

## CHAPTER 2

# INVERTEBRATE RESPONSES TO DISCING OF MOIST-SOIL VEGETATION

### INTRODUCTION

The mid-Atlantic coastal region provides habitat for a variety of nonbreeding waterbirds. Dominant physiographic features in this region include Chesapeake Bay and Delaware Bay. These estuaries are among the most important habitat features in North America for wintering waterfowl and spring migrant shorebirds, respectively (Hindman and Stotts 1989, Clark et al. 1993). One of the major energetic challenges to nonbreeding waterbirds is obtaining adequate food to provide for maintenance under potentially severe weather conditions, while building endogenous reserves to provide for migration and reproduction. In Chesapeake Bay, submerged aquatic vegetation and its associated macroinvertebrate community historically provided an abundant source of forage for wintering waterfowl (Perry et al. 1981). The timing of northward shorebird migration through Delaware Bay corresponds with peak spawning of horseshoe crabs (*Limulus polyphemus*) on sandy beaches, where eggs provide a concentrated source of high-energy food for migrant shorebirds (Botton et al. 1994). These formerly abundant sources of natural food in this region have experienced dramatic declines in recent decades, leading to management concern for the ability of natural habitats to provide for the nutritional needs of nonbreeding waterbirds.

Aquatic invertebrates also are a significant component of the diet for nonbreeding shorebirds (Rundle 1982, Baldassarre and Fischer 1984, Hicklin and Smith 1984, Weber and Haig 1997a, Davis and Smith 1998) and waterfowl (Euliss et al. 1987, 1991, Thompson et al. 1992, Batzer et al. 1993, Combs and Fredrickson 1996). Managed habitats in the coastal zone, such as moist-soil impoundments, may be manipulated to provide structural features that encourage high invertebrate production. Because invertebrate populations are often directly related to plant community structure (Krull 1970, Voigts 1976, Nelson and Kadlec 1984), such manipulations often are targeted at providing a successional stage that optimizes invertebrate

production. To the extent that wetland management practices enhance invertebrate production, managed habitats may provide waterbird foods that at least partially compensate for declines in abundance of traditional foods. Although habitat manipulations are commonly employed in managed impoundments, few studies have examined the consequences of these practices for waterbird food production.

### **Significance of Invertebrates to Shorebirds**

Delaware Bay is important for the northbound migration of semipalmated sandpipers (*Calidris pusilla*), ruddy turnstones (*Arenaria interpres*), red knots (*C. canutus*) and sanderlings (*C. alba*), and is the second largest spring shorebird staging area in the Western Hemisphere (Clark et al. 1993, Botton et al. 1994). Mudflats and sandy beach habitats along the mid-Atlantic coast also receive high use by migratory shorebirds during the horseshoe crab spawning season (J. Gallegos, Back Bay NWR, unpubl. data). Shorebird use of managed wetlands in South Carolina was significantly higher than in adjacent unmanaged mud flats, reflecting substantial differences in abundance of benthic invertebrates (Weber and Haig 1996). Thus, management of coastal impoundments may contribute to energy and protein balance, and ultimately reproductive success, of spring migrating shorebirds.

Shorebird migration strategies vary by species, with availability of high-quality food being more critical for those species that tend to travel long distances and stop few times (Skagen and Knopf 1994). Seasonally abundant foods at migratory stopovers allow shorebirds to replenish depleted reserves, providing energy for later stages of migration (Morrison and Harrington 1979) and potentially reducing number and duration of other stops along the migration corridor (Hicklin 1987). Stopover duration of semipalmated sandpipers in coastal South Carolina decreases and estimated fat mass increases throughout the spring migration period, suggesting that later migrants may minimize stopover time to enable exploitation of resources in more northerly habitats (Lyons and Haig 1995). Similarly, Pfister et al. (1998) found that return rate (i.e., survival) of semipalmated sandpipers was higher for birds with longer residence times on a migratory stopover. Thus, an important function of midcontinent migratory stopovers may be to mitigate temporal depletions in forage at more northerly and more southerly latitudes.

Substrate variation (Hicklin and Smith 1984, Colwell and Landrum 1993), tidal cycle (Burger et al. 1977, Evans and Harris 1994), water depth (Weber and Haig 1996) and vegetation density (Kaminski and Prince 1981, Murkin et al. 1982) influence the composition and density of invertebrate populations, affecting shorebird distribution. Investigations of forage availability for shorebirds have focused primarily on intertidal and sandy beach habitats (Hicklin and Smith 1984, Loegering and Fraser 1995). However, areas of exposed soil in managed wetlands also can provide habitat for migrant shorebirds. Weber and Haig (1996) documented higher invertebrate and shorebird densities in brackish impoundments compared to intertidal mud flats in South Carolina. Knowledge of the available forage base and its nutritional value would contribute to efforts to manage moist-soil impoundments for migratory shorebirds.

Chironomid larvae were the major dietary component of migratory shorebirds in Texas, although seeds of *Polygonum* spp. and *Scirpus* spp. accounted for 18-37% of diet volume (Baldassarre and Fischer 1984). Managed wetlands can produce high densities of chironomids in comparison to tidal marsh and intertidal beach habitats (A. Pinkney, USFWS, pers. comm.). Although shorebird migratory patterns are directly tied to seasonal abundance of other highly nutritious foods (i.e., horseshoe crab eggs), the relationship between temporal patterns of shorebird migration and invertebrate abundance is unknown.

### **Significance of Invertebrates to Waterfowl**

The importance of invertebrates in waterfowl diets is recognized primarily in reference to the breeding season (Krapu and Swanson 1975, Krapu 1979, Krapu and Reinecke 1992), yet the influence of late winter condition on survival and reproduction have been demonstrated (Heitmeyer and Fredrickson 1981, Alisauskas and Ankney 1992). Invertebrate-rich wetlands can attract an abundance of wintering waterfowl, including traditionally herbivorous species such as pintails (Euliss et al. 1991). Lipid reserves of pintails (Miller 1986) and mallards (Whyte and Bolen 1984) decline through early winter, but increase during late winter and early spring. The timing of late winter increases in pintail fat reserves corresponds directly to an increase in consumption of invertebrates (Miller 1987). Animal matter constituted >50% of the diet of pintails wintering in California during September and March, and 0-25% of the diet during October, January and

February (Euliss et al. 1991). Mid-winter body fat and protein of pintails are significantly lower in dry than in wet years (Miller 1986), suggesting that availability of aquatic foods is important to maintaining condition. Cyclic patterns of fat mass during winter (e.g. Whyte and Bolen 1984) also may be in part dictated by variations in availability of protein-rich invertebrates.

Molt and migration result in increased demands for energy (Hohman et al. 1992) and protein (Heitmeyer 1988). The lipid reserves of dusky Canada geese (*B. c. occidentalis*) were depleted by 52% during spring migration, a higher rate of endogenous energy expenditure than during any period of the reproductive season (Bromley and Jarvis 1993). Mallards have relatively high energy demands during fall because prealternate molt corresponds with the southward migration, although these events occur early in the fall when high-energy foods are abundant (Heitmeyer 1988). The prebasic molt of mallards on a corn diet is delayed in comparison to birds on nutritionally balanced diets (Richardson and Kaminski 1992). Energetic costs of wing and body molt can limit the capability to store lipids in preparation for fall migration and winter, influencing the timing of migration and increasing demand for high quality forage on the wintering grounds (Hohman et al. 1992). Therefore, productive costs of the non-breeding season should be an important factor in managing winter waterfowl habitats.

### **Waterbird Management Through Impoundment Manipulation**

Marsh management for breeding waterfowl is often focused on providing "hemi-marsh" habitat, which provides approximately equal interspersions of open water and standing emergent vegetation (Weller 1978). Preferential use of hemi-marsh habitats by breeding waterfowl has been attributed to increased invertebrate production (Voigts 1976). Macroinvertebrate production and waterfowl use may decline in later successional stages, when extensive areas of emergent vegetation are interspersed with only a few remnant small openings (Voigts 1976, Swanson and Meyer 1977, Weller 1978, Nelson and Kadlec 1984). Structural and nutritional characteristics of hemi-marsh habitats may be beneficial to wintering waterfowl as well, although comparatively little effort has been focused on developing these management strategies for the wintering grounds.

Physical manipulation of vegetation and/or impoundment substrate is occasionally employed to retard succession and provide optimum conditions for growth of seed-producing

annuals. Common manipulation techniques include prescribed burning, mowing and discing. Removal of a dense standing crop of herbaceous vegetation provides interspersion of cover types and contributes to plant species diversity. Because dry mass, density and species composition of invertebrate communities are correlated with vegetation structure (Krull 1970), physical manipulation of vegetation in moist-soil impoundments would be expected to directly impact the composition of the invertebrate community. Large, unprotected openings are least productive for aquatic invertebrates (Nelson and Kadlec 1984), but may mimic structural characteristics of mud flats, thereby attracting migrant shorebirds. Knowledge of the nutritional contribution of such management actions to shorebird energy balance could aid in selecting appropriate sites for physical manipulation.

Previous investigations of the effects of marsh manipulation on aquatic macroinvertebrates on Delta Marsh, Manitoba (Kaminski and Prince 1981, Murkin et al. 1982) have demonstrated the value of hemi-marsh habitats to breeding waterfowl. Kaminski and Prince (1981) observed lower overall spring invertebrate populations, but higher taxonomic diversity and numbers of large individuals, following fall mowing or rototilling. Treatment effects observed by Murkin et al. (1982) included higher dry mass of water column invertebrates and pronounced temporal variation in benthic invertebrate populations. However, these studies were conducted on a semi-permanent prairie marsh that differs markedly in hydrology and growing season length from seasonally-flooded moist-soil impoundments on the Atlantic coast. Invertebrate populations may increase (Murkin and Kadlec 1986*b*, Riley and Bookhout 1990) or decrease (Neckles et al. 1990, Batzer and Resh 1992*a*) in response to flooding, suggesting that invertebrate responses to manipulation may vary with hydrological regime.

In a study of seasonal brackish marsh manipulation, de Szalay and Resh (1997) found that invertebrate density was generally higher in burned than in unburned plots, but did not differ between mowed and unmowed plots. Batzer and Resh (1992*b*), working in the same marsh as de Szalay and Resh (1997), found that colonization by water boatmen and hydrophyliid beetles was higher in mowed than in unmowed plots. Gray et al. (in press) evaluated effects of tilling, discing and mowing on invertebrates, and found substantial spatial variation in the magnitude of

responses to treatment. Tilling and discing had no effect on invertebrate dry mass in 1 impoundment, whereas dry mass was 4.2 x and 3.0 x higher in tilled and disced areas, respectively, than in control plots.

Collectively, the above studies suggest that few generalities regarding invertebrate responses to wetland manipulation may be made. However, all have employed vegetation manipulation on areas of about 100 m<sup>2</sup>, an area that is small relative to the habitat requirements of shorebirds. Shorebird density (Recher 1966) and aggressive defense of foraging areas (Recher and Recher 1969) are directly related to the amount of available foraging space, suggesting that large-scale manipulation of habitat would enhance benefits to shorebirds. Given this goal for impoundment management in the Atlantic Coastal region, studies that accurately reflect the typical spatial extent of manipulations will most accurately characterize their value for shorebirds.

### **Waterbird Predation on Aquatic Invertebrates**

Presence and extent of predation is one of the principal factors that structures communities of aquatic prey (Paine 1966, Marsh 1986). Numerous studies have quantified predation rates of shorebirds, particularly in intertidal habitats (Goss-Custard 1977, Peer et al. 1986, Mercier and McNeil 1994). Duffy et al. (1981) concluded that predation by wintering shorebirds in Peru did not have a marked impact on food availability, suggesting that food-induced population limitation does not occur on the wintering grounds. Conversely, predation by spring migrant shorebirds in South Carolina depleted the available invertebrate forage base by up to 50% within a 3 to 4 week period (Weber and Haig 1997b). Shorebirds on the Bay of Fundy selectively preyed upon the largest invertebrates, causing minor changes in invertebrate density, but a pronounced alteration in size distribution (Peer et al. 1986). Because shorebirds forage intensively in large flocks during spring migration, predation impacts on prey abundance should be most pronounced during this period (Mercier and McNeil 1994). Any substantial depletion of prey could have important implications for energy gain by late migrants, and could be an important selective factor in the timing of migration among species (Schneider and Harrington 1981).

The impact of waterfowl predation on invertebrate abundance has been investigated in few controlled studies. Peterson et al. (1989) found that numbers and dry mass of chironomid larvae during fall were 3x to 4x higher in exclosures than in open control sites on the Delta Marsh, Manitoba. Wrubleski (1989) demonstrated that low invertebrate populations in areas of waterfowl foraging were secondary to removal of submerged aquatics by birds. Positive correlations between bird density and invertebrate density in either esophageal samples (Batzer et al. 1993) or marsh substrates (e.g., Murkin and Kadlec 1986a, Safran et al. 1997) suggest that predation impacts may occur, yet can not quantify predation rates due to lack of experimental controls. Similarly, studies reporting waterbird predation impacts on aquatic macroinvertebrates that are based on prey populations prior to and after intense bird foraging (e.g., Peer et al. 1986) are unable to distinguish temporal variation in prey populations from predation impacts. Accurate assessment of predation impacts requires an experimental approach in which the effect of predation is removed, generally through exclosures designed to eliminate predator access to prey. Sociability factors create large flocks of foraging shorebirds (Botton et al. 1994) and waterfowl (Joyner 1980), especially in the presence of abundant prey (Goss-Custard 1977, Colwell and Landrum 1993, Mercier and McNeil 1994). Thus, analyses of prey abundance in managed wetlands should account for predation impacts (Edwards et al. 1982, Weber and Haig 1997b).

Of the published studies of invertebrate responses to marsh manipulation, only Gray et al. (in press) eliminated avian predation from study plots. However, they did not attempt to quantify avian use of invertebrates relative to manipulation by including unexclosed plots in their study. Given that a response by birds to habitat manipulation was expected (Kaminski and Prince 1981, Murkin et al. 1982) and that density-dependent predation may affect invertebrate abundance (Goss-Custard 1977), this study was designed to assess invertebrate responses to habitat manipulation while experimentally controlling for waterbird predation.

## **OBJECTIVES**

The primary goal of this study was to evaluate invertebrate responses to discing of moist-soil habitat, during peak periods of waterfowl and shorebird use of the study area. Specific objectives addressed were to:

- 1) Evaluate the effect of impoundment discing on density of aquatic invertebrates during peak periods of waterfowl (fall and winter) and shorebird (late spring) use of the study site.
- 2) Evaluate numerical responses of waterbirds to impoundment discing.
- 3) Evaluate the effect of waterbird predation on aquatic invertebrate density.

## METHODS

### Study Site Description

The study was conducted at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The refuge is located on a barrier peninsula that is bordered to the east by the Atlantic Ocean and to the west by Back Bay, a freshwater sound that lacks lunar tides. Freshwater impoundments dominate the central portion of the refuge, and are separated from tidal waters by an extensive dune system to the east. Impoundment dikes are generally oriented north to south and east to west. Water depths and plant communities along the western edge of the refuge are typical of semi-permanent wetlands. Elevations gradually rise to the east, generating drier and more frequently exposed substrate. Ditches at the toe of perimeter dikes surround the impoundments, and generally hold water throughout the year.

Impoundment soil generally consists of coarse to fine sand, with a distinct surface organic layer of variable depth. The surface organic layer tends to be most pronounced in more frequently inundated areas (i.e. to the west). Plant community composition similarly varies along an east-west gradient. Cattail (*Typha angustifolia*) and black needlerush (*Juncus roemerianus*) dominate in the wettest areas. Drier habitats are characterized by a more diverse assemblage of plants, including rushes (*Juncus spp.*), bulrushes (*Scirpus spp.*), salt meadow hay (*Spartina patens*), common reed (*Phragmites australis*), switchgrasses (*Panicum spp.*), bur marigold (*Bidens cernua*) and spikerushes (*Eleocharis spp.*). Upland habitat is interspersed among the impoundments, arrayed either as small (generally <0.1 ha) hummocks or narrow linear ridges. Dominant upland vegetation includes loblolly pine (*Pinus taeda*), live oak (*Quercus virginiana*) and common waxmyrtle (*Myrica cerifera*). Many of these upland features appear to consist of remnant spoil from dike construction.

Back Bay is the primary source of water for the impoundments. A pump station located on the western edge of the impoundment complex is used to draw bay water into a central storage pool. Dikes and water control structures are configured such that water can move by gravity from the storage pool to the managed impoundments. The annual hydrological cycle is generally characterized by early fall flooding and early spring drawdowns. Drawdowns are timed so that substrate exposure coincides with arrival of early spring migrant shorebirds (generally in early April). The east-west elevation gradient allows drawdown to continue throughout migration, exposing additional foraging habitat for later migrants. Low water levels are maintained through the growing season to encourage germination of moist-soil plants. Flooding is initiated during fall (generally Nov) and maintained through winter to provide waterfowl with access to seeds of moist-soil plants. Although water level manipulation is the primary means of impoundment management, discing, mowing, burning and herbicide application are periodically used to create openings and discourage undesirable plant species (e.g., common reed, black needlerush, and marsh fleabane [*Pluchea foetida*]). Discing is generally employed in late summer, when low water levels allow tractor access to impoundments and low bird censuses minimize disturbance to wildlife.

Management goals for 3 impoundments (Pools A, B and C) include providing habitat for migrant shorebirds during spring. Elevations along the eastern edge of these impoundments are such that exposed saturated substrate is easily provided during spring drawdowns. Shorebird management efforts are focused on a strip of habitat approximately 100 meters wide along the eastern edge of these impoundments. Due to the annual exposure of these substrates, production of seed-bearing plants is highest in these areas.

Back Bay NWR is located approximately midway between Chesapeake Bay and the coastal sounds of North Carolina, both of which are recognized as significant wintering areas for Atlantic Flyway waterfowl. Accordingly, the refuge annually supports a wide diversity of wintering waterfowl. Dominant species include mallards, gadwall, American black ducks, widgeon and green-winged teal. The landscape position of the refuge also favors use by spring migrant shorebirds, as it is located midway between major stopover areas in Delaware and South

Carolina. Dominant shorebird species include Calidrid sandpipers, semipalmated plovers and yellowlegs.

### **Experimental Design**

This study was conducted in the eastern portions of Pools A and C. In the absence of this study, refuge staff intended to disc all moist-soil habitat within the shallow-water zone of both impoundments. Consequently, study plot selection was designed to identify a minimum area of habitat to remain undiscd. Each impoundment was divided approximately equally into northern, central and southern portions. One contiguous area (range of areas approximately 0.5 - 2.0 ha) within each zone was randomly selected to remain undiscd within each impoundment. This process ensured that control and discd plot locations would be adequately interspersed along the north-south axis of each impoundment.

Discing was conducted by drawing a coarse-bladed disc through standing vegetation to a depth of approximately 15 cm. All wetland habitat except for the randomly-selected control areas in the shallow water zone of both impoundments was discd. After completion of discing, the impoundments were flooded according to standard management practices. Discing was originally intended to occur during September 1995, but several factors caused a delay until November. Thus, the 1995 drawdown period was unusually prolonged, and the fall flood was unusually rapid. Although this departure from standard water level management could potentially influence subsequent invertebrate populations, interspersed discd and control study plots ensured that both experienced similar hydrological regimes.

Sixteen permanent study plot locations ( $n = 8$  per impoundment) were randomly selected from the available discd and undiscd habitat in March 1996 (Fig. 2.1). Plot locations were constrained to be >10m from habitats other than moist-soil, such as perimeter ditches and uplands. Within a selected location, a 30m x 75m plot was randomly positioned such that the eastern plot edge was 5-15 m from the perimeter ditch. Plots were oriented with the 30-m dimension parallel to the perimeter dike. Orientation and positioning of plots ensured that the range of water depths was similar among plots. Sampling was stratified across the range of water

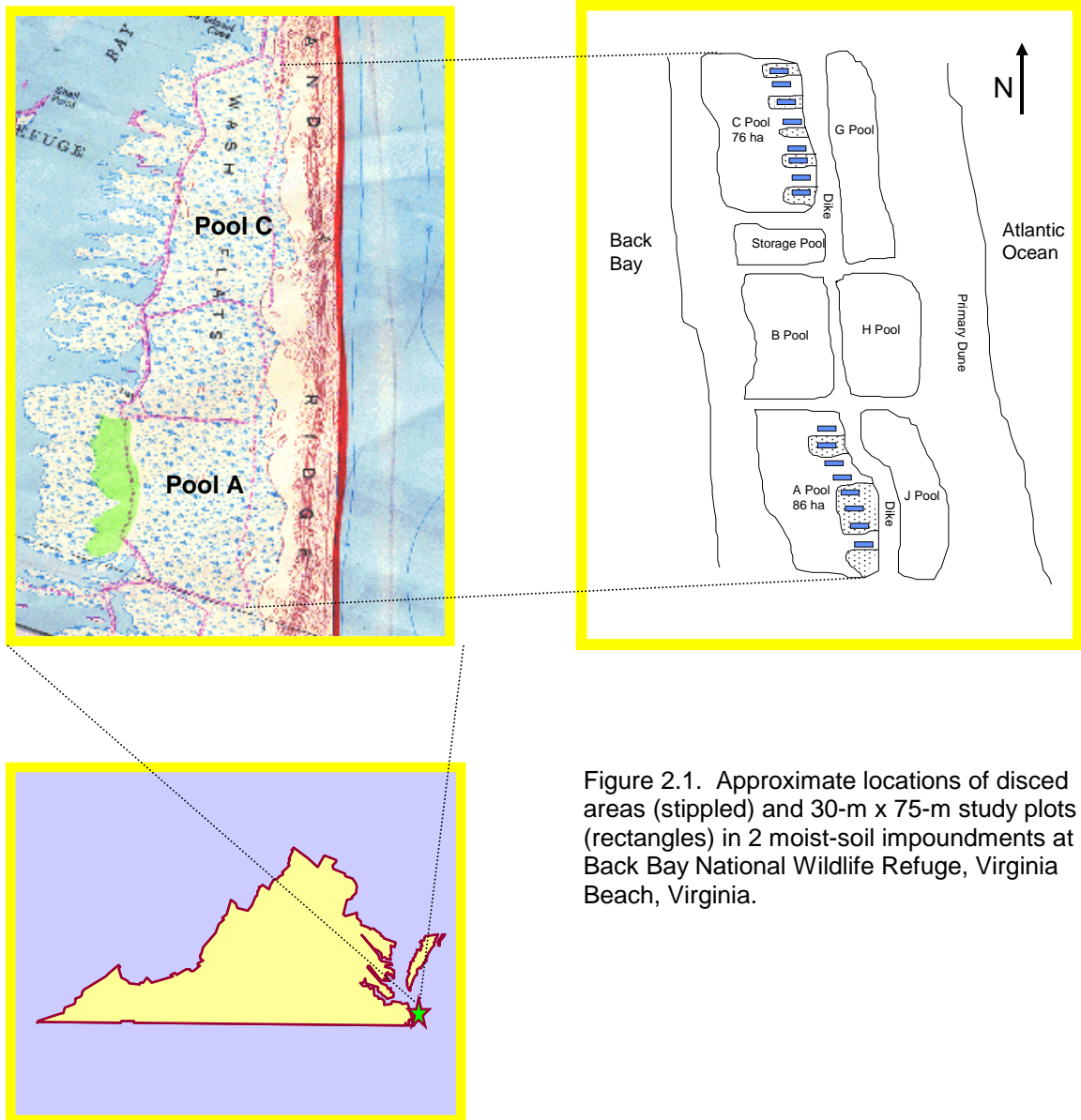


Figure 2.1. Approximate locations of disced areas (stippled) and 30-m x 75-m study plots (rectangles) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

depths by dividing each plot into 5 30m x 15m subplots (Fig. 2.2). Plot and subplot corners were marked with 45.7-cm or 61.0-cm wooden stakes.

Two permanent 1m x 1m sampling stations (1 enclosure, 1 open) were established at random locations within each subplot (Fig. 2.2). Enclosures consisted of 1.27 cm x 1.27 cm nylon mesh stapled to wooden corner stakes such that the sides and top were covered (Fig. 2.3). Corner stakes were driven into the marsh substrate so that the sides contacted the substrate. Height of enclosures was approximately 25 cm. Open sampling stations were marked at the corners with wooden stakes.

Sampling was conducted during 3 seasons following discing: spring 1996, winter 1996-7, and spring 1997. To minimize potential effects of previous sampling on invertebrate abundance during the later sampling periods, new locations for sampling stations were selected at the beginning of each season. All old enclosure and open sampling stations were removed at the end of a given season and placed at new random locations prior to the start of the subsequent season. New locations were constrained to be >2m from previous sampling station locations. This approach minimized extensive data gaps that would have occurred due to enclosure damage by black rat snakes (*Elaphe obsoleta obsoleta*), feral hogs (*Sus scrofa*) and white-tailed deer (*Odocoileus virginianus*). Because predation effects should be cumulative over time, enclosure loss could not be mitigated by replacement in the same location midway through a sampling season. Replacing all enclosures at the beginning of each season thus minimized lack of balance in the final dataset.

### **Sample Collection and Analysis**

Sampling periods were selected to correspond with peak periods of shorebird and waterfowl use of the refuge, but the frequency of sampling differed among seasons. Spring sampling was conducted at 2- to 3-week intervals, whereas fall and winter sampling were conducted at approximately 4-week intervals. These intervals reflect the relatively contracted nature of shorebird migration relative to the residence period of waterfowl on the refuge. It was also desirable to sample intensively during spring because rapid changes in invertebrate abundance during this period were anticipated.

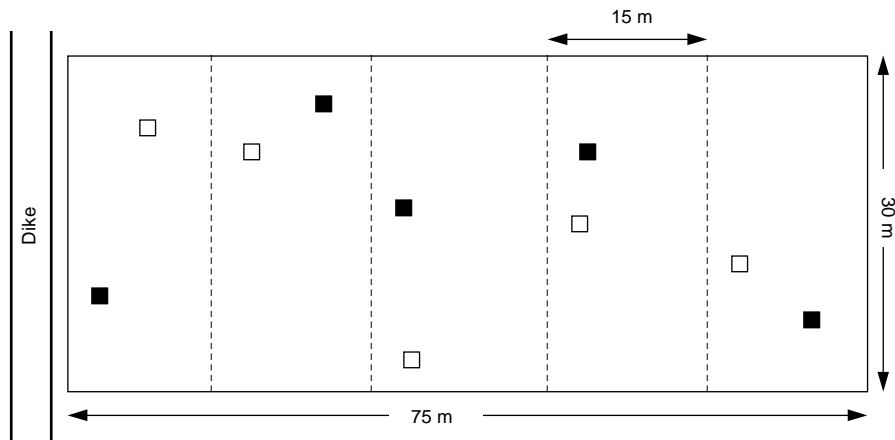


Fig. 2.2. Dimensions and configuration of sampling plots in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Solid squares represent exclosures and open squares represent open sampling stations.

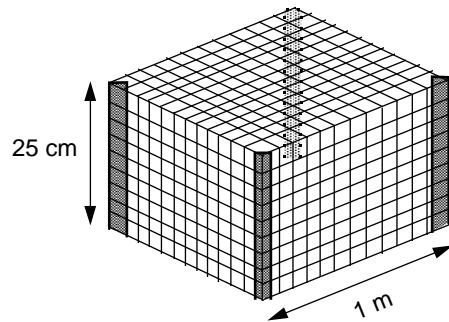


Fig. 2.3. Dimensions and configuration of nylon mesh netting for exclosure sampling stations at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Plot locations were aligned along a north-south axis (Fig. 2.1). Plots always were sampled consecutively along this axis beginning at either the northernmost or southernmost plot. The starting point (north vs. south) was alternated between sampling periods. During most sampling periods, field work was conducted by 2 individuals. Within sampling periods, all sampling for each plot was conducted by 1 person. Plot assignments were alternated between sampling periods so that no plot was sampled by the same person that had sampled it during the previous period. The exception was the final 2 sampling periods, during which I conducted all sampling. Sampling all plots generally required 2 days.

Within plots, core sample collection was started at the subplot farthest from the impoundment dike (i.e., the westernmost plot) and working back toward the dike. To reach the starting point for core sampling, the observer walked a transect from east to west along the centerline of the plot. From this transect, all locations in the plot were within 15m of the observer (i.e., half of the plot width). All waterbirds seen in or flushed from the plot while walking this transect were counted. This method of surveying waterbirds removed visibility problems encountered in attempts to count birds from impoundment dikes.

A random location was chosen within each sampling station. Sampling locations were constrained to be >20cm from previously sampled locations. Water depth, water temperature, herbaceous plant cover, submerged aquatic vegetation cover, detritus cover and detritus depth were measured at each location. Water depth ( $\pm 1$  cm) was measured using a graduated dowel rod. Additional water depth data were obtained from refuge records of periodic readings taken at permanent staff gauges near the outlet water control structure for each impoundment. Water temperature ( $\pm 1$  C) was measured at the substrate-water interface. Visual estimates of percent herbaceous plant cover and submerged aquatic vegetation cover (10% increments) within a 5-cm radius circle of the sample location were recorded. The organic layer was often thin and discontinuous, particularly in shallow-water areas. Thus, detritus cover (10% increments; visual estimate) and detritus depth ( $\pm 1$  cm; measured with a graduated dowel rod) within a 5-cm radius circle around the sample location also were recorded. All habitat variables were recorded prior to sample collection to minimize the influence of sample collection on measurements. The area in

which plant and detritus cover were estimated was selected to reflect habitat conditions at a scale potentially important to aquatic invertebrates. The 5-cm radius also ensured that habitats within sampling stations would not be double-sampled across sampling periods, because random core sample locations were constrained to be >20cm apart.

After collection of habitat data, 1 10-cm deep x 10-cm diameter benthic core sample was collected from that location. Samples were collected using a PVC pipe that had been sharpened at 1 end to facilitate substrate penetration. Sample depth was controlled by initially resting the sampler on the substrate surface at the chosen location, and marking a point on the sampler 10cm above the water surface. The sampler was driven into the substrate until this mark met the water surface (i.e., when the sampler had traveled 10cm into the substrate). The water surface was used as a reference because the substrate was not always clearly visible when water levels were high. Samples were retrieved by tilting the sampler to one side, inserting a hand into the hole in the substrate created by the sampler, and covering the bottom of the sampler by hand. The sampler was then removed from the substrate, and the sample was placed into a labelled plastic bag. Small holes drilled into the sampler 11 cm above the sharpened end allowed surface water to drain prior to placing the sample into its bag. The holes were located slightly above the top of the core sample to prevent loss of interface organisms when water was drained. Core samples were washed <30 min after collection over a 550- $\mu$ m sieve using either a washing bucket (Wildco Model 190-E20) or a self-cleaning screen (Euliss and Swanson 1989). Material remaining on the screen was preserved in ethanol with Rose Bengal stain. Samples were stored on ice in the field and in a walk-in cooler in the laboratory.

All samples were sorted in the laboratory under bright light after rinsing over a 550- $\mu$ m screen to remove ethanol. Sample contents were placed in white plastic pans and covered with a shallow layer of water. All invertebrates encountered were counted by Order (Family for coleopterans and dipterans). Macroinvertebrates were removed from samples, placed in plastic vials with ethanol, and stored in a walk-in cooler. Microinvertebrates (e.g., Cladocera, Copepoda) were counted but were not removed from samples. Taxonomy followed Merritt and Cummins (1996) and Thorp and Covich (1991).

Invertebrate dry mass was determined after combining invertebrates for both sampling station types within plots. There were originally 160 samples collected per sampling period (16 plots x 5 subplots / plot x 2 sampling stations / subplot), but low density of invertebrates for many samples led to a concern that dry mass for many taxa within samples would be less than 0.01 mg. By combining samples, 32 dry mass measures were collected per sampling period (16 plots x 2 sampling stations / plot). Invertebrates were removed from vials and assigned to 1 of 10 taxonomic groups:

Chironomids--Chironomidae larvae

Other Diptera--Larvae of all other Diptera Families

Diptera Pupae--Pupae of all Diptera Families

Coleoptera Adults--All adult Coleoptera

Coleoptera Larvae--All Coleoptera larvae

Amphipoda--*Gammarus* spp.

Isopoda--Isopoda

Oligochaetes--Earthworms and Oligochaetes

Gastropods--Gastropods

Miscellaneous Invertebrates--All other taxa (Collembola, Hemiptera, Odonata, etc.)

Invertebrates in each group were placed in individual plastic weighing dishes and dried 24hr at 60C. After drying, dishes were placed in a bell dessicator >2hr to allow equilibration with room temperature. Dry mass was determined on a Mettler balance ( $\pm 0.01$  mg) by placing dried invertebrates onto tared glasine weighing paper. To correct for missing samples, dry mass for each taxonomic group was divided by the number of samples combined. Thus, the response variable was an estimate of invertebrate dry mass per core sample.

Prior to analysis, invertebrate abundance data were summarized by assigning all organisms to 1 of the 10 groups used to group taxa for dry mass determinations. An additional response variable (Crustacea) was generated to account for abundance of microinvertebrates (primarily Cladocera, Copepoda, and Ostracoda). Because these organisms were not removed from samples, dry mass was not determined for this group.

Mean size of individual invertebrates for each taxonomic group was estimated by dividing mean dry mass per sample by mean abundance per sample. Abundance data were combined across sampling stations within plots prior to calculating mean invertebrate size.

### **Statistical Analysis**

Abundance, dry mass and invertebrate size data were analyzed using repeated measures mixed model analysis of variance (PROC MIXED, Littell et al. 1996). Specification of models where random factors are included should account for these factors to ensure that appropriate error terms are employed (Bennington and Thayne 1994). PROC MIXED uses an iterative approach to converge on variance component estimates, and is preferable to general linear models (e.g., PROC GLM, SAS Institute 1990) for analysis of mixed-factor studies (Littell et al. 1996). Models included Plot (Pool x Discing) and Sampling Station x Subplot (Plot x Pool x Discing) as random error terms. Fixed factors included Sampling Period, Pool, Discing, Predation (i.e., the enclosure effect), and all possible interactions between these factors. The null hypothesis of no discing effect on response variables was tested with the Discing and Sampling Period x Discing factors, whereas the null hypothesis of no waterbird predation effect on response variables was tested with the Predation, Predation x Sampling Period, and Predation x Discing factors. Models were analyzed for each of the 11 abundance variables, 10 total dry mass variables, and 10 invertebrate size variables. Additional models were analyzed to test for effects on total invertebrate abundance, total invertebrate dry mass, and total invertebrate size, where the response variables were the sum of all taxonomic groups for each sample. Similar models were used to test for variation in habitat variables. Although an effect of waterbird predation on habitat variables was not expected, the Predation main effect and all interactions were retained in habitat models to assess potential effects of enclosure netting on these variables.

PROC MIXED allows specification of the within-factors covariance structure (TYPE= option; Littell et al. 1996), which describes the relationship between repeated measures on a given subject (i.e., Plots for analysis of Discing effects). All models were initially analyzed with an unspecified covariance structure, which makes no assumptions about correlations among repeated measures. However, unique solutions could not be found for many of these models.

Thus, all models also were analyzed using compound symmetry and autoregressive covariance structures. The compound symmetry structure assumes that all pairs of repeated measures on a subject are equally correlated regardless of their temporal relationships, whereas the autoregressive structure assumes that correlation between repeated measures is proportional to the time period between measurements (Littell et al. 1996). Where >1 of these covariance structures resulted in convergence for a given model, the model with the highest Akaike's Information Criterion was selected as the final model (Littell et al. 1996).

Significant Sampling Period x Pool x Discing and Sampling Period x Pool x Predation interactions occurred for several taxa, suggesting that invertebrate response to discing or predation varied among time periods and impoundments. These interactions were examined by calculating indices of Relative Abundance, Relative Total Dry Mass, or Relative Invertebrate Size for significant interactions. For example, the Relative Abundance index for the Sampling Period x Pool x Discing interaction was calculated for each time period and pool as  $([ \text{Mean abundance in disced plots} ] / [ \text{Mean abundance in control plots} ]) * 100$ . Values of this index >100 indicate higher relative abundance in disced than in control plots, whereas values <100 indicate higher relative abundance in control than in disced plots. Similarly, index values >100 for Sampling Period x Pool x Predation interactions indicate higher relative abundance in exclosures, whereas values <100 indicate higher relative abundance in open sampling stations. Index values for significant interactions were examined graphically by plotting values for each Pool against Sampling Period.

All data were  $\log_{10}(x + 1)$ -transformed prior to analysis, with the exception of percentage variables (detrital cover, herbaceous plant cover, and submerged aquatic vegetation cover), which were  $\arcsin(x^{0.5})$ -transformed (Sokal and Rohlf 1995). To maintain additivity across taxonomic groups within samples, arithmetic means ( $\pm 1$  SE; PROC MEANS, SAS Institute 1990) are reported herein. As the consequences of Type I error were deemed minimal, statistical significance was accepted at  $P \leq 0.10$ .

## RESULTS

### Habitat Variables

Peak water depths in both impoundments occurred during February, whereas minimum water depths occurred during late May and early June (Table 2.1). Staff gauge readings collected by refuge biologists near outlet water control structures (i.e., the deepest portion of the impoundments) showed a pattern of water depth dynamics that was similar to water depth measurements obtained on study plots (Fig. 2.4, 2.5). Water depth did not differ between disced and control areas, but a significant Sampling Period x Discing interaction (Table 2.3) revealed deeper water depths in disced plots during some sampling periods. The maximum difference in water depth between disced and control plots occurred during the first sampling period (3.9 cm), but differences between treatments thereafter were < 2cm (Table 2.1).

Water temperature was highest in the spring sampling periods when sheet water remained on the study plots (i.e.,  $\bar{x}$  depth >0 during mid-May and mid-June sampling periods; Tables 2.1, 2.2). The Discing main effect was nonsignificant for water temperature, although the Sampling Period x Discing interaction (Table 2.3) revealed higher water temperatures in disced plots during Spring 1996 (Table 2.1). Water temperature was the only habitat variable for which the Predation (i.e., Exclosure) main effect was significant (Table 2.3), although the observed temperature difference (Exclosure =  $18.8 \pm 0.2$  C, Open =  $19.0 \pm 0.2$  C) was less than the precision with which water temperature was recorded in the field ( $\pm 1$  C).

Herbaceous plant cover was significantly higher in control than in disced plots (Discing effect; Table 2.3), and the magnitude of this difference varied among sampling periods (Sampling Period x Discing interaction; Tables 2.1, 2.3). The most pronounced differences in herbaceous plant cover occurred during spring sampling periods, when plant cover in both disced and control plots were at their annual minimum (Table 2.1). Mean herbaceous plant cover increased by 10-20% from spring 1996 to spring 1997 (Tables 2.2, 2.3). No Exclosure effects or interactions were significant for plant cover (Tables 2.2, 2.3).

Table 2.1. Mean values of 6 habitat variables at benthic core sampling locations in disced ( $n = 8$ ) and control ( $n = 8$ ) plots in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Water Depth (cm)				Water Temperature (C)				Herbaceous Plant Cover (%)				Submerged Aquatic Vegetation Cover (%)				Detritus Cover (%)				Detritus Depth (cm)			
	Control		Disced		Control		Disced		Control		Disced		Control		Disced		Control		Disced		Control		Disced	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	5.8	1.5	1.9	1.1	21.3	0.6	23.1	0.7	24.1	6.3	8.9	2.0	8.3	4.0	2.7	1.4	89.6	3.6	82.1	3.5	5.3	1.0	3.3	1.0
17 - 19 May 1996	3.4	2.4	3.1	1.1	24.8	1.4	26.6	1.4	29.9	4.6	10.5	2.1	1.8	1.0	0.2	0.1	96.9	1.3	91.9	3.2	5.6	1.1	3.7	0.9
31 May - 2 Jun 1996	-0.7	1.9	-2.9	2.0	21.4	0.7	20.3	0.6	29.6	5.2	13.5	1.7	0.6	0.4	0.0	0.0	96.6	1.4	88.3	5.8	3.6	0.8	2.9	0.7
13 - 15 Jun 1996	1.8	2.9	-0.6	1.4	26.0	0.4	27.5	0.6	29.0	5.1	23.7	3.6	0.3	0.3	0.1	0.1	99.4	0.4	82.7	5.0	5.6	1.4	2.3	0.9
25-26 Oct 1996	4.3	1.4	3.6	1.5	20.4	0.6	21.1	0.5	45.7	7.2	31.8	5.5	4.3	2.1	2.3	1.0	91.6	4.5	91.8	3.0	4.3	1.1	3.7	1.1
21-22 Nov 1996	2.7	2.2	2.7	1.9	9.1	0.9	8.4	0.8	54.6	4.8	49.7	4.6	2.1	1.0	4.2	2.1	94.7	2.4	90.7	3.3	4.3	1.2	3.3	0.9
25-26 Jan 1997	13.7	2.6	12.2	2.5	10.9	1.1	10.7	1.1	36.7	3.6	26.9	6.1	4.6	1.8	1.9	0.7	94.4	2.2	95.0	2.2	4.6	0.9	4.5	1.0
21-23 Feb 1997	23.5	2.4	20.9	2.2	15.1	1.2	15.4	1.1	22.3	4.9	15.3	3.5	1.7	0.7	4.9	1.9	98.4	0.6	93.4	2.1	4.9	0.8	4.6	0.9
19-21 Apr 1997	1.6	1.7	-0.8	3.0	16.5	1.1	16.2	1.1	31.3	4.7	17.1	5.2	1.8	0.8	1.3	0.9	97.6	0.9	91.3	4.1	2.3	0.5	1.9	0.4
1-3 May 1997	4.7	1.2	4.1	2.1	20.8	1.3	21.7	1.3	35.6	6.8	20.1	6.4	3.4	0.9	3.6	1.1	96.6	0.9	86.9	4.6	3.2	0.5	3.1	0.9
26-28 May 1997	-3.2	1.2	-4.6	2.3	20.0	0.2	20.3	0.9	47.0	6.9	31.4	7.6	1.0	1.0	0.4	0.4	98.8	1.3	92.3	4.3	1.8	0.1	1.7	0.4
Grand Means	5.2	1.4	3.6	1.5	18.7	0.2	19.2	0.3	35.1	3.7	22.6	2.8	2.7	0.7	1.9	0.5	95.9	1.1	89.6	2.9	4.1	0.5	3.2	0.4

Table 2.2. Mean values of 6 habitat variables at benthic core sampling locations in open and exclosure sampling stations in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Means were generated using plots ( $n = 16$ ) as independent sampling units (i.e., sampling stations [ $n = 5$  exclosures and 5 open sampling stations per plot] were considered subsamples).

Sampling Period	Water Depth (cm)				Water Temperature (C)				Herbaceous Plant Cover (%)				Submerged Aquatic Vegetation Cover (%)				Detritus Cover (%)				Detritus Depth (cm)			
	Open		Exclosure		Open		Exclosure		Open		Exclosure		Open		Exclosure		Open		Exclosure		Open		Exclosure	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	3.9	1.1	3.8	1.1	22.4	0.5	21.9	0.5	14.8	3.6	18.3	4.1	4.7	2.2	6.3	2.5	86.4	2.8	85.3	3.2	3.8	0.7	4.8	0.8
17 - 19 May 1996	2.7	1.6	3.8	1.1	25.8	1.0	25.6	1.0	20.1	3.7	20.3	3.8	0.6	0.5	1.3	0.7	94.8	2.3	94.0	2.0	4.1	0.8	5.2	0.8
31 May - 2 Jun 1996	-1.8	1.6	-1.7	1.3	21.0	0.4	20.6	0.5	20.0	3.0	23.0	4.2	0.5	0.5	0.2	0.2	92.1	4.1	92.7	2.6	3.0	0.6	3.5	0.5
13 - 15 Jun 1996	0.5	1.5	0.8	1.8	27.1	0.4	26.4	0.4	25.3	3.3	27.4	3.2	0.3	0.3	0.0	0.0	90.3	3.7	91.9	3.5	3.8	0.9	4.2	1.0
25-26 Oct 1996	3.8	1.0	4.1	1.1	20.9	0.5	20.7	0.4	42.8	5.5	34.8	4.7	4.1	1.7	2.5	1.0	92.8	2.9	90.6	3.0	4.1	0.8	3.9	0.8
21-22 Nov 1996	2.9	1.6	2.3	1.3	8.8	0.6	8.7	0.6	51.9	3.7	52.8	4.5	3.6	1.5	2.8	1.0	92.5	2.3	93.0	2.3	4.3	0.9	3.3	0.6
25-26 Jan 1997	13.2	1.8	12.7	1.7	10.8	0.8	10.8	0.8	30.5	4.7	33.0	3.8	3.4	1.4	3.2	1.0	95.3	1.8	93.9	2.0	4.7	0.6	4.3	0.7
21-23 Feb 1997	22.6	1.7	21.8	1.7	15.3	0.8	15.3	0.8	18.6	3.4	19.1	3.4	3.3	1.2	3.4	1.0	96.4	1.2	95.3	1.5	5.3	0.8	4.1	0.5
19-21 Apr 1997	0.0	1.8	0.8	1.7	16.4	0.8	16.3	0.8	24.1	3.9	24.3	4.1	1.5	0.6	1.6	0.7	93.9	2.5	94.9	2.0	2.2	0.4	2.0	0.3
1-3 May 1997	4.4	1.1	4.3	1.3	21.6	1.0	21.0	0.8	27.2	5.6	28.4	4.8	3.4	0.9	3.6	0.8	93.8	2.7	89.8	3.5	3.2	0.5	3.0	0.5
26-28 May 1997	-3.8	1.2	-4.1	1.4	20.1	0.5	20.1	0.5	38.6	5.2	40.0	5.9	1.1	0.7	0.4	0.4	95.2	2.7	95.8	2.6	1.8	0.2	1.8	0.3
Grand Means	4.4	0.7	4.1	0.6	18.8	0.2	19.0	0.2	28.5	1.6	28.8	1.7	2.4	0.4	2.3	0.4	93.0	1.1	92.2	1.2	3.6	0.2	92.2	3.6

Table 2.3. *P*-values from mixed model analyses of variance for 6 habitat variables at benthic core sampling locations in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The Discing effect reflects comparison of disced to control plots, whereas the Predation effect reflects comparison of open to enclosure sampling stations. Each column represents a separate analysis.

Source	df	Submerged					
		Water Depth	Water Temperature	Herbaceous Plant Cover	Aquatic Vegetation Cover	Detritus Cover	Detritus Depth
Discing <sup>a</sup>	1,12	0.387	0.516	0.021	0.409	0.029	0.060
Pool <sup>a</sup>	1,12	0.008	0.217	0.179	0.701	0.015	0.011
Pool * Discing <sup>a</sup>	1,12	0.850	0.735	0.854	0.076	0.455	0.886
Predation <sup>b</sup>	1,140	0.582	0.067	0.611	0.861	0.795	0.616
Discing * Predation <sup>b</sup>	1,140	0.951	0.988	0.557	0.989	0.542	0.312
Pool * Predation <sup>b</sup>	1,140	0.431	0.569	0.273	0.834	0.240	0.721
Pool * Discing * Predation <sup>b</sup>	1,140	0.542	0.380	0.210	0.860	0.448	0.168
Sampling Period <sup>c</sup>	101,454	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Sampling Period * Discing <sup>c</sup>	101,454	0.001	<0.001	0.018	<0.001	<0.001	<0.001
Sampling Period * Predation <sup>c</sup>	101,454	0.655	0.991	0.608	0.882	0.900	0.026
Sampling Period * Discing * Predation <sup>c</sup>	101,454	0.709	0.998	0.837	0.959	0.722	0.718
Sampling Period * Pool <sup>c</sup>	101,454	<0.001	<0.001	<0.001	<0.001	0.074	<0.001
Sampling Period * Pool * Discing <sup>c</sup>	101,454	<0.001	0.048	0.286	0.296	0.003	<0.001
Sampling Period * Pool * Predation <sup>c</sup>	101,454	0.873	0.997	0.430	0.967	0.480	0.261
Sampling Period * Pool * Discing * Predation <sup>c</sup>	101,454	0.461	0.995	0.876	0.949	0.777	0.979

<sup>a</sup> Error term = Plot (Pool x Discing)

<sup>b</sup> Error term = Predation x Subplot (Plot x Pool x Discing)

<sup>c</sup> Error term = Sampling Period x Predation (Subplot x Plot x Pool x Discing)

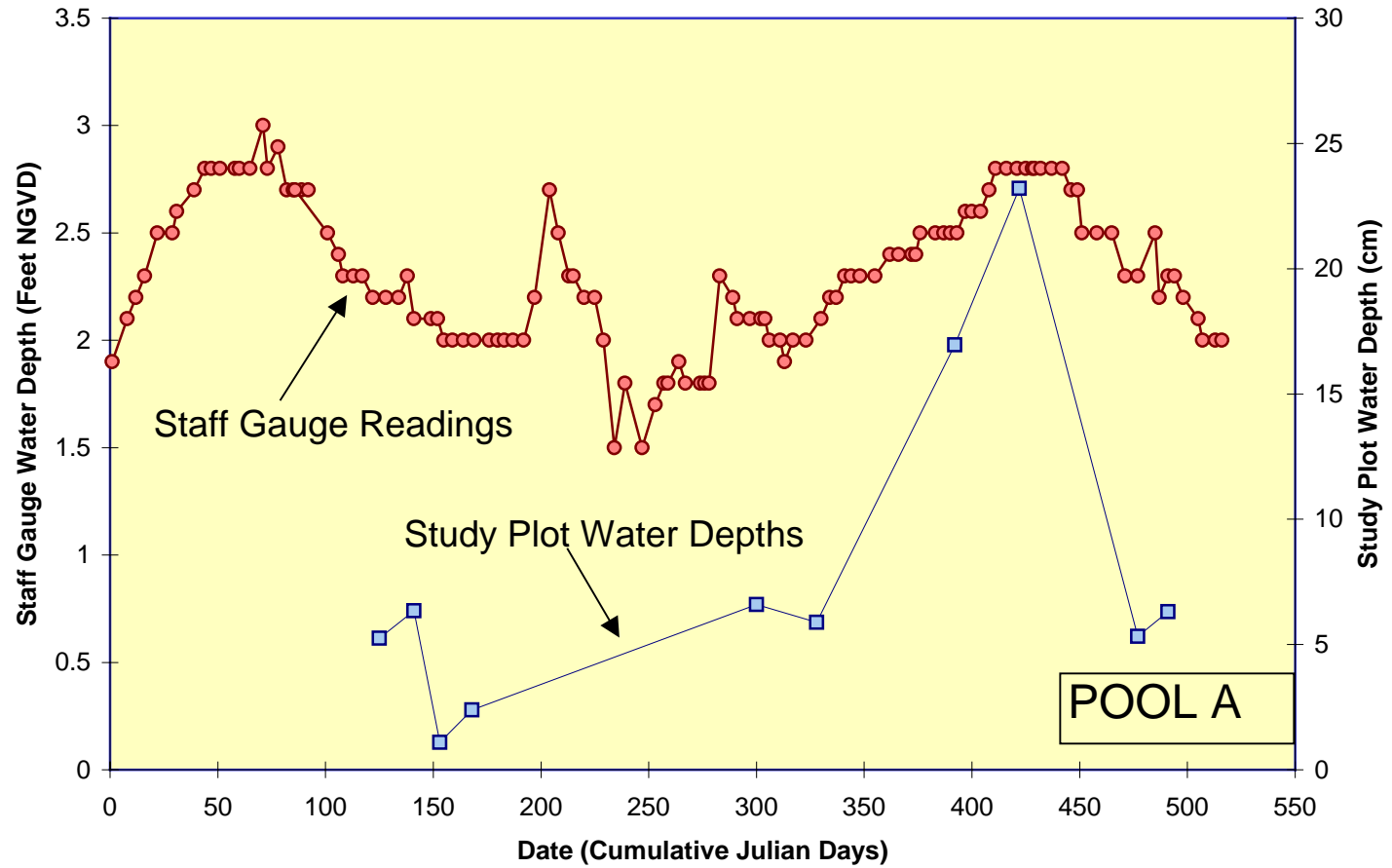


Figure 2.4. Water depth in Pool A, Back Bay National Wildlife Refuge, Virginia Beach, Virginia, Jan 1996 - May 1997. Depth data were obtained from refuge readings of staff gauges (feet NGVD) and from measurements on 8 study plots during benthic core sample collection (cm).

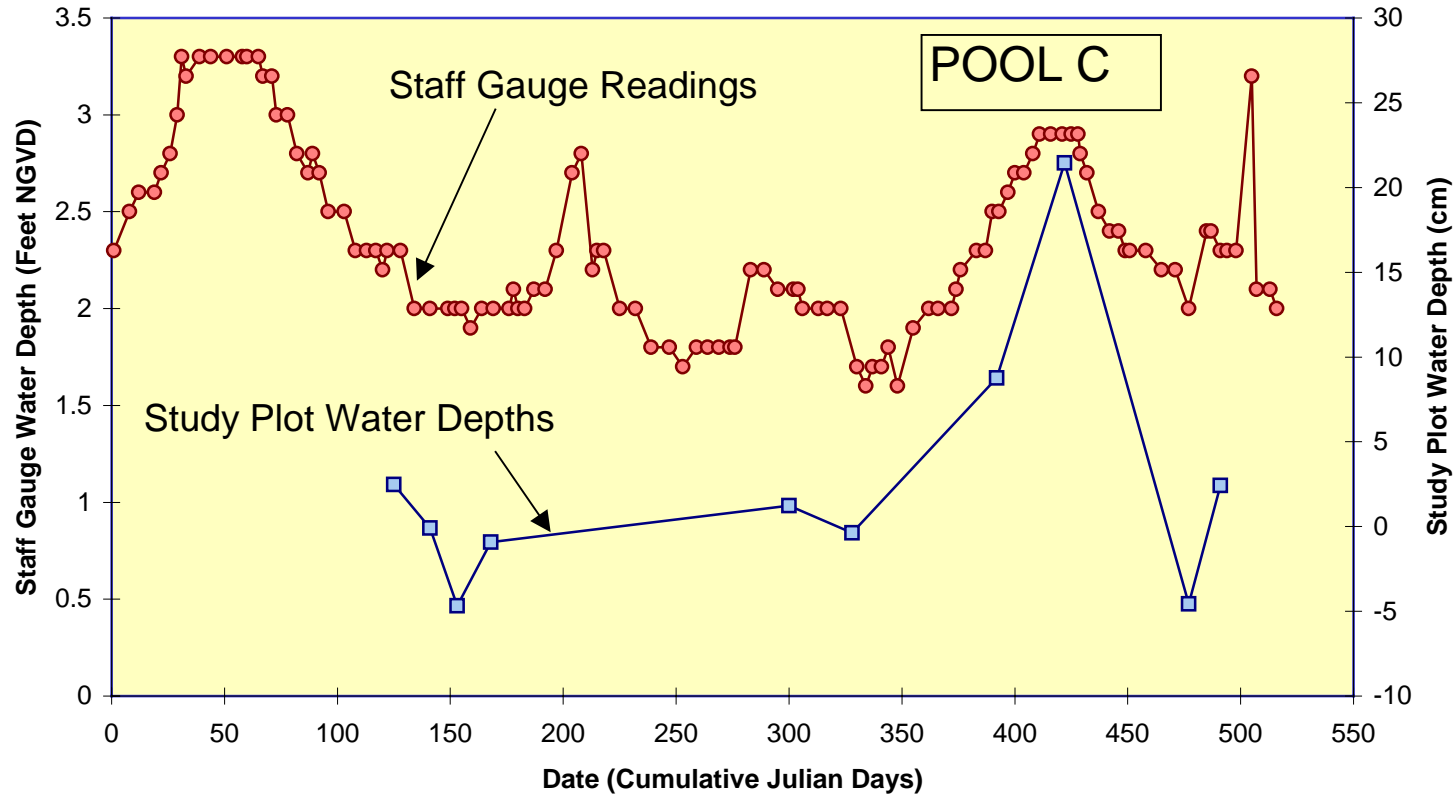


Fig. 2.5. Water depth in Pool C, Back Bay National Wildlife Refuge, Virginia Beach, Virginia, Jan 1996 - May 1997. Depth data were obtained from refuge readings of staff gauges (feet NGVD) and from measurements on 8 study plots during benthic core sample collection (cm).

Submerged aquatic vegetation cover was generally < 5% in all sampling stations and treatments (Tables 2.1, 2.2). A significant Sampling Period x Discing interaction (Table 2.3) appeared to be driven by higher submerged aquatic vegetation cover in disced plots during the first 2 sampling periods, and variable dominance between treatments from Oct 1996 to Feb 1997 (Table 2.1). No Enclosure effects or interactions were significant for submerged aquatic vegetation cover (Tables 2.2, 2.3).

Disced plots had lower mean detritus cover (Disced =  $89.6 \pm 2.9$  %, Control =  $95.9 \pm 1.1$  %) and detritus depth (Disced =  $3.2 \pm 0.4$  cm, Control =  $4.1 \pm 0.5$  cm) over the entire study period than did control plots (Discing effect; Table 2.3). Mean detritus cover was >90% in control plots for 10 of the 11 sampling periods, and for 7 of the 11 sampling periods in disced plots (Sampling Period x Discing interaction; Tables 2.1, 2.3). Detritus depth was higher in control than in disced plots during 3 of the 4 spring 1996 sampling periods, but was similar between disced and control plots during spring 1997 (Sampling Period x Discing interaction; Tables 2.1, 2.3). Detritus cover was higher in control plots during both spring sampling periods, but was similar between treatments during fall and winter (Table 2.1). Detritus depth was about 1.0 cm higher in enclosures than in open sampling stations during May 1996, but was 0.5 - 1.0 cm higher in open sampling stations than in enclosures during Oct 1996 - Jan 1997 (Sampling Period x Discing x Predation interaction, Tables 2.2, 2.3).

### **Bird Surveys**

Waterbird density varied among sampling periods and impoundments, but no Discing terms were significant in the analysis (Fig. 2.6, Table 2.4). The highest waterbird density ( $\bar{x} = 21.7 \pm 8.1$  birds / ha) occurred during the initial sampling period (4-5 May 1996; Fig. 2.6). Bird density was <1.5 birds / ha from late May - late Jan; no birds were recorded in any study plots during the January sampling period. Bird density during 4-5 May 1996 was about 3x higher than during 3-4 May 1997 ( $\bar{x} = 7.8 \pm 5.0$  birds / ha). Pool A study plots had higher bird density ( $\bar{x} = 9.3 \pm 2.2$  birds / ha) than did Pool C study plots ( $\bar{x} = 2.4 \pm 1.0$  birds / ha;  $F = 11.05$ ,  $P = 0.006$ , Table 2.4). Averaged across sampling periods, 5 study plots had mean bird densities > 10 birds / ha; 4 of these were disced plots (3 in Pool A and 1 in Pool C), but the highest mean bird density

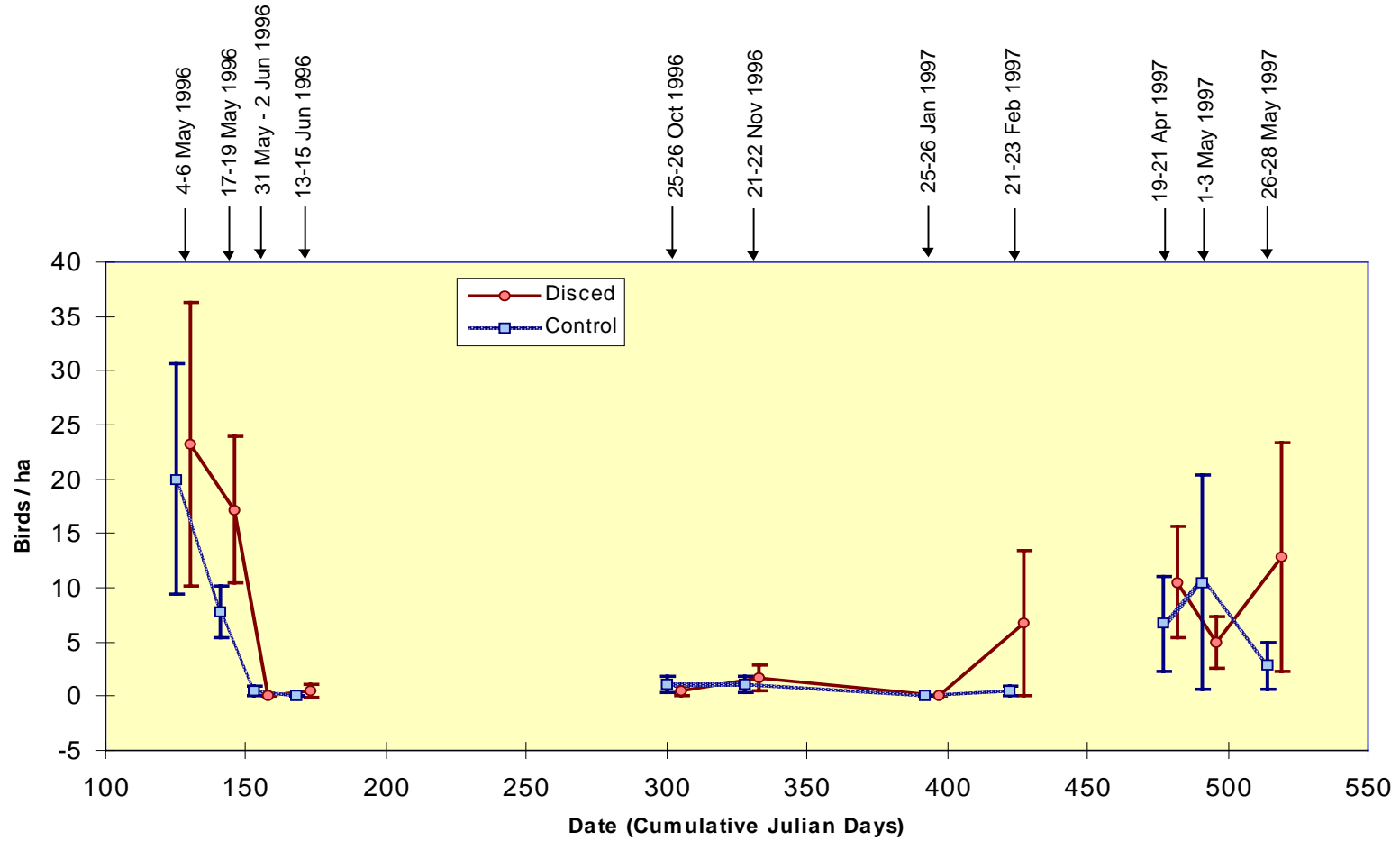


Figure 2.6. Mean ( $\pm$  SE) waterbird density (birds / ha) in disced ( $n = 8$ ) and control ( $n = 8$ ) plots in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Means for disced plots are offset +5 days for clarity.

Table 2.4. Results of repeated measures mixed model analysis of variance for the effects of Discing, Pool and Sampling Period on total waterbird density in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

<b>Source</b>	<b>df</b>	<b>F</b>	<b>P</b>
Discing <sup>a</sup>	1,12	0.95	0.333
Pool <sup>a</sup>	1,12	11.05	0.006
Discing x Pool <sup>a</sup>	1,12	0.00	0.974
Sampling Period <sup>b</sup>	10,120	5.45	<0.001
Sampling Period x Discing <sup>b</sup>	10,120	0.41	0.941
Sampling Period x Pool <sup>b</sup>	10,120	2.25	0.019
Sampling Period x Discing x Pool <sup>b</sup>	10,120	0.56	0.842

<sup>a</sup> Error term = Plot (Discing x Pool)

<sup>b</sup> Error term = Sampling Period (Plot x Discing x Pool)

( $19.8 \pm 9.8$  birds / ha) occurred in a control study plot in Pool A. No waterbirds were recorded during any foot surveys in 3 plots; all 3 were in Pool C and 2 of the 3 were control plots.

### **Invertebrate Response to Discing**

*Abundance.*--Chironomid abundance was about 2x higher in disced than in control areas during spring 1996, and 2.5 - 6.0x higher in disced areas during fall - winter (Table 2.5). Abundance of Other Diptera was 1.2 – 1.7x higher in disced than in control areas during Oct, Nov, and Feb, but similar between treatments during Jan and all spring months (Table 2.6). Mean abundance of Diptera pupae (Table 2.7), Coleoptera larvae (Table 2.8), and Coleoptera adults (Table 2.9) was generally < 1 per sample; Diptera pupae and Coleoptera larvae reached peak abundance during spring, whereas the highest abundance of Coleoptera adults occurred during Oct – Jan (Tables 2.7 – 2.9). Amphipods were 2.7 – 4.2x more abundant in disced than in control areas during Nov and Jan, but similar in abundance between treatments during the remaining sampling periods (Table 2.10). Isopods and Oligochaetes were the least and most common taxa on the study area, respectively (Tables 2.11, 2.12). Isopods were essentially undetected from Oct – Jan, and had abundance of < 2.0/sample in all other sampling periods (Table 2.11). Oligochaetes showed a similar pattern of peak abundance in spring, but abundance remained > 14/sample from Jun – Feb (Table 2.12). Gastropods were the only taxon for which abundance was consistently higher in control than in disced plots. They were 1.5 – 3.6x higher in control areas during mid Apr - mid May of both years, but abundance was similar between treatments during the remaining sampling periods (Table 2.13). Crustacea were nearly an order of magnitude more abundant in Apr – May 1997 than in Apr – May 1996, but showed little consistent variation between treatments (Table 2.14). Miscellaneous Invertebrates were 1.7x more abundant in disced than in control areas when abundance was highest (early May 1996; Table 2.15), but were substantially lower in abundance during all subsequent sampling periods. Total Invertebrate abundance in disced plots was similar to or higher than that in control plots during all sampling periods (Table 2.16). Peak Total Invertebrate abundance occurred during Spring 1997, although abundance during Spring 1996 remained up to 2x higher than that during the fall and winter sampling periods (Table 2.16). Chironomids, Diptera Pupae, Amphipods,

Table 2.5. Mean abundance, total dry mass and dry mass per individual of Chironomidae in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots												Enclosure vs. Open Sampling Stations											
	Abundance (# / sample)				Dry Mass								Abundance (# / sample)				Dry Mass							
	Control		Disced		Total (mg / sample)				Per Individual (mg)				Open		Exclosure		Total (mg / sample)				Per Individual (mg)			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	10.9	3.6	19.6	8.6	3.35	1.08	5.02	1.93	0.43	0.18	0.52	0.30	15.0	4.2	15.5	5.9	4.56	1.26	3.82	1.22	0.53	0.31	0.42	0.20
17 - 19 May 1996	8.4	4.1	15.1	6.0	3.03	1.56	3.89	1.57	0.34	0.07	0.24	0.05	11.1	3.5	12.4	4.2	3.46	1.11	3.46	1.25	0.30	0.05	0.28	0.05
31 May - 2 Jun 1996	0.9	0.4	2.1	1.2	0.20	0.09	0.43	0.22	0.14	0.04	0.11	0.02	2.5	1.1	0.4	0.1	0.57	0.23	0.05	0.02	0.16	0.04	0.08	0.02
13 - 15 Jun 1996	0.5	0.2	0.6	0.2	0.11	0.06	0.06	0.04	0.10	0.05	0.05	0.03	0.8	0.3	0.2	0.1	0.15	0.07	0.02	0.02	0.11	0.05	0.03	0.02
25-26 Oct 1996	0.8	0.2	3.0	1.8	0.01	0.01	0.06	0.04	0.00	0.00	0.01	0.00	2.3	1.0	1.5	0.9	0.05	0.03	0.02	0.02	0.01	0.00	0.00	0.00
21-22 Nov 1996	3.0	1.6	8.8	3.4	0.04	0.02	0.16	0.09	0.00	0.00	0.01	0.00	5.5	2.0	6.4	2.9	0.05	0.02	0.14	0.09	0.00	0.00	0.01	0.00
25-26 Jan 1997	3.6	2.3	11.3	6.6	0.15	0.12	0.25	0.15	0.07	0.05	0.01	0.00	7.2	4.7	8.1	3.1	0.20	0.13	0.20	0.10	0.06	0.05	0.02	0.01
21-23 Feb 1997	2.0	1.3	12.0	6.5	0.07	0.06	0.77	0.57	0.01	0.01	0.02	0.01	4.8	2.4	9.2	4.8	0.19	0.10	0.65	0.52	0.01	0.00	0.02	0.01
19-21 Apr 1997	5.5	2.6	13.8	6.2	0.50	0.37	1.24	0.53	0.06	0.03	0.08	0.04	12.1	4.8	7.2	2.4	1.26	0.53	0.47	0.16	0.07	0.02	0.06	0.02
1-3 May 1997	7.5	4.3	11.6	5.9	1.24	0.74	1.40	0.69	0.09	0.04	0.09	0.04	10.4	3.8	8.7	3.5	1.76	0.79	0.88	0.32	0.10	0.03	0.07	0.03
26-28 May 1997 <sup>a</sup>	1.8	0.7	5.1	2.0	--	--	--	--	--	--	--	--	3.6	1.3	3.4	1.2	--	--	--	--	--	--	--	--
Grand Means	4.2	1.3	9.4	3.9	0.87	0.3	1.32	0.48	0.12	0.03	0.11	0.03	6.9	1.2	6.7	1.1	1.22	0.31	0.97	0.28	0.13	0.05	0.10	0.04

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.6. Mean abundance, total dry mass and dry mass per individual of Other Diptera in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots										Enclosure vs. Open Sampling Stations															
	Abundance (# / sample)				Dry Mass						Abundance (# / sample)				Dry Mass											
	Control		Disced		Control			Disced			Control		Disced		Open		Exclosure		Open		Exclosure		Open		Exclosure	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	3.2	0.9	2.0	0.5	0.44	0.10	0.84	0.41	0.23	0.10	0.62	0.41	2.5	0.6	2.6	0.9	0.75	0.38	0.53	0.25	0.26	0.11	0.59	0.42		
17 - 19 May 1996	3.2	1.0	4.8	1.2	0.91	0.47	0.44	0.13	0.83	0.65	0.10	0.03	2.6	0.4	5.4	1.2	0.64	0.31	0.71	0.22	0.54	0.42	0.39	0.25		
31 May - 2 Jun 1996	4.0	1.0	3.5	0.9	0.51	0.17	2.71	1.83	0.13	0.03	0.44	0.18	3.0	0.5	4.5	0.9	0.71	0.23	2.51	1.86	0.21	0.05	0.37	0.20		
13 - 15 Jun 1996	3.8	0.6	3.6	0.7	1.46	0.66	1.14	0.35	0.36	0.16	0.45	0.21	3.6	0.3	3.7	0.7	1.34	0.59	1.26	0.39	0.33	0.15	0.48	0.22		
25-26 Oct 1996	10.1	2.3	16.2	2.5	4.17	1.10	3.28	1.39	0.47	0.13	0.24	0.10	11.1	1.4	15.2	3.1	1.33	0.34	6.12	1.74	0.13	0.03	0.57	0.18		
21-22 Nov 1996	8.7	1.1	12.2	2.1	3.59	1.50	8.95	4.01	0.42	0.16	0.83	0.37	8.9	1.1	11.7	1.8	7.02	3.74	5.52	1.77	0.72	0.31	0.53	0.18		
25-26 Jan 1997	11.7	3.9	12.8	2.2	6.43	1.42	5.40	2.22	0.84	0.30	0.50	0.22	9.5	1.7	15.7	3.5	5.40	1.67	6.44	2.44	0.72	0.30	0.61	0.27		
21-23 Feb 1997	9.2	1.7	15.8	1.8	6.21	2.20	5.16	2.21	0.65	0.25	0.38	0.20	10.7	1.3	15.0	2.5	2.12	1.25	9.25	2.96	0.19	0.11	0.84	0.31		
19-21 Apr 1997	6.5	1.1	5.3	0.7	6.01	1.81	2.85	1.08	1.30	0.49	0.63	0.25	5.5	0.7	6.3	0.8	3.35	1.55	5.51	1.84	0.74	0.35	1.18	0.49		
1-3 May 1997	5.2	0.6	4.9	1.1	2.48	0.96	3.68	1.77	0.42	0.11	0.78	0.38	4.5	0.8	5.5	0.6	2.29	1.08	3.87	1.83	0.36	0.11	0.84	0.40		
26-28 May 1997 <sup>a</sup>	6.7	1.1	5.5	0.9	--	--	--	--	--	--	--	--	6.3	0.8	5.7	0.8	--	--	--	--	--	--	--	--		
Grand Means	6.5	0.6	7.7	0.7	3.22	0.51	3.44	1.13	0.56	0.10	0.50	0.08	6.1	0.3	8.1	0.6	2.49	0.55	4.17	0.79	0.42	0.07	0.64	0.08		

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.7. Mean abundance, total dry mass and dry mass per individual of Diptera pupae in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots								Enclosure vs. Open Sampling Stations															
	Abundance (# / sample)				Dry Mass				Abundance (# / sample)				Dry Mass											
	Control		Disced		Total (mg / sample)		Per Individual (mg)		Open		Exclosure		Total (mg / sample)		Per Individual (mg)									
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE								
4 - 6 May 1996	0.3	0.2	0.5	0.2	0.04	0.02	0.15	0.06	0.11	0.07	0.34	0.14	0.5	0.2	0.4	0.1	0.14	0.06	0.05	0.01	0.30	0.13	0.14	0.06
17 - 19 May 1996	1.0	0.2	1.7	0.4	0.15	0.06	0.46	0.19	0.26	0.17	0.25	0.06	1.3	0.3	1.4	0.3	0.18	0.06	0.43	0.21	0.27	0.15	0.24	0.06
31 May - 2 Jun 1996	0.6	0.2	0.8	0.3	0.26	0.12	0.73	0.33	0.38	0.16	1.51	1.06	0.5	0.2	0.8	0.3	0.24	0.09	0.75	0.36	0.48	0.18	1.41	0.95
13 - 15 Jun 1996	0.6	0.2	0.8	0.2	0.13	0.03	0.53	0.26	0.19	0.06	0.59	0.28	0.7	0.2	0.7	0.2	0.21	0.05	0.44	0.26	0.44	0.18	0.34	0.17
25-26 Oct 1996	0.2	0.1	0.3	0.1	0.15	0.06	0.05	0.02	0.39	0.13	0.08	0.04	0.4	0.1	0.2	0.1	0.07	0.03	0.13	0.06	0.21	0.12	0.27	0.13
21-22 Nov 1996	0.2	0.1	0.1	0.1	0.22	0.12	0.01	0.01	0.18	0.11	0.03	0.02	0.1	0.0	0.3	0.1	0.04	0.03	0.19	0.13	0.03	0.02	0.18	0.11
25-26 Jan 1997	0.4	0.2	0.4	0.1	0.48	0.42	0.22	0.12	0.42	0.21	0.56	0.34	0.2	0.1	0.6	0.2	0.13	0.08	0.57	0.43	0.65	0.39	0.32	0.16
21-23 Feb 1997	0.3	0.2	0.4	0.1	0.43	0.40	0.10	0.05	0.22	0.15	0.38	0.25	0.3	0.1	0.4	0.2	0.09	0.05	0.44	0.40	0.33	0.26	0.27	0.16
19-21 Apr 1997	1.0	0.2	1.3	0.3	0.31	0.15	0.28	0.08	0.24	0.09	0.21	0.05	1.3	0.3	1.0	0.2	0.32	0.10	0.28	0.13	0.24	0.06	0.21	0.07
1-3 May 1997	0.7	0.1	1.5	0.4	0.15	0.05	0.27	0.07	0.16	0.04	0.20	0.05	1.1	0.3	1.0	0.2	0.17	0.06	0.24	0.06	0.11	0.03	0.24	0.05
26-28 May 1997 <sup>a</sup>	1.9	0.4	1.9	0.5	--	--	--	--	--	--	--	--	1.7	0.3	1.9	0.4	--	--	--	--	--	--	--	--
Grand Means	0.6	0.1	0.9	0.1	0.23	0.09	0.28	0.06	0.25	0.04	0.41	0.12	0.7	0.1	0.8	0.1	0.16	0.02	0.35	0.10	0.31	0.06	0.36	0.12

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.8. Mean abundance, total dry mass and dry mass per individual of Coleoptera larvae in discing and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots								Enclosure vs. Open Sampling Stations															
	Abundance (# / sample)				Dry Mass				Abundance (# / sample)				Dry Mass											
	Control		Disced		Total (mg / sample)		Per Individual (mg)		Open		Exclosure		Total (mg / sample)		Per Individual (mg)									
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE								
4 - 6 May 1996	0.6	0.1	0.5	0.2	0.33	0.13	0.62	0.54	0.45	0.15	0.55	0.27	0.6	0.1	0.5	0.2	0.32	0.14	0.63	0.52	0.48	0.15	0.52	0.29
17 - 19 May 1996	0.8	0.1	0.5	0.1	0.75	0.26	0.59	0.37	1.12	0.43	0.95	0.59	0.8	0.2	0.6	0.1	0.96	0.33	0.37	0.19	1.27	0.44	0.81	0.48
31 May - 2 Jun 1996	1.2	0.2	0.9	0.2	0.59	0.25	0.31	0.15	0.54	0.18	0.34	0.14	0.8	0.1	1.3	0.2	0.43	0.11	0.48	0.22	0.55	0.16	0.34	0.15
13 - 15 Jun 1996	1.1	0.2	0.9	0.1	0.89	0.30	0.77	0.56	0.79	0.19	0.96	0.74	1.1	0.3	0.9	0.2	0.85	0.34	0.81	0.46	1.08	0.57	0.67	0.26
25-26 Oct 1996	0.8	0.2	0.6	0.1	0.12	0.04	0.47	0.28	0.13	0.04	0.60	0.29	0.9	0.2	0.5	0.1	0.40	0.25	0.19	0.08	0.34	0.14	0.39	0.20
21-22 Nov 1996	0.7	0.2	0.7	0.2	0.24	0.09	0.38	0.20	0.45	0.29	0.33	0.15	0.8	0.1	0.6	0.2	0.37	0.17	0.25	0.09	0.45	0.21	0.33	0.12
25-26 Jan 1997	0.7	0.2	1.0	0.2	0.48	0.18	0.52	0.22	0.78	0.26	0.40	0.16	0.5	0.1	1.2	0.3	0.36	0.14	0.64	0.25	0.59	0.23	0.59	0.21
21-23 Feb 1997	0.5	0.2	0.5	0.1	0.27	0.12	0.34	0.21	0.32	0.12	0.62	0.47	0.5	0.2	0.5	0.1	0.38	0.20	0.23	0.13	0.71	0.46	0.23	0.12
19-21 Apr 1997	0.9	0.1	0.7	0.2	0.41	0.08	0.39	0.13	0.46	0.08	0.59	0.17	0.7	0.1	0.9	0.2	0.28	0.09	0.52	0.15	0.43	0.15	0.61	0.18
1-3 May 1997	1.1	0.2	0.8	0.1	0.58	0.11	0.27	0.13	0.72	0.19	0.32	0.13	0.7	0.1	1.1	0.2	0.43	0.13	0.42	0.11	0.55	0.15	0.49	0.17
26-28 May 1997 <sup>a</sup>	2.0	0.3	3.1	0.4	--	--	--	--	--	--	--	--	2.4	0.3	2.8	0.5	--	--	--	--	--	--	--	--
Grand Means	0.9	0.1	0.9	0.1	0.47	0.07	0.47	0.16	0.58	0.07	0.57	0.11	0.9	0.1	1.0	0.1	0.48	0.08	0.45	0.10	0.64	0.09	0.50	0.06

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.9. Mean abundance, total dry mass and dry mass per individual of Coleoptera adults in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots								Enclosure vs. Open Sampling Stations															
	Abundance (# / sample)				Dry Mass				Abundance (# / sample)				Dry Mass											
	Control		Disced		Total (mg / sample)		Per Individual (mg)		Open		Exclosure		Total (mg / sample)		Per Individual (mg)									
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE								
4 - 6 May 1996	0.2	0.1	0.1	0.1	2.18	1.83	0.28	0.27	5.77	4.54	0.67	0.63	0.2	0.1	0.1	0.0	0.38	0.23	2.08	1.75	0.78	0.42	5.65	4.38
17 - 19 May 1996	0.2	0.1	0.2	0.1	0.55	0.42	0.24	0.10	2.61	2.14	0.87	0.40	0.2	0.1	0.1	0.1	0.19	0.09	0.60	0.43	0.79	0.46	2.68	2.16
31 May - 2 Jun 1996	0.3	0.1	0.3	0.1	0.29	0.07	0.84	0.24	0.85	0.31	3.01	0.87	0.2	0.1	0.4	0.1	0.35	0.15	0.79	0.20	0.89	0.32	2.97	1.01
13 - 15 Jun 1996	0.4	0.1	0.3	0.1	0.57	0.22	0.81	0.28	1.79	0.75	2.17	0.65	0.3	0.1	0.4	0.1	0.62	0.23	0.77	0.21	1.69	0.63	2.26	0.84
25-26 Oct 1996	1.6	0.7	1.5	0.6	1.29	0.38	1.23	0.42	1.29	0.68	0.89	0.34	1.7	0.6	1.4	0.5	1.40	0.37	1.12	0.31	1.09	0.35	1.09	0.57
21-22 Nov 1996	2.9	0.9	1.4	0.5	1.55	0.42	1.29	0.48	0.61	0.11	1.06	0.51	2.3	0.6	1.9	0.8	1.41	0.34	1.43	0.56	0.69	0.09	0.99	0.46
25-26 Jan 1997	2.7	1.6	1.2	0.3	1.55	0.86	0.93	0.23	0.64	0.14	0.86	0.13	0.9	0.2	2.9	1.6	0.87	0.22	1.62	0.73	0.89	0.21	0.60	0.12
21-23 Feb 1997	0.7	0.2	0.6	0.1	0.64	0.29	0.35	0.08	1.93	1.44	0.56	0.14	0.5	0.1	0.8	0.2	0.63	0.29	0.36	0.08	2.03	1.44	0.46	0.08
19-21 Apr 1997	0.8	0.1	0.5	0.2	0.92	0.43	0.90	0.30	0.84	0.21	1.29	0.42	0.6	0.1	0.8	0.2	0.49	0.20	1.32	0.48	0.73	0.19	1.41	0.37
1-3 May 1997	0.8	0.2	0.9	0.4	1.03	0.54	0.83	0.36	0.97	0.31	0.57	0.19	0.6	0.1	1.1	0.4	0.47	0.12	1.40	0.62	0.65	0.18	0.90	0.31
26-28 May 1997 <sup>a</sup>	1.3	0.2	0.9	0.2	--	--	--	--	--	--	--	--	1.1	0.2	1.2	0.2	--	--	--	--	--	--	--	--
Grand Means	1.1	0.2	0.7	0.1	1.05	0.30	0.77	0.07	1.73	0.53	1.19	0.17	0.77	0.10	1.01	0.24	0.68	0.08	1.15	0.29	1.02	0.15	1.90	0.50

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.10. Mean abundance, total dry mass and dry mass per individual of Amphipoda in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots												Enclosure vs. Open Sampling Stations													
	Abundance (# / sample)				Dry Mass								Abundance (# / sample)				Dry Mass									
	Control		Disced		Total (mg / sample)				Per Individual (mg)				Open		Exclosure		Total (mg / sample)				Per Individual (mg)					
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	12.7	3.4	11.8	2.1	3.73	0.92	2.53	0.55	0.36	0.11	0.22	0.06	10.7	2.5	13.9	2.0	2.49	0.81	3.77	0.71	0.31	0.10	0.28	0.05		
17 - 19 May 1996	17.4	6.5	16.9	8.2	9.71	6.40	4.14	3.05	0.67	0.18	0.20	0.05	12.3	3.9	22.0	9.5	2.08	0.57	11.77	6.95	0.38	0.12	0.49	0.17		
31 May - 2 Jun 1996	7.3	2.0	7.0	3.1	6.16	3.74	0.29	0.09	0.76	0.20	0.25	0.17	7.9	2.9	6.4	1.8	0.98	0.37	5.47	3.65	0.32	0.14	0.69	0.22		
13 - 15 Jun 1996	3.2	0.9	1.6	0.7	2.76	0.73	0.21	0.12	0.80	0.22	0.07	0.05	2.1	0.5	2.7	0.7	1.35	0.64	1.62	0.61	0.31	0.11	0.56	0.22		
25-26 Oct 1996	4.0	1.6	8.5	4.6	0.65	0.22	0.86	0.39	0.39	0.17	0.10	0.05	7.7	3.2	4.8	1.8	0.98	0.30	0.54	0.16	0.37	0.18	0.12	0.04		
21-22 Nov 1996	3.6	2.2	15.3	11.5	1.91	0.43	2.13	1.07	1.20	0.33	0.28	0.16	11.2	7.8	7.7	4.0	2.12	0.77	1.91	0.47	0.59	0.25	0.89	0.31		
25-26 Jan 1997	7.1	3.7	19.7	13.9	0.86	0.45	1.33	0.81	0.13	0.05	0.05	0.02	10.7	5.2	16.2	9.1	0.86	0.32	1.33	0.59	0.10	0.04	0.08	0.02		
21-23 Feb 1997	7.4	3.8	11.7	5.8	1.11	0.44	1.67	0.68	0.19	0.09	0.21	0.04	9.6	3.5	9.5	3.4	1.12	0.32	1.66	0.62	0.20	0.08	0.19	0.03		
19-21 Apr 1997	21.7	6.4	22.3	10.0	6.67	1.54	7.29	3.64	0.36	0.10	0.38	0.17	19.2	6.3	24.7	5.9	6.40	3.15	7.56	1.54	0.30	0.09	0.44	0.14		
1-3 May 1997	27.0	13.7	25.7	12.2	4.47	1.21	3.62	1.37	0.29	0.05	0.16	0.05	20.9	7.0	31.8	11.0	2.45	0.57	5.64	1.38	0.22	0.06	0.23	0.06		
26-28 May 1997 <sup>a</sup>	25.7	7.9	21.1	7.9	--	--	--	--	--	--	--	--	23.5	5.8	23.5	6.2	--	--	--	--	--	--	--	--		
Grand Means	12.3	3.3	14.8	6.2	3.80	0.94	2.41	0.92	0.51	0.06	0.19	0.03	12.4	1.6	14.8	1.8	2.08	0.48	4.13	1.08	0.31	0.04	0.40	0.08		

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.11. Mean abundance, total dry mass and dry mass per individual of Isopoda in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots												Enclosure vs. Open Sampling Stations											
	Abundance (# / sample)				Dry Mass								Abundance (# / sample)				Dry Mass							
	Control		Disced		Total (mg / sample)				Per Individual (mg)				Open		Exclosure		Total (mg / sample)				Per Individual (mg)			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	1.3	0.3	2.0	0.6	0.45	0.12	0.76	0.26	0.35	0.11	0.41	0.12	1.0	0.3	2.3	0.6	0.44	0.13	0.77	0.25	0.37	0.12	0.38	0.09
17 - 19 May 1996	1.4	0.5	0.6	0.1	0.30	0.10	0.12	0.03	0.23	0.07	0.22	0.07	0.9	0.3	1.1	0.3	0.19	0.10	0.22	0.07	0.20	0.07	0.25	0.09
31 May - 2 Jun 1996	0.4	0.1	0.7	0.5	0.03	0.01	0.07	0.06	0.05	0.02	0.06	0.03	0.7	0.5	0.3	0.1	0.09	0.06	0.02	0.01	0.08	0.03	0.03	0.01
13 - 15 Jun 1996	0.4	0.2	0.8	0.6	0.02	0.01	0.06	0.04	0.03	0.02	0.04	0.02	0.5	0.2	0.8	0.6	0.06	0.04	0.03	0.02	0.05	0.03	0.02	0.01
25-26 Oct 1996	0.0	0.0	0.1	0.0	0.01	0.01	0.02	0.01	0.02	0.02	0.06	0.03	0.1	0.0	0.0	0.0	0.02	0.01	0.01	0.01	0.06	0.03	0.02	0.02
21-22 Nov 1996	0.1	0.1	0.0	0.0	0.04	0.03	0.00	0.00	0.14	0.11	0.02	0.02	0.0	0.0	0.1	0.0	0.02	0.02	0.03	0.02	0.03	0.03	0.13	0.08
25-26 Jan 1997	0.1	0.1	0.1	0.1	0.08	0.07	0.27	0.14	0.39	0.36	0.68	0.32	0.1	0.1	0.2	0.1	0.15	0.12	0.21	0.11	0.23	0.15	0.83	0.45
21-23 Feb 1997	0.4	0.3	0.2	0.1	0.27	0.18	0.06	0.03	0.22	0.11	0.10	0.05	0.3	0.1	0.3	0.1	0.20	0.13	0.13	0.07	0.18	0.07	0.14	0.06
19-21 Apr 1997	1.1	0.5	1.2	0.6	0.29	0.15	0.13	0.10	0.12	0.06	0.05	0.03	1.2	0.5	1.0	0.6	0.30	0.14	0.12	0.07	0.10	0.03	0.08	0.04
1-3 May 1997	1.2	0.6	1.8	1.2	0.24	0.14	0.32	0.18	0.09	0.06	0.08	0.04	0.8	0.4	2.2	1.3	0.19	0.11	0.37	0.20	0.06	0.03	0.10	0.05
26-28 May 1997 <sup>a</sup>	1.3	1.0	0.9	0.6	--	--	--	--	--	--	--	--	0.9	0.7	1.3	0.7	--	--	--	--	--	--	--	--
Grand Means	0.7	0.2	0.8	0.3	0.17	0.06	0.18	0.06	0.16	0.04	0.17	0.04	0.6	0.1	0.9	0.2	0.16	0.04	0.19	0.05	0.14	0.03	0.20	0.08

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.12. Mean abundance, total dry mass and dry mass per individual of Oligochaetes in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots										Enclosure vs. Control Sampling Stations													
	Abundance (# / sample)				Dry Mass						Abundance (# / sample)				Dry Mass									
	Control		Disced		Control			Disced			Control		Disced		Open		Exclosure		Open		Exclosure			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
4 - 6 May 1996	27.6	9.7	28.2	5.8	2.25	0.86	2.96	0.87	0.16	0.08	0.18	0.07	25.8	5.5	30.0	6.3	2.19	0.81	3.02	0.81	0.15	0.07	0.19	0.07
17 - 19 May 1996	16.0	3.2	29.5	5.3	2.40	1.36	3.72	1.44	0.29	0.17	0.19	0.08	21.5	3.9	24.0	4.5	3.58	1.29	2.54	0.86	0.33	0.15	0.14	0.04
31 May - 2 Jun 1996	20.0	9.4	35.4	15.7	3.77	2.07	3.35	1.05	0.47	0.29	0.38	0.15	33.2	13.3	22.2	5.8	5.71	2.27	1.40	0.45	0.73	0.31	0.12	0.04
13 - 15 Jun 1996	14.1	4.6	18.0	3.6	2.59	1.02	4.85	2.33	0.36	0.15	0.73	0.39	16.8	4.1	15.3	4.1	3.84	1.33	3.60	1.47	0.54	0.18	0.54	0.25
25-26 Oct 1996	16.0	6.2	17.0	8.6	5.20	1.91	4.44	1.63	1.05	0.48	0.60	0.22	15.1	4.2	17.9	6.3	4.70	1.80	4.94	1.62	0.76	0.29	0.88	0.39
21-22 Nov 1996	19.2	6.0	24.0	14.2	3.99	1.15	6.69	2.14	0.48	0.14	0.70	0.22	20.0	9.9	22.3	5.8	3.67	1.29	7.02	1.62	0.42	0.12	0.76	0.19
25-26 Jan 1997	18.1	5.5	43.6	22.5	3.64	1.18	8.63	3.69	0.34	0.15	0.47	0.22	34.1	14.4	27.3	9.3	3.50	1.03	8.78	3.75	0.23	0.07	0.58	0.23
21-23 Feb 1997	25.3	8.7	47.6	19.9	1.13	0.36	5.65	2.65	0.06	0.02	0.32	0.11	31.9	11.3	41.1	13.0	2.64	1.17	4.13	1.83	0.14	0.05	0.24	0.10
19-21 Apr 1997	45.9	20.1	42.5	14.1	2.48	0.63	6.07	2.13	0.14	0.07	0.41	0.18	33.3	8.1	55.1	17.1	2.37	0.59	6.18	1.91	0.19	0.06	0.37	0.16
1-3 May 1997	33.4	10.4	41.4	12.1	3.02	0.69	5.47	2.00	0.23	0.09	0.26	0.12	38.7	9.0	36.1	7.8	4.27	0.88	4.22	1.49	0.23	0.07	0.25	0.09
26-28 May 1997 <sup>a</sup>	23.6	8.9	42.9	14.8	--	--	--	--	--	--	--	--	26.7	7.6	41.9	10.7	--	--	--	--	--	--	--	--
Grand Means	23.6	6.3	33.7	10.9	3.05	0.79	5.18	1.34	0.35	0.07	0.42	0.06	27.3	3.5	30.2	3.3	3.65	0.76	4.58	0.95	0.37	0.07	0.41	0.08

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.13. Mean abundance, total dry mass and dry mass per individual of Gastropods in discing and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Discing vs. Control Plots										Enclosure vs. Open Sampling Stations													
	Abundance (# / sample)				Dry Mass						Abundance (# / sample)				Dry Mass									
	Control		Discing		Total (mg / sample)			Per Individual (mg)			Open		Enclosure		Total (mg / sample)			Per Individual (mg)						
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	5.8	4.1	1.6	0.8	7.56	4.31	2.00	0.90	1.96	0.62	1.25	0.31	5.4	3.5	2.0	0.8	5.84	3.01	3.72	1.79	1.29	0.42	1.92	0.42
17 - 19 May 1996	4.7	2.5	2.3	1.2	10.11	3.49	3.66	1.39	3.32	1.08	2.22	0.67	3.0	1.0	4.1	2.0	6.48	1.56	7.29	3.12	2.44	0.60	3.10	1.23
31 May - 2 Jun 1996	1.8	1.0	2.0	0.9	2.64	0.85	2.54	1.33	2.26	0.80	0.72	0.31	1.8	0.7	1.9	1.0	2.13	0.72	3.05	1.35	1.42	0.50	1.56	0.50
13 - 15 Jun 1996	1.0	0.3	1.3	0.5	3.44	2.35	4.12	2.28	2.04	0.81	1.92	0.87	1.2	0.3	1.2	0.4	4.85	2.28	2.72	1.45	2.70	0.77	1.26	0.53
25-26 Oct 1996	0.3	0.1	0.2	0.1	0.86	0.34	0.43	0.17	2.13	0.82	1.28	0.44	0.3	0.1	0.2	0.1	0.55	0.23	0.74	0.25	1.21	0.40	2.19	0.68
21-22 Nov 1996	0.5	0.2	0.4	0.2	3.00	1.58	2.30	1.21	3.33	0.98	3.22	0.96	0.4	0.1	0.6	0.2	1.87	0.62	3.43	1.67	3.11	0.88	3.43	0.83
25-26 Jan 1997	3.7	1.3	2.7	1.1	7.60	3.60	2.82	0.92	2.11	0.49	1.19	0.31	2.7	0.7	3.7	1.2	3.95	0.96	6.47	3.37	1.64	0.31	1.66	0.48
21-23 Feb 1997	2.5	0.9	3.9	1.2	3.70	0.79	3.51	0.76	1.63	0.37	1.03	0.23	3.0	0.7	3.4	0.9	2.98	0.64	4.23	0.94	1.41	0.38	1.25	0.23
19-21 Apr 1997	10.1	2.2	5.3	1.7	10.42	2.85	9.22	2.99	1.13	0.28	2.04	0.42	8.9	2.3	6.5	1.4	12.74	3.24	6.90	1.76	1.94	0.44	1.23	0.20
1-3 May 1997	10.0	3.5	6.5	2.8	10.50	3.90	8.77	4.49	1.01	0.11	1.50	0.66	7.5	1.9	9.0	2.9	6.11	1.60	13.16	4.45	1.14	0.22	1.37	0.49
26-28 May 1997 <sup>a</sup>	5.0	1.3	4.5	1.3	--	--	--	--	--	--	--	--	6.2	1.6	2.9	0.8	--	--	--	--	--	--	--	--
Grand Means	4.2	0.8	2.8	0.5	5.98	1.43	3.93	0.84	2.09	0.22	1.63	0.19	3.7	0.4	3.4	0.3	4.75	0.73	5.17	1.01	1.83	0.22	1.90	0.25

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.14. Mean abundance of Crustacea in disced and control plots ( $n = 8$  per treatment) and exclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Dry mass was not determined for this taxonomic group.

Sampling Period	Disced vs. Control				Exclosure vs. Open			
	Control		Disced		Open		Exclosure	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	4.6	1.7	5.4	1.7	4.4	0.9	5.5	1.7
17 - 19 May 1996	3.9	1.9	6.4	2.3	5.6	1.9	4.7	1.4
31 May - 2 Jun 1996	5.7	1.5	5.9	1.4	6.0	1.4	5.6	1.2
13 - 15 Jun 1996	3.3	0.8	4.7	1.4	4.7	1.1	3.2	0.7
25-26 Oct 1996	2.5	1.0	2.4	0.7	2.3	0.6	2.6	0.6
21-22 Nov 1996	2.1	0.7	3.5	0.8	2.4	0.7	3.1	0.7
25-26 Jan 1997	27.0	7.9	32.7	8.4	32.8	7.4	26.5	4.5
21-23 Feb 1997	47.1	15.5	36.1	6.8	42.9	9.1	40.8	8.3
19-21 Apr 1997	38.6	12.9	31.3	9.1	38.1	7.8	31.8	8.8
1-3 May 1997	16.7	4.9	26.6	7.6	20.4	4.1	22.9	5.5
26-28 May 1997	29.3	11.1	25.5	7.4	29.0	8.1	23.0	5.3
Grand Means	16.3	2.6	16.3	2.5	17.5	1.5	15.2	1.1

Table 2.15. Mean abundance, total dry mass and dry mass per individual of Miscellaneous Invertebrates in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots												Enclosure vs. Open Sampling Stations											
	Abundance (# / sample)				Dry Mass								Abundance (# / sample)				Dry Mass							
	Control		Disced		Total (mg / sample)				Per Individual (mg)				Open		Exclosure		Total (mg / sample)				Per Individual (mg)			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
4 - 6 May 1996	11.9	5.5	20.7	10.8	2.38	1.08	1.27	0.61	0.77	0.41	0.46	0.25	17.2	7.0	15.4	6.5	1.28	0.71	2.37	0.81	0.28	0.11	0.96	0.39
17 - 19 May 1996	3.0	1.5	4.8	3.2	0.73	0.33	1.93	1.04	0.75	0.42	1.80	0.92	4.0	2.7	3.8	1.6	0.50	0.17	2.15	0.96	0.98	0.46	1.57	0.75
31 May - 2 Jun 1996	1.2	0.2	1.8	0.4	0.68	0.35	1.32	0.80	0.49	0.24	1.26	0.77	1.2	0.4	1.8	0.4	1.35	0.67	0.65	0.25	1.25	0.60	0.50	0.20
13 - 15 Jun 1996	2.0	0.7	0.8	0.1	0.46	0.26	0.71	0.20	0.30	0.18	1.28	0.73	1.2	0.2	1.6	0.7	0.62	0.25	0.55	0.28	0.51	0.20	1.06	0.78
25-26 Oct 1996	2.4	0.3	2.3	0.2	0.90	0.32	1.41	0.50	0.43	0.17	0.91	0.35	2.7	0.3	2.0	0.2	1.08	0.24	1.23	0.49	0.47	0.11	0.87	0.37
21-22 Nov 1996	2.6	0.4	2.4	0.4	1.84	0.46	3.02	1.76	0.92	0.23	1.08	0.44	2.5	0.4	2.5	0.3	1.45	0.49	3.41	1.38	0.54	0.12	1.46	0.42
25-26 Jan 1997	3.0	1.1	2.9	0.9	1.15	0.49	1.21	0.60	0.41	0.17	0.47	0.28	2.6	0.8	3.1	0.7	1.14	0.46	1.23	0.46	0.49	0.20	0.40	0.14
21-23 Feb 1997	2.5	1.0	3.8	0.8	0.70	0.28	6.01	4.84	0.50	0.28	2.02	1.42	2.7	0.7	3.5	0.9	0.89	0.28	5.82	4.91	0.56	0.30	1.95	1.46
19-21 Apr 1997	3.5	0.8	2.7	0.5	4.12	2.02	2.33	0.68	1.99	1.30	1.16	0.35	3.3	0.6	2.9	0.6	2.43	0.94	4.02	1.38	1.17	0.51	1.98	0.94
1-3 May 1997	3.2	1.1	4.0	1.5	4.57	1.47	3.85	1.61	1.65	0.58	0.89	0.30	3.6	0.9	3.6	1.1	4.16	1.33	4.27	1.33	1.29	0.51	1.25	0.48
26-28 May 1997 <sup>a</sup>	4.6	1.6	2.6	1.1	--	--	--	--	--	--	--	--	4.6	1.6	2.8	0.7	--	--	--	--	--	--	--	--
Grand Means	3.6	0.8	4.5	1.4	1.75	0.30	2.30	0.85	0.82	0.16	1.13	0.21	4.2	0.7	4.0	0.6	1.49	0.23	2.57	0.81	0.75	0.12	1.20	0.17

<sup>a</sup> Logistical constraints precluded dry mass analysis for this sampling period.

Table 2.16. Mean abundance, total dry mass and dry mass per individual of Total Invertebrates in disced and control plots ( $n = 8$  per treatment) and enclosure and open sampling stations ( $n = 80$  per station type) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia.

Sampling Period	Disced vs. Control Plots												Enclosure vs. Open Sampling Stations											
	Abundance (# / sample)				Dry Mass								Abundance (# / sample)				Dry Mass							
	Control		Disced		Total (mg / sample)				Per Individual (mg)				Open		Exclosure		Total (mg / sample)				Per Individual (mg)			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
4 - 6 May 1996	79.2	20.0	92.3	20.7	22.73	5.14	16.42	2.92	0.38	0.11	0.22	0.04	83.2	15.9	88.3	14.9	18.38	4.10	20.76	2.76	0.28	0.06	0.32	0.07
17 - 19 May 1996	60.1	9.4	82.6	15.9	28.64	5.95	19.18	4.23	0.53	0.08	0.26	0.04	63.2	8.7	79.5	12.7	18.27	1.98	29.56	6.97	0.40	0.07	0.39	0.05
31 May - 2 Jun 1996	43.3	10.9	60.2	20.6	15.15	3.65	12.60	2.52	0.53	0.18	0.36	0.08	58.0	17.2	45.5	7.2	12.57	1.96	15.18	4.82	0.55	0.18	0.34	0.09
13 - 15 Jun 1996	30.2	4.4	33.4	4.0	12.44	4.01	13.26	2.46	0.53	0.23	0.58	0.19	33.0	4.5	30.7	4.3	13.89	2.93	11.81	2.06	0.60	0.20	0.51	0.14
25-26 Oct 1996	38.8	8.3	51.9	12.5	13.35	2.19	12.26	2.72	0.50	0.12	0.29	0.08	44.4	6.9	46.4	8.5	10.57	2.07	15.04	2.50	0.33	0.09	0.46	0.10
21-22 Nov 1996	43.6	8.3	68.8	28.0	16.42	1.23	24.92	6.31	0.49	0.08	0.60	0.21	54.1	19.9	57.1	10.1	18.03	4.11	23.31	3.57	0.55	0.15	0.54	0.09
25-26 Jan 1997	78.1	11.0	128.5	49.8	22.44	4.55	21.58	4.13	0.34	0.07	0.25	0.06	101.4	28.6	105.5	23.5	16.54	2.07	27.48	4.96	0.26	0.05	0.33	0.06
21-23 Feb 1997	97.8	22.4	132.5	36.2	14.54	2.25	23.62	6.86	0.18	0.04	0.24	0.06	107.2	20.8	124.5	24.6	11.24	1.95	26.91	6.66	0.17	0.04	0.26	0.06
19-21 Apr 1997	135.5	36.6	126.7	33.5	32.14	5.26	30.70	5.52	0.33	0.06	0.35	0.09	124.1	22.5	138.2	28.3	29.96	5.02	32.88	3.69	0.31	0.05	0.38	0.07
1-3 May 1997	106.7	32.8	125.6	39.1	28.29	3.99	28.47	7.22	0.37	0.07	0.37	0.14	109.3	23.3	122.9	27.2	22.29	2.24	34.47	6.85	0.33	0.07	0.41	0.13
26-28 May 1997 <sup>a</sup>	103.3	25.7	114.0	30.7	--	--	--	--	--	--	--	--	105.9	19.7	110.3	20.3	--	--	--	--	--	--	--	--
Grand Mean	74.3	13.3	92.6	23.8	20.61	1.46	20.30	2.54	0.42	0.04	0.35	0.04	81.1	7.2	86.1	6.5	17.17	1.26	23.74	1.76	0.38	0.04	0.39	0.03

<sup>a</sup> Logistical constraints precluded biomass analysis for this sampling period.

Isopods, Oligochaetes, and Total Invertebrates were more abundant in Pool A than in Pool C, but no taxon was more abundant in Pool C than in Pool A (Table 2.17).

The Discing main effect was significant only for Diptera pupae, which were about 1.5 x as abundant in disced ( $\bar{x} = 0.9 \pm 0.1$  individuals / sample) as in control areas ( $\bar{x} = 0.6 \pm 0.1$  individuals / sample) across the entire study period (Tables 2.7, 2.18). At least 1 Discing interaction was significant for abundance of all other taxa except for Isopods, Crustacea and Total Invertebrates (Table 2.18). Sampling Period x Discing interactions were significant for 5 taxa (Table 2.18), indicating higher abundance during some sampling periods in disced than in control areas for 4 (Chironomidae, Other Diptera, Coleoptera Larvae and Amphipoda; Tables 2.5, 2.6, 2.8, 2.10), and higher abundance in control than in disced areas for 1 (Gastropoda; Table 2.13). The only significant Discing terms for Coleoptera adults, Oligochaetes, and Miscellaneous Invertebrates were either 3- or 4-way interactions (Table 2.18).

*Dry Mass*--The Discing main effect was significant for total dry mass and dry mass per individual of Amphipoda (Tables 2.19, 2.20) due to decreased total dry mass (Control =  $3.8 \pm 0.9$  mg / sample, Disced =  $2.4 \pm 0.9$  mg / sample) and mean dry mass per individual (Control =  $0.41 \pm 0.02$  mg / individual, Disced =  $0.06 \pm 0.01$  mg / individual) across all sampling periods. Discing was not a significant main effect in any other dry mass models (Tables 2.19, 2.20). Total Amphipod dry mass per sample was higher in control areas than in disced areas during May - Jun 1996, but was similar between treatments thereafter (Sampling Period x Discing interaction; Tables 2.10, 2.19). Mean dry mass per individual of Coleoptera adults was 3.2 x higher in control than in disced areas during early May 1996, but 2.3 x higher in disced areas than in controls during late May 1996 (Sampling Period x Discing interaction; Tables 2.9, 2.20). Mean dry mass per individual amphipod was 1.5 - 7.0 x higher in control areas from May - Nov 1996, but similar between treatments thereafter (Sampling Period x Discing interaction; Tables 2.10, 2.20). Sampling Period x Discing interactions were nonsignificant for total dry mass and dry mass per individual of all other taxa (Tables 2.19, 2.20).

Seasonal trends in abundance were generally similar to trends in total dry mass, but did not necessarily reflect variation in mean size per individual. Mean abundance and mean total dry

Table 2.17. Mean abundance (# / sample) of 12 invertebrate taxonomic groups in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia, April 1996 - May 1997. Means were generated by averaging across treatments (disced vs. control) and sampling stations (exclosure vs. open), with Plot(Sampling Period) as independent sampling units ( $n = 88$  per pool).

Taxon	Pool A		Pool C	
	Mean	SE	Mean	SE
Chironomids	10.5	1.6	2.9	0.5
Other Diptera	6.9	0.6	7.5	0.7
Diptera Pupae	0.8	0.1	0.7	0.1
Coleoptera Larvae	0.9	0.1	0.9	0.1
Coleoptera Adults	1.1	0.2	0.6	0.1
Amphipods	20.3	2.7	6.8	1.2
Isopods	1.1	0.2	0.3	0.1
Gastropods	4.1	0.6	2.7	0.5
Oligochaetes	42.8	4.3	14.3	1.3
Miscellaneous Invertebrates	4.8	1.2	3.2	0.3
Crustacea	21.0	3.1	11.8	1.3
Total Invertebrates	114.6	9.7	52.0	3.5

Table 2.18. *P*-values from mixed model analyses of variance for abundance of 12 invertebrate taxa in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The Discing effect reflects comparison of disced to control plots, whereas the Predation effect reflects comparison of enclosure to open sampling stations. Each column represents a separate analysis.

Source	df	Chironomids	Other Diptera	Diptera Pupae	Coleoptera Larvae	Coleoptera Adults	Amphipods	Isopods	Oligochaetes	Gastropods	Crustacea	Miscellaneous Invertebrates	Total Invertebrates
Discing <sup>a</sup>	1,12	0.167	0.211	0.060	0.656	0.174	0.929	0.449	0.129	0.473	0.422	0.814	0.291
Pool <sup>a</sup>	1,12	0.098	0.249	0.092	0.892	0.162	0.005	0.005	0.049	0.102	0.188	0.236	0.011
Pool * Discing <sup>a</sup>	1,12	0.374	0.176	0.238	0.456	0.710	0.434	0.650	0.740	0.255	0.671	0.025	0.422
Predation <sup>b</sup>	1,140	0.889	0.027	0.276	0.134	0.101	0.073	0.628	0.401	0.711	0.791	0.363	0.261
Discing * Predation <sup>b</sup>	1,140	0.160	0.798	0.693	0.603	0.923	0.421	0.534	0.409	0.090	0.559	0.777	0.958
Pool * Predation <sup>b</sup>	1,140	0.164	0.657	0.661	0.202	0.208	0.641	0.915	0.972	0.369	0.660	0.336	0.458
Pool * Discing * Predation <sup>b</sup>	1,140	0.117	0.281	0.600	0.026	0.210	0.497	0.923	0.462	0.762	0.382	0.638	0.840
Sampling Period <sup>c</sup>	101,426	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Sampling Period * Discing <sup>c</sup>	101,426	0.006	0.001	0.317	0.091	0.228	0.087	0.620	0.409	<0.001	0.158	0.557	0.269
Sampling Period * Predation <sup>c</sup>	101,426	0.054	0.213	0.568	0.007	0.696	0.893	0.621	0.291	0.622	0.848	0.189	0.982
Sampling Period * Discing * Predation <sup>c</sup>	101,426	0.572	0.687	0.101	0.871	0.900	0.470	0.386	0.634	0.306	0.484	0.391	0.708
Sampling Period * Pool <sup>c</sup>	101,426	<0.001	<0.001	0.134	0.001	0.003	<0.001	<0.001	0.021	<0.001	<0.001	<0.001	<0.001
Sampling Period * Pool * Discing <sup>c</sup>	101,426	0.186	0.009	0.241	0.941	0.407	0.007	0.262	0.072	0.024	0.463	0.001	0.144
Sampling Period * Pool * Predation <sup>c</sup>	101,426	0.709	0.923	0.178	0.072	0.922	0.300	0.914	0.805	0.542	0.362	0.422	0.685
Sampling Period * Pool * Discing * Predation <sup>c</sup>	101,426	0.129	0.238	0.482	0.038	0.057	0.922	0.434	0.669	0.991	0.926	0.357	0.778
Covariance Structure <sup>d</sup>		A	A	A	A	A	CS	A	A	A	A	A	CS

<sup>a</sup> Error term = Plot (Discing x Pool)

<sup>b</sup> Error term = Predation x Subplot (Plot x Discing x Pool)

<sup>c</sup> Error term = Sampling Period x Predation (Subplot x Plot x Discing x Pool)

<sup>d</sup> A = Autoregressive, CS = Compound Symmetry

Table 2.19. *P*-values from mixed model analyses of variance for total dry mass of 11 invertebrate taxa in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The Discing effect reflects comparison of disced to control plots, whereas the Predation effect reflects comparison of enclosure to open sampling stations. Each column represents a separate analysis.

Source	df	Chironomids	Other Diptera	Diptera Pupae	Coleoptera Larvae	Coleoptera Adults	Amphipods	Isopods	Oligochaetes	Gastropods	Miscellaneous Invertebrates	Total Invertebrates
Discing <sup>a</sup>	1,12	0.404	0.945	0.337	0.573	0.634	0.043	0.857	0.163	0.241	0.760	0.762
Pool <sup>a</sup>	1,12	0.017	0.028	0.418	0.091	0.101	0.001	0.004	0.025	0.182	0.136	0.092
Pool * Discing <sup>a</sup>	1,12	0.451	0.878	0.253	0.420	0.576	0.045	0.701	0.392	0.259	0.260	0.212
Predation <sup>b</sup>	1,12	0.362	0.006	0.154	0.538	0.147	0.031	0.722	0.224	0.753	0.112	<0.001
Discing * Predation <sup>b</sup>	1,12	0.681	0.471	0.620	0.549	0.771	0.366	0.746	0.759	0.192	0.310	0.043
Pool * Predation <sup>b</sup>	1,12	0.478	0.040	0.658	0.174	0.446	0.964	0.696	0.489	0.868	0.080	0.738
Pool * Discing * Predation <sup>b</sup>	1,12	0.881	0.760	0.188	0.831	0.103	0.655	0.190	0.711	0.459	0.781	0.332
Sampling Period <sup>c</sup>	9,216	<0.001	<0.001	0.037	0.085	0.001	<0.001	<0.001	0.017	<0.001	<0.001	<0.001
Sampling Period * Discing <sup>c</sup>	9,216	0.806	0.149	0.144	0.606	0.604	0.014	0.116	0.635	0.704	0.510	0.392
Sampling Period * Predation <sup>c</sup>	9,216	0.744	0.055	0.726	0.523	0.622	0.649	0.446	0.010	0.750	0.589	0.274
Sampling Period * Discing * Predation <sup>c</sup>	9,216	0.846	0.866	0.033	0.533	0.706	0.314	0.973	0.309	0.996	0.813	0.580
Sampling Period * Pool <sup>c</sup>	9,216	<0.001	0.059	0.007	0.136	0.243	<0.001	0.003	0.022	<0.001	0.016	<0.001
Sampling Period * Pool * Discing <sup>c</sup>	9,216	0.914	0.622	0.547	0.239	0.191	0.094	0.059	0.378	0.544	0.013	0.664
Sampling Period * Pool * Predation <sup>c</sup>	9,216	0.880	0.052	0.279	0.430	0.159	0.025	0.010	0.328	0.335	0.390	0.070
Sampling Period * Pool * Discing * Predation <sup>c</sup>	9,216	0.167	0.146	0.161	0.012	0.819	0.778	0.955	0.020	0.962	0.712	0.087
Covariance Structure		A	UN	CS	A	A	A	UN	A	UN	CS	CS

<sup>a</sup> Error term = Plot (Discing x Pool)

<sup>b</sup> Error term = Predation x Subplot (Plot x Discing x Pool)

<sup>c</sup> Error term = Sampling Period x Predation (Subplot x Plot x Discing x Pool)

<sup>d</sup> A = Autoregressive, CS = Compound Symmetry, UN = Unspecified

Table 2.20. *P*-values from mixed model analyses of variance for dry mass per individual of 11 invertebrate taxa in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. The Discing effect reflects comparison of disced to control plots, whereas the Predation effect reflects comparison of enclosure to open sampling stations. Each column represents a separate analysis.

Source	df	Chironomids	Other Diptera	Diptera Pupae	Coleoptera Larvae	Coleoptera Adults	Amphipods	Isopods	Oligochaetes	Gastropods	Miscellaneous Invertebrates	Total Invertebrates
Discing <sup>a</sup>	1,12	0.586	0.657	0.284	0.559	0.882	0.004	0.907	0.492	0.210	0.437	0.400
Pool <sup>a</sup>	1,12	0.360	0.015	0.875	0.045	0.744	0.733	0.134	0.006	0.143	0.258	0.186
Pool * Discing <sup>a</sup>	1,12	0.420	0.455	0.779	0.434	0.434	0.181	0.255	0.454	0.228	0.967	0.716
Predation <sup>b</sup>	1,12	0.362	0.049	0.722	0.146	0.131	0.055	0.422	0.751	0.913	0.112	0.450
Discing * Predation <sup>b</sup>	1,12	0.640	0.224	0.693	0.560	0.780	0.556	0.362	0.323	0.602	0.136	0.183
Pool * Predation <sup>b</sup>	1,12	0.627	0.080	0.643	0.184	0.616	0.965	0.593	0.422	0.912	0.055	0.645
Pool * Discing * Predation <sup>b</sup>	1,12	0.591	0.500	0.286	0.734	0.225	0.629	0.007	0.701	0.831	0.606	0.333
Sampling Period <sup>c</sup>	9,216	<0.001	0.066	0.039	0.134	0.367	<0.001	<0.001	<0.001	0.095	0.115	0.001
Sampling Period * Discing <sup>c</sup>	9,216	0.927	0.185	0.260	0.475	0.049	0.003	0.277	0.494	0.405	0.542	0.244
Sampling Period * Predation <sup>c</sup>	9,216	0.987	0.480	0.776	0.884	0.303	0.579	0.510	0.061	0.454	0.710	0.822
Sampling Period * Discing * Predation <sup>c</sup>	9,216	0.006	0.832	0.481	0.433	0.479	0.470	0.989	0.721	0.908	0.214	0.572
Sampling Period * Pool <sup>c</sup>	9,216	0.003	0.006	0.042	0.146	0.645	0.022	0.580	0.092	0.015	<0.001	0.479
Sampling Period * Pool * Discing <sup>c</sup>	9,216	0.967	0.310	0.015	0.044	0.009	0.822	0.694	0.019	0.186	0.185	0.245
Sampling Period * Pool * Predation <sup>c</sup>	9,216	0.995	0.050	0.971	0.731	0.015	0.134	0.952	0.066	0.581	0.378	0.091
Sampling Period * Pool * Discing * Predation <sup>c</sup>	9,216	0.198	0.500	0.448	0.001	0.861	0.615	0.243	0.128	0.846	0.887	0.345
Covariance Structure		A	A	A	UN	UN	CS	UN	A	UN	UN	A

<sup>a</sup> Error term = Plot (Discing x Pool)

<sup>b</sup> Error term = Predation x Subplot (Plot x Discing x Pool)

<sup>c</sup> Error term = Sampling Period x Predation (Subplot x Plot x Discing x Pool)

<sup>d</sup> A = Autoregressive, CS = Compound Symmetry, UN = Unspecified

mass per sample were positively correlated ( $r = 0.34 - 0.78$ ;  $P < 0.001$ ) for all taxa except Oligochaetes, but Isopods were the only taxon for which mean abundance and mean dry mass per individual were positively (albeit weakly) correlated (Table 2.21). Mean abundance and mean dry mass per individual were negatively correlated for Amphipods, Oligochaetes, and Total Invertebrates (Table 2.21), whereas total dry mass and mean dry mass per individual were positively correlated ( $r = 0.38 - 0.72$ ;  $P < 0.001$ ) for all taxa (Table 2.21).

### **Invertebrate Response to Predation**

*Abundance*--Mean abundance of Other Diptera and Amphipods was lower in open sampling stations than in enclosures (Other Diptera: Open =  $6.1 \pm 0.3$  individuals / sample, Enclosure =  $8.1 \pm 0.6$  individuals / sample; Amphipods: Open =  $12.4 \pm 3.3$  individuals / sample, Enclosure =  $14.8 \pm 6.2$  individuals / sample; significant Predation main effect, Table 2.18). Chironomids were 1.9 x more abundant in enclosures than in open sampling stations during Feb, but were 4 - 6 x more abundant in open sampling stations during Jun 1996 (Table 2.5; Sampling Period x Predation interaction, Table 2.18). Coleoptera larvae were 2.4 x more abundant in enclosures than in open sampling stations during Jan, but were similar in abundance between sampling stations during the remaining periods (Table 2.8; Sampling Period x Predation interaction, Table 2.18). Predation effects were similar across pools for all taxa (i.e., nonsignificant Pool x Predation interactions; Table 2.18). All Predation terms were nonsignificant for abundance of Diptera Pupae, Isopods, Oligochaetes, Crustacea, Miscellaneous Invertebrates, and Total Invertebrates (Table 2.18).

*Dry Mass*--Significant Predation main effects revealed higher total dry mass of Other Diptera in enclosures ( $4.2 \pm 0.8$  mg/sample) than in open sampling stations ( $2.5 \pm 0.5$  mg/sample) (Table 2.6, 2.19). However, the magnitude of this effect varied between pools (Pool x Predation interaction, Table 2.19); Other Diptera dry mass was higher in enclosures ( $6.3 \pm 1.1$  mg/sample) than in open sampling stations ( $3.1 \pm 1.0$  mg/sample) in Pool A, but similar between enclosures ( $1.8 \pm 0.4$  mg/sample) and open sampling stations ( $2.0 \pm 0.2$  mg/sample) in Pool C. Other Diptera were also larger in enclosures ( $0.15 \pm 0.02$  mg/individual) than in open sampling stations ( $0.11 \pm 0.01$  mg/individual) (Table 2.19; Predation main effect, Table 2.20).

Table 2.21. Pearson correlation coefficients for abundance (# / sample), total dry mass (mg / sample) and individual size (mg / individual) for 11 taxa of invertebrates from disced and control plots in moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Correlations were conducted on log-transformed data using Sampling Stations(Plots x Sampling Period) as independent sampling units ( $n = 320$ ).

Taxon	Abundance vs. Total Dry Mass		Abundance vs. Individual Size		Total Dry Mass vs. Individual Size	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Chironomidae	0.77	<0.001	0.09	0.124	0.38	<0.001
Other Diptera	0.45	<0.001	-0.05	0.327	0.70	<0.001
Diptera Pupae	0.51	<0.001	0.06	0.314	0.58	<0.001
Coleoptera Larvae	0.50	<0.001	0.05	0.414	0.72	<0.001
Coleoptera Adults	0.64	<0.001	-0.02	0.675	0.55	<0.001
Amphipoda	0.67	<0.001	-0.11	0.052	0.47	<0.001
Isopoda	0.75	<0.001	0.18	0.001	0.51	<0.001
Gastropoda	0.78	<0.001	-0.01	0.922	0.47	<0.001
Oligochaeta	0.03	0.532	-0.31	<0.001	0.71	<0.001
Miscellaneous Invertebrates	0.34	<0.001	-0.04	0.437	0.70	<0.001
Total Invertebrates	0.39	<0.001	-0.42	<0.001	0.46	<0.001

Total dry mass of Other Diptera was about 4.5 x higher in enclosure than in open sampling stations during Oct and Feb (Table 2.6; Sampling Period x Predation interaction, Table 2.19). Total dry mass and dry mass per individual of Oligochaetes were higher in enclosures than in open sampling stations during Nov and Jan, but both metrics were higher in open sampling stations than in enclosures during May 1996 (Table 2.12; Sampling Period x Predation interactions, Tables 2.19, 2.20). Sampling Period x Predation interactions were nonsignificant for both dry mass metrics in all other taxa (Tables 2.19, 2.20).

The Total Invertebrate total dry mass model contained 4 significant Predation terms (Table 2.19). Mean Total Invertebrate total dry mass was 38% higher in enclosures ( $23.7 \pm 1.8$  mg / sample) than in open sampling stations ( $17.2 \pm 1.3$  mg / sample) across all sampling periods (Predation effect, Table 2.19). However, the magnitude of predation effects on Total Invertebrate total dry mass varied between disced and control areas (Discing x Predation interaction, Table 2.19). Total Invertebrate total dry mass was 25% higher in control plot enclosures than in control plot open sampling stations, but was 52% higher in disced plot enclosures than in disced plot open sampling stations (Fig. 2.7).

### **Spatial Variation in Invertebrate Response**

*Discing*--Sampling Period x Pool x Discing interactions were significant for abundance of Other Diptera, Amphipoda, Oligochaetes, Gastropods, and Miscellaneous Invertebrates, total dry mass of Isopoda, Miscellaneous Invertebrates, and Amphipods, and mean dry mass per individual of Diptera pupae, Coleoptera larvae, Coleoptera adults, and Oligochaetes (Tables 2.18 – 2.20). All 5 taxa for which Sampling Period x Pool x Discing interactions were significant for abundance were at least 2x more abundant in disced than control plots in Pool A during winter, but were approximately equal in abundance between treatments in Pool C during this period (Fig. 2.8). The discing effect on abundance of Gastropods and Miscellaneous Invertebrates also was more pronounced in Pool A than in Pool C during spring 1996 (Fig. 2.8 D, E). However, the discing effect on abundance of Other Diptera was more pronounced in Pool C than in Pool A during spring - fall 1996 (Fig. 2.8 A).

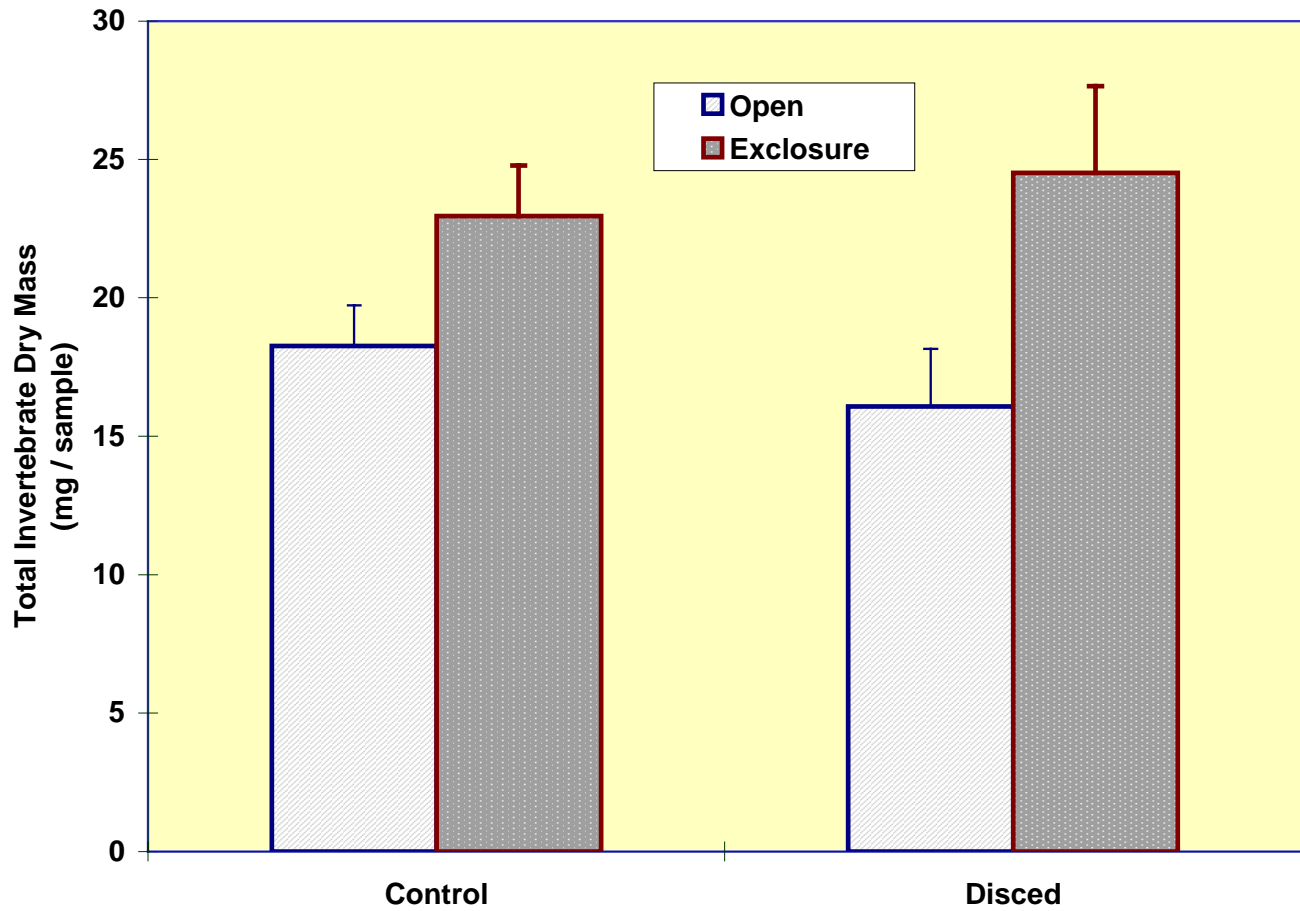


Fig. 2.7. Mean (+ SE) total invertebrate dry mass (mg / sample; all taxa included) in disced and control plots, as measured in open and exclosure sampling stations in moist-soil impoundments at Back Bay National Wildlife Refuge, Apr 1996 - May 1997. Means were generated using plots as independent sampling units ( $n = 8$  per mean).

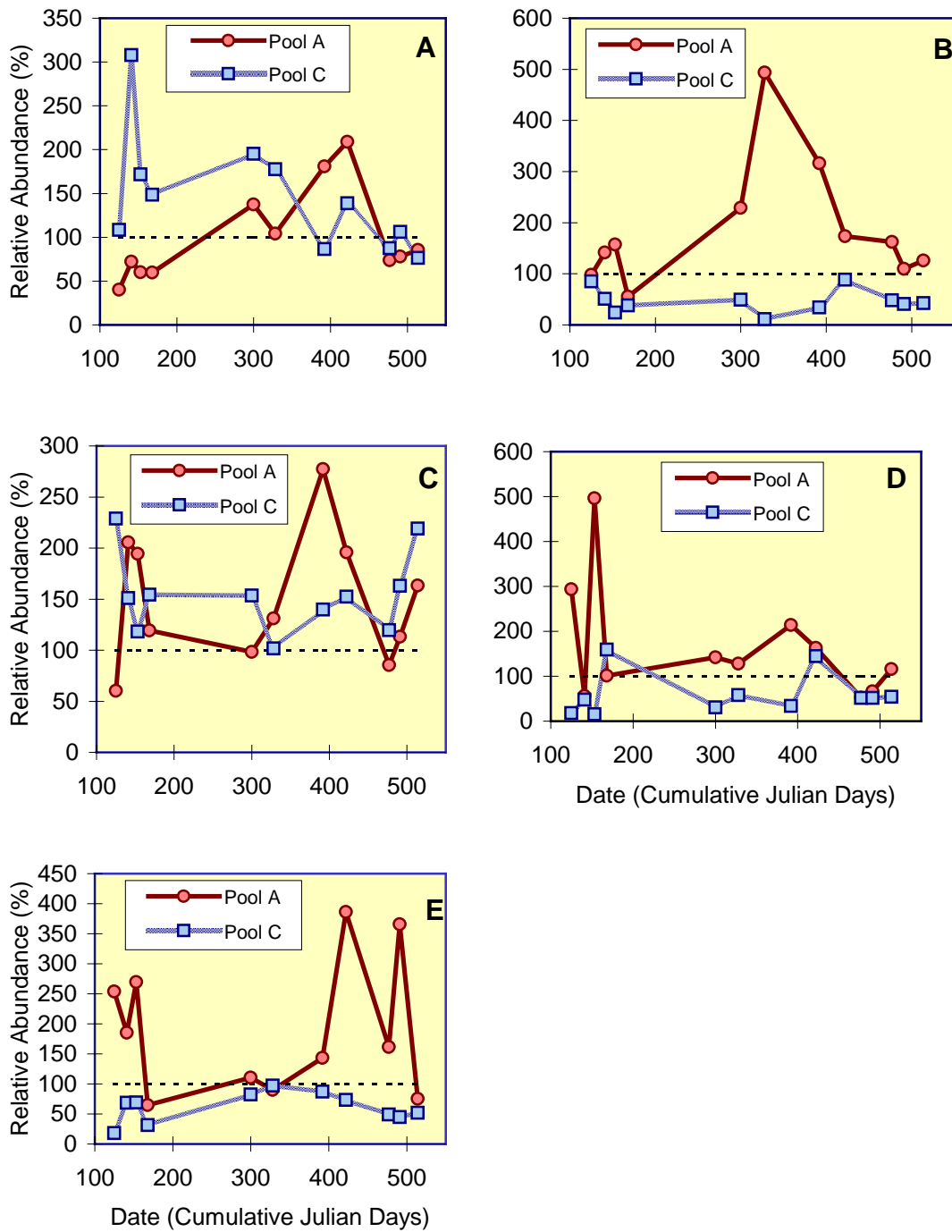


Fig. 2.8. Abundance relative to discing (% Relative Abundance = [(Mean # / sample in disced plots) / (Mean # / sample in control plots)] \* 100) of Other Diptera (A), Amphipods (B), Oligochaetes (C), Gastropods (D), and Miscellaneous Invertebrates (E) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal dashed line indicates equal mean abundance in disced and control plots (i.e., Relative Abundance = 100%). Points above the dashed line indicate higher Relative abundance in disced plots.

Total dry mass of Isopods was several orders of magnitude higher in disced than in control Plots in Pool C during 2 sampling periods, but this taxon did not occur in Pool C plots during other time periods (Fig. 2.9 A). Dry mass of Miscellaneous Invertebrates responded positively to discing in Pool A during late winter, and in Pool C during spring 1996 (Fig. 2.9 B). Amphipods showed a strongly divergent pattern of dry mass response to discing between pools; dry mass was up to 2 orders of magnitude lower in disced than in control plots in Pool C, but was higher in disced than in control plots in Pool A during most of the same time periods (Fig. 2.9 C).

Discing produced substantially larger Diptera pupae in Pool A during 2 spring 1996 sampling periods and in Pool C during 1 spring 1996 sampling period (Fig. 2.10 A). During late winter - spring 1997, discing produced substantially larger Diptera pupae in Pool C, but reduced Diptera pupa size in Pool A (Fig. 2.10 A). Individual size of Coleoptera adults and larvae responded positively to discing in Pool A during late spring and fall 1996, but no such response occurred in Pool C during this period (Fig. 2.10 B,C). Discing effects on Coleoptera adult size were of similar magnitude between pools during early spring 1996 (Fig. 2.10 C). Discing produced larger Oligochaetes in Pool C and smaller Oligochaetes in Pool A during late spring 1996, but mean size of this taxon responded similarly to discing between pools thereafter (Fig. 2.10 D).

*Predation*--Sampling Period x Pool x Predation interaction terms were significant for abundance of Coleoptera Larvae, total dry mass of Isopods, Other Diptera, Amphipods, and Total Invertebrates, and dry mass per individual of Other Diptera, Coleoptera Adults, and Total Invertebrates (Tables 2.18 – 2.20). Coleoptera adults were about 3.5 x more abundant in exclosures than in open sampling stations in Pool C during 1 winter sampling period, and about 1.5 x more abundant in exclosures than open sampling stations in Pool A during spring 1997 (Fig. 2.11). Abundance of Coleoptera adults was about 50% lower in exclosures than in open sampling stations in Pool A during fall 1996 (Fig. 2.11). Isopods were absent from Pool A exclosures during 4 sampling periods, and showed no other consistent trend in dry mass between sampling stations (Fig. 2.12 A). Total dry mass of Other Diptera and Amphipods tended to be higher in exclosures than in open sampling stations

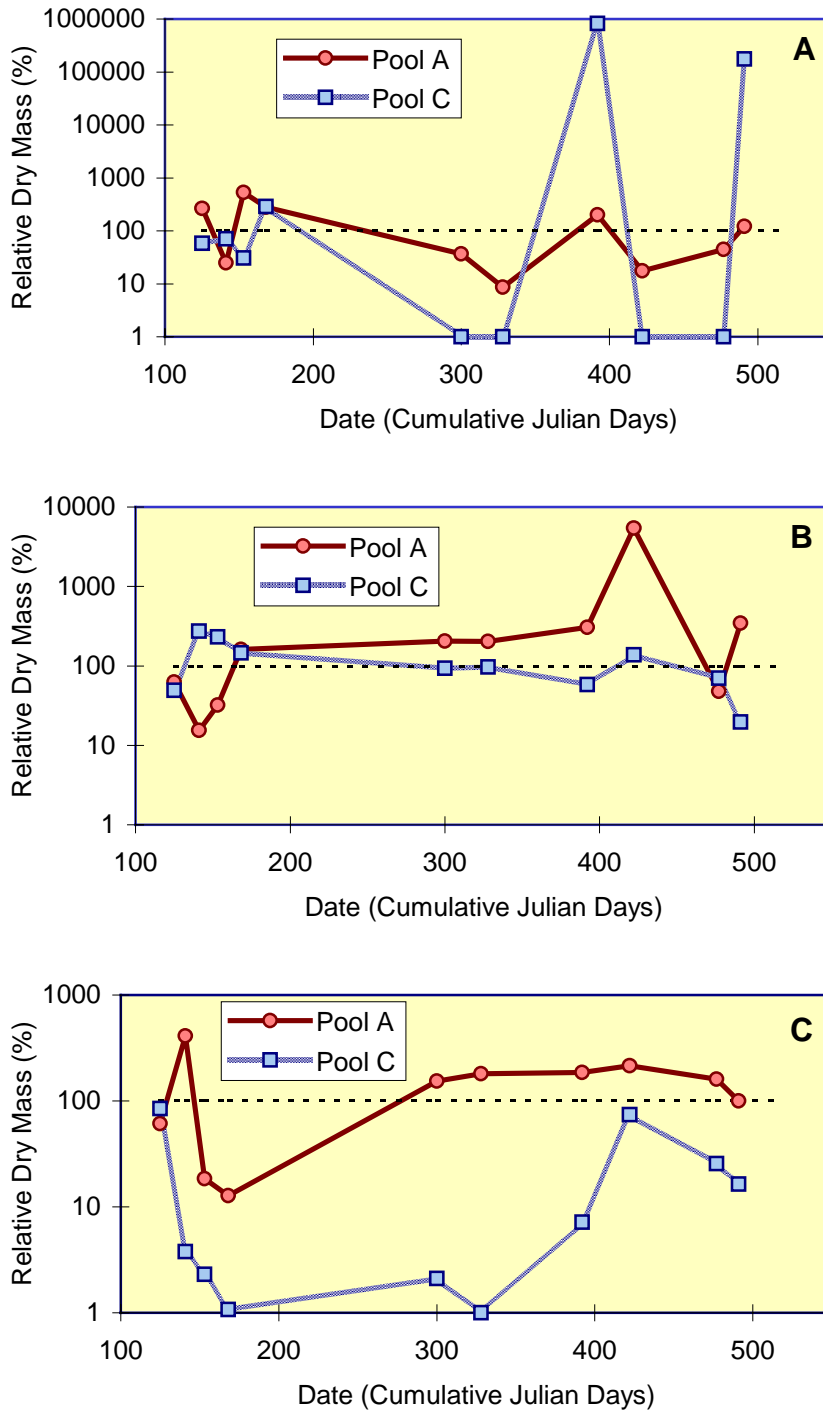


Fig. 2.9. Dry mass relative to discing (% Relative Dry Mass = [(Mean dry mass (mg) / sample in discing plots) / (Mean dry mass (mg) / sample in control plots)] \* 100) of Isopoda (A), Miscellaneous Invertebrates (B), and Amphipods (C) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal dashed line represents equal mean dry mass between discing and control plots. Points above the line indicate higher Relative Dry Mass in discing plots. Note logarithmic scales. Zero values resulted from lack of occurrence in 1 or both treatments.

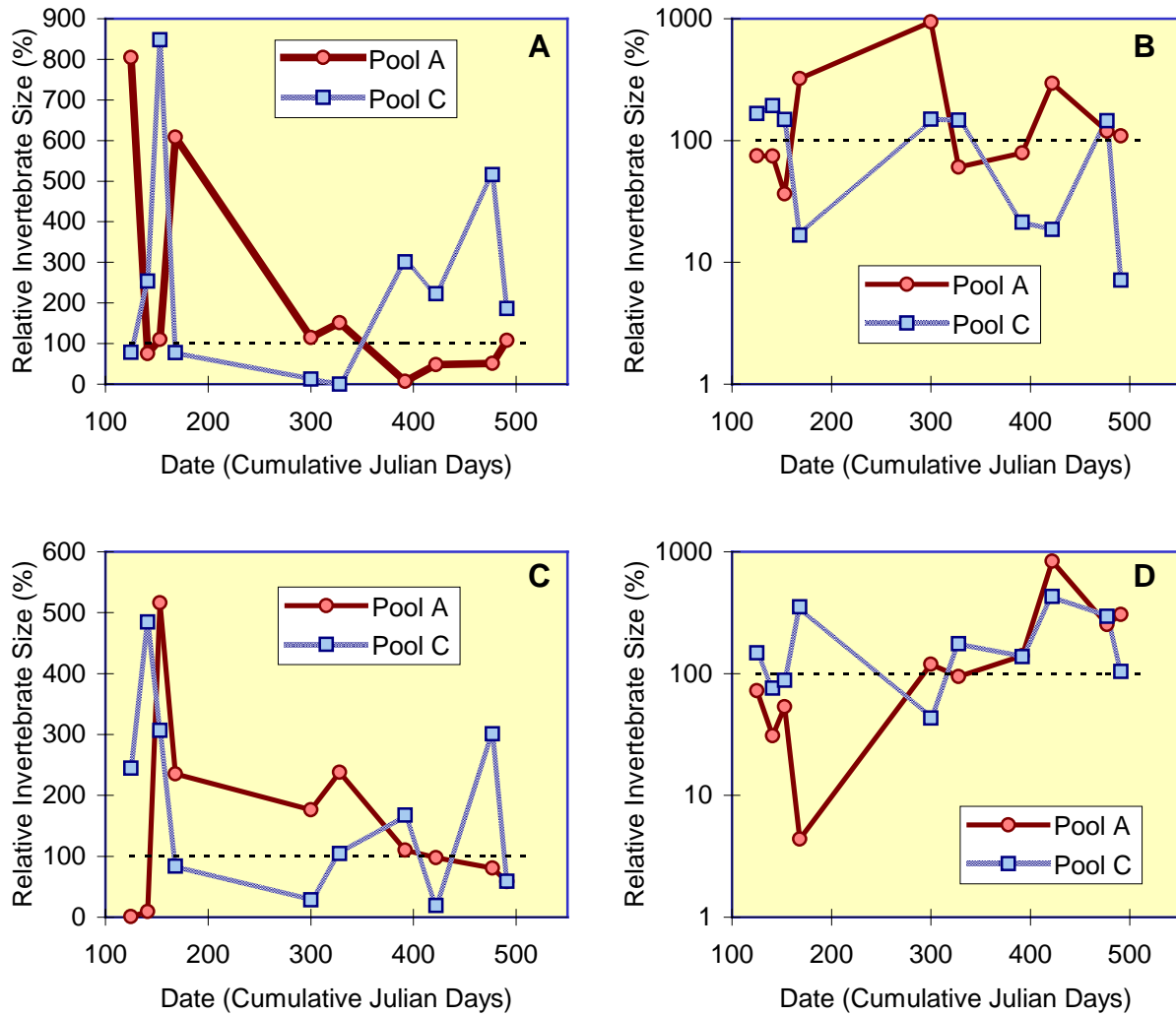


Fig. 2.10. Invertebrate size relative to discing (% Relative Size = [(Mean size [mg / individual] in discing plots) / (Mean size [mg / individual] in control plots)] \* 100) of Diptera Pupae (A), Coleoptera Larvae (B), Coleoptera Adults (C), and Oligochaetes (D) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal dashed line represents equal mean abundance between discing and control plots. Points above the line indicate higher mean abundance in discing plots. Note logarithmic scale in B and D. Julian days represent the following time periods: 125 - 175 = May - Jun 1996, 300 - 425 = Oct 1996 - Feb 1997, 475 - 500 = Apr - May 1997.

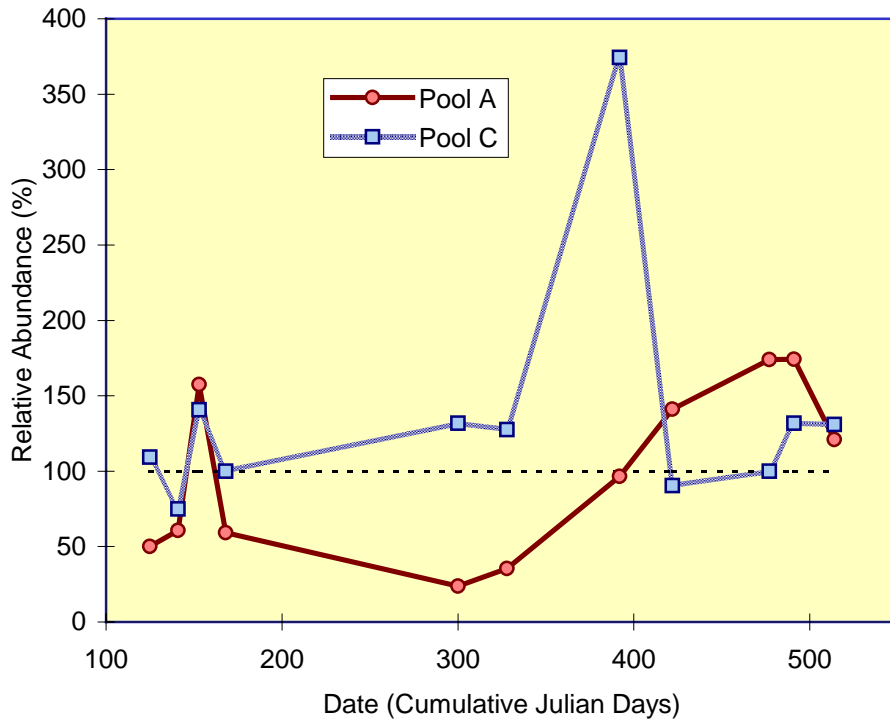


Fig. 2.11. Abundance relative to enclosure effects (% Relative Abundance = [(Mean # / sample in exclosures) / (Mean # / sample in open sampling stations)] \* 100) of Coleoptera Larvae in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal dashed line indicates equal mean abundance in enclosure and open sampling stations. Points above the line indicate higher Relative Abundance in exclosures.

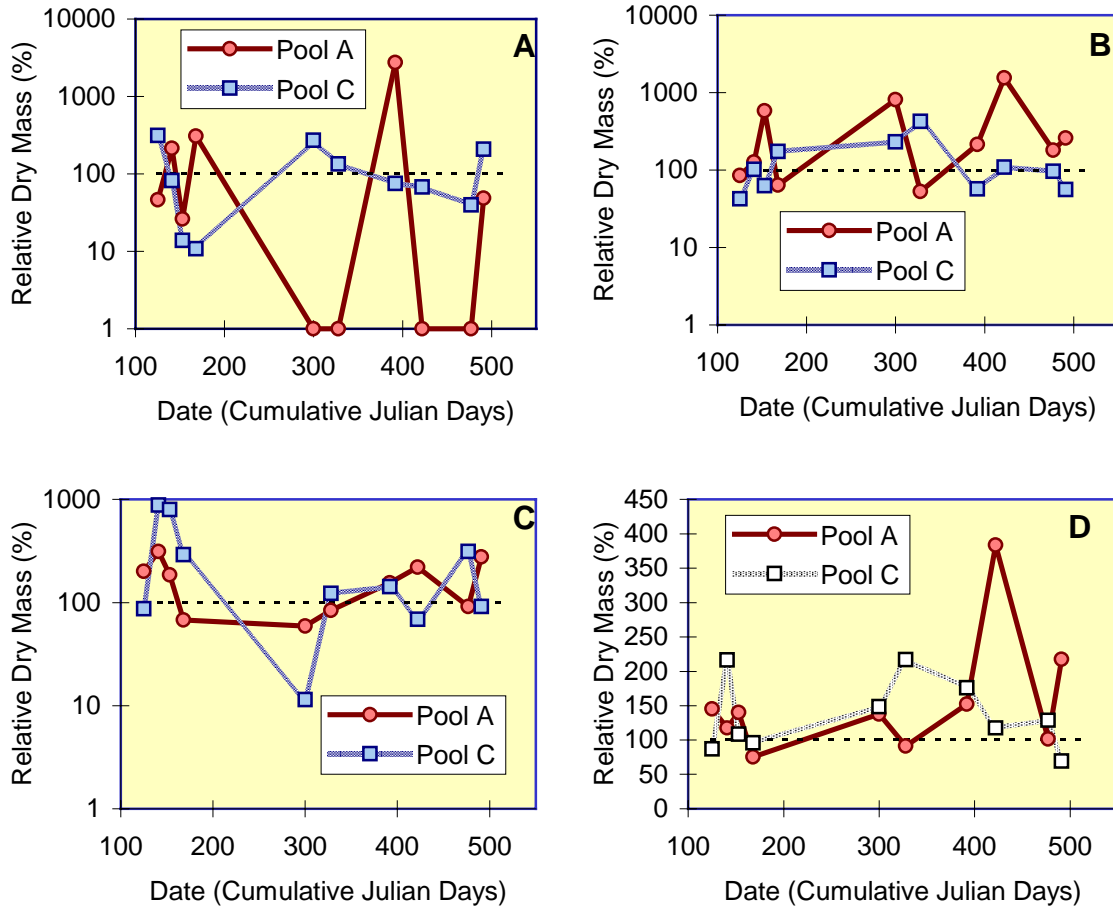


Fig 2.12. Dry mass relative to enclosure effects (% Relative dry mass = [(Mean total dry mass (mg) / sample in enclosures) / (Mean total dry mass (mg) / sample in open sampling stations)] \*100) of Isopoda (A), Other Diptera (B), Amphipoda (C) and Total Invertebrates (D) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal dashed line represents equal mean dry mass between enclosure and open sampling stations. Points above the dashed line indicate higher mean dry mass in enclosures. Note logarithmic scale for A, B and C. Zero values for Isopoda occurred during 4 sampling periods due to lack of occurrence in 1 or both sampling station types.

during most time periods, although the most pronounced enclosure effects did not coincide between pools (Fig. 2.12 B, C). Similarly, Total Invertebrate dry mass was up to 3.5 x higher in enclosures than in open sampling stations, but the most pronounced effects were observed during late winter in Pool A and late fall and spring 1996 in Pool C (Fig. 2.12 D).

Other Diptera tended to be larger in enclosures than in open sampling stations in both pools, although the most pronounced effects occurred in late spring in Pool C and in late winter in Pool A (Fig. 2.13 A). Coleoptera adults were larger in enclosures than in open sampling stations in both pools during spring 1996, but showed no consistent pattern in size between pools thereafter (Fig. 2.13 B). There was a pronounced enclosure effect on mean size of all invertebrates in Pool A during late winter and in Pool C during late fall (Fig. 2.13 C). This pattern closely resembled the pattern observed in total invertebrate dry mass (Fig. 2.12 D).

## DISCUSSION

### Experimental Effects on Habitat Variables

There was pronounced temporal variation in herbaceous plant cover, water temperature and water depth. Among these variables, a pronounced discing effect was observed only for herbaceous plant cover (Table 2.1). Plant cover was higher in control than in disced plots during all sampling periods, particularly during spring sampling periods. Both herbaceous plant cover and detritus cover were higher in control than in disced plots during spring 1997 (Table 2.1), suggesting that the discing influence on habitat conditions is not limited to 1 growing season after fall discing. Mean water depth and detritus depth were higher in control than in disced plots during spring 1996, but similar between treatments during spring 1997 (Table 2.1). This variation likely reflects a physical alteration of the substrate, wherein increases in aeration and incorporation of surface organic matter occur in disced areas. Although such alterations persisted through the initial flooding cycle after discing (Fall 1995), they were largely eliminated by the second flooding cycle (Fall 1996).

Detritus depth was the only habitat variable that differed between open and enclosure sampling stations. Detritus was slightly deeper in enclosures during the first 2 sampling periods, and slightly deeper in open sampling stations during the Oct 1996 – Feb 1997 sampling periods

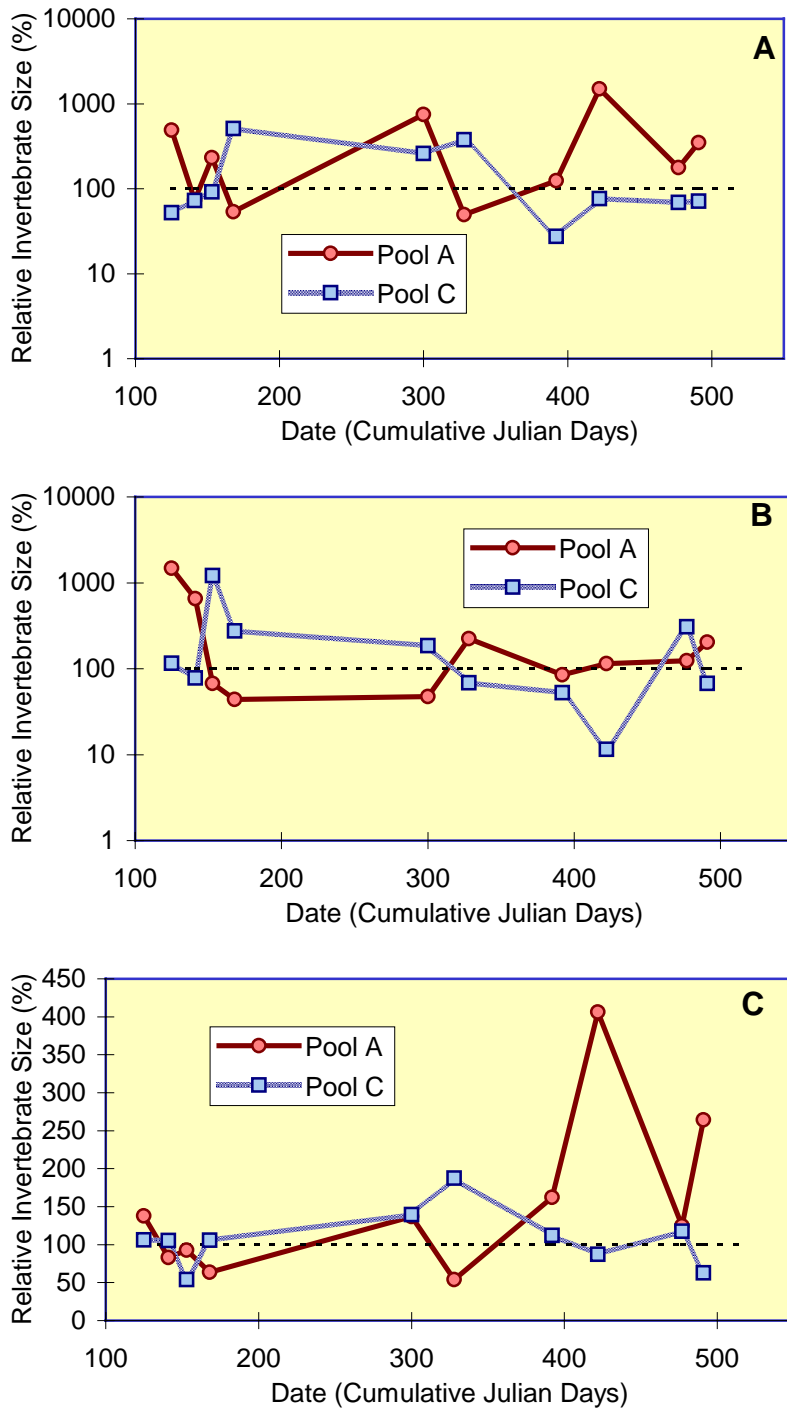


Fig. 2.13. Invertebrate size relative to enclosure effects (% Relative Size = [(Mean invertebrate size (mg/individual) in enclosures) / (Mean invertebrate size (mg/individual) in open sampling stations)] \* 100) for Other Diptera (A), Coleoptera Adults (B) and Total Invertebrates (C) in 2 moist-soil impoundments at Back Bay National Wildlife Refuge, Virginia Beach, Virginia. Horizontal lines represent equal invertebrate size between enclosure and open sampling stations. Points above the line represent higher mean invertebrate size in enclosures. Note logarithmic scale in A and B. Julian days represent the following time periods: 125 - 175 = May - Jun 1996, 300 - 425 = Oct 1996 - Feb 1997, 425 - 500 = Apr - May 1997.

(Table 2.2). These results suggest that enclosure netting may impede horizontal movement of surface organic material, tending to trap detritus during drawdowns (e.g., spring 1996) and prevent detrital accumulation during floods (e.g., fall-winter 1996-97). Variation in organic matter accumulation may affect suitability of habitat for benthic organisms, potentially compromising the ability to detect waterbird predation effects on invertebrate abundance. Apart from detritus depth, the lack of enclosure effects on other habitat variables suggests that habitat conditions for aquatic invertebrates were largely similar between enclosure and open sampling stations.

### **Bird Response to Discing**

Burning and mowing have been promoted as habitat management techniques that enhance production of invertebrates significant in waterbird diets, yet responses to both techniques are variable among taxa (Batzer and Resh 1992a, b, de Szalay and Resh 1997). Other studies (e.g., Kaminski and Prince 1981, Murkin et al. 1982) have shown disproportionate use of 50% cover-removal treatments by waterbirds, suggesting that management-induced enhancement of invertebrate production should be evident in increased bird use. However, bird survey data in this study did not reveal such a pattern (Table 2.4, Fig. 2.6). Anecdotal observations suggested that portions of Pool A with relatively low plant cover received higher bird use, particularly by shorebirds. Inability to detect bird responses to discing may have resulted from the relatively low frequency of bird surveys, and several biases inherent in the survey technique. An initial attempt was made to survey all plots from a vehicle on the impoundment dike, but this method was strongly biased toward detection of birds in disced plots because detection rates are a function of vegetative cover. Foot surveys conducted during sample collection likely minimized bias in detection rates because a single observer could flush all birds from a plot regardless of vegetative cover. However, birds in adjacent plots frequently flushed during surveys, yielding low detection rates during most surveys. A survey technique that minimizes both detection bias between treatments and unintentional flushing of birds prior to surveys would have enhanced this aspect of the study.

Contrary to the inability of surveys to detect bird responses to discing, invertebrate data from enclosures suggested that waterbird foraging effort was higher in disced areas. The

magnitude of the exclosure effect on Total Invertebrate dry mass was >2x higher in disced (+52%) than in control (+25%) plots (Fig. 2.7). In the absence of direct behavioral observations, survey data can not distinguish high-quality roosting and foraging habitats. Thus, lack of variation in bird density between treatments may not accurately reflect their relative value as foraging habitat (Van Horne 1983).

### **Discing Effects on Invertebrates**

The magnitude and extent of invertebrate responses to discing were variable among taxa. Chironomidae showed the most consistent response to discing, with abundance being higher in disced than in control plots during all sampling periods (Table 2.5). Chironomids are among the most common invertebrates in waterbird diets (Baldassarre and Fischer 1984, Euliss et al. 1991), and accordingly are often the focus of impoundment management practices (Fredrickson and Taylor 1982). The magnitude of chironomid response to discing was highest during peak periods of waterbird use of the refuge (e.g., May, Jan-Feb), suggesting that enhanced production in disced areas should benefit waterbirds.

Many other taxa showed enhanced production in disced areas during a few sampling periods. Other Diptera, Amphipods, and Oligochaetes were more abundant in disced areas during the winter months, but were generally similar in abundance between disced and control areas during the spring months (Tables 2.6, 2.10, 2.12). Accordingly, the highest proportional increase in total invertebrate abundance occurred during Jan and Feb (Table 2.16). The winter months represent the completion of the first full growing season after discing, suggesting that the presence of openings during the summer drawdown may be an important factor contributing to invertebrate colonization of disced habitats.

The only evidence for negative effects of discing on invertebrates was reduced total dry mass and mean dry mass per individual of Amphipods (Table 2.10) and reduced abundance of Gastropods during spring sampling periods (Table 2.13). Conversely, most other taxonomic groups showed increased abundance or dry mass in response to discing, although such responses were spatially variable for many taxa (e.g., Sampling Period x Pool x Discing interaction for Other Diptera; Table 2.6). Amphipods were reduced in total dry mass and mean

dry mass per individual, but were higher in abundance in disced areas. This suggests that undisced habitat would be characterized by relatively few, large individuals, whereas disced habitat would be characterized by an abundance of small individuals. Changes in size distribution of invertebrates may influence their availability to waterbirds as much as changes in abundance, given that many waterbirds prey selectively on specific size classes of organisms (Armstrong and Nudds 1985, Weber and Haig 1997a).

The main effect of Discing was significant only for abundance of Diptera pupae (Table 2.18) and both dry mass metrics for Amphipods (Tables 2.19, 2.20). All other significant Discing effects were evident as interactions with Sampling Period (Tables 2.18 – 2.20). Herbaceous plant cover and water temperature and depth also varied seasonally (Tables 2.1 – 2.3), and are likely the major ecological factors influencing invertebrate abundance and distribution (Krull 1970, Voigts 1976, Nelson and Kadlec 1984). Consequently, all taxa showed seasonal variation in abundance, with discing effects tending to be most evident during peak periods of abundance for most taxa. Given variation among taxa in life history, habitat use and seasonal patterns of abundance, it is not surprising that few analyses showed universal trends in responses to discing across all sampling periods.

The 3 response variables analyzed per taxon should each reflect a unique response to habitat manipulation. Changes in abundance would reflect movement or reproductive changes, whereas total dry mass would also reflect changes in growth patterns between treatments. Dry mass per individual would reflect changes in size-specific mortality or movement, as well as changes in growth patterns within taxa. Abundance data generally showed more statistically significant and numerically pronounced responses to discing than did total dry mass or dry mass per individual. There was a significant positive correlation between abundance and total dry mass for all taxa except Oligochaetes (Table 2.21), yet the 2 metrics did not respond identically. Assuming no error in dry mass measurements, these results would suggest that changes in growth rate of many taxa occurred in response to discing. However, it should be noted that variation among samples within plots was removed by the methods used to determine dry mass, but retained in abundance analyses. Further, dry mass metrics include an additional source of

measurement error (mass) that is excluded from abundance metrics. Despite the combining of samples to reduce measurement error, invertebrate dry mass often approached the limits of detectability on the electronic balance. Consequently, measurement error may have contributed to the relatively few significant treatment effects that were detected for dry mass metrics.

The lack of significant discing effects on Total Invertebrate abundance should not be interpreted as indication of no discing response by invertebrates. There were effects on individual taxa (i.e. Sampling Period x Discing), but variation among taxa in seasonality of effects likely was masked in the Total Invertebrates variable. The Total Invertebrates response variable is a useful index of habitat productivity, yet likely does not reflect availability of invertebrates to waterbirds due to variation in habits and habitats among taxa. Although the sampling methods used in this study targeted benthic organisms, water-column and epiphytic invertebrates also occurred in core samples. Thus, the Total Invertebrates response variable may overestimate invertebrate availability to shorebirds that forage by probing or waterfowl that filter invertebrates from the substrate-water column interface.

Previous research has failed to reveal a paradigm for invertebrate responses to habitat manipulation in freshwater wetlands. However, Gray et al. (in press) reported a trend in spatial variability of invertebrate responses to discing that was similar to the trend observed at Back Bay NWR. Invertebrate dry mass in 4 impoundments at Noxubee NWR, Mississippi either did not differ between disced and control plots or was lower in disced plots. One of the 4 produced an order of magnitude higher invertebrate dry mass than the other 3; dry mass in this impoundment was 3x higher in disced than in control plots. Significant Sampling Period x Pool x Discing interactions occurred for 6 invertebrate taxa at Back Bay NWR. These interactions generally resulted from increased abundance or dry mass in Pool A disced plots relative to Pool A control plots, and decreased abundance or dry mass in Pool C disced plots relative to Pool C controls (Fig. 2.8, 2.9). Significant 2- and 3-way interactions among various combinations of year, sampling period within year, wetland, and cover type within wetland are common in studies of aquatic invertebrate abundance (e.g., Solberg and Higgins 1993), suggesting that enhanced invertebrate populations should not be expected to occur in all disced habitats.

### **Waterbird Predation**

Differences in invertebrate abundance between open and enclosure sampling stations did not occur during either spring sampling period, suggesting that shorebird foraging removes a relatively small proportion of invertebrate production. Enclosures were located in both disced and control plots, but favorable shorebird habitat was generally only available in disced plots. Consequently, the influence of shorebird predation should be manifested through significance of Discing x Predation interactions. Inability of these analyses to detect predation likely reflects several factors. Shorebird abundance on the study area appeared to be low relative to other Atlantic coastal migratory stopovers. Weber and Haig (1996) recorded mean shorebird densities of 125 - 150/ ha, whereas mean density observed in this study was nearly an order of magnitude less (Fig. 2.6). Densities in the range of 150/ha occurred only in 1 or 2 study plots during 1 sampling period per spring season. One plot in which waterbird numbers were consistently among the highest was a control plot in Pool A. This plot was characterized by a soft, moist, highly organic substrate and low plant cover, despite the lack of discing treatment for this study. Low shorebird use of Back Bay impoundments during migration may reflect its location midway between major stopovers in South Carolina and Delaware. Given superior habitat conditions on South Carolina stopovers, most birds may be able to acquire sufficient reserves to fuel flight directly to Delaware Bay. The value of midlatitude impoundments to migrating shorebirds may therefore be strongly dependent on habitat conditions in more southerly regions. Finally, the extent of high-quality habitat on Back Bay NWR may be insufficient to attract large numbers of shorebirds. In the absence of intense habitat management, Back Bay impoundments during spring are characterized by dense moist-soil vegetation in shallow-water zones. Discing can create structural habitat characteristics favored by shorebirds, but these habitats are generally ephemeral, often reverting to dense stands of herbaceous vegetation within 1 or 2 growing seasons. A long-term habitat management program that consistently provides relatively large areas of shallowly-flooded unvegetated habitat during spring may be required to enhance shorebird use of the refuge.

There was, however, some evidence that waterfowl foraged extensively on invertebrates during winter 1996-97. For example, chironomid abundance and total dry mass were 1.9 and 3.5 x higher, respectively, in exclosures than in open sampling stations during Feb 1997 (Table 2.5). This observation is consistent with increasing consumption of invertebrates by waterfowl in late winter (Miller 1987, Euliss et al. 1991). Combs and Fredrickson (1996) found that invertebrate consumption by mallards was highest in mid-winter, whereas among habitats, invertebrate consumption was highest in open marshes. The latter observation also was supported by this study through the higher predation rates observed in disced than in control plots (Fig. 2.7).

### **Spatial Variability of Responses**

Indices of relative abundance and dry mass (Figs. 2.8 – 2.13) revealed marked spatial variation in responses to both discing and predation. Responses to discing were generally more pronounced in Pool A, although some taxa responded positively to discing in Pool C during periods when no positive response was evident in Pool A (e.g., Other Diptera, Fig. 2.8.A). Three-way interactions with Pool also may reflect spatial variation in species composition of taxonomic groups. Because the 2 impoundments differed in substrate composition and moisture content, broad taxonomic groups (e.g., Other Diptera) may have consisted of different taxa between pools. Moisture content also may influence the depth distribution of benthic organisms, altering vulnerability to collection by core samplers and predation by waterbirds between pools. The extent and nature of 3-way interactions suggest that the 2 pools functioned independently and may require separate water and vegetation management practices to optimize invertebrate production.

### **Value of Discing for Waterbird Habitat Management**

Availability of invertebrates to foraging waterbirds may vary among invertebrate taxa. Sedentary benthic organisms, such as Chironomids and Oligochaetes, should be more vulnerable to predation by shorebirds that forage by probing than should mobile organisms that occur more frequently in the water column (e.g., Amphipods, Coleopterans). However, at the conclusion of the spring 1996 shorebird migration (31 May – 2 Jun 1996), abundance and total dry mass of these taxa were higher in open sampling stations than in exclosures (Tables 2.8 – 2.10). This

suggests the occurrence of a combination of low shorebird foraging effort and a negative influence of exclosures on invertebrate production.

Invertebrate populations were higher and responses to discing were more pronounced in Pool A, in which the substrate was wetter and of higher organic matter content than in Pool C. Because adjacent undiscd habitat could serve as a source for immigration of invertebrates to discd habitats, invertebrate responses to discing may be dependent on habitat conditions and distance to adjacent undiscd areas. Moist, organic substrate may also provide microhabitat conditions that contribute to survival of aquatic organisms through drawdown periods, enhancing the response to discing. These conditions, however, present a logistical challenge to implementing this management tool. As moisture and organic matter content of the substrate increase, so will difficulty of access for discing.

Enhancement of invertebrate production is a common goal in use of discing in impoundment management. However, this represents only 1 component of the broader concept of impoundment habitat. Moist-soil impoundments may provide habitat for other bird species (e.g., passerines, rails, raptors) that are not directly dependent on invertebrate foods. Further, extensive marsh openings could reduce the quantity and quality of habitat available to those species that favor densely vegetated habitats. Although the technique appears to positively influence invertebrate production in artificial openings, this resource benefit should be weighed against the potential cost in temporary loss of habitats for other species.

The "hemi-marsh" has been advanced as a conceptual goal for the management of marshes for breeding waterfowl (Weller 1978). The interspersion of vegetation and open water provided by such habitats is believed to enhance invertebrate production and provide optimal cover for breeding birds. However, the application of this concept to marsh habitats for wintering birds has been largely ignored in the literature. Residual cover may provide thermally favorable conditions for wintering birds, yet this value of vegetated habitats to waterfowl remains unquantified. Highly productive remnant stands of herbaceous vegetation could provide abundant seed resources that may be important waterfowl foods as well as a source of propagules for

establishing moist-soil plants in openings. Manipulation of vegetative cover should therefore be conducted with the ecological functions of unmanipulated habitats in mind.

The temporal nature of invertebrate responses to discing in this study suggest that annual maintenance of disced habitats is not required to maintain enhanced invertebrate production. Some taxa (e.g., chironomids, oligochaetes) were more abundant in disced than in control plots during the second spring after discing, suggesting that these plots represented higher quality foraging habitat for shorebirds, even after a complete growing season. Recher (1966) and Recher and Recher (1969) point out the importance of social factors and aggressive behavior in the spacing and habitat use of migrant shorebird flocks. Given the influence of these factors on habitat selection, large, unvegetated openings are likely to be favored as roosting or resting habitats in the absence of enhanced invertebrate production.

This study has demonstrated that manipulation of marsh habitats enhances invertebrate production during periods of peak resource demand by migrant birds. However, an accurate description of the benefit of such enhanced production to birds depends upon habitat conditions on the surrounding landscape. The spatial relationship between a manipulated habitat and other high-quality habitats may substantially influence the extent to which enhanced food production is realized through enhanced bird use. In the absence of impoundment openings, high-quality shorebird habitat in the vicinity of Back Bay NWR consists primarily of narrow intertidal sandy beaches. Such habitats may be favored by species such as red knots and sanderlings, but are unlikely to attract large flocks of calidrid sandpipers and other species that typically favor mudflats (Weber and Haig 1996). Consequently, habitat management that increases local acreage of such habitats is likely to be of value to shorebirds. In other landscapes where mudflats are abundant, disced impoundments may represent a relatively small proportion of the locally available habitat.

## **CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS**

The results of this study support the tenet that physical manipulation of impoundment vegetation enhances production of aquatic invertebrates, at least within mid-Atlantic coastal systems. Given that variation between impoundments in invertebrate responses to discing was high, caution is warranted in extrapolating these results to other wetland systems, even within the

mid-Atlantic coast. Even in the absence of a positive influence on invertebrate production, discing can enhance the value of impoundments to waterbirds by enhancing production of moist-soil seeds (see Chapter 3), and providing openings that may be used as roosting habitat by waterbirds. These benefits should be weighed against the potential negative influence on habitat quality for other species that favor dense herbaceous vegetation (e.g., passerines, rails).

Total invertebrate abundance was substantially higher in Pool A than in Pool C, suggesting that habitat characteristics do not favor invertebrates in Pool C. Substrate in this impoundment generally contained higher proportions of sand and lower proportions of organic detritus than substrate in Pool A. The substrate also was often completely dry during spring sampling periods when Pool A substrate still held residual moisture. Future management efforts for Pool C should be targeted at improving substrate moisture and organic matter content to enhance habitat quality for invertebrates. This may be accomplished through deeper and longer floods to encourage decomposition of organic detritus and the development of a substrate that is more suitable for benthic organisms.

Back Bay NWR represents a relatively small area of shorebird habitat relative to the critical stopover areas in North America identified by Senner and Howe (1984). However, areas of relatively low current value to shorebirds are perhaps equally significant from a management perspective. Sites such as Back Bay that appear to be underused by shorebirds could serve as buffer habitat to the major stopover areas. In the event of continued declines in horseshoe crab populations or a catastrophic event in one of the major stopover areas (e.g., an oil spill in Delaware Bay), additional habitat will be needed to support spring migrants. Consequently, habitat management practices that consistently encourage shorebird use of the refuge may contribute to its long-term function as a stopover area.

As a management tool, discing is labor- and cost-intensive. Habitat alterations produced by discing are not sustainable, generating recurring maintenance requirements. These requirements, however, do not likely differ substantially from those incurred under other management practices designed to create openings (e.g., burning). To the extent that habitat alterations generated by discing are desirable over long time periods, an appropriate maintenance

cycle should be identified that maximizes the resource benefits of discing while minimizing labor costs. Because dramatic alteration of fall hydrology may be required to facilitate discing, water level management should be adequate to ensure that fall floods are not delayed beyond the arrival of early migrant waterfowl.

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