberg and D. M. Lodge, *unpublished manuscript*), the typically high water levels at our site are not favorable for use by seed-consuming dabbling ducks, nor were dabbling ducks seen feeding at the site in winter.

CONCLUSION

Even though migratory waterfowl may be present for only a short duration in aquatic habitats, they provide an intense pulse of consumption during the winter that can have significant impacts on belowground biomass. Efforts to restore *Vallisneria* populations have sometimes been unsuccessful due to herbivory by waterfowl and muskrats (Carter and Rybicki 1985), highlighting the importance of herbivory in regulating these populations. However, aboveground biomass of an established population of *Vallisneria* does not appear to respond to such herbivory. The lack of an effect on aboveground production is in sharp contrast to studies of Snow Goose (*Chen caerulescens*) herbivory in emergent wetlands, where consumption of belowground tubers results in a near total loss of aboveground vegetation (Smith and Odum 1981, Bazely and Jefferies 1986, Giroux and Bedard 1987). Based on this and other studies at Lake Mattamuskeet (Lovvorn and Gillingham 1996), it appears that constraints on energetic profitability limit the ability of waterfowl to deplete tubers to population levels that cause extinction, or even to levels that affect aboveground biomass in the subsequent growing season. Studies of other species of waterfowl foraging on a different submerged macrophyte in Europe (Jonzén et al. 2002) and Canada (LaMontagne et al. 2003) are consistent with our results, suggesting that foraging thresholds and density-dependent feeding of waterfowl may be common in waterfowl–plant interactions.

Because waterfowl foraging on *Vallisneria* is density dependent, *Vallisneria* is able to persist at Lake Mattamuskeet despite repeated, intense bouts of grazing on tubers during the winter. Thus, as found in studies on a variety of benthivores (such as other waterfowl, crabs, and rays), foraging thresholds provide a refuge for prey items (Eggleston et al. 1992, Hines et al. 1997) and, hence, a mechanism for stabilizing the effects of consumption on prey populations (Mitchell and Brown 1990, Jonzén et al. 2002). Although the lack of studies on belowground herbivory in terrestrial ecosystems limits our ability to draw comparisons, Andersen (1987) notes that belowground herbivores tend to have abundances more variable in time than those of aboveground herbivores, and limited evidence suggests that some plants and their belowground herbivores may have coevolved toward a mutualistic relationship. Thus, intense, seasonal belowground herbivory with little long-term impact on the plant population, such as we have found at Lake Mattamuskeet, may occur in terrestrial ecosystems as well.

LITERATURE CITED

Andersen, D. C. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. Quarterly Review of Biology **62**(3):261–286.

Anderson, M. G., and J. B. Low. 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. Journal of Wildlife Management **40**:233–242.

Bazely, D. R., and R. L. Jefferies. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. Journal of Ecology **74**:693–706.

Beekman, J. H., M. R. van Eerden, and S. Dirksen. 1991. Bewick's swans *Cygnus columbianus bewickii* utilising the changing resource of *Potamogeton pectinatus* during autumn in the Netherlands. Pages 238–248 *in* J. Sears and P. J. Bacon, editors. Proceedings of the Third International Swan Symposium, Oxford, UK.

Blossey, B., and T. R. Hunt-Joshi. 2003. Belowground herbivory in insects: influence on plants and aboveground herbivores. Annual Review of Entomology **48**:521–547.

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

Comin, F. A., and J. A. Herrera-Silveira. 2000. The role of birds on the trophic structure and nutrient cycles of aquatic ecosystems: a review. Pages 205–218 *in* F. A. Comin, J. A. Herrera, and J. Ramirez, editors. Limnology and aquatic birds. Monitoring, modelling and management. Universidad Autonoma de Yucatan, Merida, Yucatan, Mexico.

Crawley, M. J. 1997. Plant–herbivore dynamics. Pages 401–474 *in* M. J. Crawley, editor. Plant ecology. Blackwell Science, Oxford, UK.

Eggleston, D. B., R. N. Lipcius, and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Marine Ecology Progress Series **85**:55–68.

Firbank, L. G., and A. R. Watkinson. 1990. On the effects of competition: from monocultures to mixtures. Pages 165–192 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competitions. Academic Press, San Diego, California, USA.

Fourqurean, J. W., G. V. N. Powell, W. J. Kenworthy, and J. C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. Oikos **72**:349–358.

Gaines, S. D., and J. Lubchenco. 1982. A unified approach to marine plant–herbivore interactions. II. Biogeography. Annual Review of Ecology and Systematics 13:111–138.

Giroux, J. F., and J. Bédard. 1987. The effects of grazing by greater snow geese on the vegetation of tidal marshes in the St. Lawrence estuary. Journal of Applied Ecology 24: 773–788.

Handa, I. T., R. Harmsen, and R. L. Jefferies. 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. Journal of Ecology 90:86–99.

Hay, M. E. 1991. Marine–terrestrial contrasts in the ecology of plant chemical defenses against herbivores. Trends in Ecology and Evolution 6:362–365.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology 67:283–335.

Hines, A. H., R. B. Whitlatch, S. F. Thrush, J. E. Hewitt, V. J. Cummings, P. K. Dayton, and P. Legendre. 1997. Non-linear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. Journal of Experimental Marine Biology and Ecology 216:191–210.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation in the European pine sawfly. Canadian Entomologist 91:293–320.

Howe, H. F., and J. S. Brown. 2001. Ghost of granivory past. Ecology Letters 4:371–378.

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

Jonzén, N., B. A. Nolet, L. Santamaría, and M. G. E. Svensson. 2002. Seasonal herbivory and mortality compensation in a swan–pondweed system. Ecological Modelling 147: 209–219.

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 stopover areas. Aquatic Botany 76:235–244.

Lodge, D. M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41:195–224.

Lodge, D. M., G. Cronin, E. van Donk, and A. J. Froelich. 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. Pages 149–174 in E. Jeppesen, M. Sondergaard, M. Sondergaard, and K. Christoffersen, editors. The structuring role of submerged macrophytes in lakes. Springer-Verlag, New York, New York, USA.

Lovvorn, J. R. 1994. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 279/280:223–233.

Lovvorn, J. R., and M. P. Gillingham. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 77:435–451.

Mitchell, S. F., and M. R. Perrow. 1998. Interactions between grazing birds and macrophytes. Pages 175–196 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. The structuring role of submerged macrophytes in lakes. Springer-Verlag, New York, New York, USA.

Mitchell, W. A., and J. S. Brown. 1990. Density-dependent harvest rates by optimal foragers. Oikos 57:14–24.

Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. Journal of the North American Benthological Society 10:89–114.

Nolet, B., O. Langevoord, R. M. Bevan, K. Engelaar, M. Klaassen, R. J. W. Mulder, and S. van Dijk. 2001. Spatial variation in tuber depletion by swans explained by differences in net intake rate. Ecology 82:1655–1667.

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

Powell, G. V. N., J. W. Fourqurean, W. J. Kenworthy, and J. C. Zieman. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. Estuarine, Coastal and Shelf Science 32:567–579.

Rosenthal, G. A., and M. R. Berenbaum. 1992. Herbivores: their interactions with secondary plant metabolites. Volume II. Evolutionary and ecological processes. Academic Press, New York, New York, USA.

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

Sondergaard, M., L. Bruun, T. Lauridsen, E. Jeppesen, and T. V. Madsen. 1996. The impact of grazing waterfowl on submerged macrophytes: in situ experiments in a shallow lake. Aquatic Botany 53:73–84.

Takekawa, J. Y. 1987. Energetics of canvasbacks staging on an upper Mississippi River pool during fall migration. Dissertation. Iowa State University, Ames, Iowa, USA.

Tubbs, C. R., and J. M. Tubbs. 1983. The distribution of *Zostera* and its exploitation by wildfowl in the Solent, southern England. Aquatic Botany 15:223–239.

Watkinson, A. R. 1997. Population dynamics. Pages 359–400 in M. J. Crawley, editor. Plant ecology. Blackwells Science, Oxford, UK.