CHAPTER 4

INVERTEBRATE RESPONSE TO SNOW GOOSE HERBIVORY ON MOIST-SOIL VEGETATION

INTRODUCTION

Management of moist-soil impoundments for shorebirds and waterfowl is often aimed at creating and maintaining marsh openings. Manipulation techniques such as mowing, discing and burning may be employed to provide habitat features favored by shorebirds and waterfowl. These methods generally are targeted at increasing production of waterbird foods, particularly aquatic invertebrates. The composition and presence of impoundment vegetation also may be altered by the foraging activity of herbivorous wildlife. Greater snow geese (*Anser caerulescens atlantica*) are one species that have a profound influence on vegetation density in arctic and temperate marshes. Geese forage by grazing above-ground vegetative shoots (Smith and Odum 1981) or grubbing for below-ground roots and rhizomes (Miller et al. 1997), often causing dramatic long-term effects on the persistence of perennial marsh vegetation (Kerbes et al. 1990, Iacobelli and Jefferies 1991).

The Delmarva Peninsula is an important wintering area for Atlantic Flyway waterfowl, and has been recognized as a shorebird stopover area of hemispheric significance (Clark et al. 1993). The region also is a significant wintering area for greater snow geese (Abraham and Jefferies 1997). Moist-soil impoundments are among the habitats that may be used by snow geese, waterfowl and shorebirds in this region. Bombay Hook and Prime Hook National Wildlife Refuges, Delaware, provide roosting and foraging habitat for snow geese in brackish and freshwater impoundments. Foraging by geese on impoundment vegetation at both refuges creates extensive denuded areas (“eat-outs”). Although the habitat conditions created by snow geese are consistent with the habitat requirements of other nonbreeding waterbirds, secondary impacts of goose foraging on other species have not been documented in the literature. The high levels of use by snow geese, waterfowl and shorebirds in this region present an ideal opportunity to assess secondary impacts of goose herbivory on other species.

Range and Habitat Use of Wintering Greater Snow Geese

North American snow geese breed in the Canadian arctic and winter in midlatitude habitats in the United States and Mexico. Lesser snow geese (*Anser caerulescens caerulescens*) breed in discrete colonies across the arctic from eastern James Bay to Wrangel Island, Russia (Abraham and Jefferies 1997). Similarly, wintering birds are concentrated in discrete areas, including the Gulf Coast of Texas and Louisiana, south-central New Mexico, and the Central Valley of California (Cooke et al. 1995). In contrast, the greater snow goose population is relatively unstructured. Birds breed in several discrete colonies in the Baffin Island region of the Northwest Territories, and winter on the mid-Atlantic coast, with heavy concentrations on the Delmarva Peninsula (Abraham and Jefferies 1997).

Despite differences in population structure, both subspecies have experienced dramatic population growth in recent decades. The midwinter index of midcontinent lesser snow geese rose from 0.8 million birds in 1969 to 2.7 million birds in 1994; counts on the breeding grounds indicate that the mid-winter index accounts for approximately 50% of breeding birds (Abraham and Jefferies 1997). Similarly, the greater snow goose population grew from about 50,000 birds in the mid-1960's to over 600,000 birds in the mid-1990's (Abraham and Jefferies 1997). Several factors are believed to have contributed to population expansion: 1) Increasing availability of agricultural foods on the wintering grounds has improved winter survival; 2) Establishment of refuges with abundant food and no-harvest zones has enhanced survival during fall migration; 3) Declining hunter numbers and success rates have reduced the major source of adult mortality; and, 4) Climatic change in the arctic has led to a broader window of breeding opportunity, improving brood survival and recruitment rates (Abraham and Jefferies 1997).

Coastal marshes of the Delmarva peninsula are the primary wintering area for greater snow geese. Freshwater impoundments and tidal marshes are used primarily as roosting habitat by snow geese (Hill and Frederick 1997). Natural marsh habitats favored by wintering birds include tidal marshes dominated by *Scirpus americanus*, *Spartina patens*, and *S. alterniflora* (Smith and Odum 1981, Miller et al. 1997). However, foraging pressure on native coastal marshes is attenuated by the availability of abundant agricultural foraging habitat. Geese forage extensively in agricultural fields where these habitats provide abundant food, but also forage in freshwater impoundments where these habitats are available (Hill and Frederick 1997).

Goose-Habitat Interactions

Direct impacts of snow goose herbivory on marsh vegetation have been documented in breeding (Cargill and Jefferies 1984, Iacobelli and Jefferies 1991, Chou et al. 1992, Ganter et al. 1996, Batt 1998), staging (Smith and Odum 1981, Kerbes et al. 1990) and wintering habitats (Robertson and Slack 1995, Miller et al. 1996). Analysis of these impacts has typically been directed at assessing the ability of these habitats to support rapidly expanding goose populations. Long-term vegetation changes in heavily grazed habitats include complete vegetation removal and alteration of plant community composition, potentially rendering grazed habitats unsuitable for goose nesting or brood-rearing (Ganter et al. 1996, Batt 1998).

Extensive goose herbivory occurs primarily in freshwater arctic marshes and coastal salt marshes. The perennial vegetation communities that dominate arctic habitats do not recover in a single growing season (Abraham and Jefferies 1997), although Atlantic coastal marshes may regenerate after 2 years of exclosure from goose foraging (Smith and Odum 1981). Other abiotic factors, such as soil salinity and growing season length, may exacerbate goose impacts by limiting the number of plant species that can colonize denuded areas. In contrast, freshwater marshes typically contain an extensive seed bank, from which herbaceous annuals may regenerate in a single growing season (Van der Valk and Davis 1978, Van der Valk 1986).

Vegetation recovery after goose herbivory is likely to differ markedly between goose breeding and wintering habitats. Geese are present in breeding habitats during the growing season, and favor the emerging shoots in previously grazed areas. Although these new shoots are highly nutritious, the energetic demands of a rapidly expanding breeding population result in annual expansion of denuded areas (Abraham and Jefferies 1997). In contrast, denuded habitats on the wintering grounds have a full growing season to recover prior to arrival of geese in the subsequent fall. Previously denuded wintering habitats thus provide an entire growing season's plant biomass for geese in the subsequent season. Plant communities dominated by annuals may regenerate rapidly through seed germination, although recovery of temperate-zone perennial plants also may be rapid relative to arctic perennials (Smith and Odum 1981).

Several studies have shown changes in abundance and biomass of aquatic invertebrates following direct manipulation of vegetative cover (Kaminski and Prince 1981, Murkin et al. 1982, Batzer and Resh 1992, de Szalay and Resh 1997; see also Chapter 2) and manipulation of water levels (Murkin and Kadlec 1986, Neckles et al. 1990, Riley and Bookhout 1990, Murkin et al. 1991) in managed wetlands. Given the dependence of aquatic invertebrate abundance on plant community structure, a response by invertebrates to plant removal by snow geese could occur. Although the direct impacts of snow geese on marsh vegetation have been studied in detail, few studies have addressed potential secondary impacts of snow geese on other marsh birds. Abraham and Jefferies (1997) provide a brief discussion of lesser snow goose impacts on arctic breeding habitat of shorebirds, but do not address potential impacts on food availability for other wintering birds. The importance of the Delmarva Peninsula to nonbreeding waterfowl and shorebirds suggests that any impact of goose foraging activity on invertebrate abundance may have consequences for survival of these species.

The level of population expansion and destruction of arctic habitats of lesser snow geese generally exceeds that of greater snow geese. Description of negative impacts of geese on habitats (Abraham and Jefferies 1997) and management prescriptions for ameliorating impacts of high goose populations (Johnson 1997, Rockwell et al. 1997) have thus focused primarily on midcontinent lesser snow geese. However, greater snow goose populations are similarly increasing, and the wintering range of this subspecies coincides directly with some of the highest quality waterfowl and shorebird habitat on the Atlantic coast. Consequently, potential impacts of greater snow geese on other waterbirds should be considered in selecting management options for this species.

OBJECTIVES

The primary goal of this study was to evaluate responses of aquatic invertebrates to goose herbivory on moist-soil impoundment vegetation. Invertebrates are a significant source of food for other nonbreeding waterbirds on the study area. Thus, the study was designed to assess this impact during peak periods of residence for waterfowl and shorebirds, and to evaluate the level of invertebrate use in goose eat-outs by spring migrant shorebirds. Specific objectives of the study were to

1) Determine aquatic invertebrate abundance in areas with and without snow goose foraging activity and,
2) Determine aquatic invertebrate abundance in areas with and without predation by migrant shorebirds.

METHODS

Study Area

The study was conducted at Prime Hook National Wildlife Refuge, Milton, Delaware. The refuge is bordered to the east by Delaware Bay, and to the north, west and south by a mixture of agricultural fields, small woodlots, and nontidal marshes. Four freshwater to slightly brackish impoundments are located along the eastern edge of the refuge. Dominant emergent vegetation in the impoundments includes cattail (*Typha spp*), three-square bulrushes (*Scirpus americanus* and *S. pungens*), beggarticks (*Bidens cernua*), and common reed (*Phragmites australis*). Precipitation is the primary source of irrigation for the impoundments, although brackish water from Delaware Bay occasionally intrudes through water control structures. Drawdowns are generally conducted during late spring - early fall to stimulate germination of seed-producing annuals and submerged aquatics as food for waterfowl. Impoundment substrates are deep, soft, and highly organic. Aggregations (generally < 1cm diameter) of clay particles are common.

Peak use of Prime Hook impoundments by waterfowl occurs during winter. Dominant duck species are green-winged teal (*Anas crecca*) and northern pintail (*A. acuta*), although mallards (*A. platyrhynchos*), American black ducks (*A. rubripes*), northern shovelers (*A. clypeata*), and gadwalls (*A. strepera*) also occur. The refuge also supports approximately 100,000 greater snow geese each winter. Goose activity patterns generally include daily flights to and from adjacent agricultural fields to forage on waste grain and emergent shoots of winter wheat crops (Hill and Frederick 1997). Emergent vegetation in the impoundments also is a significant source of winter forage. Geese consume tubers and rhizomes of emergent plants, particularly cattail and three-square bulrush. Grubbing activity is concentrated in discrete areas within impoundments, creating large areas (‘eat-outs’) that are devoid of vegetation. Geese appear to exhibit philopatry to areas in which foraging activity has been high during previous winters (G. O’Shea, Prime Hook NWR, personal communication).

Sampling Plot Layout

Locations for six circular study plots were selected based on refuge records of the historical distribution of eat-outs. Study plots were equally divided among 3 impoundments (Unit II [607 ha], Unit III [1012 ha], and Unit IV [81 ha]; Fig. 4.1). As the goal of the study was to assess herbivory effects, study plot locations were not random. Rather, areas were selected in which heavy foraging activity by snow geese was deemed likely. No attempt was made to control for among-plot similarity in vegetation communities or extent of previous use by snow geese, although all plot locations had been denuded previously by geese. Within each area, a random plot center location was chosen. Plot centers were constrained such that the plot dimensions (50-m radius) would not extend beyond the likely extent of goose foraging activity.

Each plot was marked at the center with a 2.5m white PVC plastic pole, and was subdivided into 4 subplots (quarters). Within subplots, one goose exclosure and one open sampling station (both 1.2 m x 1.2 m) were located at random distance (1-50 m) and bearing from the plot center (Fig. 4.2). Goose exclosures were constructed by stapling a 0.4 m-wide strip of 1.5 cm x 1.5 cm plastic mesh to 150 cm x 2.5 cm x 1.2 cm wooden corner stakes. Additional 90-cm wooden stakes were added at the mid-point of exclosure sides for stability. Stakes were driven into the substrate until the bottom of the plastic mesh contacted the substrate surface. Plastic flagging in a high visibility color (pink or blaze orange) was tied in a criss-cross pattern over the open top of exclosures. The height of exclosures above the substrate (about 0.75 m) prevented geese from obtaining plant material by reaching over the sides. Open sampling stations were marked at the corners with wooden stakes. Goose exclosures and open sampling stations were installed in late September and early October 1996, prior to the arrival of snow geese on the study area.

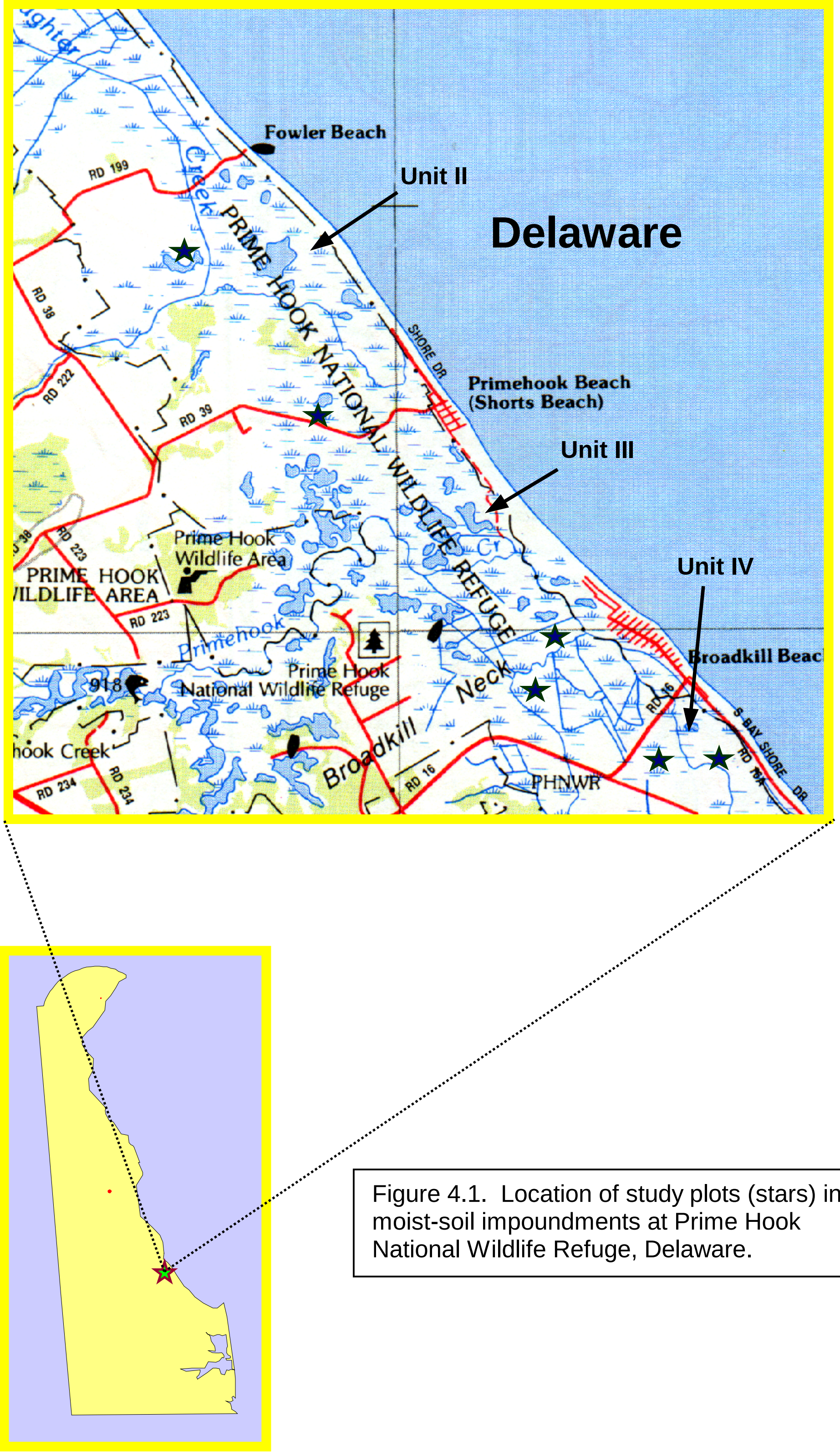

Figure 4.1. Location of study plots (stars) in moist-soil impoundments at Prime Hook National Wildlife Refuge, Delaware.

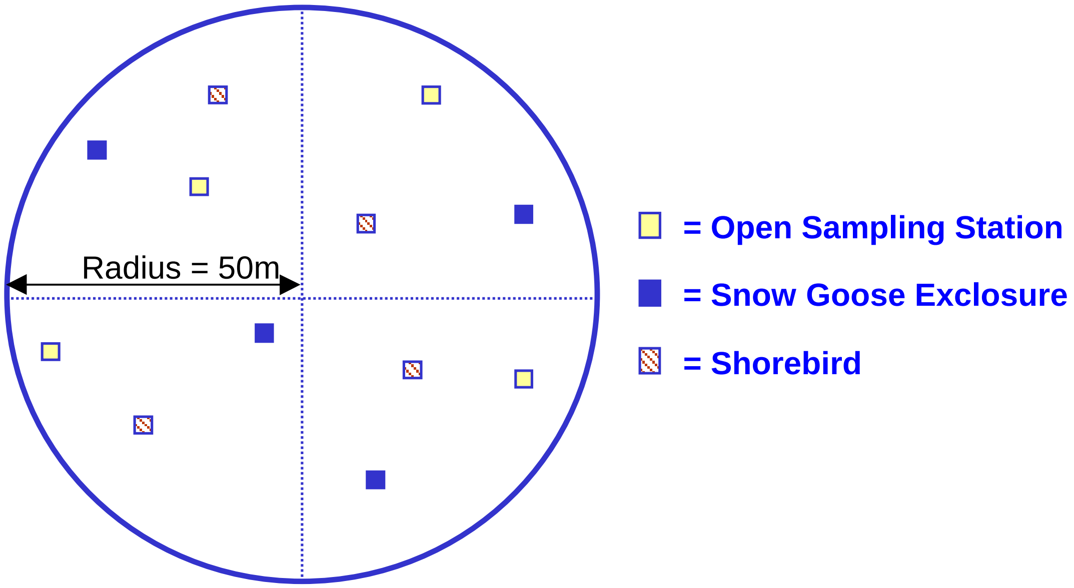

Figure 4.2. Dimensions and configuration of invertebrate sampling plots in moist-soil impoundments at Prime Hook National Wildlife Refuge, Delaware.

A second exclosure was added to a random location in each plot quarter during March 1997 to assess the impact of shorebird predation on invertebrate abundance. Shorebird exclosures were 1m x 1m in size with sides rising about 30 cm above the impoundment substrate, and lacked the extra anchor stakes at the mid-point of the sides. Flagging also was tied across the top of shorebird exclosures.

Sampling Methods

Sampling was conducted during fall 1996 (Nov), winter 1997 (Jan and Feb) and spring 1997 (Early April and Late April). Only plots in which vegetation had been completely removed by snow geese were sampled. During the Nov sampling period, geese had only removed vegetation from 2 of the 6 plots (1 in Unit IV and 1 in Unit II). Geese removed vegetation from 2 additional plots (1 in Unit IV and 1 in Unit II) between Nov and Jan, but never foraged in either of the plots in Unit III. Consequently, only 2 plots were sampled during Nov, and 4 plots were sampled for the remaining 4 sampling periods. During each sampling period, 1 core sample (10 cm diameter x 5 cm depth) was extracted from a random location within each sampling station. Sampling locations were constrained to be >20 cm from previously sampled locations and > 20 cm from the edges of sampling stations. At each sampling location, water depth (±1 cm) and temperature (±1 C) were measured and an estimate of total plant cover for the entire sampling station was recorded. Core samples were washed in the field over a 550-μm sieve and preserved in 95% ethanol stained with Rose Bengal. Samples were stored on ice in the field and in a walk-in cooler in the laboratory.

Sample volume was not appreciably reduced by field washing due to high proportions of fine organic material and clay. Visibility of invertebrates during sorting was reduced by excess organic material. Thus, sugar flotation (Lackey and May 1971) was used to separate invertebrates from organic material. Samples were washed over a 550-μm sieve in the laboratory to remove ethanol, and covered with a sugar solution in shallow plastic pans under bright light. Macroinvertebrates were removed and identified using Merritt and Cummins (1996) and Thorp and Covich (1993).

Statistical Analysis

Invertebrate density data were analyzed using repeated measures mixed linear models (PROC MIXED, Littell et al. 1996). Mixed models use an iterative approach based on maximum likelihoods to converge on variance component estimates and *F*-statistics (Littell et al. 1996). This method is preferable to general linear models (i.e., PROC GLM, SAS Institute 1990) for field studies that include both fixed and random factors. Testing of null hypotheses in such designs should account for random factors in specification of error terms (Bennington and Thayne 1994). For the purposes of these analyses, random factors of Plot(Pool), Subplot(Plot*Pool) and Sampling Station*Subplot(Plot*Pool) were included as error terms, where Pool represents the main blocking factor (impoundments).

The goal of data analysis was to test null hypotheses of 1) no change in invertebrate abundance in response to goose foraging (H_{O1}), and 2) no change in invertebrate abundance in response to shorebird predation (H_{O2}). Goose exclosures and open sampling stations were sampled during all sampling periods, whereas shorebird exclosures were present only during the last 2 sampling periods of the study. The study design was thus incomplete with respect to sampling stations and time (Table 4.1). Further, only 2 of the 3 possible comparisons among sampling stations were of interest. The design allowed testing of H_{O1} by comparing invertebrate abundance between open sampling stations and goose exclosures. Similarly, H_{O2} could be tested by comparing invertebrate abundance between open sampling stations and shorebird exclosures. It was also desirable to examine patterns of abundance both across and within months. The comparisons of interest thus constituted *a priori* hypotheses for which linear contrasts are appropriate (Mason et al. 1989). Due to the incomplete nature of the design, orthogonality of contrasts could not be maintained using one analysis with a single independent variable for sampling station type (i.e., goose exclosure, shorebird exclosure, open). However, a balanced design could be maintained by conducting a separate analysis for each of the main hypotheses. This was accomplished by generating 2 data sets, each of which was balanced and complete (Table 4.1). The first contained all observations from goose exclosures and open sampling stations for all months, and was used to test H_{O1}. The second contained all

Table 4.1. Number of goose exclosures, open sampling stations, and shorebird exclosures sampled during 5 periods at Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Datasets used to test null hypotheses of no goose herbivory effects on invertebrate abundance (H_{O1}) and no shorebird predation effects on invertebrate abundance (H_{O2}) are indicated in boxes.

	Nov	Jan	Feb	Early Apr	Late Apr	
Goose Exclosures	8	16	16	16	16	
Open Sampling Stations	8	14	16	16	16	H_{O1}
Shorebird Exclosures				16	16	H_{O2}

observations from shorebird exclosures and open sampling stations for Early Apr and Late Apr, and was used to test H_{O2}. Each analysis included a single classification variable that corresponded to sampling station type; the *F*-statistic associated with this variable was used to test the overall hypothesis of interest. Month * Sampling Station interactions were examined using linear contrasts to test hypotheses of no difference in invertebrate abundance between sampling stations and within months. Both analyses consisted of a full mixed linear model, including Month, Pool (i.e., impoundment), Treatment (Goose Herbivory or Shorebird Predation), and all 2- and 3-way interaction terms.

The above analyses were conducted for each of 7 response variables, each of which corresponded to one or more taxonomic groups (Table 4.2). A separate test of H_{O1} (goose herbivory effects) also was conducted for water temperature, water depth and plant cover. H_{O2} was not tested for these variables because an influence of shorebird predation was deemed unlikely. Invertebrate abundance was expressed as number of individuals / core sample. Water temperature, water depth, and all invertebrate abundance data were $\log_{10}(x + 1)$-transformed prior to analysis; plant cover data were $\arcsin(x^{0.5})$-transformed (Sokal and Rohlf 1995). All means are presented ± 1 SE. As the consequences of Type II error were deemed minimal, statistical significance was accepted at $P < 0.10$.

RESULTS

Habitat Variables

Goose herbivory significantly reduced herbaceous plant cover (Fig. 4.3, Table 4.3) and water temperature (Fig. 4.4, Table 4.4). Residual plant cover remained in exclosures in Nov; percent cover estimates in both open sampling stations and exclosures declined from Nov to Late Apr (Fig. 4.3). The maximum water temperature difference between open sampling stations (8.4 ± 0.4 C) and exclosures (10.4 ± 0.3 C) occurred during February (Fig. 4.4), although the Month * Herbivory interaction was nonsignificant for water temperature (Table 4.4). Water temperature was highest during Late Apr and lowest during Jan (Fig. 4.4). Water depth was substantially lower during early Apr than in other months (Fig. 4.5). The Herbivory main effect, interactions with

Table 4.2. Mean abundance (# / core sample) of invertebrate taxa in open sampling stations, snow goose exclosures, and shorebird exclosures in 2 moist-soil impoundments at Prime Hook National Wildlife Refuge, Delaware, Fall 1996 – Spring 1997.

	November				**January**				**February**			
	Open		**Goose Exclosure**		**Open**		**Goose Exclosure**		**Open**		**Goose Exclosure**	
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Chironomidae	**6.4**	**1.9**	**4.6**	**1.2**	**5.1**	**2.2**	**24.4**	**7.0**	**1.9**	**0.8**	**3.2**	**1.1**
Other Diptera												
Certaopogonidae	0.6	0.3	0.5	0.2	1.9	0.9	1.6	0.3	0.3	0.1	0.2	0.1
Dolichopodidae	0.2	0.2	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.1
Ephydridae	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Muscidae	0.5	0.3	0.9	0.4	0.0	0.0	4.0	0.2	0.2	0.1	0.5	0.2
Stratiomyidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tabanidae	0.0	0.0	0.6	0.4	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.1
Tipulidae	0.4	0.4	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.1
Unknown Diptera	0.5	0.3	0.4	0.2	1.3	0.7	0.1	0.1	0.1	0.1	0.5	0.4
Diptera Adults	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Diptera Pupae	1.1	0.7	0.7	0.5	0.2	0.1	0.2	0.1	0.2	0.1	1.3	0.6
Total	**3.4**	**0.5**	**3.4**	**0.8**	**3.8**	**1.2**	**2.3**	**0.5**	**0.9**	**0.2**	**2.9**	**0.8**
Coleoptera												
Adults	0.2	0.2	0.4	0.2	0.5	0.2	0.8	0.3	0.0	0.0	0.8	0.6
Larvae	2.4	0.8	4.0	1.7	1.1	0.5	0.8	0.3	0.2	0.1	1.0	0.3
Total	**2.6**	**1.0**	**4.4**	**1.7**	**1.6**	**0.5**	**1.6**	**0.4**	**0.2**	**0.1**	**1.8**	**0.6**
Other Insects												
Collembola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corixidae	0.2	0.2	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odonata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Total	**0.2**	**0.2**	**0.0**	**0.0**	**0.1**	**0.1**	**0.0**	**0.0**	**0.0**	**0.0**	**0.1**	**0.1**
Oligochaeta	**8.6**	**1.7**	**8.1**	**1.5**	**2.9**	**0.7**	**5.6**	**1.8**	**9.2**	**1.6**	**31.4**	**12.2**

Table 4.2 Cont'd.

	November				**January**				**February**			
	Open		**Goose Exclosure**		**Open**		**Goose Exclosure**		**Open**		**Goose Exclosure**	
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Other Invertebrates												
Arachnid	0.0	0.0	0.4	0.2	0.0	0.0	0.2	0.1	0.0	0.0	0.2	0.1
Copepoda	11.4	5.3	1.1	0.6	3.6	2.3	1.4	0.6	2.9	1.0	7.7	2.9
Daphnia	3.1	1.8	2.4	1.0	0.7	0.5	1.1	0.6	0.7	0.3	0.7	0.2
Egg Masses	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1
Gammaridae	0.1	0.1	0.2	0.2	0.0	0.0	0.1	0.1	0.1	0.1	0.3	0.2
Isopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	1.2	0.9	0.9	0.4	0.3	0.2	0.3	0.2	0.3	0.2	0.3	0.2
Misc. / Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**15.9**	**6.4**	**5.0**	**1.5**	**4.6**	**2.4**	**3.3**	**0.7**	**4.0**	**1.1**	**9.5**	**3.1**
Total Invertebrates	**37.1**	**7.5**	**25.5**	**2.3**	**18.2**	**4.6**	**37.2**	**8.1**	**16.2**	**2.4**	**48.9**	**14.7**

Table 4.2 Cont’d.

	Early April						**Late April**					
	Open		**Goose Exclosure**		**Shorebird Exclosure**		**Open**		**Goose Exclosure**		**Shorebird Exclosure**	
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Chironomidae	**3.3**	**0.7**	**32.0**	**13.5**	**3.1**	**1.2**	**2.9**	**1.2**	**4.9**	**2.1**	**8.6**	**3.8**
Other Diptera												
Certaopogonidae	0.7	0.3	1.0	0.4	1.2	0.8	0.4	0.2	0.6	0.2	1.1	0.7
Dolichopodidae	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.1	0.1	0.1	0.1
Ephydridae	2.1	0.8	0.9	0.4	1.4	0.7	12.2	6.1	3.4	1.4	7.4	3.5
Muscidae	1.1	0.4	1.3	1.1	0.4	0.3	0.7	0.3	1.2	0.4	0.2	0.1
Stratiomyidae	0.0	0.0	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1
Tabanidae	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Tipulidae	0.7	0.4	6.7	3.6	0.6	0.5	0.9	0.4	3.7	2.0	1.3	1.0
Unknown Diptera	0.1	0.1	0.1	0.1	0.6	0.4	0.1	0.1	0.1	0.1	0.3	0.2
Diptera Adults	0.1	0.1	0.9	0.5	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.0
Diptera Pupae	3.2	1.1	14.5	7.6	1.2	0.7	1.9	0.9	4.1	1.8	1.2	0.3
Total	**8.1**	**0.7**	**24.9**	**11.6**	**5.5**	**1.8**	**16.7**	**6.3**	**13.4**	**4.0**	**11.8**	**3.4**
Coleoptera												
Adults	0.1	0.1	1.2	0.5	0.1	0.1	0.2	0.2	0.8	0.6	0.6	0.6
Larvae	0.5	0.2	0.3	0.1	0.6	0.4	0.4	0.1	0.6	0.2	0.5	0.2
Total	**0.6**	**0.2**	**1.6**	**0.5**	**0.7**	**0.5**	**0.6**	**0.3**	**1.4**	**0.6**	**1.1**	**0.5**
Other Insects												
Collembola	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.0
Corixidae	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Hemiptera	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Odonata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**0.1**	**0.1**	**0.1**	**0.1**	**0.0**	**0.0**	**0.1**	**0.1**	**0.1**	**0.1**	**0.1**	**0.1**
Oligochaeta	**136.2**	**37.3**	**155.9**	**47.2**	**191.3**	**66.6**	**69.0**	**30.4**	**75.9**	**23.0**	**120.1**	**65.6**

Table 4.2 Cont'd.

	Early April						**Late April**					
	Open		**Goose Exclosure**		**Shorebird Exclosure**		**Open**		**Goose Exclosure**		**Shorebird Exclosure**	
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Other Invertebrates												
Arachnid	0.0	0.0	0.7	0.4	0.5	0.5	0.1	0.1	0.4	0.2	0.1	0.1
Copepoda	19.1	10.2	23.9	12.5	15.1	6.9	8.6	3.5	22.4	11.8	15.0	7.6
Daphnia	0.6	0.3	0.7	0.5	0.3	0.2	1.5	1.0	2.2	1.4	1.7	1.6
Egg Masses	0.4	0.2	1.2	0.9	0.1	0.1	1.2	0.8	1.0	0.7	0.0	0.0
Gammaridae	0.3	0.1	0.7	0.3	1.0	0.6	0.2	0.1	0.1	0.1	0.8	0.4
Isopoda	0.1	0.1	0.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.4	0.3	1.8	1.6	1.4	0.9	0.2	0.1	1.8	1.8	1.4	1.4
Misc. / Other	0.2	0.1	1.1	1.0	0.1	0.1	0.2	0.1	0.1	0.1	0.6	0.3
Total	**21.2**	**10.2**	**31.9**	**12.6**	**18.5**	**7.2**	**12.0**	**3.7**	**28.1**	**11.6**	**19.6**	**7.8**
Total Invertebrates	**169.4**	**36.8**	**246.4**	**47.7**	**219.1**	**67.4**	**101.3**	**31.5**	**123.8**	**29.3**	**161.2**	**68.6**

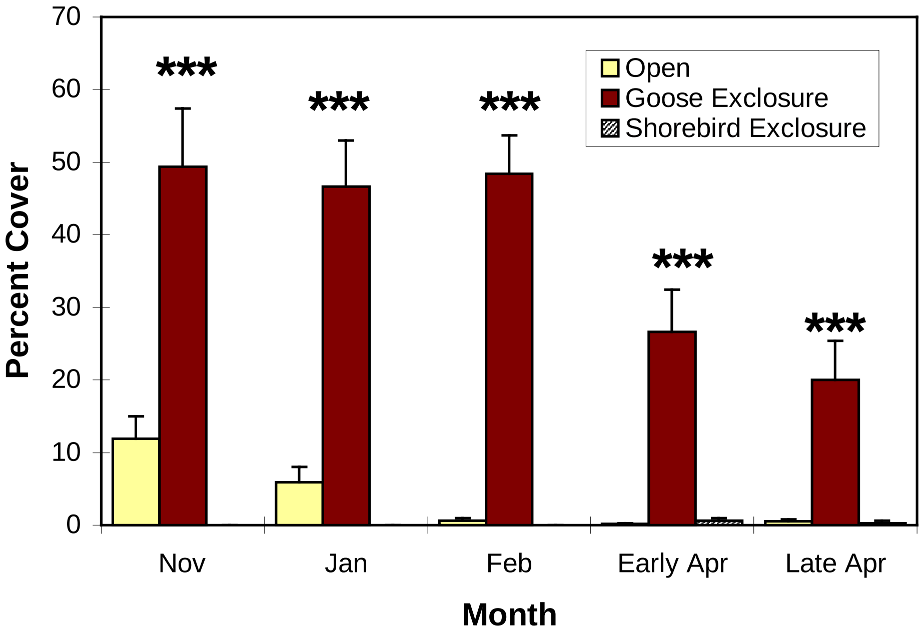

Figure 4.3 Mean (+ SE) percent cover of herbaceous plants in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: $P < 0.10$, **: $P < 0.05$, ***: $P < 0.01$) difference between snow goose exclosures and open sampling stations within months.

Table 4.3. Results of mixed model analysis of variance for Pool, snow goose Herbivory, and Month effects on herbaceous plant cover in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97.

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.04	0.857			
Herbivory	1,14	103.79	<0.001			
Pool * Herbivory	1,14	2.80	0.116			
Month	4,96	24.40	<0.001			
Month * Pool	4,96	1.00	0.409			
Month * Herbivory	4,96	6.93	<0.001			
Nov				1,96	32.62	<0.001
Jan				1,96	69.69	<0.001
Feb				1,96	114.90	<0.001
Early Apr				1,96	46.88	<0.001
Late Apr				1,96	29.09	<0.001
Month * Pool * Herbivory	4,96	2.90	0.026			

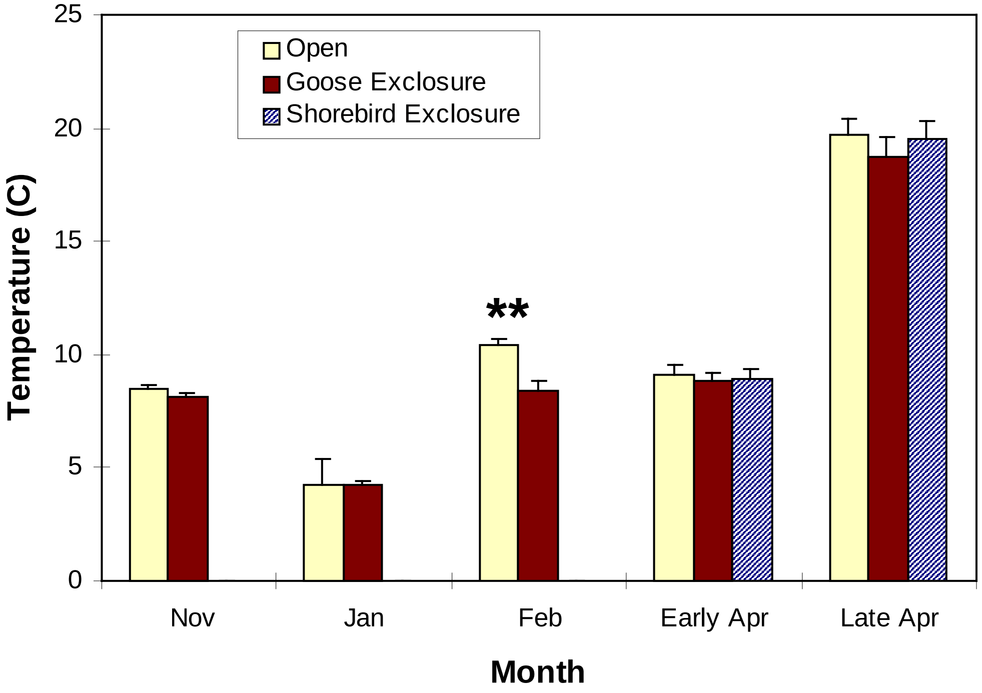

Figure 4.4. Mean (+ SE) water temperature (C) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: P < 0.10, **: P < 0.05, ***: P < 0.01) difference between snow goose exclosures and open sampling stations within months.

Table 4.4. Results of mixed model analysis of variance for Pool, snow goose Herbivory, and Month effects on water temperature in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97.

	Main Effects			Contrasts		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.91	0.442			
Herbivory	1,14	3.98	0.066			
Pool * Herbivory	1,14	0.63	0.442			
Month	4,96	503.95	<0.001			
Month * Pool	4,96	10.04	<0.001			
Month * Herbivory	4,96	0.71	0.588			
Nov				1,96	0.46	0.500
Jan				1,96	0.03	0.864
Feb				1,96	4.66	0.033
Early Apr				1,96	0.53	0.467
Late Apr				1,96	1.47	0.228
Month * Pool * Herbivory	4,96	0.25	0.907			

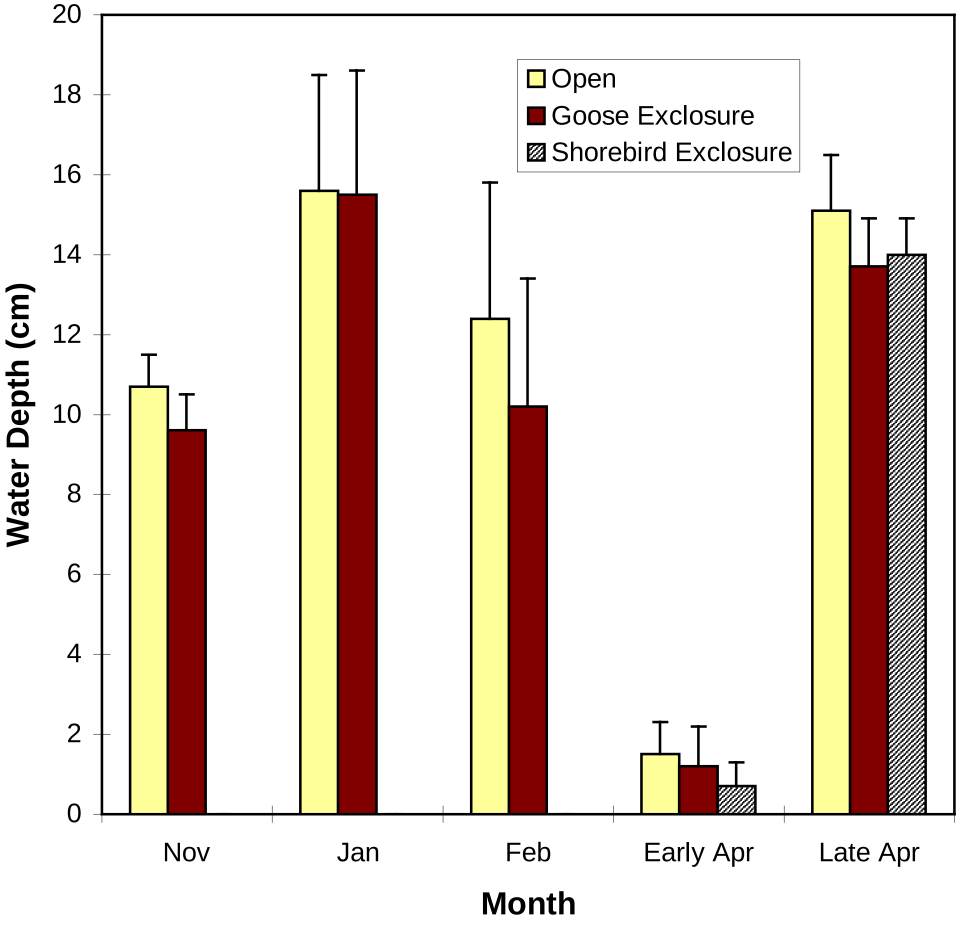

Figure 4.5. Mean (+ SE) water depth (cm) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97.

Table 4.5. Results of mixed model analysis of variance for Pool, snow goose Herbivory, and Month effects on water depth in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97.

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.05	0.846			
Herbivory	1,14	1.61	0.226			
Pool * Herbivory	1,14	0.16	0.699			
Month	4,96	57.36	<0.001			
Month * Pool	4,96	11.29	<0.001			
Month * Herbivory	4,96	0.14	0.969			
Nov				1,96	0.10	0.749
Jan				1,96	0.10	0.757
Feb				1,96	1.45	0.232
Early Apr				1,96	0.60	0.440
Late Apr				1,96	0.13	0.719
Month * Pool * Herbivory	4,96	0.22	0.929			

Herbivory, and linear contrasts for the Month * Herbivory interaction were all nonsignificant for water depth (Table 4.5). Among habitat variables, spatial variation (i.e., significant Pool effect or interaction) was evident only for plant cover (Month * Pool * Herbivory; Table 4.3).

Herbivory Effects on Invertebrates

Total Invertebrates.—Among months, Total Invertebrate density was significantly higher in exclosures than in open sampling stations during Jan and Feb (Fig. 4.6). Total Invertebrate density was substantially lower during Nov – Feb than during April (Fig. 4.6). Total invertebrate density across all months was higher (*P* = 0.051) in goose exclosures (104.2 ± 16.1 individuals / sample) than in open sampling stations (73.5 ± 13.2 individuals / sample) (Table 4.6). The Pool effect and both interactions with Pool were nonsignificant (*P* > 0.14; Table 4.6).

Diptera.—Chironomid density was 4.8 and 9.7 x higher in goose exclosures than in open sampling stations during January and Early Apr, respectively (Table 4.2, Fig. 4.7). However, no herbivory effect was detected during Feb (*P* = 0.305; Fig. 4.7, Table 4.7). Mean density in goose exclosures during Jan and Early Apr was substantially higher than in all other sampling station x month combinations (Fig. 4.7). Density of Other Diptera was higher in goose exclosures only during Feb (*P* = 0.081, Fig. 4.8, Table 4.8). However, densities during this period were among the lowest of the observed means (Fig. 4.8).

Other Insect Orders.—Coleoptera density was 6.0 and 2.7 x higher in goose exclosures than in open sampling stations during February and Early Apr, respectively (Fig. 4.9, Table 4.9). Coleoptera density was highest during Nov, but exhibited little variation from Jan to late Apr (Fig. 4.9). Density of Other Insects was extremely low; these taxa generally occurred in about 10% of samples (Table 4.2). Accordingly, differences in density between goose exclosures and open sampling stations were significant only during Nov, when no Other Insects occurred in goose exclosures (Fig. 4.10). The Month * Pool * Herbivory interaction was significant for Coleoptera (*P* = 0.069; Table 4.9), but not for Other Insects (*P* = 0.388; Table 4.10).

Other Invertebrate Taxa.—Oligochaetes were among the most abundant invertebrates on the study area (Table 4.2). Accordingly, temporal patterns of Total Invertebrate abundance

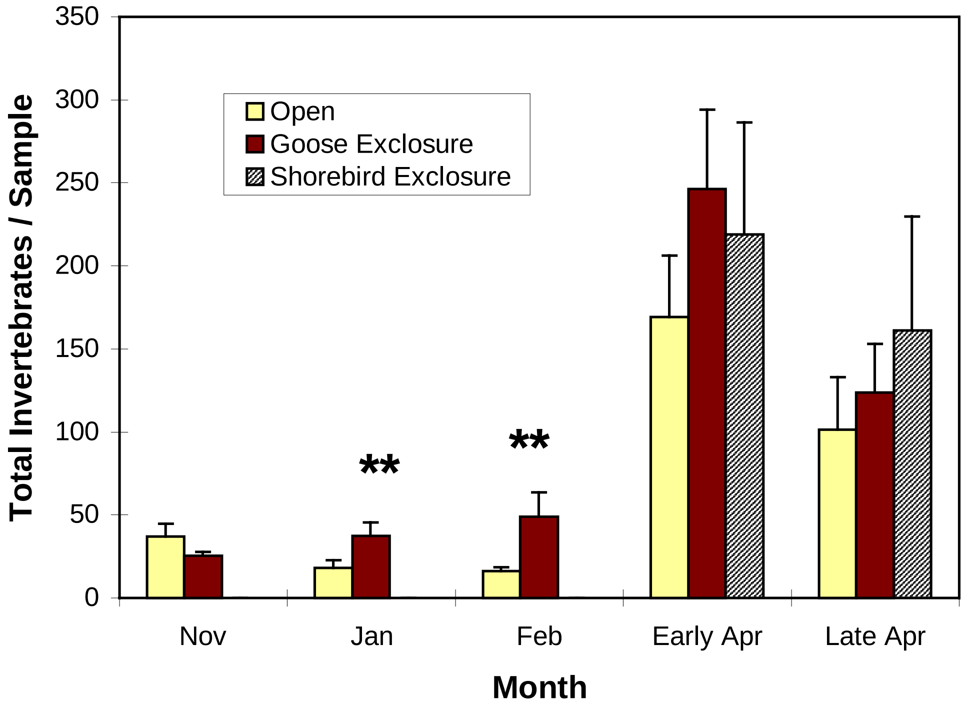

Figure 4.6. Mean (+ SE) density (# / sample) of Total Invertebrates (all taxa) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: $P < 0.10$, **: $P < 0.05$, ***: $P < 0.01$) difference in abundance between snow goose exclosures and open sampling stations within months.

Table 4.6. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on total invertebrate abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	5.68	0.140			
Herbivory	1,14	4.58	0.051			
Pool * Herbivory	1,14	1.02	0.330			
Month	4,96	29.10	<0.001			
Month * Pool	4,96	1.60	0.180			
Month * Herbivory	4,96	1.41	0.235			
Nov				1,96	0.37	0.547
Jan				1,96	4.40	0.039
Feb				1,96	6.32	0.014
Early Apr				1,96	1.45	0.232
Late Apr				1,96	0.05	0.818
Month * Pool * Herbivory	4,96	0.64	0.639			
Shorebird Predation						
Pool	1,2	2.54	0.252			
Predation	1,14	0.37	0.551			
Pool * Predation	1,14	0.30	0.591			
Month	1,28	7.54	0.010			
Month * Pool	1,28	7.87	0.009			
Month * Predation	1,28	0.31	0.583			
Early Apr				1,28	0.00	0.966
Late Apr				1,28	0.68	0.416
Month * Pool * Predation	1,28	0.13	0.717			

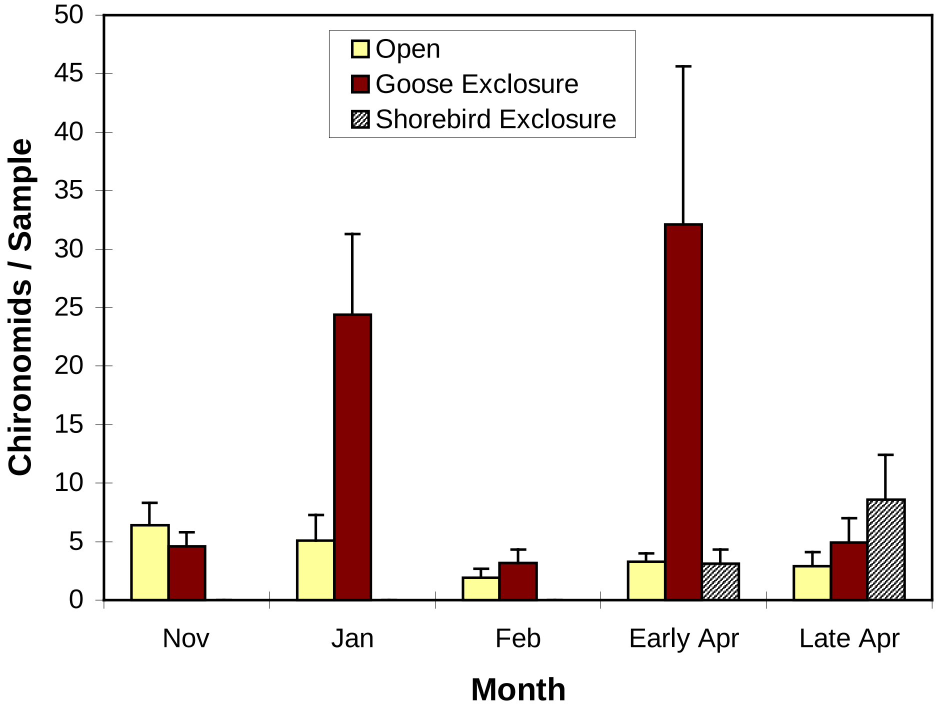

Figure 4.7. Mean (+ SE) density (# / sample) of Chironomidae in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: P < 0.10, **: P < 0.05, ***: P < 0.01) difference in abundance between snow goose exclosures and open sampling stations within months.

Table 4.7. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Chironomid abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.62	0.515			
Herbivory	1,14	9.17	0.009			
Pool * Herbivory	1,14	6.40	0.024			
Month	4,96	5.94	<0.001			
Month * Pool	4,96	5.01	0.001			
Month * Herbivory	4,96	2.43	0.053			
Nov				1,96	0.11	0.740
Jan				1,96	15.71	<0.001
Feb				1,96	1.06	0.305
Early Apr				1,96	4.82	0.031
Late Apr				1,96	0.35	0.557
Month * Pool * Herbivory	4,96	2.37	0.058			
Shorebird Predation						
Pool	1,2	2.26	0.272			
Predation	1,14	0.14	0.719			
Pool * Predation	1,14	6.91	0.020			
Month	1,28	0.00	0.984			
Month * Pool	1,28	0.55	0.466			
Month * Predation	1,28	3.22	0.084			
Early Apr				1,28	1.02	0.322
Late Apr				1,28	2.34	0.138
Month * Pool * Predation	1,28	0.86	0.363			

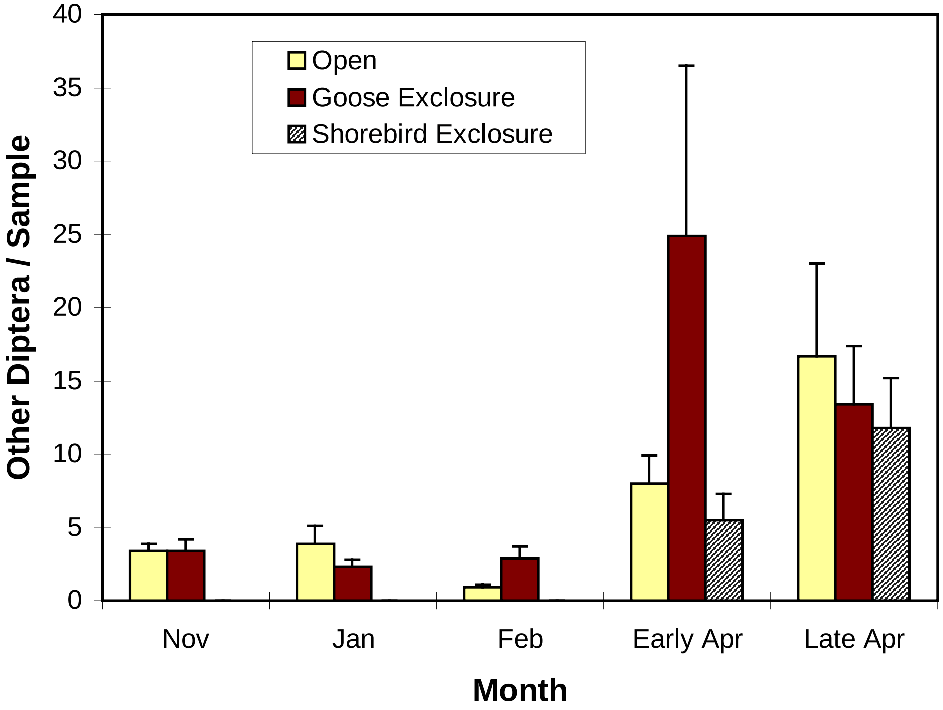

Figure 4.8. Mean (+ SE) density (# / sample) of Other Diptera (Chironomidae excluded) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: $P < 0.10$, **: $P < 0.05$, ***: $P < 0.01$) difference in abundance between snow goose exclosures and open sampling stations within months.

Table 4.8. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Other Diptera abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	3.82	0.190			
Herbivory	1,14	0.81	0.383			
Pool * Herbivory	1,14	0.43	0.522			
Month	4,96	16.79	<0.001			
Month * Pool	4,96	4.26	0.003			
Month * Herbivory	4,96	0.98	0.423			
Nov				1,96	0.20	0.656
Jan				1,96	0.16	0.692
Feb				1,96	3.11	0.081
Early Apr				1,96	1.86	0.176
Late Apr				1,96	0.11	0.737
Month * Pool * Herbivory	4,96	1.93	0.111			
Shorebird Predation						
Pool	1,2	14.18	0.064			
Predation	1,14	1.63	0.222			
Pool * Predation	1,14	0.79	0.388			
Month	1,28	2.63	0.116			
Month * Pool	1,28	0.87	0.360			
Month * Predation	1,28	0.53	0.474			
Early Apr				1,28	2.01	0.168
Late Apr				1,28	0.15	0.699
Month * Pool * Predation	1,28	0.82	0.373			

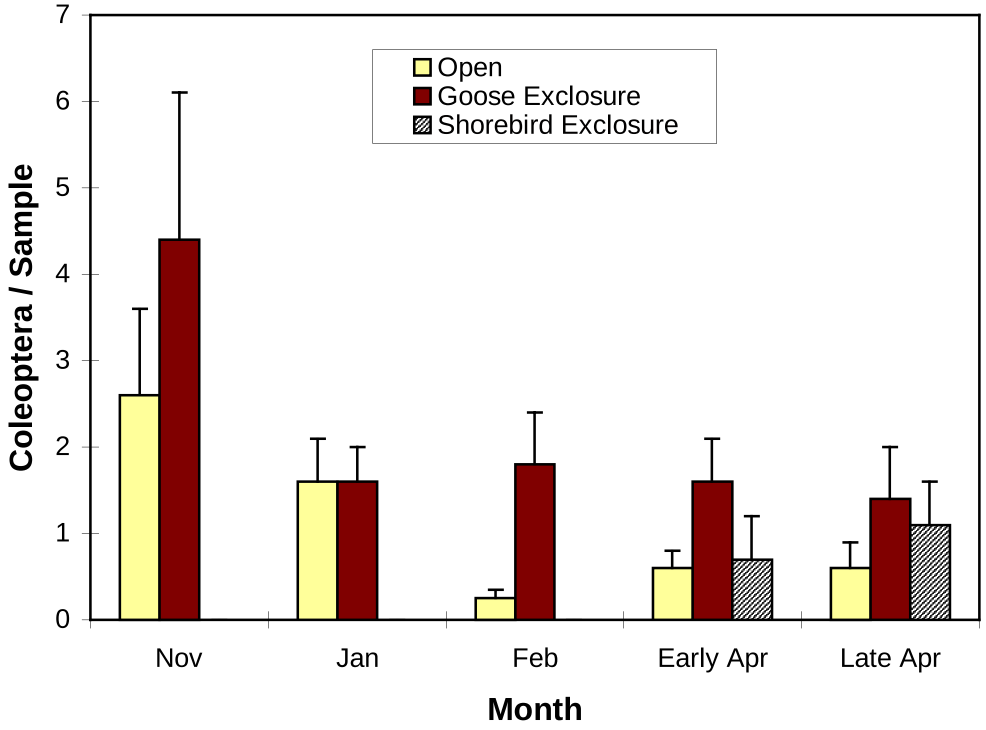

Figure 4.9. Mean (+ SE) density (# / sample) of Coleoptera adults and larvae in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: P < 0.10, **: P < 0.05, ***: P < 0.01) difference in abundance between snow goose exclosures and open sampling stations within months.

Table 4.9. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Coleoptera abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.44	0.575			
Herbivory	1,14	7.92	0.014			
Pool * Herbivory	1,14	0.38	0.549			
Month	4,96	6.57	<0.001			
Month * Pool	4,96	4.02	0.005			
Month * Herbivory	4,96	1.22	0.308			
Nov				1,96	0.95	0.333
Jan				1,96	0.00	0.839
Feb				1,96	9.93	0.002
Early Apr				1,96	3.81	0.054
Late Apr				1,96	1.71	0.195
Month * Pool * Herbivory	4,96	2.25	0.069			
Shorebird Predation						
Pool	1,2	0.47	0.562			
Predation	1,14	0.15	0.703			
Pool * Predation	1,14	0.15	0.703			
Month	1,28	1.29	0.266			
Month * Pool	1,28	1.29	0.266			
Month * Predation	1,28	0.45	0.507			
Early Apr				1,28	0.00	0.971
Late Apr				1,28	0.48	0.495
Month * Pool * Predation	1,28	1.15	0.292			

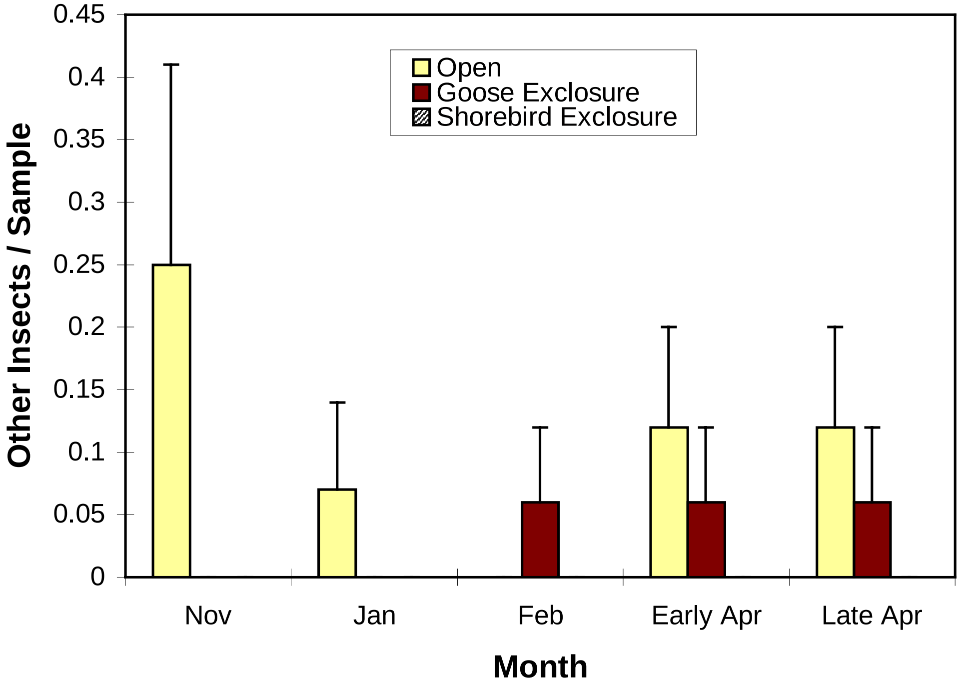

Figure 4.10. Mean (+ SE) density (# / sample) of Other Insects (Diptera and Coleoptera excluded) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: $P < 0.10$, **: $P < 0.05$, ***: $P < 0.01$) difference in abundance between snow goose exclosures and open sampling stations within months. Missing bars reflect 0 abundance for goose exclosures in Nov and Jan and shorebird exclosures in Early Apr and Late Apr.

Table 4.10. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Other Insect abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	0.56	0.531			
Herbivory	1,14	3.21	0.095			
Pool * Herbivory	1,14	3.21	0.095			
Month	1,96	0.51	0.729			
Month * Pool	4,96	1.16	0.332			
Month * Herbivory	4,96	1.05	0.388			
Nov				1,96	3.90	0.051
Jan				1,96	0.80	0.374
Feb				1,96	0.49	0.487
Early Apr				1,96	0.49	0.487
Late Apr				1,96	0.49	0.487
Month * Pool * Herbivory	4,96	1.05	0.388			
Shorebird Predation						
Pool	1,2	0.15	0.737			
Predation	1,14	1.34	0.266			
Pool * Predation	1,14	0.15	0.705			
Month	1,28	0.30	0.586			
Month * Pool	1,28	0.30	0.586			
Month * Predation	1,28	0.30	0.586			
Early Apr				1,28	1.60	0.216
Late Apr				1,28	0.40	0.532
Month * Pool * Predation	1,28	0.30	0.586			

generally reflected the pattern observed in Oligochaetes (Fig. 4.6, 4.11). Oligochaete density was higher in goose exclosures than in open sampling stations during Feb (*P* = 0.064; Table 4.11), but herbivory effects were nonsignificant during the period of peak abundance (Early and Late Apr; Fig. 4.11). Peak density of Other Invertebrates also occurred during Early and Late Apr (Fig. 4.12), but no herbivory effects were detected (Table 4.12). Copepods were the dominant Other Invertebrate taxon (Table 4.2).

Shorebird Predation Effects on Invertebrates

Mixed models for shorebird predation effects did not include significant Predation or Month * Pool * Predation effects for any taxonomic group (Tables 4.7 – 4.12). The Pool * Predation and Month * Predation effects were significant for Chironomids (Table 4.7), but were nonsignificant for all other taxa (Tables 4.7 – 4.12). Despite marginal significance of the Month * Predation effect for Chironomids, examination of this interaction did not reveal significant effects within months (Table 4.7).

DISCUSSION

Herbivory Effects on Invertebrates

The results of this study provide strong evidence that snow goose foraging activity results in substantial reduction of invertebrate abundance during some time periods. The observed effects varied among taxa and time periods, but tended to be most pronounced for benthic organisms during Jan - Early Apr, such as Diptera larvae. Dipterans were among the most abundant organisms on the study area (Table 4.2), and are also common food items for waterfowl (Euliss and Harris 1987, Miller 1987, Batzer et al. 1993, Euliss et al. 1997) and shorebirds (Baker 1977, Baldassare and Fischer 1984, Weber and Haig 1997). Production of invertebrate foods is often a significant impoundment management goal (Fredrickson and Taylor 1982, USFWS 1996), but snow goose herbivory appears to counteract efforts to provide these foods through moist-soil management.

Significant depletion of several invertebrate taxa occurred in snow goose eat-outs, despite variation in life history among invertebrate taxa and substantial variation in habitat conditions among time periods. Herbivory effects generally were not spatially confined, as Pool

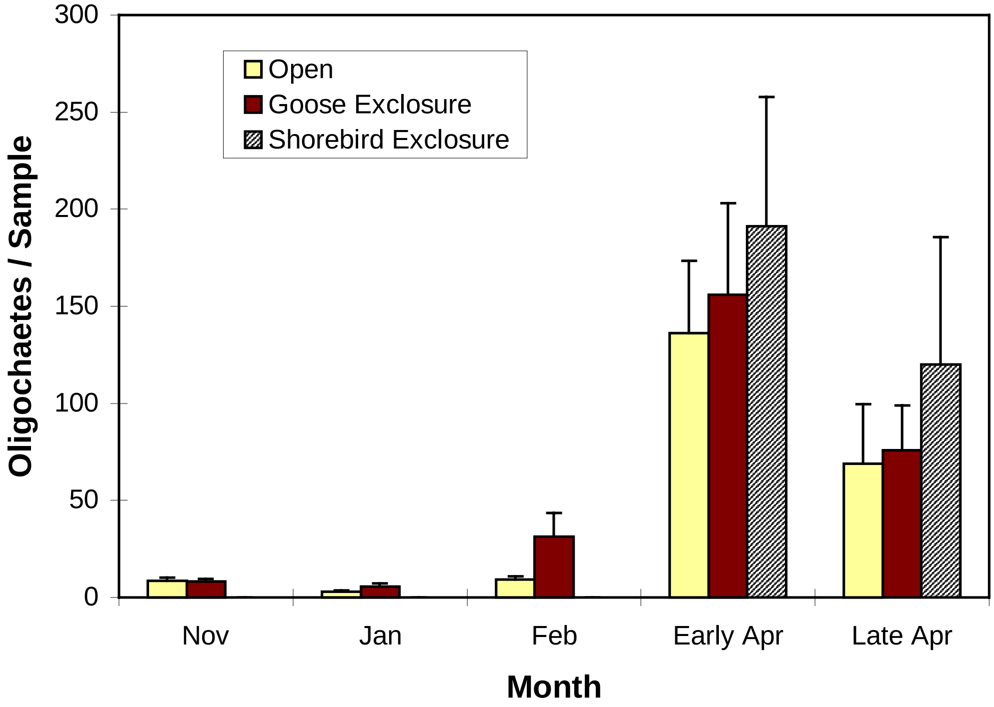

Figure 4.11. Mean (+ SE) density (# / sample) of Oligochaeta in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97. Asterisks indicate significant (*: $P < 0.10$, **: $P < 0.05$, ***: $P < 0.01$) difference in abundance between snow goose exclosures and open sampling stations within months.

Table 4.11. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Oligochaete abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	5.95	0.135			
Herbivory	1,14	1.62	0.224			
Pool * Herbivory	1,14	0.00	0.960			
Month	4,96	38.66	<0.001			
Month * Pool	4,96	1.70	0.157			
Month * Herbivory	4,96	0.52	0.722			
Nov				1,96	0.03	0.856
Jan				1,96	0.59	0.445
Feb				1,96	3.50	0.064
Early Apr				1,96	0.09	0.764
Late Apr				1,96	0.18	0.674
Month * Pool * Herbivory	4,96	0.49	0.745			
Shorebird Predation						
Pool	1,2	4.30	0.174			
Predation	1,14	0.45	0.512			
Pool * Predation	1,14	0.02	0.880			
Month	1,28	16.19	<0.001			
Month * Pool	1,28	0.11	0.737			
Month * Predation	1,28	0.06	0.814			
Early Apr				1,28	0.09	0.761
Late Apr				1,28	0.42	0.524
Month * Pool * Predation	1,28	0.39	0.535			

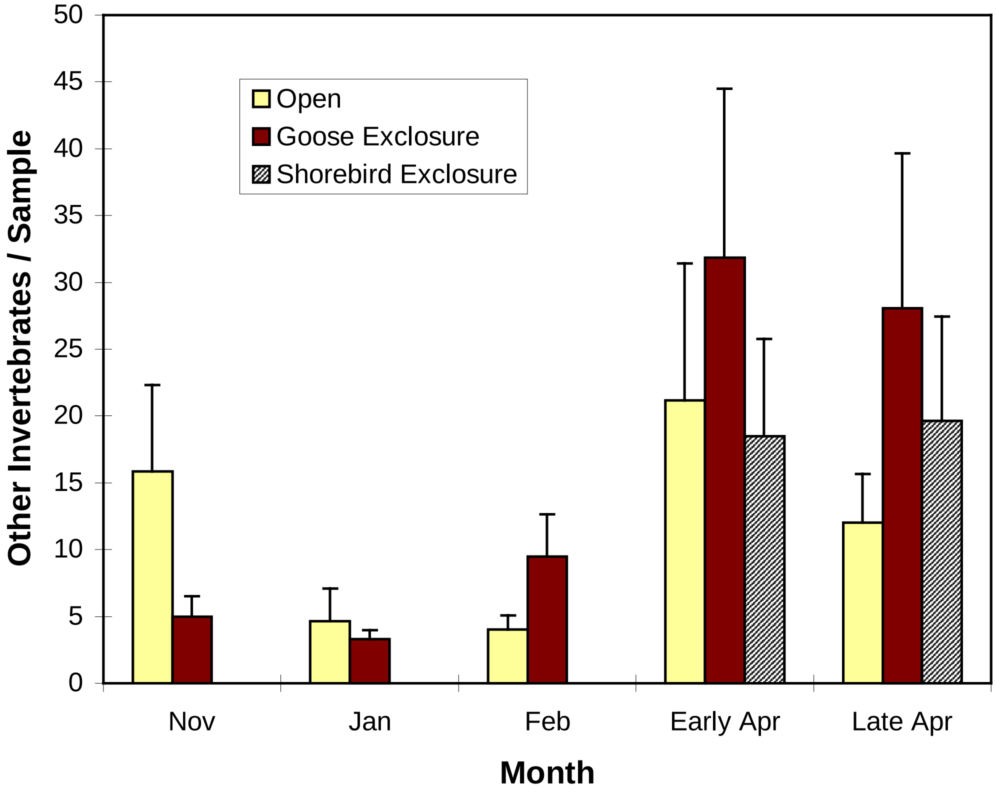

Figure 4.12. Mean (+ SE) density (# / sample) of Other Invertebrates (Insects and Oligochaetes excluded) in open sampling stations, snow goose exclosures, and shorebird exclosures, Prime Hook National Wildlife Refuge, Milton, Delaware, 1996-97.

Table 4.12. Results of mixed model analyses of variance for Snow Goose Herbivory and Shorebird Predation effects on Other Invertebrate abundance in moist-soil impoundments at Prime Hook National Wildlife Refuge, Milton, Delaware, during winter 1996-97. The Goose Herbivory model was based on data from goose exclosures and open sampling stations during all 5 sampling periods. The Shorebird Predation model was based on data from shorebird exclosures and open sampling stations during the 2 spring sampling periods (see Table 4.1 for sample sizes).

	Main Effects			**Contrasts**		
Source	**df**	***F***	***P***	**df**	***F***	***P***
Goose Herbivory						
Pool	1,2	2.08	0.286			
Herbivory	1,14	0.10	0.757			
Pool * Herbivory	1,14	1.03	0.328			
Month	4,96	4.27	0.003			
Month * Pool	4,96	3.89	0.006			
Month * Herbivory	4,96	0.49	0.745			
Nov				1,96	1.07	0.303
Jan				1,96	0.28	0.595
Feb				1,96	0.71	0.402
Early Apr				1,96	0.23	0.631
Late Apr				1,96	0.13	0.715
Month * Pool * Herbivory	4,96	0.82	0.516			
Shorebird Predation						
Pool	1,2	0.12	0.766			
Predation	1,14	0.02	0.884			
Pool * Predation	1,14	0.22	0.646			
Month	1,28	1.72	0.201			
Month * Pool	1,28	9.68	0.004			
Month * Predation	1,28	0.00	0.999			
Early Apr				1,28	0.01	0.917
Late Apr				1,28	0.01	0.917
Month * Pool * Predation	1,28	0.93	0.343			

* Herbivory interactions were nonsignificant for most taxa. That the observed effects were not limited to a single taxon, sampling period or spatial location suggests that depletion of invertebrate resources is a common response to goose herbivory on moist-soil vegetation. There are several possible explanations for the observed differences in invertebrate density between goose exclosures and open sampling stations:

Incidental Consumption by Geese.--Many organisms for which significant herbivory effects were detected were either benthic (e.g., Chironomidae) or associated with the mud-water interface (e.g., Oligochaeta). These organisms may have been incidentally consumed or killed by geese grubbing for rhizomes and tubers. Soft-bodied organisms (e.g., Diptera larvae) would be expected to be particularly vulnerable to this cause of mortality.

Under the hypothesis that goose consumption of invertebrates caused the observed effects, an invertebrate response should coincide with herbivory. Conversely, exclosure effects were not evident for any taxonomic group early in the study, whereas most taxa exhibited higher density in goose exclosures during either Jan or Feb. Analysis of data only for the 2 plots in which herbivory occurred later (between Nov and Jan) indicated significant herbivory effects on abundance of Chironomids, Oligochaetes, and Total Invertebrates during Jan (all $P < 0.05$). This result is consistent with the goose consumption hypothesis because effects on invertebrate abundance occurred during the sampling period immediately subsequent to goose herbivory.

Movement or Habitat Selection by Invertebrates.--Differences in habitat structure, particularly plant cover, may have influenced movement of invertebrates between goose exclosures and open sampling stations. Such movements could occur as active selection of vegetated areas by mobile invertebrates, or wind-induced accumulation of invertebrates among plants remaining in exclosures. In controlled experiments, Baker and Ball (1995) demonstrated that lateral movements up to 45 cm by late-instar chironomids may occur in response to changes in predator communities and food availability. Such movements are more likely for early instars, in which a planktonic life history is common (Oliver 1971, Baker and Ball 1995). Exclosure samples collected in this study were ≤60cm from habitat edges, and most of the chironomids collected appeared to be in the second instar. Consequently, lateral movement of these organisms is a plausible explanation for the observed differences in abundance between exclosure and open sampling stations.

Influence on Invertebrate Developmental Rates.--Temperature is the primary factor influencing growth and development rates of invertebrates (Pinder 1986). Growth and development are enhanced at higher temperatures, and may stop completely under cold temperatures (Merritt and Cummins 1996). The only difference in water temperature between sampling stations occurred in Feb, when mean temperature in open sampling stations (10.4 ± 0.3 C) was higher than that in goose exclosures (9.4 ± 0.4) (Fig. 4.4). This pattern is inconsistent with elevated invertebrate populations in goose exclosures during and subsequent to this period. Consequently, differences in temperature-mediated growth and development rates between experimental treatments probably did not occur.

Invertebrate growth and development also may be influenced by oxygenation and the quantity and quality of food (Danks 1971, Pinder 1986). Sampling during 1995 at Prime Hook NWR revealed that chironomids were primarily detritivores (USFWS 1996). Goose foraging likely would increase availability of coarse organic matter for these invertebrates due to the presence of plant shoots discarded by geese. Despite the apparently favorable conditions for invertebrate growth and development in eat-outs, invertebrate abundance was lower or similar to that in vegetated areas during all sampling periods.

Exclosure Effects.--Use of exclosures to manipulate predation or herbivory rates by wildlife presents an unavoidable confounding between the main effect of interest and secondary effects of the exclosures. In aquatic systems, exclosures used to control avian herbivory also may alter hydrology, detrital accumulation, and density of other organisms. Exclosures in this study produced substantial alterations in herbaceous plant density (Fig. 4.3), but this result was the intended consequence of their use. Any differences in habitat characteristics between exclosed and open locations that could be directly attributed to presence or absence of plants should thus be viewed as experimental treatment effects of interest rather than unavoidable exclosure effects.

Wind-induced drift can cause accumulation of organic debris in exclosures, potentially providing enhanced habitat quality for detritovores. However, the primary effect created by exclosures in this study was to cause the plant community to remain in the absence of goose herbivory. In the absence of exclosure netting, similar levels of detrital accumulation would likely be caused by dense stands of emergent vegetation in areas where geese did not forage. Exclosures created a hard edge between vegetated and unvegetated habitat, but a similarly abrupt transition between habitats also occurred at the periphery of eat-outs. Consequently, any accumulation of detritus within exclosures likely was similar to that that naturally occurs at the edges of snow goose eat-outs, and any concomitant effects on invertebrate abundance would likely occur in the absence of exclosure netting.

Predation by Other Organisms.--Presence of predators in confined habitats can markedly alter invertebrate density (Murkin et al. 1983) and the distribution of size classes for remaining individuals (Ball and Baker 1995). Carp (*Cyprinus carpio*) were commonly observed in unvegetated shallow-water habitats on the study area, including snow goose eat-outs. The exclosures in this study would have eliminated carp, as may dense stands of vegetation (e.g., cattail) in other unexclosed habitats (Wrubleski 1989). Carp consumption of invertebrates may therefore have differed between exclosed and open sampling locations, potentially contributing to reduced invertebrate populations in eat-outs. Snow goose eat-outs also would have been available as foraging habitat for wintering waterfowl. Waterfowl feeding can alter composition and density of invertebrate communities (Peterson et al. 1989, Wrubleski 1989) and can not be eliminated as a potential cause of low invertebrate density in snow goose eat-outs.

Shorebird Use of Invertebrates

There were no overt differences in the measured habitat variables between open sampling stations and shorebird exclosures (Figs. 4.3 – 4.5), suggesting that shorebird predation was the major ecological difference between treatments. Despite marginal evidence for a difference in chironomid density between shorebird exclosures and open sampling stations in Late Apr, the observed pattern is inconsistent with the pattern expected from shorebird predation. Chironomid density was similar in shorebird exclosures and open sampling stations in Early Apr

(Fig. 4.7), suggesting that substantial shorebird predation had not occurred at that time. An added influence of shorebird predation should be manifested as decreased density in open sampling stations relative to this baseline. Conversely, chironomid density in Late Apr was higher in shorebird exclosures than in either sampling station during Early Apr. This response could result from nutrient enrichment of exclosures relative to open sampling stations due to trapping of coarse organic material by exclosure netting. This hypothesis implies either active selection of exclosures by chironomids or enhanced development of larvae from eggs in exclosures during this period.

The lack of evidence for shorebird predation effects on invertebrate density suggests that shorebird use of snow goose eat-outs was low during the study period. Because shorebirds select habitat on the basis of invertebrate density (Colwell and Landrum 1993), impacts of snow goose foraging may render eat-outs unsuitable as shorebird foraging habitat. Other factors, such as water depth, also may influence distribution of shorebirds. The observed water depths during Late Apr (Fig. 4.5) were higher than the maximum water depth used by most species of shorebirds in South Carolina (10cm; Weber and Haig 1997), suggesting that these areas may not be favorable shorebird habitat, regardless of invertebrate density.

Predation impacts on invertebrate density should be cumulative over time, and should thus be most evident at the conclusion of the peak shorebird use period. Peak concentrations of migrant shorebirds in the Delaware Bay area generally occur during mid to late May (Clark et al. 1993, USFWS 1996), although logistical constraints prevented sampling during May for this study. Consequently, lack of detectable shorebird predation may be an artifact of migration chronology rather than disproportionate distribution of foraging birds among available habitats. An exclosure study that includes the entire period of shorebird residence on the study area may be required to adequately characterize the value of snow goose eat-outs as shorebird habitat.

Value of Eat-Outs as Waterbird Habitat

Abundance of most invertebrate taxa was substantially lower in open sampling stations than in goose exclosures during at least 1 of the sampling periods. Effects of goose herbivory were most pronounced during Jan, Feb and Early Apr, corresponding to increased consumption of animal foods by some waterfowl (Euliss and Harris 1987, Miller 1987, Euliss et al. 1997). Although the habitat structure induced by goose foraging may favor waterfowl use, invertebrate abundance in openings created by geese would support fewer birds than adjacent vegetated areas. Given goose herbivory effects on invertebrate abundance and the significance of these foods to waterfowl during late winter, eat-outs are probably relatively low-quality waterfowl foraging habitat.

In the absence of goose herbivory, moderate to dense stands of herbaceous vegetation would persist through winter and early spring. Waterfowl generally use habitats that vary widely in vegetation height and density, often preferring habitats that provide interspersion of open water and vegetation. Experimentally manipulated marshes with interspersed open water and vegetation often are used more heavily by waterfowl than unmanipulated marshes (Murkin et al. 1982, 1997, Kaminski and Prince 1981, Linz et al. 1996). These studies generally indicate that interspersion is an important waterfowl habitat characteristic at relatively small spatial scales. For example, Murkin et al. (1982) found that waterfowl use was highest in plots where 50% of the plant cover had been removed from 6m x 6m blocks. In contrast, goose foraging at Prime Hook NWR created large, continuous unvegetated areas that bordered directly on dense stands of emergent vegetation.

Shorebirds typically favor habitats with sparse to absent vegetation (Baker 1979, Weber and Haig 1997). Were goose herbivory to have no effect on invertebrate density, eat-outs and adjacent vegetated stands would differ markedly in their relative value to shorebirds. The absence of vegetation in eat-outs suggests that these habitats would be strongly favored by shorebirds relative to adjacent vegetated areas, although decreased invertebrate abundance in eat-outs may render these habitats unsuitable for shorebirds. Spring shorebird migration through Delaware Bay coincides with spawning of horseshoe crabs (*Limulus polyphemus*) on intertidal beaches, where eggs provide a major source of shorebird food (Clark et al. 1993, Botton et al. 1994). It is probable that impoundment invertebrates serve as a secondary source of food for shorebirds, yet the highest invertebrate densities occur in areas that are otherwise unsuitable as shorebird foraging habitat.

In the absence of goose herbivory, shorebird habitat in Prime Hook NWR impoundments would be limited to marsh openings created by ice scour, vegetation senescence, variation in hydrology, or other natural processes. Vegetation interspersion at a spatial scale favored by waterfowl is more likely to be maintained during winter by these processes. Areas in which snow goose foraging activity does not occur may therefore provide foraging habitat for waterfowl, but are unlikely to attract shorebirds. However, openings created by geese may serve other functions (i.e., roosting habitat) that otherwise contribute to energy balance and survival of waterfowl and shorebirds.

Consequences of Goose Herbivory for Management of Other Waterbirds

The results of this study are useful as a preliminary indication of invertebrate responses to snow goose foraging activity in coastal impoundments. However, this study has addressed only 1 of several potential interactions between snow geese and other waterbirds. Several areas in which goose foraging was concentrated were dominated by seed-producing plants (e.g., *Scirpus americanus*). Geese appeared to feed exclusively on rhizomes of these species, although the effect of this disturbance on seed availability to waterfowl is unknown. Snow geese on Prime Hook NWR also have been observed grubbing for rhizomes of submerged aquatic vegetation, an important source of winter forage for other wintering waterfowl (USFWS 1996). However, observations by refuge staff suggest that waterfowl fed heavily on stems of submerged aquatics discarded by geese (USFWS 1996).

Euliss and Grodhaus (1987) suggest that small ponds within wetlands can serve as sources of invertebrate introduction to adjacent areas as water levels rise. The results of this study suggest that impoundment habitats free from goose foraging may play a similar role. Areas in which vegetation remains may develop greater invertebrate abundance and diversity over time, enhancing development of the invertebrate community in adjacent areas affected by geese. Remaining vegetated habitat may provide a source of emerging adult dipterans that may subsequently deposit eggs in adjacent eat-outs. However, Oliver (1971) concluded that the relatively high mobility of first instar chironomid larvae minimizes the importance of habitat selection by ovipositing females. Regardless of the mode of recolonization, the value of vegetated habitat as a source of invertebrates would be enhanced by its proximity to eat-outs.

Hill and Frederick (1997) concluded that the extent of tidal marsh eat-outs at Bombay Hook NWR (about 50 km north of Prime Hook NWR) had not appreciably changed during recent years, although rates of Gulf Coast marsh loss have essentially paralleled increases in lesser snow goose populations (Miller et al. 1996). Efforts to deter goose foraging in agricultural fields would be expected to increase as populations grow, suggesting that goose use of Prime Hook NWR impoundments may increase as geese seek alternative forage. A conservative approach to migratory bird management would be to consider goose eat-outs as low-quality shorebird foraging habitat, and to expect annual increases in the extent of these habitats that correspond to goose population increases.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Increasing populations of lesser snow geese have led to increasing management concern for the long-term integrity of arctic and Gulf coastal marsh habitats. Greater snow geese have exhibited similar population trends in recent decades, although the consequences of this trend have received less attention in the literature. Studies of lesser snow goose wintering habitats have shown increasing habitat degradation with increasing goose populations (Miller et al. 1996). Goose herbivory in Prime Hook NWR impoundments appears to have a substantial negative influence on production of invertebrates that coincides with periods of residence by waterfowl and shorebirds. Despite these results, goose herbivory is confined to discrete areas within the impoundments and does not appear to generate irreversible alterations to habitat structure. Nonetheless, the short-term effect of goose herbivory appears to be a biologically significant impact on resource availability for other waterbirds. In light of trends in greater snow goose populations, less certainty can be ascribed to future habitat conditions on Prime Hook NWR. A temporally replicated exclosure study would allow conclusions regarding the strength of trophic interactions between snow geese and other waterbirds (Pace et al. 1998), and could enable analysis of other responses to goose herbivory, such as waterbird habitat use, moist-soil seed production, and long-term vegetation dynamics.

The consequences of goose herbivory to other waterbirds should be examined relative to the availability of other habitats for these species. Waterfowl may be less sensitive to goose-induced habitat alterations because they use habitats varying widely in plant community composition and density. Conversely, shorebirds require specific habitat characteristics (e.g., unvegetated mudflats) that may be limited in availability outside of goose eat-outs. Knowledge of the spatial patterns of waterbird habitat use on the study area would clarify the implications of goose herbivory for other nonbreeding birds.

Management intervention to reduce goose populations, such as that recommended for mid-continent lesser snow geese (Ankney 1996, Rockwell et al. 1997), is one mechanism by which goose impacts on impoundment vegetation and invertebrate communities could be addressed. Local management actions, such as disturbance or crop manipulation, may be effective in causing short-term redistribution of birds, but may negatively affect non-target species and fail to address the continental issue of goose overpopulation (Ankney 1996, Hill and Frederick 1997).

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