

Influence of migrant tundra swans (*Cygnus columbianus*) and Canada geese (*Branta canadensis*) on aquatic vegetation at Long Point, Lake Erie, Ontario

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Abstract

Numerous studies have shown that large, herbivorous waterfowl can reduce quantity of aquatic plants during the breeding or wintering season, but relatively few document herbivory effects at staging areas. This study was done to determine if feeding activities of tundra swans (*Cygnus columbianus columbianus*) and Canada geese (*Branta canadensis*) had a measurable additive influence on the amount of aquatic plants, primarily muskgrass (*Chara vulgaris*), wild celery (*Vallisneria americana*), and sago pondweed (*Potamogeton pectinatus*), removed during the fall migration period at Long Point, Lake Erie, Ontario. Exclosure experiments done in fall 1998 and 1999 showed that, as compared to ducks and abiotic factors, these two large herbivorous waterfowl did not have any additional impact on above or below ground biomass of those aquatic plants. As expected, however, there were substantial seasonal reductions in above-ground and below-ground biomass of aquatic plants in wetlands that were heavily used by all waterfowl. We suggest that differences in large- and small-scale habitat use, feeding activity, and food preferences between tundra swans and other smaller waterfowl as well as compensatory herbivory contributed to our main finding that large waterfowl did not increase fall reductions of *Chara* spp., *V. americana*, and *P. pectinatus* biomass.

Introduction

Submerged and emergent aquatic macrophytes provide important foods for many migratory waterfowl and several other species of aquatic herbivores (Thayer et al., 1984; Lodge et al., 1998; Knapton & Petrie, 1999). The relationship between waterfowl and their aquatic food resources is dynamic, resulting from seasonal changes in their feeding behaviour that ultimately is a response to herbivory and other biotic and abiotic factors

affecting the abundance and distribution of aquatic macrophytes (Lodge, 1991). Waterfowl congregate in and select areas with large concentrations of macrophytes, especially those that contain preferred forage species (Dirksen et al., 1991; Wicker & Endres, 1995; Mitchell & Wass, 1996; Nolet et al., 2001). Concentrations of waterfowl can cause large reductions in above- and below-ground biomass of their preferred forage species (Anderson & Low, 1976; Giroux & Bédard, 1987; Beekman et al., 1991; Evers et al., 1998; Idestam-Almqvist,

1998) and may even change species composition of some plant communities over longer periods of time (Jefferies et al., 1994; Kotanen & Jefferies, 1997). Abiotic factors, such as wave action and ice scour, and senescence also are major factors that contribute to biomass reduction in some aquatic macrophyte communities (Beekman et al., 1991; Crowder & Painter, 1991; Idestam-Almquist, 2000).

Recently, there has been concern about increasing populations of large herbivorous waterfowl and the influence these birds have on food resources in critical aquatic and terrestrial habitats (Conover & Kania, 1994; Ankney, 1996; Abraham & Jefferies, 1997; Petrie et al., 2002). There is a growing body of evidence showing that large numbers of geese can have pronounced and detrimental effects on the structure, quality, and quantity of habitat at breeding, staging, and wintering areas (Cargill & Jefferies, 1984; Bazely & Jefferies, 1986; Giroux & Bédard, 1987; Jefferies et al., 1994; Kotanen & Jefferies, 1997). These effects not only have population-level ramifications for species that are the main consumer of foods (Cooke et al., 1995; Abraham & Jefferies, 1997; Leafloor et al., 2000), but potentially also for other organisms that use the same habitats (Abraham & Jefferies, 1997). Purportedly, increasing populations of exotic mute swans, *Cygnus olor* (Gmelin), in eastern North America can have some negative impacts on submerged aquatic macrophytes (Reese, 1975; Petrie & Francis, 2003; but see Conover & Kania, 1994). Further, tundra swans, *Cygnus columbianus columbianus* (Ord), and Bewick's swans, *Cygnus columbianus bewickii* (Ord [Yarrell]), can substantially reduce densities of wild celery, *Vallisneria americana* (Michaux), and sago pondweed, *Potamogeton pectinatus* (L.), tubers at some of their major staging and wintering areas (Beekman et al., 1991; Nolet & Drent, 1998; Froelich & Lodge, 2000; Nolet et al., 2001).

Tundra swan populations in North America have increased since the early 1970s (Serie et al., 2002), causing concern that they may directly or indirectly influence aquatic plant and waterfowl communities at some of their staging areas (Petrie, 1998; Petrie et al., 2002). Thousands of these large, herbivorous waterfowl often congregate at traditional staging and wintering areas where they co-occur with large concentrations of many other

waterfowl species (Limpert & Earnst, 1994; Petrie et al., 2002). At fall staging areas, tundra swans spend much time feeding in aquatic habitats where they excavate and eat tubers and rhizomes of several different aquatic plants (Earnst, 1994; Limpert & Earnst, 1994; Badzinski, 2003). Tundra swans also consume above-ground parts of aquatic macrophytes and charophytes when available (Beekman et al., 1991; Earnst, 1994; Limpert & Earnst, 1994; Nolet et al., 2001). Some aquatic plant species consumed by tundra swans, including wild celery, sago pondweed, and muskgrass, *Chara* spp. (L.), also are preferred or common foods of many other staging waterfowl (Korschgen & Green, 1988; Korschgen et al., 1988; Kantrud, 1990; Rees & Bowler, 1991; Knapton & Petrie, 1999).

The wetland complex associated with Long Point, Lake Erie is a continentally important staging area for tundra swans and several other waterfowl species (Petrie, 1998) (Fig. 1). Considerable numbers of Canada geese also use these wetlands, but their numbers have decreased at Long Point, despite a large increase in the giant Canada goose population in southern Ontario, since the early 1970s (Petrie, 1998). Further, based on average peak numbers during fall aerial surveys flown from 1991 to 2002, tundra swans are much more abundant (~4 times: 6831 swans vs. 1714 geese) than Canada geese at Long Point, which also is reflected at much smaller spatial scales (Badzinski, 2003; this study). Tundra swan use has increased substantially at this staging area over the past 30 years (Petrie et al., 2002), mirroring this species' increase throughout North America (Serie et al., 2002). In light of their relatively recent population increase and the general lack of information concerning tundra swan staging ecology, it is important to determine the degree that staging tundra swans and other large herbivorous waterfowl affect seasonal abundance of aquatic plants and smaller waterfowl (Petrie, 1998; Petrie et al., 2002; Badzinski, 2003).

In this study, we designed an enclosure experiment to determine if large numbers of relatively large herbivorous waterfowl (primarily tundra swans) substantially reduce the availability of above- and below-ground vegetation beyond that resulting from activities of smaller aquatic consumers (mainly ducks) and abiotic factors during

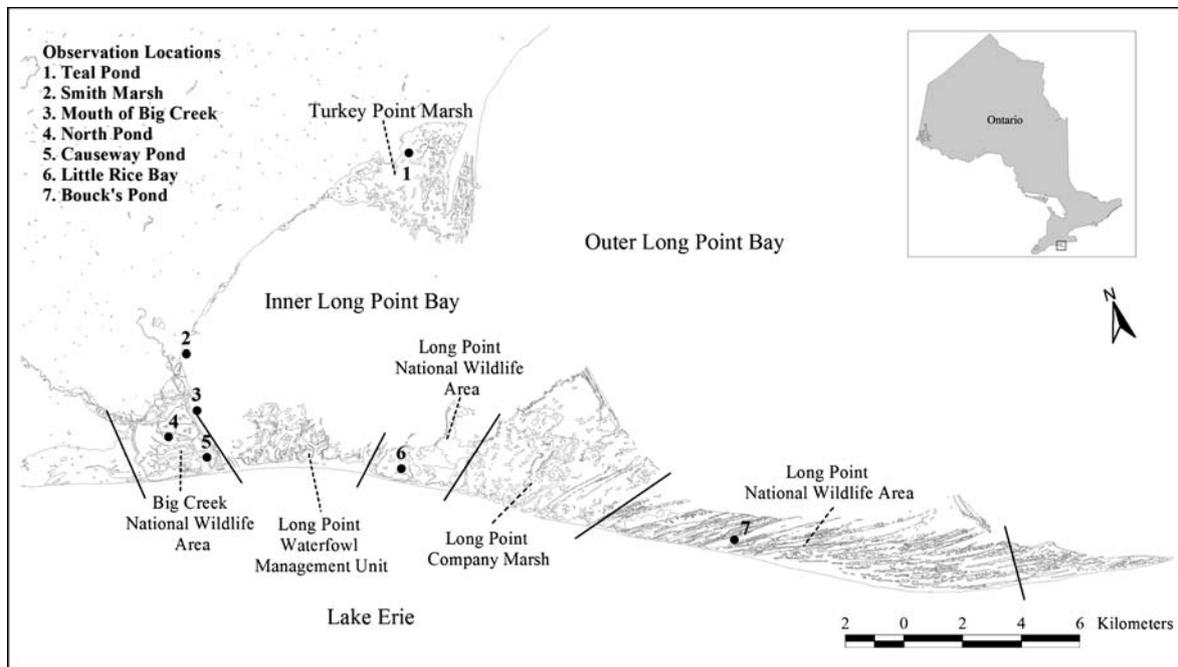


Figure 1. Map showing major wetland complexes and public, private, and government owned areas at Long Point, Lake Erie, Ontario. Locations where vegetation sampling and behavioural observations were conducted are shown as numbered points.

the fall staging season. More specifically, we sought to determine if activities of tundra swans (and Canada geese) exerted a measurable removal effect on total below-ground biomass and tuber mass and density of important waterfowl (duck) foods (i.e., wild celery, sago pondweed, and muskgrass) at locations that traditionally receive heavy fall-use by tundra swans and other waterfowl.

Study area

This study was conducted during fall 1998 and 1999 at Long Point, Ontario (80° 24' W, 42° 38' N) (Fig. 1). Long Point is a sand-spit extending 35 km east from the southern shore of Ontario into Lake Erie that has facilitated the formation of the Inner and Outer Long Point Bays and their associated freshwater marsh complexes (Petrie, 1998). The extensive wetlands where this study was conducted were classified as lacustrine, emergent and/or aquatic bed wetland habitats (Cowardin et al., 1979).

During 1998, three study locations were used: Bouck's Pond, North Pond, and Teal Pond,

whereas in 1999, four locations were used: Bouck's Pond, North Pond, Smith Marsh, and the Mouth of Big Creek (Fig. 1). Limnological characteristics of major wetland complexes associated with the inner and outer Long Point Bays have been summarized and discussed by Leach (1981) and Petrie (1998); in general, all locations containing enclosures were considered to be eutrophic and had maximum water depths ≤ 1.0 m.

Emergent plant species commonly found at nearly all of the study locations included cattails, *Typha latifolia* (L.) and *T. angustifolia*, (L.), common reed grass, *Phragmites australis* (Cavannes), hardstem bulrush, *Scirpus acutus* (Muhlenberg), softstem bulrush, *Scirpus validus* (Kuntze), pickerelweed, *Pontedaria cordata* (L.), wild rice, *Zizania palustris* (L.), and arrowheads, *Sagittaria latifolia* (Willdenow) and *S. rigida* (Pursh). Yellow water lily, *Nuphar variegatum* (Engelmann), and white water lily, *Nymphaea odorata* (Aiton), were common floating-leaved macrophytes. Common submerged macrophytes included bladderworts, *Utricularia* spp, Canada waterweed, *Elodea canadensis* (Michaux), coontail, *Ceratophyllum demersum* (L.), floating-leaved

pondweed, *Potamogeton natans* (L.), sago pondweed, slender pondweed, *Potamogeton pusillus* (L.), muskgrass, Richardson's pondweed, *Potamogeton richardsonii* (Rydberg), water-milfoils, *Myriophyllum* spp, water niads, *Najas* spp, and wild celery.

Methods

Exclosure design

Two types of structures, exclosures and reference (or control) plots, were placed in aquatic habitats to determine influence that large waterfowl have on aquatic vegetation (Fig. 2). Exclosures were square structures ($6 \times 6 \times 1.25 \text{ m}^3$) made by wiring modified

pieces of concrete reinforcing mesh (mesh dimensions: $15.3 \times 15.3 \text{ cm}^2$) to eight fence posts. Exclosures were designed to restrict only swans and Canada geese, but not ducks (and other small herbivores), from aquatic vegetation (Fig. 2). Once situated around a patch of vegetation, the bottoms of exclosures were pushed into the substrate so their height above the substrate-water interface was about 1.0 m. Tops of the exclosures were left uncovered so ducks could land inside of them, but the relatively small size of exclosures precluded larger waterfowl from doing so. Reference (or control) plots were $6 \times 6 \text{ m}^2$ plots demarcated by four corner posts extending approximately 1.0 m above the marsh bottom (Fig. 2). These plots represented plant community characteristics after exposure to all biotic and abiotic factors that could

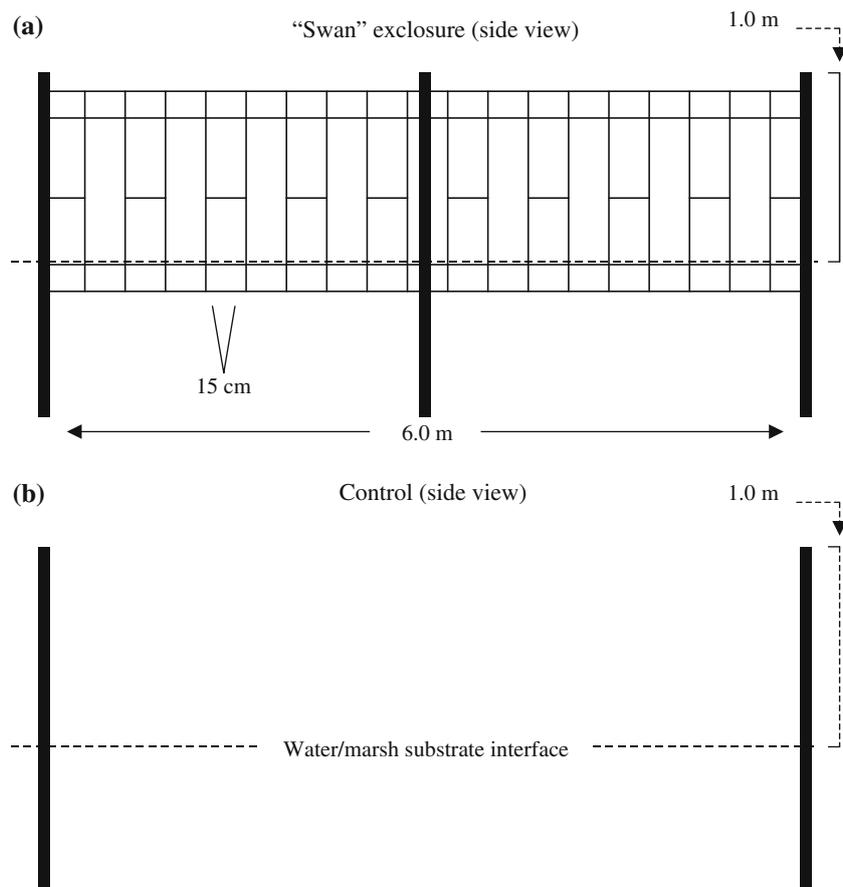


Figure 2. Design and dimensions of swan exclosures (a), and reference/control plots placed in wetlands during fall 1998 and 1999 at Long Point, Lake Erie, Ontario.

influence late season mass and seasonal change in aquatic plants. Most importantly, however, these plots were areas where large herbivores could freely access aquatic plants.

Exclosure placement

During late summer each year (18–25 September 1998 and 10–19 September 1999), three sets of experimental structures were placed in each of three (1998) or four (1999) geographically separate locations (see Fig. 1). Each experimental set consisted of one control and one “swan” exclosure. Several weeks before waterfowl arrival, locations of experimental sets were chosen and marked at each location. Structures at each location were placed in similar depths (0.3–0.9 m) of water at similar distances from shore or emergent vegetation. The range of water depths where exclosures were placed reduced the likelihood that they would become dry and unsuitable for waterfowl as water levels declined throughout the fall. Locations for each experimental set were chosen such that all had visually similar plant species composition and biomasses. Further, each set was situated in relatively dense, contiguous patches of *Chara* spp or *V. americana* and *P. pectinatus*, all of which are known to be very important foods for ducks at Long Point (Petrie, 1998). Structures within each set were grouped relatively close (range: 18–24 m) together, but much larger distances (range: 50–200 m) separated structures of different sets at the same locations. A few days prior to taking the early season sample, we randomly assigned treatments (control plot or “swan” exclosure) to each set of structures and then fastened the exclosure materials to the appropriate fence posts. Drought conditions forced us to change some study locations between years. If the same study location was used in consecutive years, structures within it were relocated so the destructive sampling during the previous year would not affect results the following season.

Aquatic vegetation sampling

Each year the fall was divided into early (27 September–8 October 1998 and 20 September–7 October 1999) and late (5–13 December 1998 and 3–10 December 1999) sampling periods. The early

period preceded arrival of large numbers of waterfowl, which usually occurs at Long Point during the first or second week of October. The late sampling period was late enough to allow for several weeks of waterfowl use, but early enough to reduce the chance that water at study locations would freeze. Comparison of early and late samples allowed us to determine the effect that large waterfowl (and other factors) had on the reduction of aquatic plants during fall.

To ensure that the vegetation samples were representative of their treatment, samples were taken ≥ 1.0 m from the edge of exclosures. This sampling area was further sub-divided into 2.0×2.0 m² quadrants, each of which was divided into 16 (0.25 m²) possible sampling locations. Potential sampling locations were sequentially assigned numbers. The actual sampling locations within each structure were chosen randomly by drawing numbers, without replacement, until two were assigned in each quadrant for each sampling period. A grid system using three ropes marked at 0.5 m increments was used to locate specific sampling locations in the field.

A small flat-bottomed boat was used to enter structures in order to take vegetation samples without destroying other potential sample locations. Once the appropriate sampling point was located, a metal sampling box ($0.5 \times 0.5 \times 0.75$ m³) was pushed into the marsh substrate and the water depth (± 1 cm) was recorded. Above-ground samples were obtained by clipping all plant stems within the sampling box at the substrate level. Samples were then sorted by species and placed into separate plastic bags labeled with date, sampling period, location, exclosure number, exclosure type, sampling coordinates, water depth, and plant species.

Below-ground samples were obtained by taking nine scoops of the marsh substrate with a perforated coffee can (total sample volume: 0.03 m³) at each of the eight sampling locations in an exclosure. Sampling in this way approximated the size and depth (~ 0.5 m) of feeding craters created by swans and ensured that all below-ground parts available to swans and ducks were collected (Beekman et al., 1991). These samples were passed through a fine mesh (2×2 mm²) sieve to separate the roots, rhizomes, and tubers from the marsh

substrate and were then sorted by species and part (roots, tubers, and rhizomes). Individual below-ground samples were placed into separate plastic bags and labeled as previously described for the above-ground samples.

At the end of the sampling day, all above- and below-ground samples were kept cool ($\sim 5^\circ\text{C}$) until they could be processed in the laboratory. Some large, heterogeneous samples were not processed in the field and were sorted, bagged, and labeled later in the laboratory.

Laboratory procedures

All species-specific above-ground vegetation samples were blotted dry with paper towels, and then weighed on a digital balance ($\pm 0.01\text{ g}$) to obtain the wet mass. Approximately 30 sub-samples of above-ground parts for each species from the 1998 vegetation sample were selected and then separately oven-dried at 80°C to constant mass ($\pm 0.01\text{ g}$); this was done so species-specific dry mass could be estimated from its wet mass via regression (Badzinski, 2003, p. 157, Appendix 2). All species-specific below-ground plant parts (roots, tubers, and rhizomes) were processed separately and oven-dried as previously described for above-ground samples.

Waterfowl use of enclosure locations

Several aerial surveys conducted by the Long Point Waterfowl and Wetlands Research Fund (1998: $N=10$ from 24 September to 10 December; 1999: $N=5$, 25 September–28 November) were used to estimate numbers of swans, Canada geese, dabbling ducks (*Anas* spp), and diving ducks (*Aythya* spp) in areas where enclosures were located. Surveys were done between 10:00 and 14:00 h EST by flying predetermined transects over Long Point's wetlands. Normally, two observers (S. Petrie and R. Ridout) would estimate waterfowl numbers on each transect without reference to individual ponds (Petrie, 1998). However, during fall 1998 and 1999, the survey protocol was modified so that waterfowl also were counted on individual "ponds" where enclosures were located.

Survey data were used to develop a seasonal index of waterfowl use (waterfowl use-days) at each

study location. Data were included in calculations only if they were collected after initial enclosure placement and before late-season sampling was done at each location. Because Inner Long Point Bay is an extensive, open water area that could not be reduced into discrete "ponds", waterfowl numbers were counted on transects flown over the Smith Marsh and mouth of Big Creek; those numbers were used in site-specific waterfowl use-day calculations. Numbers of waterfowl were converted to use-days by multiplying the average number of birds (by species or group) counted on two successive surveys by the number of days between those surveys; these individual survey pair values were then summed to provide total waterfowl use-days during fall (see Dennis et al., 1984).

Exclosure observations

Observers who were documenting diurnal and nocturnal activities of waterfowl for another study (Badzinski, 2003) monitored and recorded use of exclosures at Bouck's pond (1998 and 1999), North Pond (1999), and Smith Marsh (1999). A total of 302 observation-hours confirmed that: (1) other aquatic herbivores were present, but waterfowl were the most abundant consumers at each location, (2) ducks and tundra swans (to a lesser extent Canada geese) fed at these locations (see Badzinski, 2003, p. 89, Table 3.9), (3) ducks entered and fed in both control plots and exclosures, (4) tundra swans (rarely Canada geese) fed in reference plots, (5) large waterfowl species could not enter exclosures.

Response variable specification

Prior to data analysis, the individual vegetation samples (above-ground = 0.25 m^2 quadrats and below-ground = 0.03 m^3 scoop samples) in each enclosure were combined and averaged to provide one sample for above-ground, below-ground, and species-specific biomass estimates for each structure within each sampling period. Above-ground biomass is reported as g/m^2 and below-ground biomass is reported as g/m^3 .

Several different response variables were used in the analyses that follow. Above-ground biomass was the total dry mass of the plant parts for all species that were above the marsh substrate,

whereas below-ground biomass was the total dry mass of all subterranean plant parts of all species. The dry mass of *Chara* spp and above-ground and below-ground biomasses of wild celery and sago pondweed (combined) were also analyzed separately; combined tuber dry mass and tuber density of these species were also included in analyses. All of the preceding response variables were used to determine if plant biomass differed among treatments in the early and late sampling periods, but another set variables was used to determine if the treatments showed different relative changes from the early to late sampling periods. The following formula was used to calculate proportional change in biomass (Y) during fall:

$$\exp(\ln(a + \text{min}) - \ln(b + \text{min})) - 1 \quad (1)$$

where \exp = the natural logarithm raised to the power specified in the parentheses, \ln = the natural logarithm, a = late season sample mass, b = early season sample mass, and min = the minimum observed value for either a or b in the dataset for a response variable. The minimum value of the variable of interest in the dataset was added as a constant to both a and b because the natural logarithm of zero is undefined (Zar, 1996).

Statistical model selection and parameter estimation

We used an information-theoretic approach to evaluate statistical models and to provide estimates for effects of biological interest (Burnham & Anderson, 1998). This analytical method evaluates the strength of evidence favoring each statistical model specified in a candidate set of models and reduces bias in estimation of effect sizes and precision when model-averaging techniques are used (see Burnham & Anderson, 1998; Anderson et al., 2000). Akaike's Information Criterion with correction for small sample size (AIC_c) was used to select the best statistical model (i.e., the one with the lowest AIC_c or ΔAIC_c of zero) from a predetermined set of biologically meaningful candidate models. We used model averaging to incorporate model selection uncertainty into estimation of the treatment effect and its measure of precision (Burnham & Anderson, 1998). Model selection was done separately for analyses evaluating treat-

ment effects for: (1) early season plant biomass and tuber density (pre-waterfowl exposure), (2) late season plant biomass and tuber density (post-waterfowl exposure), and (3) relative (%) change in plant biomass or tuber density during fall (PROC MIXED; SAS Institute Inc., 1990).

Analyses using only early season data were done to determine if treatments or treatments within enclosure locations showed any differences in biomass or tuber density before exposure to waterfowl feeding activities. If differences were detected, we could then control for them by including early season biomass estimates as covariates in other analyses. To assess variation in initial plant biomass and tuber density estimates among treatments, three candidate models were developed that included effects and interactions of location (1998: North Pond, Bouck's Pond, & Teal Pond; 1999: North Pond, Bouck's Pond, Mouth of Big Creek, and Smith Marsh), enclosure set (1, 2, and 3) nested within location, and treatment (swan access [control plot] & no swan access [enclosure]) (see Table 4 for similar models). We included a model in the candidate set that lacked all treatment effects, {L, S(L)} (i.e., a candidate set "null" model), which assessed the strength of evidence for treatment effects in these data.

The amount of vegetation or density of below-ground plant parts remaining late in the fall was used as a response variable in evaluating if large herbivorous waterfowl removed more aquatic plants during fall than did other biotic and abiotic factors. Three candidate models, identical to those listed above, were specified to evaluate the strength of evidence for the prediction that control plots, as compared to enclosures, would have both reduced biomass and tuber densities during late fall (see Table 3). In this analysis, we have included an additional explanatory variable (P), early season (initial) plant biomass, to control for any effect that potential differences in early season biomass may possibly have on among enclosure differences observed later in the season. Again, one model lacking treatment effects was included to evaluate if treatment effects were substantially different between enclosure types.

We also evaluated the proportional change in aquatic vegetation during fall because it was another relative measure of the intensity of plant removal. If large waterfowl, as compared to other

biotic and abiotic factors, had an additive effect on removal of aquatic plants, then proportional seasonal changes in plant biomasses and tuber densities in control plots should be larger than those within exclosures. We developed three candidate models, one of which lacked treatment effects, to determine if seasonal removal intensity of plant biomass and tubers differed between treatments (see Table 4).

To aid in assessing the strength of evidence for each candidate model, relevant model selection information (R^2 [explained variation], K [number of parameters], N [sample size], ΔAIC_c , and $^W AIC_c$) were reported in tables. Model averaged least-squares means and $\pm 95\%$ confidence intervals ($\pm 95\%$ CI) for treatment effects were reported in all tables and text.

Results

Waterfowl and other herbivore use of exclosure locations

All study locations received much use by waterfowl during 1998 (range: 45,764–1,009,313 water-

fowl use-days) and 1999 (range: 57,393–924,623) (Table 1). During fall both years, Bouck's Pond had the highest number of waterfowl use-days, largely as a result of relatively greater use by diving ducks as compared to the other locations; this site also had the highest use by tundra swans each year. Ducks, especially dabbling ducks, showed much higher use of exclosure ponds than did larger herbivores; this pattern was evident at each location during both study seasons (Table 1). Further, a notable number and percentage of all waterfowl and duck use-days were recorded at each study location before swan arrival each year (Table 2).

Waterfowl exclosure and vegetation study

Early season plant biomass

For all six sets of analyses, there was no support ($^W AIC_c = 0.00$) that any estimate of initial above- and below-ground biomass or tuber density differed substantially between treatments within study locations (L×T) during fall; there also was virtually no support ($^W AIC_c = 0.01$ for all analyses) for an overall treatment effect in these data. Further, inspection of model averaged least

Table 1. Use of exclosure locations by waterfowl during fall 1998 and 1999 at Long Point, Ontario

Year and location (area)	Tundra swan		Canada geese		Large waterfowl ^a		<i>Anas</i> spp		<i>Aythya</i> spp		Total waterfowl	
	Use-days	#	Use-days	#	Use-days	#	Use-days	#	Use-days	#	Use-days	#
<i>1998</i>												
North pond (0.02 km ²)	2625	63	899	7	3577	70	42177	343	0	0	45764	412
	6		2		8		92		0			
Bouck's pond (0.25 km ²)	43523	813	435	4	44570	817	735305	7477	229438	1845	1009313	10138
	4		<1		4		73		23			
Teal pond (0.05 km ²)	2500	44	2156	15	4796	59	63970	513	0	0	68766	572
	4		3		7		93		0			
<i>1999</i>												
North pond (0.02 km ²)	28000	450	10390	74	3844	524	87985	700	0	0	126433	1224
	22		8		30		70		0			
Bouck's pond (0.25 km ²)	35315	667	9549	59	46462	726	557912	4473	320250	2870	924623	8069
	4		1		5		60		35			
Big creek mouth and Smith marsh (0.75 km ²)	5422	229	0	0	5837	229	1926	15	49630	1026	57393	1271
	10		0		11		3		86			

Species/group-specific and total number of use-days, average number of individuals counted (#), and the percentage of total waterfowl use-days (% shown below Use-days) are shown for each exclosure location.

^aLarge waterfowl = combined use-days and numbers of tundra swans, mute swans (*Cygnus olor*), and Canada geese; thus, percentages will not sum to 100%.

Table 2. Waterfowl use of enclosure locations before (Pre) and after (Post) tundra swan arrival during fall 1998 and 1999 at Long Point, Ontario

Year and location	Waterfowl use-days (% of use-days)									
	Canada geese		<i>Anas</i> spp		<i>Aythya</i> spp		Total duck		Total waterfowl	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
<i>1998</i>										
North pond	468	431	29070	13107	0	0	29070	13107	29538	13538
	52	48	69	31	0	0	69	31	69	31
Bouck's pond	60	375	144341	590964	8475	220963	152816	811927	152876	812302
	14	86	20	80	4	96	16	84	16	84
Teal pond	2156	0	40430	23540	0	0	40430	23540	32597	33529
	100	0	63	37	0	0	63	37	49	51
<i>1999</i>										
North pond	2900	7490	18633	69353	0	0	18633	69353	21533	76843
	28	72	21	79	0	0	21	79	22	78
Bouck's pond	3466	6083	50185	507728	0	320250	50185	827978	53650	834061
	36	64	9	91	0	100	6	94	6	94
Big creek mouth and Smith marsh	0	0	1044	882	0	49630	1044	50512	1044	50512
	0	0	54	46	0	100	2	98	2	98

Species/group-specific and total number of use-days and the percentage (% are shown below pre- and post-use-days) of use-days are shown for each enclosure location.

squares means and their 95% confidence intervals clearly showed no difference in any initial above-ground, below-ground, and tuber biomass estimate obtained from exclosures and reference plots (Figure 3). However, because there was some (albeit very weak) support of an overall treatment effect, we decided to include early season biomass estimates in models describing variation in late season biomass as covariates to control for any possible confounding effect.

Late season plant biomass

The best model describing variation in all estimates of late season above-ground (total, *Chara* spp, and combined *V. americana* and *P. pectinatus*), below-ground (total and combined *V. americana* and *P. pectinatus*) and tuber (combined *V. americana* and *P. pectinatus*) biomass overwhelmingly ($^W\text{AIC}_c$: 0.99–1.00) was one that contained only effects of study location, exclosure set nested within location, and early season biomass (i.e., the candidate set null model, {L, S(L), P}) (Table 3). The two other models, {L, S(L), P, T} and {L, S(L), P, T, L×T} both had extremely low model weights in the six sets of analyses ($^W\text{AIC}_c \leq 0.01$), which suggested there was virtually no support for any kind of

treatment effect. Thus, model averaged means showed that there were no real differences in the amount of remaining above-ground, below-ground, and tuber biomass in areas where large waterfowl had access to aquatic plants (control plots) as compared to where their access was restricted (exclosures) (Figure 3).

Proportional change in plant biomass

Model selection criterion indicated the candidate set null model, {L, S(L)}, was overwhelmingly ($^W\text{AIC}_c$: 0.93–0.99) the best model describing variation in each of the six measures of relative change in above- and below-ground biomass (Table 4). As such, there again was only very weak support ($^W\text{AIC}_c$: 0.01–0.07) for an overall treatment effect ({L, S(L), T}) and no support ($^W\text{AIC}_c=0.00$) for an added effect of treatment dependent on study area ({L, S(L), T, L×T}) in these six sets of analyses (Table 4). Above-ground and below-ground biomass of all focal plant species (or species-groups) showed substantial reductions throughout fall, but there was no real difference in relative change between areas where large waterfowl could and could not access aquatic plants (Fig. 4). For example, in both controls and

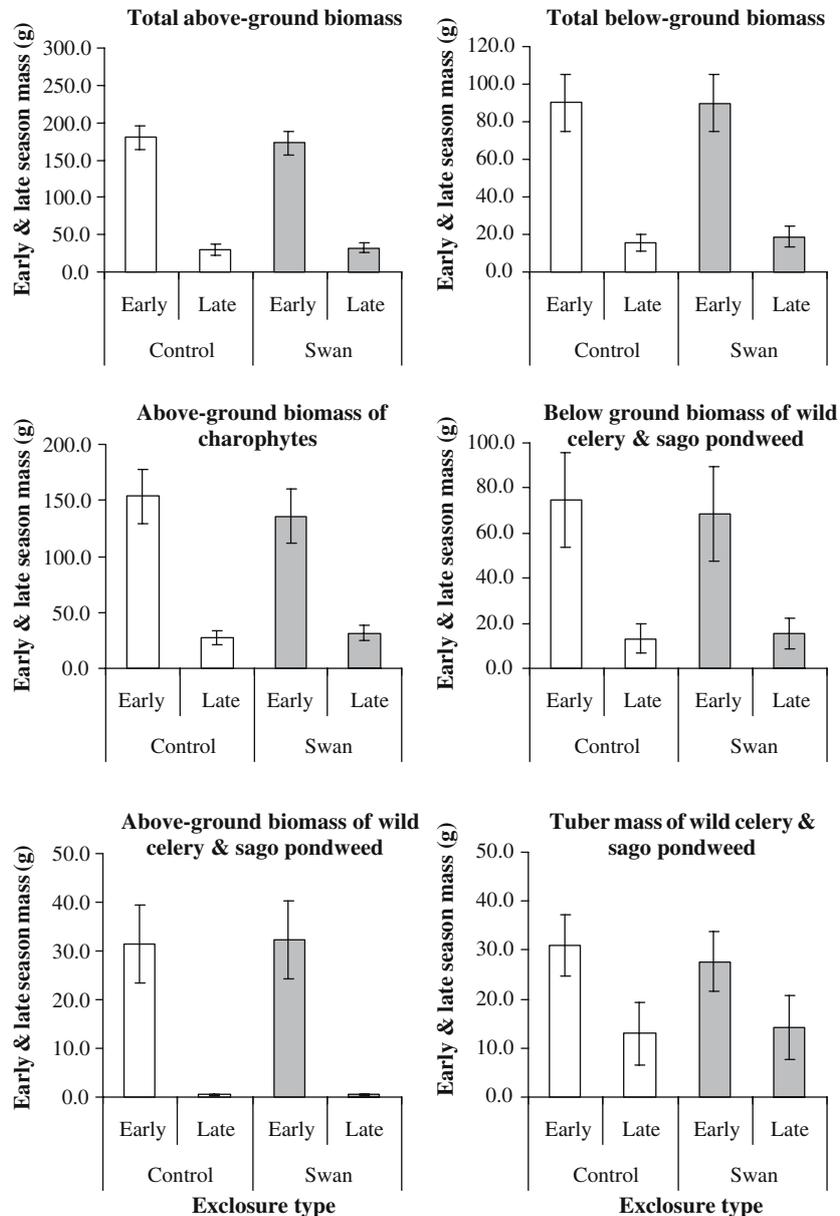


Figure 3. Early and late season estimates for the amount of dry above-ground (g m^{-2}), below-ground (g m^{-3}), and tuber (g m^{-3}) biomass present in reference/control plots (control) and swan enclosures (swan) during the 1998 and 1999 fall staging seasons at Long Point, Lake Erie, Ontario.

enclosures, total above- and below-ground biomass decreased by about $80 \pm 7\%$ during fall, whereas biomass of *Chara* spp declined by about $73 \pm 6\%$. Regardless of treatment, nearly all ($100 \pm 1\%$) above ground parts of both *V. Americana* and *P. pectinatus* were gone by early December each year, but below ground biomass of these species declined by $76 \pm 6\%$ throughout the

fall, whereas combined tuber mass of these two species declined by about $43 \pm 28\%$.

Discussion

The primary impetus for this study was concern that large numbers of large-bodied, herbivorous

Table 3. Model selection information for among enclosure variation in above- and below-ground biomass of aquatic plants after they were exposed to waterfowl during fall at Long Point, Ontario

Response variable (Y =) late season biomass	Model	<i>n</i>	<i>R</i> ²	<i>K</i>	AIC _c	ΔAIC _c	^W AIC _c
<i>Above-ground (g/m²)</i>							
Total above-ground	{L, S(L), P}	42	0.86	23	422.42	0.00	0.99
	{L, S(L), P, T}		0.86	24	432.97	10.55	0.01
	{L, S(L), P, T, L×T}		0.92	30	521.05	98.62	0.00
<i>Chara</i> spp	{L, S(L), P}	28	0.93	16	273.50	0.00	1.00
	{L, S(L), P, T}		0.94	17	284.90	11.40	0.00
	{L, S(L), P, T, L×T}		0.98	21	358.17	84.68	0.00
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.47	21	-34.19	0.00	0.99
	{L, S(L), P, T}		0.50	22	-24.70	9.49	0.01
	{L, S(L), P, T, L×T}		0.54	28	97.75	131.94	0.00
<i>Below-ground (g/m³)</i>							
Total below-ground	{L, S(L), P}	38	0.78	21	493.92	0.00	1.00
	{L, S(L), P, T}		0.78	22	500.12	10.95	0.00
	{L, S(L), P, T, L×T}		0.87	28	596.39	116.25	0.00
<i>Vallisneria americana</i> and <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.80	21	376.60	0.00	1.00
	{L, S(L), P, T}		0.80	22	387.80	11.20	0.00
	{L, S(L), P, T, L×T}		0.87	28	496.29	119.69	0.00
<i>Tubers (g/m³)</i>							
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.80	21	373.24	0.00	1.00
	{L, S(L), P, T}		0.80	22	384.81	11.57	0.00
	{L, S(L), P, T, L×T}		0.87	28	493.27	120.02	0.00

Under Model, L=location (three in 1998 & four in 1999), S=enclosure set (1, 2, and 3), S(L)=enclosure sets nested within locations, P=early season (initial) biomass of Y in enclosures, T=enclosure treatment (swan and control), L×T=interaction among locations and treatments. Shown for each candidate model are: sample size (*n*), proportion of explained variation (*R*²), number of model parameters (*K*), Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c difference (ΔAIC_c), and model weight (^WAIC_c).

waterfowl could substantially reduce the biomass of aquatic plants, and thus, directly or indirectly affect aquatic vegetation and waterfowl communities at Long Point (Petrie et al., 2002; Badzinski, 2003). Our results, however, showed that fall migrant tundra swans and Canada geese did not greatly add to the substantial seasonal reductions in total above- and below-ground biomass of aquatic vegetation, above-ground biomass of *Chara* spp, or the combined above-ground, below-ground, and tuber biomass of *V. Americana*, and *P. pectinatus*.

It was our original intent to provide data on the effect that large waterfowl may have on reducing food availability to smaller waterfowl that co-occur in time and space at a major staging area. However, within the temporal and spatial limitations of this study, it seems that diving and dabbling ducks may influence availability of some

aquatic plants, mainly *V. americana*, *P. pectinatus*, and *Chara* spp, and in turn may influence the behaviour and feeding activities of large waterfowl, especially tundra swans. There were several lines of supportive reasoning and circumstantial evidence. First, even though they are smaller, ducks were far more abundant than swans and geese. Secondly, ducks, especially dabbling ducks, begin to arrive at Long Point in sizable numbers during mid-September with peak numbers occurring in mid- to late October, whereas tundra swans generally begin to arrive late in October and reach their peak numbers during early- to mid-November (Long Point Waterfowl and Wetlands Research Fund, unpubl. data). Thus, by the time tundra swans and many Canada geese arrive, dabbling and diving ducks have been using (see Table 2) and feeding in aquatic habitats for a considerable amount of time and have already

Table 4. Model selection information for proportional changes in above- and below-ground biomass of aquatic plants among exclosures during fall at Long Point, Ontario

Response variable (Y =) Proportional change	Model	<i>n</i>	<i>R</i> ²	<i>K</i>	AIC _c	ΔAIC _c	^w AIC _c
<i>Above-ground (g/m²)</i>							
Total above-ground	{L, S(L)}	42	0.75	22	8.40	0.00	0.99
	{L, S(L), T}		0.75	23	18.44	10.04	0.01
	{L, S(L), T, L×T}		0.80	29	104.53	96.13	0.00
<i>Chara</i> spp	{L, S(L)}	28	0.77	15	2.29	0.00	0.99
	{L, S(L), T}		0.78	16	12.11	9.82	0.01
	{L, S(L), T, L×T}		0.90	20	68.74	66.45	0.00
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.47	20	-255.47	0.00	0.93
	{L, S(L), T}		0.54	21	-250.28	5.19	0.07
	{L, S(L), T, L×T}		0.65	27	-154.89	100.59	0.00
<i>Below-ground (g/m³)</i>							
Total below-ground	{L, S(L)}	38	0.84	20	274.71	0.00	0.99
	{L, S(L), T}		0.84	21	282.20	9.98	0.01
	{L, S(L), T, L×T}		0.89	27	364.85	101.86	0.00
<i>Vallisneria americana</i> and <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.44	20	79.98	0.00	0.99
	{L, S(L), T}		0.45	21	89.98	10.01	0.01
	{L, S(L), T, L×T}		0.53	27	189.43	109.46	0.00
<i>Tubers (g/m³)</i>							
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.72	20	128.81	0.00	0.99
	{L, S(L), T}		0.72	21	138.26	9.45	0.01
	{L, S(L), T, L×T}		0.76	27	238.23	109.42	0.00

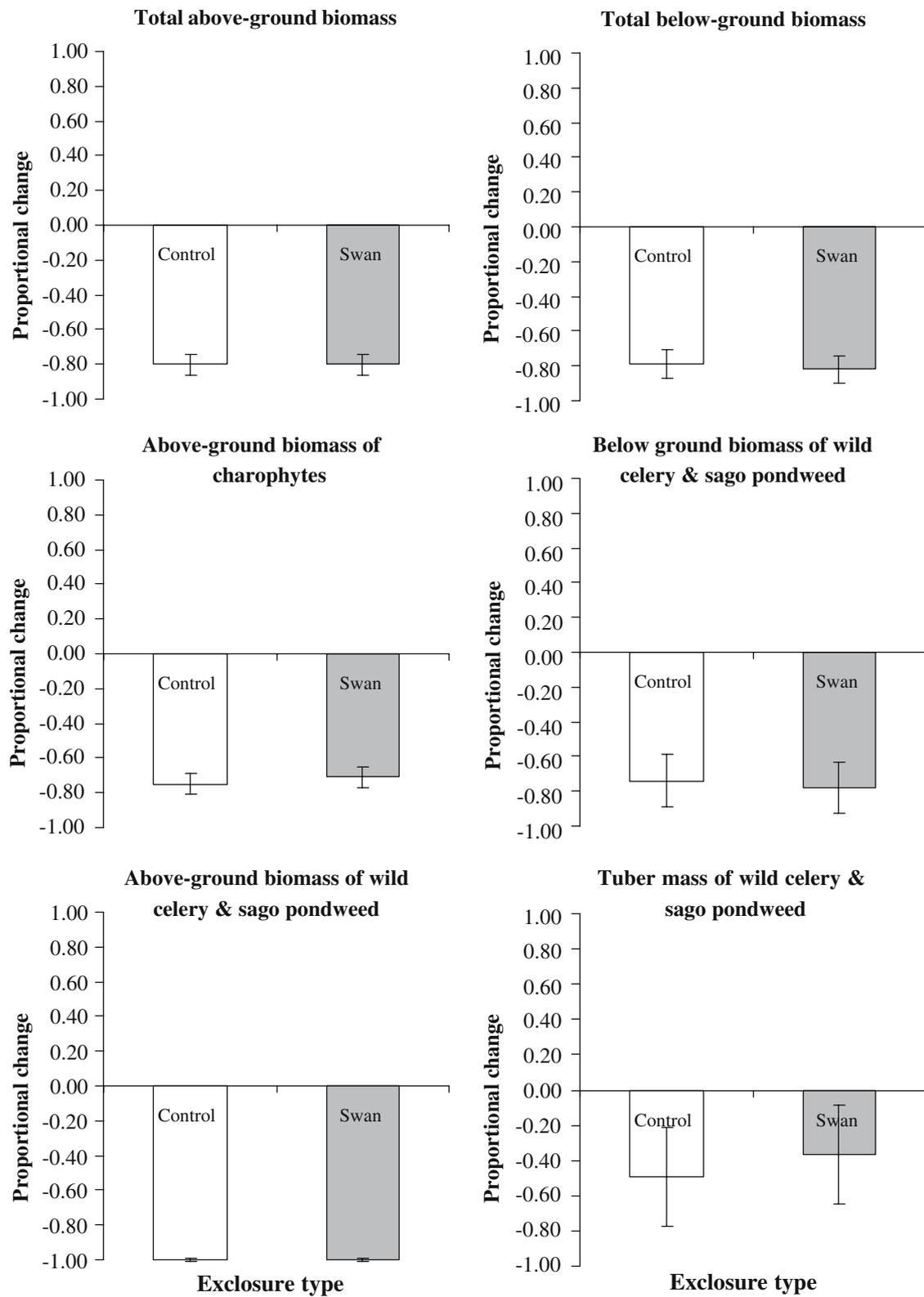
Under Model, L=location (three in 1998 and four in 1999), S=exclosure set (1, 2, and 3), S(L)=exclosure sets nested within locations, T=exclosure treatment (swan and control), L×T=interaction among locations and treatments. Shown for each candidate model are: sample size (*n*), proportion of explained variation (*R*²), number of model parameters (*K*), Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c difference (ΔAIC_c), and model weight (^wAIC_c).

consumed much of the aquatic vegetation at study locations (S. Badzinski, pers. obs.). Further, tundra swans and Canada geese only spent from 3% to 10% of the day feeding at two study locations (Badzinski, 2003), Big Creek North Pond and Little Rice Bay, both of which had high duck densities and were used heavily by many species of waterfowl before swan arrival (see Table 2). Sampling immediately before swan arrival would allow determination of how much aquatic biomass ducks, early arriving geese, and other aquatic herbivores, remove and the potential these consumers have for influencing tundra swan feeding behaviour and energetics at staging areas.

Even though large waterfowl did not further reduce the amount of aquatic plants removed from wetlands throughout the fall, the substantial seasonal decline in aquatic plant availability and biomass warrants mention. Removal of aquatic

macrophytes by waterfowl and other small aquatic consumers, wave action, and senescence all can be important factors contributing to seasonal reductions in plant biomass (see reviews Lodge, 1991; Lodge et al., 1998). Clearly, because a true control (i.e., total herbivore exclusion) was not included in this study, biomass removal effects could not be partitioned unequivocally into those attributable to each of these factors and all likely contributed, in varying degrees, to the overall decline in plant availability during fall. Despite the presence of relatively small numbers of muskrat (*Ondatra zibethicus*, Linnaeus), fish, and turtles and the occurrence of wave action and senescence, both

Figure 4. Proportional change in dry above-ground, below-ground, and tuber biomass in reference/control plots (control) and swan exclosures (swan) throughout the 1998 and 1999 fall staging seasons at Long Point, Lake Erie, Ontario.



before and during the fall staging season, the combined effect of each of these factors on biomass of *Chara* spp and below-ground and tuber biomass of *V. americana* and *P. pectinatus* likely was less than that caused by the hundreds (sometimes thousands) of migrant waterfowl (primarily ducks) that fed in and used each of these study locations each day (Badzinski, 2003; see also Tables 1 and 2).

The main finding of this study, which was that large herbivores had no additional removal effect on aquatic vegetation, should not be interpreted as evidence that tundra swans and Canada geese had no effect at all on the seasonal biomass of aquatic plants at Long Point. In fact, both of these species used study locations and foraged in them to varying degrees. Canada geese, for example, used those locations primarily as diurnal roost sites between foraging bouts to agricultural fields, and thus spent less than 3% of their time feeding there (Badzinski, 2003); geese were, however, present and fed more in aquatic habitats earlier in the fall (S. Badzinski, pers. obs.). Tundra swans almost exclusively use aquatic habitats during fall (Petrie et al., 2002) where they spend 6–54% of their time feeding (Badzinski, 2003; S. Badzinski, unpubl. data). Further, individual tundra and Bewick's swans can eat 3–5 kg (wet mass) of tubers each day at staging areas (Limpert, 1974; Beekman et al., 1991). Thus, given that tundra swans were present at study locations in sizeable numbers and were feeding on aquatic plant rhizomes and tubers (Badzinski, 2003), it was notable that we did not detect an added effect of herbivory on *V. americana* and *P. Pectinatus* tubers (see Beekman et al., 1991; Limpert & Earnst, 1994; Froelich & Lodge, 2000).

There are several possible explanations regarding why a large waterfowl did not remove considerably more vegetation from unprotected areas during this study. One reason may be that tubers in both the control plots and swan enclosures were depleted to a threshold level beyond which it became unprofitable for waterfowl to continue foraging on them (Tome, 1988; Beekman et al., 1991; Lovvorn, 1994). Such a lower feeding threshold (7.2 ± 3.4 g tuber dry-mass m^{-2}) was detected for Bewick's swans feeding on *P. pectinatus* tubers during fall in the Netherlands (Beekman et al., 1991). Our estimates of combined tuber mass (control plot: 13.3 ± 6.6 g dry-mass m^{-2} and

enclosure: 15.4 ± 6.7 g dry-mass m^{-2}) were close to the lower threshold values reported by Beekman et al. (1991), showing that tuber densities at our study locations were very low by the end of the fall staging period. Low aquatic food availability also may partly explain why tundra swans (and Canada geese) increase their use of agricultural fields during late fall and spring at Long Point (Petrie et al., 2002) and the considerable time spent feeding on crops during those periods (S. Badzinski & S. Petrie, unpubl. data).

The similarity in late season tuber densities between "enclosure" types also suggested that even if tundra swans and Canada geese did contribute to some of the removal of tubers from control plots, other waterfowl likely removed tubers to an identical, low density in areas where swans could not forage, i.e., removal by ducks compensated for the lack of "large waterfowl" herbivory. Many other herbivory studies have been done at locations where only one species or ecological group of consumers (e.g., geese) was present and biomass removal effects could be reliably attributed to one specific consumer (or group) (e.g., Bazely & Jeffries, 1986; Giroux & Bédard, 1987; Beekman et al., 1991; Conover & Kania, 1994; Mitchell & Wass, 1996). However, the potential for compensatory herbivory in aquatic habitats at Long Point, where many different species and types of consumers and removal agents were present, was very high. Thus, it was not entirely unexpected that we did not detect an additive effect due to removal of aquatic vegetation attributable solely to large waterfowl during this short-term study.

Differences in food preferences between ducks and larger waterfowl, particularly tundra swans, are another possible explanation why a "large waterfowl" herbivory effect was not detected. For example, observations and collections of foraging tundra swans showed that some of the same plants that are important duck foods, specifically *V. americana* and *P. pectinatus* tubers, were eaten by swans (Badzinski, 2003, Appendix 1). However, tundra swans also spent much time feeding in shallow water in areas dominated by emergent or floating leaved aquatic plants where they excavated and consumed the relatively large tubers (and rhizomes) of *Sagittaria latifolia*, *Sagittaria rigida*, *Nuphar variegatum*, and likely *Scirpus* spp (S. Badzinski, pers. obs., see also Limpert, 1974;

Limpert & Earnst, 1994). This was notable because smaller waterfowl at Long Point commonly consumed *Chara* spp (*Anas* and *Aythya* spp), seeds of various aquatic plants (primarily *Anas* spp), and the relatively small tubers of *V. americana* and *P. pectinatus* (primarily *Aythya* spp) (Petrie, 1998; Knapton & Petrie, 1999). Near the end of fall, however, tundra swans began to feed much more in deeper water, where large *V. americana* and *P. pectinatus* beds were located and where thousands of diving ducks had been feeding earlier (S. Badzinski, pers. obs.). This seasonal change in foraging behaviour suggests that swans had depleted other more energetically profitable and preferred foods (see also Beekman et al., 1991; Nolet & Drent, 1998). Thus, the impact that large numbers of tundra swans (and other large waterfowl) have on *V. americana* and *P. pectinatus* tuber banks may be more important during winter or during spring migration, especially at staging or wintering areas that have extensive shallow wetlands that are dominated by these plants and/or have limited availability of large tuber-producing plants (Froelich & Lodge, 2000). Wetlands such as these are present in some of the large, private hunting clubs at Long Point, so results from our study locations may not be entirely representative what is occurring throughout this large staging area. Further reductions of the tuber bank during spring in these types of wetlands could decrease primary plant production later during the growing season, which may in turn have future, longer-term consequences for plant, thus waterfowl, abundance or distribution (Anderson & Low, 1976; Tubbs & Tubbs, 1983; Idestam-Almquist, 1998; Lodge et al., 1998).

Longer-term impacts of waterfowl herbivory on the aquatic plant community remain to be determined at Long Point, but its evaluation is necessary to understand better plant–herbivore dynamics at staging areas used by tundra swans and other waterfowl. Given the importance of *Sagittaria* spp, *Nuphar* spp, and *Scirpus* spp as foods for staging tundra swans, the short-term and longer-term effects that swan herbivory have on the seasonal abundance and distribution of these plants should be determined. Future studies also should try to assess how much different consumer

groups overlap in use of specific aquatic forage plants and how herbivores affect relative abundances, compositions, and distributions of these plant species in the short-term (i.e., fall and spring staging or winter periods) and over the longer term (i.e., over several years of exposure). The relative contribution of each group of herbivores and other removal agents could be investigated by designing a more complex enclosure experiment, which also might allow more subtle indirect effects, such as compensatory herbivory, to be detected (e.g., see Evers et al., 1998; Hamilton, 2000). Broader scale and longer-term studies of aquatic plant abundance and distributions could be combined with similar investigations of waterfowl at staging areas. Doing so would greatly increase our understanding of waterfowl–plant interactions/associations and provide the framework necessary for improved monitoring of aquatic macrophyte and waterfowl populations at important waterfowl staging and wintering areas.

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