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UNIVERSITY OF ALBERTA

CHIRONOMIDAE (DIPTERA) COMMUNITY DEVELOPMENT FOLLOWING EXPERIMENTAL MANIPULATION OF WATER LEVELS AND AQUATIC VEGETATION

BY

Dale A. Wrubleski

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

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SUBMITTED BY DALE A. WRUBLESKI

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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Date: 12 April 1991

DEDICATION

I dedicate this thesis to Anita, Kristin and Amanda
for their patience, encouragement and love.

ABSTRACT

The importance of aquatic vegetation in structuring invertebrate communities of a northern prairie marsh are investigated in two field experiments.

In the first experiment, responses by the Chironomidae (Diptera) to the experimental flooding of ten diked marshes in the Delta Marsh, Manitoba were followed over four years. Emergence traps were used in three 'preflood' vegetation types (the terrestrial annual *Aster laurentianus*, and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) flooded at two water depths (shallow: 20-40 cm, deep: 50-70 cm). Highest number of chironomids (9,168 m^{-2} yr^{-1}) emerged from the deep *Aster* sites in the first year. The highest biomass of chironomids (22,007 mg m^{-2} yr^{-1}) was from the deep *Scirpus* sites in the fourth year. In *Aster*, a diverse group of chironomids, including epiphytic and bottom-dwelling species, were present from the first application of water. Numbers, biomass and size classes were similar over the four years. In the two emergent macrophyte habitats, small epiphytic species, particularly *Corynoneura* cf. *scutellata*, dominated emergence during the first two years. Prolonged flooding contributed to the death of the emergent macrophytes, epiphytic species declined in abundance and benthic species, particularly *Chironomus tentans* and *Glyptotendipes barbipes*, increased in numbers. The potential of chironomids as a food resource for waterfowl was initially greatest from the *Aster* habitat but became greater from the *Scolochloa* and *Scirpus* habitats in the third and fourth years. Comparisons are made with developmental sequences reported for reservoirs, and the unmanaged Delta Marsh.

A second field experiment examined how the seasonal development of submersed vegetation affects benthic invertebrates. *Potamogeton pectinatus* was either removed via clipping or permitted to grow in fenced plots. Invertebrates (primarily copepods) were more abundant in the clipped plots. Chironomid larval numbers and adult emergence did not differ between treatments, although *Polypedilum halterale* and *Cladotanytarsus* sp. were more abundant in clipped plots, and more *Corynoneura* cf. *scutellata* emerged from pondweed plots. Algal biomass beneath the pondweed tended to be lower than in the clipped plots suggesting that by shading the bottom, submersed macrophytes reduced algal biomass and indirectly affected benthic invertebrate abundances.

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I would like to thank Lisette Ross and Karen Tome for supervising the field crews during the collection of emergence trap samples in the MERP cells. Field assistants were provided through the MacMillan and Webster Fellowship Programs. Colleen Barber, Rosie Bolen and Bruce Pollard helped in the field with the pondweed manipulation experiment. Sharon Gurney advised on the collection and analysis of algal samples and Lorie Shortreed sorted many of the core samples from the pondweed manipulation experiment. Ray Weingardt graciously offered his time and expertise with statistical matters. Don Oliver verified many of my chironomid determinations.

Finally, I would to thank my fellow graduate students at Delta and the University of Alberta for their lively discussions and warm friendship.

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1. INTRODUCTION

Agriculture, urban expansion and other human activities contribute to a continuing loss of North American wetlands. Interest in wetland preservation is increasing, although the rate of loss is still very high (Millar 1989; Wilen 1989). Wetlands are important for many reasons including water storage and purification, protection of shorelines from erosion, recreation and wildlife habitat (Brande 1980). However, much of the concern for wetland preservation comes from recognition that these habitats are crucial to migratory waterfowl populations. Wetlands of the prairie pothole region for example, produce between 50 and 75% of North American waterfowl (Batt et al. 1989). Along with the increasing demand to protect and conserve remaining wetlands, there is also pressure to manage intensively many of the protected areas to maintain high waterfowl productivity in the face of continued habitat loss.

Recent studies of waterfowl feeding have revealed that aquatic invertebrates are a crucial food resource for waterfowl, especially during reproduction and early growth of broods (Murkin and Batt 1987; Swanson and Duebbert 1989). These organisms also are involved in a number of important ecosystem functions such as food chain support, decomposition and nutrient cycling within wetlands (Murkin and Wrubleski 1988). For these reasons the study of the aquatic invertebrate fauna of wetlands is extremely important, and consideration must be given to the effects of wetland management practices on invertebrate communities.

1.1 Previous studies of wetland invertebrates. Most work on the invertebrates of North American freshwater marshes[1] has been descriptive faunal surveys (e.g., Judd 1949, 1953; Watts 1970; Smith 1968; Hanson and Swanson 1989; Wrubleski and Rosenberg 1990). Because of the taxonomic challenges with important groups and the perceived lack of importance of wetland invertebrates, other than pestiferous species, very little process-level work has been undertaken (Rosenberg and Danks 1987b). However, before detailed ecological work can proceed a basic knowledge of the fauna present is required. The Biological Survey of Canada recognized the need for more information on the taxonomy and ecology of aquatic insects of Canadian wetland habitats and established a project to coordinate interest in this area and to summarize existing knowledge. The culmination of this effort was the publication of a conference proceedings "Aquatic Insects of Peatlands and Marshes in Canada" (Rosenberg and Danks 1987a) which summarizes our present knowledge of the insect fauna of Canadian wetlands. This thorough and informative publication provides a much needed basis for future work on the aquatic insects of wetland habitats.

Ecological studies within freshwater wetlands have concentrated on the role of habitat features such as aquatic vegetation and water levels, and their

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[1] For the purposes of this review the term marsh is used in a very general sense to include most shallow freshwater habitats but not peatland or swamp type habitats (Zoltai 1987).

effects on invertebrate communities. Krull (1970), Voigts (1976), Henson (1988), and Wrubleski and Rosenberg (1990) have examined invertebrate abundances and community composition in different aquatic plant communities. Driver (1977) attempted to correlate chironomid community composition with permanence of prairie potholes. Murkin and Kadlec (1986b) reported on the effects of prolonged flooding on the invertebrate communities of a series of experimental marshes in the Delta Marsh, Manitoba, and Neckles et al. (1990) examined the role of water levels on the invertebrate community of seasonal marshes. Corkum (1984) and Wrubleski and Ross (1989) have reported on diel activities of the invertebrate fauna of marshes. Unfortunately, almost no autecological studies have been done (but see Corkum 1985).

A number of investigations of aquatic invertebrate communities of wetland habitats have been done in conjunction with waterfowl studies. Waterfowl production and habitat use have been correlated with invertebrate abundances by McKnight and Low (1969), Kaminski and Prince (1981), Murkin et al. (1982), Talent et al. (1982), and Murkin and Kadlec (1986a), and the effects of waterfowl feeding and disturbance on invertebrate populations have been examined by Collins and Resh (1985), Smith et al. (1986), Peterson et al. (1989), and Wrubleski (1989).

Field experiments are only recently being undertaken within wetland habitats. Smith et al. (1986), Peterson et al. (1989) and Wrubleski (1989) used exclosures to determine impacts of waterfowl feeding on invertebrate communities. Campeau (1990) examined the roles of detritus and algae in supporting invertebrate populations in wetlands. Morrill and Neal (1990) investigated the impact of an experimental application of the insecticide deltamethrin on the Chironomidae of prairie ponds.

Descriptive studies still are needed to provide basic information about the aquatic invertebrate fauna of wetland habitats. However, field experiments provide a greater understanding of their ecological and functional relationships in this habitat, and this approach should be encouraged.

1.2 Wetland management and aquatic invertebrates. Much of the interest in the aquatic invertebrates of North American wetlands has been generated by studies of waterfowl food habits which have revealed that breeding hens and their young are dependent upon invertebrates as a primary source of protein (Murkin and Batt 1987; Swanson and Duebbert 1989). As noted above, waterfowl habitat use is often correlated with availability of invertebrates. The now widely recognized importance of aquatic invertebrates to waterfowl has provided evidence needed to justify study of the effects of wetland management techniques on aquatic invertebrate communities.

Wetland management, however, is still in its infancy and much of its practice is based on trial and error rather than sound scientific principles (Weller 1978). Most management practices are designed to provide food and cover for waterfowl through manipulation of plant communities (Fredrickson and Taylor 1982), and it is the effects of management on vegetation that has received the greatest emphasis. Nevertheless, several investigations have considered aquatic invertebrate responses to wetland management practices, and in particular the impacts of drawdown (artificial drainage and reflooding). The first such study was by Kadlec (1962) who concluded that drawdown of waterfowl impoundments in Michigan was detrimental to invertebrate populations. McKnight and Low (1969) provided qualitative evidence that drawdown of salt marshes in Utah actually enhanced aquatic invertebrate numbers. Whitman (1974), studying impoundments within the Tintamarre and Missaquash Marshes of Nova Scotia, found that those less than four years old provided the highest numbers of invertebrates as food for waterfowl. Danell and Sjöberg (1982) reported that in a Swedish lake highest numbers of chironomids occurred in the fifth year of flooding, coincident with peak production of waterfowl broods. Kenow and Rusch (1989) reported that nektonic invertebrates increased in numbers over a three year period following flooding of impoundments within the Horicon Marsh, in Wisconsin. Except for the study of Kadlec (1962), drawdown has generally been reported to increase invertebrate numbers over those found in nearby mature (older) areas.

However, with the exception of Kenow and Rusch (1989), none of the studies listed above have followed invertebrate responses within a single wetland from the first application of water, and except for Danell and Sjöberg (1982) none of these studies have attempted to identify invertebrates further than the order or family level. Interpretation of management effects at these higher taxonomic levels can be problematic (e.g., Resh and Unzicker 1975; Rosenberg et al. 1986). Therefore, additional work is necessary to understand responses of the aquatic invertebrates to drawdown and other wetland management practices.

1.3 Marsh ecology research program. To understand further the effects of wetland management practices, and in particular drawdown, the Delta Waterfowl and Wetlands Research Station and Ducks Unlimited Canada established the Marsh Ecology Research Program (MERP) in 1979. This was a long-term (10 years), interdisciplinary program, centred around a series of ten experimental marshes situated within the Delta Marsh in south-central Manitoba (Figure 1.1). Its stated purpose was to develop a clearer understanding of ecological processes in northern prairie marshes and how these processes influence the distribution and abundance of the flora and fauna within marshes. The aquatic invertebrates were identified as one of seven specific research interests within the program (Batt et al. 1983; Murkin et al. 1984).

1.4. Objectives of this thesis. In Chapter 2, I describe the development of the chironomid community following reflooding of these experimental marshes which had undergone a drawdown. The Chironomidae were selected for intensive study for several reasons: 1) they are one of the most abundant and diverse invertebrate groups in the Delta Marsh, as well as other freshwater marshes (Wrubleski 1987), 2) they perform a number of important ecological functions within wetlands and are also an important waterfowl food resource (Wrubleski 1987), 3) emergence traps can be used to sample adults which can then be identified to species much more readily than immature stages, and 4) a previous study of chironomids within the unmanaged Delta Marsh provides information for comparative purposes (Wrubleski and Rosenberg 1990). The present study describes the most intensively sampled and longest running data set for any specific invertebrate group within a wetland habitat to date. Biological requirements of dominant species, derived from the published literature, are used to help explain observed patterns of overall chironomid community development. The effects of aquatic plant communities and water depth on community development are also discussed.

In Chapter 3, I use a condensed data set from Chapter 2 to provide information for wetland managers as to the observed responses of the chironomids to drawdown in a northern prairie marsh. Because of the known importance of these insects, their responses to this management technique are important. Numbers, biomass and size class information are used to evaluate chironomid production from different plant communities and water depths within the experimental cells.

In Chapter 4, I describe a field experiment which examined the effects of submersed vegetation on the benthic community of a shallow marsh. Hall et al. (1970), Danell and Sjöberg (1982), Johnson and Mulla (1983) and Wrubleski (1989) have noted differences between benthic invertebrate communities when submersed vegetation is present or absent. Aquatic macrophytes are known to alter their physical environment (e.g., Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983), but the effects of these modifications on invertebrate communities of wetlands and other aquatic habitats has not been well documented.

In Chapter 5, I summarize my findings and make suggestions as to future research needs. I also comment on the present state of invertebrate research in wetlands. Problems with sampling and identification greatly hamper our understanding of aquatic invertebrates in these habitats. Increased effort will be required if we are to progress in our understanding of invertebrate community dynamics in these habitats.

Figure removed for copyright reasons.

Figure 1.1. Location of the experimental cells of the Marsh Ecology Research Program in the Delta Marsh, Manitoba. Cells are numbered 1 to 10 from west to east (from Murkin et al. 1984).

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2. CHIRONOMID (DIPTERA: CHIRONOMIDAE) COMMUNITY DEVELOPMENT FOLLOWING EXPERIMENTAL WATER-LEVEL MANIPULATIONS IN A NORTHERN PRAIRIE MARSH, DELTA MARSH, MANITOBA, CANADA

2.1 SYNOPSIS

This study describes the development of the chironomid community in a series of newly flooded marshes. Emergence traps were used to compare chironomid communities among three 'preflood' vegetation types (the terrestrial annual *Aster laurentianus* and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) and two water depths, over a four year period. Chironomids colonized the marshes rapidly with high numbers of individuals and species found in the first year of flooding. Patterns of community development differed between the *Aster* habitat and the two emergent macrophytes. In *Aster*, a diverse group of chironomids, including epiphytic and bottom-dwelling species, were present from the first application of water. In the two habitats with emergent macrophytes, epiphytic species, particularly *Corynoneura* cf. *scutellata*, dominated chironomid emergence during the first two years. Prolonged flooding resulted in the death of the macrophytes, epiphytic species declined in abundance and benthic species, particularly *Chironomus tentans* and *Glyptotendipes barbipes*, increased in numbers. Comparisons are made with developmental sequences reported for chironomid communities in reservoirs, and an area of the unmanaged Delta Marsh.

2.2 INTRODUCTION

Chironomids are an abundant and diverse family of aquatic insects. They dominate benthic assemblages of many freshwater habitats and are one of the first groups to colonize newly created water bodies. Chironomid colonization and succession have been studied in a variety of new reservoirs (e.g., Armitage 1977, 1983; Sephton et al. 1983; Brown and Oldham 1984; Rosenberg et al. 1984) and other shallow water habitats (e.g., Clement et al. 1977; Street and Titmus 1979; Titmus 1979; Danell and Sjöberg 1982; Barnes 1983), but the dynamics of chironomid assemblages have not been examined in newly created wetland habitats.

The flooding of a series of experimental marshes in southern Manitoba enabled me to study chironomid colonization and succession within these structurally complex habitats. During the drawdown phase, marsh bottoms were colonized by a variety of terrestrial and aquatic macrophytes (van der Valk et al. 1989; van der Valk and Welling 1988; Welling et al. 1988). Flooding of this 'preflood' vegetation provided a diverse array of habitats for chironomid colonization. Marsh vegetation does influence chironomid community composition (Wrubleski 1987; Wrubleski and Rosenberg 1990), but how these effects are manifested is not well understood. In the experimental cells, terrestrial plants were drowned and aquatic macrophytes survived for varying periods of time, depending upon depth of flooding (van der Valk, unpubl. data). Death of these plants contributed to an abundance of plant litter on the bottom and additional habitat for chironomids. Thus, within these experimental cells, habitats available for colonization by the chironomids varied in form, abundance and duration.

In this paper, I describe changes in the abundance, diversity and species composition of the chironomid community within these experimentally flooded marshes. Observations were made over a period of four years to evaluate changes in the chironomid community and their relationship to changes in the plant communities. Information about habitat requirements of the dominant species are used to explain underlying patterns of chironomid community development. Comparisons are made with sequences of community development reported for reservoir habitats (e.g., McLachlan 1974). Comparisons are also made with an unmanaged area of the Delta Marsh (Wrubleski and Rosenberg 1990) to determine the effects of this disturbance on chironomid community parameters such as diversity and dominance.

2.3 STUDY AREA

A complex of 10 contiguous, rectangular, 4-6 ha experimental marshes (cells) were established in 1979 by the Marsh Ecology Research Program (MERP) in the Delta Marsh, in south-central Manitoba (50° 11' N, 98° 19' W). The dikes were built of earth excavated from within each cell. Water levels were manipulated and maintained by electric pumps. In 1980-1982 the cells were flooded to a depth 1 m above average Delta Marsh water levels (Batt et al. 1983; Murkin et al. 1984). The cells were drained (drawdown) during 1983 and 1984, and then reflooded in June-August of 1985. Vegetation and water chemistry in the cells have been described by Kadlec (1986a,b, 1989), van der Valk (1986), van der Valk and Welling (1988), Gurney and Robinson (1988) and van der Valk et al. (1989).

2.4 MATERIALS AND METHODS

2.4.1 Sampling. The design of the reflooding experiment for the Marsh Ecology Research Program (MERP) called for three cells to be flooded at the long-term average of the Delta Marsh ('low' treatment), three flooded to a depth 60 cm above average ('high' treatment), and four to be flooded to a depth 30 cm above average ('medium' treatment) (Batt et al. 1983; Murkin et al. 1984). The experimental cells varied widely in the development of plant communities on the drawdown surfaces (van der Valk et al. 1989; van der Valk and Welling 1988; Welling et al. 1988), and water depths following reflooding increased from north to south within the cells. This variation rendered the cells unsuitable as 'replicates' for the study of chironomid community responses, and therefore I selected the following habitats, based on preflood vegetation, as treatments rather than the cells: *Aster*, *Scolochloa* and *Scirpus*. These plant species formed extensive stands on the drawdown surfaces of the experimental cells (van der Valk, unpubl. data). Each habitat was sampled at two water depths, shallow (20-40 cm) and deep (50-70 cm). The deep flooding sites were anticipated to lose their emergent macrophyte cover faster than the shallow sites.

Aster laurentianus Fern. was one of the dominant terrestrial annuals to grow on the dry marsh bottoms (van der Valk 1986, as *A. brachyactis* Blake) and was drowned following flooding. *Scolochloa festucacea* (Willd.) Link (whitetop) and *Scirpus lacustris* L. ssp. *validus* (Wahl.) Koyama (softstem bulrush) were selected to represent emergent macrophyte habitats from the five species that dominated the drawdown surfaces of the cells (Welling et al. 1988; van der Valk and Welling 1988). *Scolochloa festucacea* is tolerant to seasonal flooding but not to prolonged flooding (Millar 1973; Neckles et al. 1985). *Scirpus lacustris validus* is more tolerant to flooding than *S. festucacea,* but intolerant to long periods of flooding (Harris and Marshall 1963; Shay and Shay 1986).

Each vegetation-water depth combination was sampled with six emergence traps, for a total of 36 traps. I used a modified LeSage and Harrison (1979) model 'week' trap (basal area = 0.5 m^2). Traps were set out when there was sufficient water at a site to float them. The same trap sites were used for each of the four years of this study (1985-88). At each site, three stakes, 2 m apart and in a line, were driven into the substrate. The emergence trap was anchored to the centre stake and one of the outside stakes, and switched to the opposite outside stake at approximately monthly intervals to reduce trap and disturbance effects below the trap.

Deep water sites, which were at lower elevations, were flooded earlier than shallow water sites at higher elevations. Initiation of sampling varied between 16 May and 20 July, 1985. Within each habitat-water depth combination the six emergence trap sites were not flooded at the same time, but all were flooded within two weeks of each other, except for two shallow *Scirpus* sites that were flooded 9 weeks before the other four sites (data from these 9 weeks were excluded from the analyses). In 1987 and 1988 traps were set out in the last week of April and emptied weekly through the third week of October, providing data for 24 weekly sample periods. In 1986, traps were not set out until the first week of May and data were collected over 23 weeks.

2.4.2 Identification of Chironomidae. All adults were identified to species. Nomenclature follows Oliver et al. (1990). Determinations were verified by Dr. Don Oliver, Biosystematics Research Centre, Ottawa, and representative specimens have been deposited in the Canadian National Collection, Ottawa.

2.4.3 Lost traps, missing data and data summation. Samples were lost in the fall of each year, particularly in 1985, because traps were sunk or damaged by muskrats. Other traps were occasionally upset by strong winds throughout the year. In some instances when a trap was damaged or upset it was replaced immediately. For these samples, the number of individuals present in the sample was adjusted proportionately to estimate the catch as if the trap had been in place for the full 7 days (e.g., a sample from a trap in place for 3 days was multiplied by 2.3 to equal a 7 day sampling period). Most traps, however, were not replaced until their next regularly scheduled visit. Highest number of complete sample losses was 23 of 138 samples (16.7%) for shallow *Scolochloa* sites in 1986. Total sample losses in the shallow sites were 0.7% and 5.8% in the deep sites over the four years.

Numbers collected from each trap during every week were summed for the entire sampling season, multiplied by 2 to give no. m^{-2} and then used to determine mean annual emergence (no. $m^{-2} yr^{-1}$ ± SE, n=6) for each habitat-water depth combination. To determine the chironomid emergence from each trap over the entire season the data lost during each week that a trap was not operating were estimated using the procedure outlined in Appendix 1.

2.4.4 Community parameters. The chironomid assemblages collected within each habitat-depth combination were compared by several methods. Number of species (species richness) collected within each was determined. Species diversity was estimated using the Shannon-Wiener (H') function (Krebs 1989, p. 361). The relative dominance index (RDI) of McNaughton (1967, after Driver 1977), the proportion of emergence represented by the two most abundant species, was also determined for each habitat-depth combination. Two similarity indices were used to compare communities and changes within and among communities over time. Jaccard's similarity coefficient is a binary index based on presence-absence and therefore gives equal weight to all species (Krebs 1989, p. 295). The percentage similarity index of Renkonen (1938, from Krebs 1989, p. 304) uses relative abundances and is influenced heavily by dominant species. Non-transformed data were used for the determination of all similarity and dominance indices.

2.4.5 Statistical analysis. Emergence data were $\log_{10}(x+1)$ transformed prior to analysis to stabilize the variances. Year comparisons were done within habitat and depths by one-way ANOVA followed by Tukey's test ($P<.05$) to compare individual year means as recommended by Day and Quinn (1989). Habitats were compared within years and depths with one-way ANOVA and Tukey's test to compare individual habitats, and depths were compared within habitat and year by *t*-tests ($P<.05$). All analyses were done with SYSTAT (vers. 3.2) on a Macintosh computer.

2.5 RESULTS

2.5.1 Total Chironomidae. Chironomids colonized the marsh cells rapidly and large populations were found during the first year of flooding (Table 2.1). The highest number of total chironomids collected in any one year was during the first year of flooding in the deep *Aster* sites (Table 2.1). *Scolochloa* and *Scirpus* sites had their highest numbers emerging during the fourth year but these numbers were not significantly different from numbers observed in the first year.

The trends for total numbers emerging over the four years did not differ among habitats but did differ between depths. In the shallow sites little change was found among years, except for a significant increase in numbers emerging from the *Scirpus* sites between the third and fourth years of flooding. In the deep sites there was a trend for high numbers emerging in the first year of flooding followed by a decline in the second and/or third years and a subsequent increase in the fourth year of flooding.

Comparisons of total chironomid numbers emerging among the three habitats showed few differences (Table 2.1). Among shallow sites *Aster* tended to have higher numbers emerging than the two emergent vegetation habitats but these differences were only significant in 1987. Among the deep sites *Aster* tended to be higher during the first two years but then numbers of emerging chironomids increased from the two emergent habitats, particularly in the fourth year. The only significant difference, however, was a very low number emerging from the *Scirpus* habitat in 1986.

Few differences were found between numbers of total chironomids emerging between depths within each habitat (Table 2.1). In 1985, deep *Aster* and *Scirpus* sites had higher emergence than their corresponding shallow sites, however this was a function of the longer flooding times in the deeper sites (Chapter 3). In 1987 and 1988, deep *Scirpus* sites had higher numbers emerging than the shallow sites.

Seasonal trends in emergence for total chironomids varied among years (Figures 2.1-3). In 1985, patterns of emergence differed among the three habitats. Emergence peaked in period 13 (early August) for both depths in the *Aster* habitat. In the *Scolochloa* habitat emergence peaked in late August - early September (period 17) in the deep sites but showed a low continuous emergence in the shallow sites. Weekly numbers emerging rose much more slowly in deep *Scolochloa* sites than the other two habitats. In the *Scirpus* habitat no readily obvious peaks were observed at either depth. Emergence in all three habitats shifted to a primarily early spring emergence in subsequent years (Figures 2.1-3). The large July-August peaks in emergence from the deep sites in 1985, were not observed in subsequent years. *Aster* continued to have a low continuous emergence throughout the summer in 1986, 1987 and 1988, particularly from the shallow sites, whereas *Scolochloa* and *Scirpus* had very low emergence after the end of June in 1986 and 1987, but in 1988 a greater proportion of emergence was found later in the summer, but from the deep sites rather than the shallow sites as found in *Aster*.

2.5.2 Species composition. Underlying the changes in the numbers of Chironomidae are changes in the abundances of the subfamilies, tribes and species. Although patterns in total numbers were similar among habitats over the four years (Table 2.1), species composition differed among habitats and varied over the duration of this experiment, as outlined below.

2.5.2.1 Chironomini. *Aster* sites were dominated by the Chironomini during all four years (Table 2.1). In the first year of flooding, the deep *Aster* sites were dominated by *Chironomus atrella* (Townes), which represented 39.7% of the chironomids collected (Table 2.2). This species represented only 6.7% of emergence from shallow *Aster* sites in the first year, where another member of this tribe, *Chironomus tentans* Fab., was the most abundant species. *Chironomus tentans* was the most abundant species from this habitat at both depths during the next three years, whereas *Chironomus atrella* had much lower emergence in subsequent years (Table 2.2; Appendix 2A). *Glyptotendipes barbipes* (Staeg.) was also very abundant in this habitat over the four years (Table 2.2).

During the first two years of flooding, members of the Chironomini were a much smaller proportion of the emergence from the two emergent vegetation habitats (Table 2.1). *Dicrotendipes nervosus* (Staeg.) was abundant during these first two years (Tables 2.3,2.4). However, by the fourth year in the shallow sites (66.0 - 76.7%) and the third year in the deep sites (66.2 - 75.2%), Chironomini represented a much greater proportion of the emergence from these two habitats (Table 2.1). This increase in abundance was due primarily to *Chironomus tentans* and *Glyptotendipes barbipes* (Tables 2.3,2.4).

2.5.2.2 Orthocladiinae. During the first few years in the *Scolochloa* and *Scirpus* habitats the Orthocladiinae, and specifically *Corynoneura* cf. *scutellata* Winn., dominated emergence numbers (Tables. 2.1,2.3,2.4). However, by the third year this species declined considerably in number and proportion of emergence in these two habitats and was not among the five most abundant species in the fourth year (Tables 2.3,2.4). Orthocladiinae represented a small but constant proportion of chironomid emergence from the *Aster* habitat (Table 2.1). *Corynoneura* cf. *scutellata* was present in this habitat (Table 2.2; Appendix 2A) but did not dominate emergence as it had in the two emergent vegetation habitats.

Other orthoclads were also important components of emergence from the experimental cells. *Cricotopus sylvestris* (Fab.) and/or *C. ornatus* (Meig.) were consistently among the five most abundant species in *Aster* and *Scolochloa* sites but were not as abundant in the *Scirpus* habitat (Tables 2.2-4). *Limnophyes prolongatus* (Kieff.), a semi-terrestrial species, had very low abundances in the *Aster* sites (Appendix 2A) but was abundant in *Scolochloa* and *Scirpus* sites in the first two years of flooding and then declined in abundance (Tables 2.3,2.4; Appendix 2B,C).

2.5.2.3 Tanytarsini. The Tanytarsini showed almost no significant changes in total numbers over the four year period (Table 2.1). In the shallow sites, it was significantly less abundant in *Scirpus* than in *Aster* during the first three years. The most abundant species was *Paratanytarsus* sp. 1 which was particularly numerous in the first few years of flooding (Tables 2.2-4). *Tanytarsus* sp. 1 was the most abundant species in shallow *Scolochloa* sites in 1987, and the second most abundant species in deep *Aster* sites in the same year (Table 2.2). Numbers were considerably greater in deep *Aster* sites in the first year but it was third in abundance after *Chironomus tentans* and *C. atrella* (Table 2.2).

2.5.2.4 Tanypodinae. This group had very low numbers in the first years of flooding but showed significant increases by the fourth year in shallow *Aster*, deep *Scolochloa*, and both *Scirpus* sites (Table 2.1). Much of the increase over the four years was due to *Tanypus punctipennis* Meig (Tables 2.2-3), but almost all species showed some increase in numbers over the four year period (Appendix 2).

2.5.2.5 Pseudochironomini. This tribe was represented by one species, *Pseudochironomus middlekauffi* Town. (Appendix 2). It showed consistent increases in abundance in all three habitats and at both depths during the four years, and was the third most abundant species in shallow *Scolochloa* in the fourth year (Table 2.3).

2.5.3 Chironomid community parameters. As with the number of chironomids collected, high numbers of species were present within the experimental cells in the first year of flooding (Figure 2.4A). *Aster* had higher numbers in the first year at both depths and maintained this higher number of species in the shallow sites over the four year period. In the deep sites however, *Scolochloa* and *Scirpus* reached comparable numbers by the third or fourth years of flooding (Figure 2.4A). Numbers of species collected increased steadily in the deep sites over the four years and by the fourth year were higher than in the shallow sites.

Aster had the highest species diversity in the first year of flooding (Figure 2.4B) and the lowest relative dominance (Figure 2.4C), whereas the deep *Scirpus* sites had very low diversity in the first year of flooding (Figure 2.4B) due to the dominance of emergence by *Corynoneura* cf. *scutellata* and *Paratanytarsus* sp. 1 (Table 2.4; Figure 2.4C). In the shallow *Aster* sites diversity dropped in the second year and then increased steadily in the third and fourth years (Figure 2.4B) and relative dominance showed the opposite pattern (Figure 2.4C). The deep *Aster* sites exhibited a steady increase in diversity from the first year onwards whereas the dominance of the two most abundant species declined in the second year and then remained stable. Both *Scolochloa* and *Scirpus* had increasing diversities up to the the third year of flooding but then exhibited a decrease in diversity with a concurrent increase in dominance due to a large increase in the emergence of *Chironomus tentans* and *Glyptotendipes barbipes* in both habitats and at both depths (Tables 2.3,2.4). Diversity was highest and dominance lowest about the time that some emergent vegetation still remained and large amounts of plant litter had been deposited on the bottom. The greatest amount of microhabitat, both in terms of emergent vegetation and plant litter, was available at this time. With the subsequent elimination of the emergent macrophytes, diversity dropped and dominance by benthic species increased.

The two similarity indices displayed different patterns (Figures 2.5-2.7). Jaccard's coefficient revealed *Aster* and *Scolochloa* habitats to be more similar in species composition in the first year of flooding, but the percentage similarity coefficient indicated *Scolochloa* and *Scirpus* as the most similar habitats over the entire four years (Figure 2.5). The percentage similarity values were heavily influenced by the dominance of emergence by *Corynoneura* cf. *scutellata* during the first few years in *Scolochloa* and *Scirpus*, and by the subsequent shift to *Chironomus tentans* by the fourth year, which was also the dominant species in the *Aster* habitat (Tables 2.2,3,4). This explains the increasing percentage similarity between *Aster* and the two emergent vegetation habitats over the four years (Figure 2.5B).

When comparing the chironomid communities between depths within each habitat, Jaccard's coefficient revealed very similar communities in the first year of flooding (Figure 2.6A). *Aster* increased in similarity over the four years and *Scirpus* declined slightly to have the least similar communities in its shallow and deep sites by the fourth year of flooding. The percentage similarity index indicated relatively similar communities between the two depths within each of the three habitats (Figure 2.6B).

When comparing changes in the chironomid communities over the four years the percentage similarity index indicated much less change within the *Aster* habitat than in the two emergent vegetation habitats (Figure 2.7B). The dramatic changes in percentage similarity within the two emergent vegetation habitats is a reflection of the domination of emergence by *Corynoneura* cf. *scutellata* during the first two years and the subsequent shift to *Chironomus tentans*. In the two emergent vegetation habitats greatest percentage similarity among years was between 1985-1986 whereas Jaccard's coefficient revealed greatest similarity in species composition among years to be between 1987-1988 (Figure 2.7).

2.6 DISCUSSION

2.6.1 Chironomid habitat and species biology. The chironomid assemblage within the experimental cells was dramatically influenced by changes in the aquatic macrophyte community following water level manipulations. Two very different patterns of chironomid community development were observed in the *Aster* and the emergent macrophyte habitats.

Aster was drowned following flooding and little live vegetation remained. The large input of plant litter contributed to a highly structured habitat, and along with the abundant metaphyton that developed in this habitat (Wrubleski, pers. observ.), a wide range of microhabitats became available for chironomid colonization. *Aster* had a varied community with both small epiphytic chironomids (e.g., *Corynoneura, Cricotopus, Paratanytarsus*) and larger benthic or mining species (*Chironomus, Glyptotendipes*) abundant over the four years. *Aster* litter seems to resist decay and can persist within the cells for many years (Murkin, pers. comm.), thereby providing a relatively stable habitat. This may explain the lack of significant changes within this community over the four year period.

Scolochloa and *Scirpus* habitats showed more dynamic changes in chironomid community composition over time. During the first two years these habitats were dominated by *Corynoneura* cf. *scutellata*. Larvae of *Corynoneura* are very small free-living grazers dependent upon submersed surfaces (Table 2.5). The live stems and leaves of *Scolochloa* and *Scirpus* provided ideal habitat for this species, as well as other epiphytic species such as *Paratanytarsus* sp.1 and several *Cricotopus* species (Table 2.5). The survival of these plants during the initial flooding delayed deposition of plant litter at that time (Wrubleski, pers. observ.) and this may have prevented large populations of mining species such as *Chironomus tentans* and *Glyptotendipes barbipes* from becoming established in the first few years. Although both of these species have been reported to mine plant litter or other soft materials, they are more often reported to live in soft highly organic bottom sediments (Table 2.5) which would have been present in these two habitats. Their absence in the two emergent vegetation habitats could indicate that factors other than availability of plant litter were responsible for the absence of bottom-dwelling species. Emergent macrophytes can produce unfavourable conditions on the bottom. They restrict algal growth, an important food resource for these species (Table 2.5), through shading (Straskraba and Pieczynska 1970; Gurney and Robinson 1988). They can also prevent mixing of the water column and contribute to low oxygen conditions on the bottom (Dvorak 1969; Suthers and Gee 1986).

Prolonged flooding, particularly at the deeper depths, eliminated emergent macrophytes by the fourth year (van der Valk, pers. comm.; Figure 2.8). The death of these plants contributed to a large deposition of plant litter and reduced shading of the bottom. Epiphytic species declined in numbers and benthic species dominated the chironomid assemblage. *Corynoneura* cf. *scutellata* declined to levels similar to that found in the *Aster* habitat. *Chironomus tentans* and *Glyptotendipes barbipes*, species that were abundant in the *Aster* habitat from the time of initial flooding, also became abundant in both the *Scolochloa* and *Scirpus* habitats after the death of the emergent plants. Driver (1977) reported that *C. tentans* increased in abundance following increased water levels on a prairie pond. He suggested that the increase in this species was attributed to its ability to use not only the dead stems and roots of *Scirpus americanus* Pers. but also the open areas created by the loss of vegetation. My results concur with Driver's observation that *Chironomus tentans* increases in abundance when emergent vegetation was flooded, but without information on larval distributions the basis for this response is unclear.

The death of *Aster*, *Scolochloa* and *Scirpus* due to flooding resulted in the deposition of abundant plant litter to the bottom. In wetland habitats, plant litter has been thought to be an important food resource for invertebrate production (Mann 1988), but recent developments have indicated that algae may be a more important food resource for invertebrates in freshwater wetlands (Murkin 1989; Campeau 1990; Chapter 4). A review of food habits of the dominant chironomid species present in the experimental cells indicates that algae are indeed important (Table 2.5). Street and Titmus (1982) were able to separate the effects of food and habitat provided by straw additions to a gravel-pit lake. Their findings indicated that habitat structure was a more important determinant of animal distributions than the availability of plant litter as food. Aquatic macrophytes and their resultant plant litter provide an important habitat for chironomids, but it may be the highly productive algal communities of wetlands (Crumpton 1989) that are the most important food resource for chironomids.

Changes in the chironomid community of the experimental cells can be related to observed changes in habitat structure. However, interactions between individual species are unknown in this habitat and cannot be ruled out as unimportant. Cantrell and McLachlan (1977), for example, found that competition between two benthic chironomids determined habitat distribution in a newly created reservoir. In the *Scolochloa* and *Scirpus* habitats of the experimental cells, a striking shift from an assemblage dominated by *Corynoneura* cf. *scutellata* to one dominated by *Chironomus tentans* was observed (Figure 2.9). In Aster, *Corynoneura* did not contribute significantly to emergence so no relationship is apparent, but in the *Scolochloa* and *Scirpus* habitats there was a clear negative relationship of abundance between these two species. Published information indicates that neither species use the same microhabitat (Table 2.5) and so a negative relationship between them is more likely to be explained by changes in habitat structure over time and the requirements of these two species than by competitive effects. Interactions between other species pairs, however, must be studied by direct experiments before conclusions about possible interactions may be drawn.

2.6.2. Comparisons with reservoir studies. Studies of aquatic invertebrate colonization and succession have been done primarily in man-made reservoirs (e.g., Nursall 1952; Paterson and Fernando 1970; Sephton et al. 1983; Brown and Oldman 1984; Voshell and Simmons 1984). Invertebrate community development in reservoirs has been characterized by four phases (McLachlan 1974, after Morduchai-Boltovskoi 1961). 1) The first phase is short and occurs during the initial filling of impoundments when river fauna and terrestrial invertebrates are present within the reservoir. 2) A second productive phase coincides with the final filling of the reservoir. This high productivity has been attributed to the release of nutrients from the flooded vegetation and surface soils. The length of time needed to reach peak abundances (often reported to be between 1 to 4 years) is determined by such factors as basin morphology, climate, water chemistry and invertebrate population structure (Armitage 1977; Sephton et al. 1983). This peak in invertebrate numbers is often dominated by chironomids, particularly *Chironomus plumosus*-type larvae (McLachlan 1974). 3) A subsequent decline in invertebrate abundances has been attributed to loss of the flooded terrestrial vegetation through decomposition, consumption by invertebrates and sedimentation. Increasing populations of fish and predatory invertebrates (e.g. leeches, odonates) have also been suggested as contributing to the decline in invertebrate densities (Andersson and Danell 1982). 4) Eventually invertebrate abundances reach an equilibrium which is determined by prevailing conditions within and outside the water body. Although this general pattern of invertebrate community development has been reported often (now considered part of the 'reservoir paradigm'; Hecky et al. 1984), Wiens and Rosenberg (1984) found little evidence of McLachlan's (1974) four phases in the responses of benthic invertebrates to reservoir formation in Southern Indian Lake, Manitoba.

The generalized pattern observed in reservoirs can be compared with development of the chironomid community in the diked marshes of the present study. The first phase of reservoir fauna development can be seen in the experimental cells in the abundance of semi-terrestrial chironomids, such as *Limnophyes prolongatus,* in *Scolochloa* and *Scirpus* during the first few years following flooding. However, with continued flooding this species declined in abundance. A similar response was also noted when these experimental cells were flooded as part of an earlier water level manipulation (Murkin and Kadlec 1986; Wrubleski, unpubl. data).

The second or 'productive' phase in reservoirs varies in duration and timing and is generally the result of high production by a single species. In the *Aster* habitat numbers were highest in the second year in the shallow sites and in the first year in the deep sites, but these numbers were not significantly different from most other years. Biomass of emerging chironomids showed much the same pattern (Chapter 3). The composition of the chironomid community did not show great differences over time as indicated by the high similarity values among years (Figure 2.7), and the community was not dominated by one or two species as was the case in the two emergent vegetation habitats (Figure 2.4C).

In the *Scolochloa* and *Scirpus* habitats, few differences in total numbers were observed in the shallow sites over the four years, but in the deep sites numbers were high in the first and fourth years of flooding. Biomass was highest in the fourth year (Chapter 3). *Corynoneura* cf. *scutellata* dominated during the first two years and *Chironomus tentans* dominated in the fourth year. The high abundances of *Chironomus tentans*, following the death of the emergent macrophytes and the addition of litter to the bottom, are consistent with reservoir studies where *Chironomus* species often dominate following flooding of the terrestrial vegetation (McLachlan 1974).

Few reservoir studies have reported high numbers of Orthocladiinae during reservoir formation. This is probably due to several factors; 1) orthoclads prefer vegetated habitats and most reservoir studies tend to focus on the deeper open-water or profundal habitats where few aquatic macrophytes are found. Paterson and Fernando (1970), Armitage (1977, 1983) and Ertlová (1980) sampled littoral habitats during reservoir formation and reported high numbers of orthoclads. 2) In reservoir studies bottom sediments are usually sampled rather than submersed or emergent vegetation, and 3) *Corynoneura* larvae, in particular, are extremely small and easily overlooked in any benthic sampling program. Street and Titmus (1979) reported that very different results were obtained when larval sampling and emergence trap sampling programs were used to describe the colonization of several small gravel-pit ponds by chironomids, and suggested that the importance of larger benthic species as pioneers may have been overestimated in previous colonization studies where larval sampling alone had been done. If a benthic sampling program had been used in the experimental cells this phase in the development of the chironomid community would have been missed entirely.

Whether it serves as food or habitat, the eventual loss of the plant litter to consumption, decomposition or siltation results in a decline in invertebrate numbers in reservoirs. In the experimental cells, chironomid abundances within the *Scolochloa* and *Scirpus* habitat, and probably *Aster* as well, can be expected to decline over the next few years. Decomposition of *Scirpus* and *Scolochloa* litter is rapid (Murkin et al. 1989) and little of it will remain as habitat for invertebrates. As more flood-tolerant emergent macrophytes or submersed macrophytes develop within the cells and provide new habitat, numbers of chironomids and other invertebrates can be expected to recover.

As in reservoir studies, my results suggest that the contribution of plant litter following flooding was the principal factor regulating the development of the chironomid community of the experimental cells. In the experimental cells however, chironomid responses to the additions of litter took place in two phases. First was the death of the terrestrial annuals which provide an immediate pulse of coarse detritus to the bottom. Prolonged flooding caused the death of emergent macrophytes and a second pulse of plant litter was added to the marsh bottom, resulting in a second pulse of chironomid production.

2.6.3 Comparisons with the unmanaged Delta Marsh. Data presented in Wrubleski and Rosenberg (1990) permit a comparison of the chironomid assemblages within the experimental cells with Bone Pile Pond (BPP, see Chapter 4 for a description), an unmanipulated area of the Delta Marsh. Although many newly created water bodies are reported to produce higher numbers of chironomids than older, mature areas (see Chapter 3 for references), this was not so for the experimental cells. Numbers emerging from the cells were comparable to those found in emergent vegetation habitats of BPP, but did not match the high numbers found in the *Potamogeton* habitat (Chapter 3). Numbers of species were higher in the *Potamogeton* habitat of BPP than in the experimental cells, but by year four species richness from the experimental cells was similar to that found in the *Scirpus* and *Typha* habitats of BPP (Table 2.6, Figure 2.4).

Chironomid species diversity in the two emergent vegetation habitats of the experimental cells was related to habitat structural diversity. In the first few years chironomid habitat was principally the emergent vegetation and by the fourth year it was the litter on the bottom. In year three, both emergent vegetation and litter were present and provided a greater variety of habitats and consequently chironomid diversity was greatest at this time. Diversity was greater in the *Aster* habitat than the two emergent vegetation habitats and probably this was related also to higher habitat diversity in *Aster* sites. Species diversities in the experimental cells in the third year of flooding were comparable to values for BPP. Diversity was lower in the *Potamogeton* habitat of BPP in 1980 due to a large number of *Tanypus punctipennis* (Wrubleski and Rosenberg 1990). Relative dominance values tended to be lower in BPP, somewhat comparable to those in the deep *Aster* sites in the second to fourth years of flooding.

The *Scirpus* and *Typha* habitats in BPP had an abundance of semi-terrestrial chironomid species, including *Limnophyes immucronatus* and *L. prolongatus* (Table 2.6; Wrubleski and Rosenberg 1990). This was not so in the two emergent vegetation habitats of the experimental cells. *Limnophyes prolongatus* was abundant initially in *Scolochloa* and *Scirpus* habitats but then declined in abundance with prolonged flooding (Tables 2.3,2.4). Water levels within BPP fluctuated greatly and occasionally there was no surface water present in the *Scirpus* and *Typha* habitats. This would explain the abundances of semi-terrestrial species in these habitats. Flooding to depths of 20-40 cm greatly reduced the abundances of these species in the experimental cells.

Tanypus punctipennis was a dominant species in the *Potamogeton* habitat of BPP (Table 2.6). *Tanypus* species prefer soft mud substrates through which they can move easily (e.g., Parkin and Stahl 1981; Titmus and Badcock 1981). Their gradual increase in numbers in the experimental cells (Tables 2.2-4, Appendix 2) may be an indication of changing substrate conditions within the cells, however, the exact reason remains unknown.

2.6.4 Conclusions. Freshwater wetlands are dynamic habitats. Vegetation and water chemistry vary with water levels which fluctuate within and among years. The aquatic macrophytes, which typify wetlands, provide structurally complex habitats for aquatic invertebrates such as chironomids. Species composition and abundances of the chironomid assemblages within these habitats can change considerably among years (e.g., Morrill and Neal 1990; Wrubleski and Rosenberg 1990) but the factors responsible are not known. The results of the present study indicate that habitat changes, and specifically changes in vegetation, are important factors regulating chironomid communities in northern prairie wetlands.

The exact mechanisms of this regulation remain unknown. We do know that aquatic macrophytes provide habitat for many species. For example, in this study the two emergent macrophytes provided habitat for *Corynoneura* cf. *scutellata* and other epiphytic species. Death of the these plants due to excessive flooding benefited larger benthic species. This benefit may be in one or all of the following forms. 1) Plant litter provides a soft material in which these species could burrow. 2) Algae and bacteria would colonize the abundant surface area provided by the litter and in turn provide an excellent food resource for chironomids. 3) The absence of emergent macrophytes would contribute to increased mixing of the water column and greater algal production on the bottom. Further studies are needed to determine how dense stands of emergent macrophytes inhibit benthic chironomids. Field experiments, such as those described in Chapter 4 and Straskraba and Pieczynska (1970), are needed to tease apart the interactions between emergent macrophytes and chironomids. Much of this effort must use information about larvae. Emergence trap samples provide detailed descriptions of patterns, but are not capable of providing the information necessary to evaluate larval responses, the life cycle stage at which habitat manipulations have their true effects.

Table 2.1. Mean annual emergence [no. m^{-2} (±SE), n=6] of the four major chironomid taxa[1] and total Chironomidae from the three habitats and two water depths in the experimental cells. Means underlined with the same line are not significantly different (Tukey's HSD test following a significant one-way ANOVA, $P<.05$). A dashed line is used to connect a solid line when the habitats that do not differ significantly are separated by a habitat that does differ significantly from those underlined. * indicates a significant difference between depths within years (*t*-test, $P<.05$). Habitat means with the same subscripts do not differ significantly within year and depth (Tukey's HSD test following a significant one-way ANOVA, $P<.05$).

	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
Tanypodinae								
Aster	20.0_a	85.0_a	433.3_b	1078.3_b	66.7_a	247.3_a	148.7_a	263.7_a
	(6.3)	(30.0)	(215.6)	(489.9)	(21.9)	(116.8)	(76.0)	(142.2)
Scolochloa	20.4_a	25.6_{ab}	7.4_a	161.0_a	17.4_a	44.6_a	50.6_a	566.4_a
	(6.8)	(9.6)	(1.4)	(103.0)	(5.6)	(11.4)	(28.2)	(169.2)
Scirpus	24.3^{*}_{a}	6.0^{*}_{b}	5.7^{*}_{a}	65.3^{*}_{a}	39.7_a	38.3_a	48.0_a	444.0_a
	(6.6)	(3.1)	(2.7)	(18.8)	(3.2)	(15.8)	(15.6)	(129.2)
Orthocladiinae								
Aster	736.7_a	706.3_a	718.3_a	626.7_a	1425.7_a	1309.7_{ab}	263.0_a	638.3_a
	(177.5)	(300.9)	(206.6)	(235.3)	(292.1)	(224.1)	(49.4)	(86.1)
Scolochloa	961.4^{*}_{a}	1852.6_a	251.0_a	400.0^{*}_{a}	4952.0_a	3559.4_a	422.4_a	912.6_a
	(381.8)	(626.8)	(74.4)	(99.4)	(1640.8)	(932.4)	(157.6)	(169.8)
Scirpus	724.7^{*}_{a}	634.3_a	262.0^{*}_{a}	414.0_a	4744.3_a	1065.3_b	775.7_b	866.0_a
	(353.1)	(118.1)	(67.4)	(95.6)	(2425.0)	(471.0)	(81.5)	(293.5)

Table 2.1. continued...

		Shallow				Deep			
		1985	1986	1987	1988	1985	1986	1987	1988
Chironomini									
	Aster	1295.7^*_b	3962.7_b	3219.3_b	2292.0_a	5726.0_b	3173.0_a	1568.0_a	2909.3_a
		(229.3)	(1308.5)	(1012.9)	(740.7)	(1838.4)	(641.3)	(542.2)	(516.0)
	Scolochloa	295.0_a	407.4_a	357.7_a	2322.3_a	580.4_a	1001.3_{ab}	1784.3_a	6247.3_a
		(154.4)	(186.2)	(102.0)	(551.5)	(174.8)	(312.0)	(1219.8)	(1755.7)
	Scirpus	358.7^*_a	673.3_a	178.0^*_a	1193.3^*_a	700.0_a	385.3_b	1841.6_a	6695.0_a
		(156.8)	(271.2)	(64.8)	(351.7)	(145.2)	(128.3)	(686.7)	(1182.4)
Tanytarsini									
	Aster	683.0_a	547.7_a	666.3_a	599.3_a	1949.3_a	1028.7_a	659.7_b	561.0_a
		(101.9)	(177.6)	(184.9)	(256.5)	(664.2)	(802.2)	(232.1)	(117.1)
	Scolochloa	724.6_{ab}	300.0_{ab}	223.0_{ab}	215.6_a	615.6_a	107.0_a	115.4_a	192.6_{ab}
		(459.8)	(186.2)	(93.2)	(71.4)	(204.8)	(20.0)	(53.8)	(64.4)
	Scirpus	71.7^*_b	86.3_b	82.7_b	169.7_a	513.0_a	48.7_a	120.7_a	114.0_b
		(22.6)	(39.4)	(27.7)	(81.2)	(162.4)	(25.3)	(22.9)	(31.3)

Table 2.1. continued...

	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
Total Chironomidae								
Aster	$2735.3^{*}{}_{a}$	5302.0_{a}	5038.7_{b}	4650.7_{a}	9168.0_{a}	5758.7_{a}	2643.3_{a}	4438.7_{a}
	(422.1)	(1673.8)	(1356.4)	(1562.5)	(2406.7)	(1282.6)	(650.3)	(447.8)
Scolochloa	2003.4_{a}	2585.6_{a}	841.0_{a}	3340.4_{a}	6165.4_{a}	4713.4_{a}	2373.6_{a}	7983.6_{a}
	(917.6)	(967.8)	(164.0)	(820.4)	(1860.4)	(1049.6)	(1406.6)	(2005.2)
Scirpus	$1179.7^{*}{}_{a}$	1400.0_{a}	$529.3^{*}{}_{a}$	$1910.0^{*}{}_{a}$	5997.0_{a}	1537.7_{b}	2789.3_{a}	8148.0_{a}
	(333.9)	(275.9)	(67.3)	(459.2)	(2663.5)	(599.6)	(725.8)	(1355.0)

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[1] The tribe Pseudochironomini was represented by one species, *Pseudochironomus middlekauffi Town.*, and is included in the Total Chironomidae but not listed separately in this table.

Table 2.2. The five most abundant species (mean m^{-2} ± SE, n=6) collected from the *Aster* habitat for each year and depth, listed in decreasing order of abundance.

Aster	1985	1986	1987	1988
Shallow	*Chironomus tentans* 725.0 ± 144.1	*Chironomus tentans* 2106.0 ± 684.0	*Chironomus tentans* 1954.3 ± 827.7	*Chironomus tentans* 1292.3 ± 414.5
	Paratanytarsus sp. 1 357.7 ± 96.6	*Glyptotendipes barbipes* 1322.7 ± 533.8	*Glyptotendipes barbipes* 999.3 ± 276.4	*Tanypus punctipennis* 847.0 ± 408.6
	Corynoneura cf. *scutellata* 232.7 ± 127.7	*Tanytarsus* sp. 1 344.0 ± 186.3	*Tanypus punctipennis* 338.7 ± 200.5	*Glyptotendipes barbipes* 782.3 ± 444.8
	Cricotopus ornatus 231.3 ± 64.8	*Corynoneura* cf. *scutellata* 273.3 ± 134.7	*Cricotopus sylvestris* 290.7 ± 92.2	*Cladotanytarsus* sp. 405.3 ± 270.1
	Glyptotendipes barbipes 206.0 ± 56.7	*Cricotopus ornatus* 248.3 ± 157.7	*Cricotopus ornatus* 278.0 ± 93.6	*Cricotopus ornatus* 267.3 ± 173.2
Deep	*Chironomus atrella* 3637.3 ± 972.6	*Chironomus tentans* 1391.7 ± 493.6	*Chironomus tentans* 850.7 ± 286.0	*Chironomus tentans* 1568.3 ± 303.2
	Chironomus tentans 1292.3 ± 809.6	*Glyptotendipes barbipes* 1077.3 ± 544.7	*Tanytarsus* sp. 1 324.0 ± 185.5	*Glyptotendipes barbipes* 387.3 ± 183.0
	Tanytarsus sp. 1 1152.0 ± 655.9	*Tanytarsus* sp. 1 948.0 ± 750.6	*Paratanytarsus* sp. 3 297.7 ± 211.8	*Dicrotendipes nervosus* 357.3 ± 191.4
	Tanytarsus sp. 4 701.0 ± 441.9	*Corynoneura* cf. *scutellata* 883.0 ± 197.4	*Cladopelma viridula* 271.7 ± 165.7	*Cricotopus sylvestris* 238.7 ± 60.5
	Glyptotendipes barbipes 547.3 ± 235.7	*Chironomus atrella* 313.3 ± 146.6	*Glyptotendipes barbipes* 190.0 ± 104.1	*Paratanytarsus* sp. 3 226.3 ± 119.0

Table 2.3. The five most abundant species (mean m^{-2}± SE, n=6) collected from the *Scolochloa* habitat for each year and depth, listed in decreasing order of abundance.

Scolochloa	1985	1986	1987	1988
Shallow	*Corynoneura* cf. *scutellata* 782.3 ± 344.1	*Corynoneura* cf. *scutellata* 1175.3 ± 433.5	*Tanytarsus* sp. 1 163.7 ± 92.6	*Chironomus tentans* 1266.0 ± 317.9
	Paratanytarsus sp. 1 686.3 ± 446.1	*Limnophyes prolongatus* 275.3 ± 150.4	*Chironomus tentans* 162.3 ± 89.4	*Glyptotendipes barbipes* 849.7 ± 274.1
	Dicrotendipes nervosus 125.3 ± 74.9	*Paratanytarsus* sp. 1 257.0 ± 171.6	*Acricotopus nitidellus* 119.3 ± 85.9	*Pseudochiron. middlekauffi* 241.3 ± 105.9
	Limnophyes prolongatus 93.3 ± 37.2	*Chironomus riparius* 206.0 ± 111.7	*Corynoneura* cf. *scutellata* 99.7 ± 34.8	*Cricotopus sylvestris* 171.0 ± 65.0
	Parachironomus tenuicaudatus 78.7 ± 47.9	*Cricotopus ornatus* 186.0 ± 104.9	*Chironomus atrella* 68.0 ± 26.3	*Dicrotendipes nervosus* 114.0 ± 43.1
Deep	*Corynoneura* cf. *scutellata* 3128.3 ± 1778.1	*Corynoneura* cf. *scutellata* 2739.3 ± 945.4	*Chironomus tentans* 978.3 ± 762.5	*Chironomus tentans* 4525.0 ± 1252.8
	Cricotopus sylvestris 1074.3 ± 452.5	*Dicrotendipes nervosus* 366.0 ± 79.7	*Glyptotendipes barbipes* 340.3 ± 266.2	Glyptotendipes barbipes 820.3 ± 367.5
	Paratanytarsus sp. 1 586.3 ± 198.6	*Glyptotendipes barbipes* 340.3 ± 208.9	*Corynoneura* cf. *scutellata* 187.7 ± 117.0	*Dicrotendipes nervosus* 549.3 ± 328.6
	Cricotopus ornatus 584.0 ± 312.0	*Cricotopus sylvestris* 282.3 ± 82.9	*Dicrotendipes nervosus* 166.3 ± 66.1	*Cricotopus sylvestris* 445.7 ± 178.2
	Dicrotendipes nervosus 218.3 ± 72.3	*Psectrocladius edwardsi* 272.3 ± 32.4	*Cricotopus sylvestris* 148.3 ± 35.9	*Tanypus punctipennis* 279.3 ± 174.3

Table 2.4. The five most abundant species (mean m^{-2} ± SE, n=6) collected from the *Scirpus* habitat for each year and depth, listed in decreasing order of abundance.

Scirpus	1985	1986	1987	1988
Shallow	*Corynoneura* cf. *scutellata* 596.0 ± 322.6	*Corynoneura* cf. *scutellata* 565.3 ± 123.9	*Corynoneura* cf. scutellata 120.7 ± 78.7	*Chironomus tentans* 582.0 ± 180.8
	Dicrotendipes nervosus 187.0 ± 88.1	*Dicrotendipes nervosus* 310.0 ± 90.5	*Acricotopus nitidellus* 101.0 ± 47.2	*Glyptotendipes barbipes* 361.7 ± 186.5
	Limnophyes prolongatus 94.0 ± 34.1	*Chironomus tentans* 143.3 ± 108.8	*Paratanytarsus* sp. 1 71.0 ± 25.0	*Acricotopus nitidellus* 307.3 ± 88.6
	Chironomus staegeri 56.7 ± 38.6	*Chironomus riparius* 117.3 ± 66.0	*Dicrotendipes nervosus* 44.7 ± 11.9	*Cladopelma viridula* 100.3 ± 74.9
	Paratanytarsus sp. 1 54.0 ± 22.5	*Paratanytarsus* sp. 1 83.3 ± 38.2	*Chironomus atrella* 28.7 ± 13.1	*Chironomus atrella* 85.7 ± 24.2
Deep	*Corynoneura* cf. *scutellata* 4600.0 ± 2415.6	*Corynoneura* cf. *scutellata* 895.0 ± 424.3	*Chironomus tentans* 678.0 ± 324.9	*Chironomus tentans* 4522.0 ± 575.2
	Paratanytarsus sp. 1 504.3 ± 162.0	*Dicrotendipes nervosus* 155.3 ± 67.8	*Chironomus atrella* 491.0 ± 289.2	*Glyptotendipes barbipes* 1523.3 ± 636.7
	Dicrotendipes nervosus 417.3 ± 90.0	*Chironomus atrella* 64.0 ± 27.4	*Corynoneura* cf. *scutellata* 341.3 ± 54.2	*Cricotopus sylvestris* 352.3 ± 175.3
	Parachironomus sp. 3 102.3 ± 25.8	*Limnophyes prolongatus* 48.7 ± 24.8	*Cricotopus sylvestris* 336.3 ± 66.8	*Dicrotendipes nervosus* 223.7 ± 55.9
	Parachironomus tenuicaudatus 101.7 ± 28.5	*Paratanytarsus* sp. 1 44.7 ± 25.0	*Dicrotendipes nervosus* 220.3 ± 31.7	*Cricotopus ornatus* 212.0 ± 144.0

Table 2.5. Literature references for habitat and food habits of dominant chironomid species collected from the experimental cells.

Reference	Habitat	Food Habits
Tanypus punctipennis		
Fellton (1940)	- lake bottom	- predacious; feeding on newly hatched and older chironomid larvae
Oláh (1976)	- lake; open water sediments	- fed mainly on diatoms
Titmus and Badcock (1981)	- gravel pit-lake bottom	- fed mainly on unicellular algae
Corynoneura scutellata		
Kesler (1981)	- free-living on submerged surfaces	- grazers of periphyton
Cricotopus sylvestris		
Darby (1962)	- tubes *on the surface of the mud,* bottom debris or submersed vegetation	- *fed on diatoms, algal debris, and* green algae
Menzie (1981)	- on submersed plants when present or on the bottom	
Cricotopus ornatus		
Swanson and Hammer (1983)	- tubes on the sediment, algal mats and submersed vegetation	- not reported
Chironomus tentans		
Sadler (1935)	- tubes in the sediment or algae	- will eat whatever is offered, but where algae are present in sufficient quantities they comprise the main bulk of the diet
Palmén and Aho (1966)	- shallow water with large amounts of detritus as substratum	- not reported

Table 2.5. continued...

Reference	Habitat	Food Habits
Hall et al. (1970)	- tubes in the sediment	- filters plankton during the day and searches the sediment surface at night for larger food items
Topping (1971)	- soft ooze and detritus	- not reported
Mason and Bryant (1975)	- within dead *Typha* stems	- brown detrital material of rotting *Typha* and no living algae
Dicrotendipes nervosus		
Fellton (1940)	- restricted to green algal mats	- not reported
Moore (1980)	- organically rich lake sediments	- detritus, very little algae
Glyptotendipes barbipes		
Kimerle and Anderson (1971)	- tubes in the sediments	- irrigation of the tube supplies sestonic food particles, primarily algal cells
Driver (1977)	- axiles of *Scolochloa*	- not reported
Wrubleski and Rosenberg (1984)	- miner of polystyrene foam	- not reported
Paratanytarsus sp. 1		
Wrubleski (unpubl. observ.)	- tubes on flooded vegetation	- grazing algae

Table 2.6. Species richness, diversity, relative dominance and the most abundant species of Chironomidae collected from Bone Pile Pond, Delta Marsh in 1980 and 1981 (calculated from data in Wrubleski and Rosenberg 1990). Abundant species are listed in decreasing order of abundance.

		Potamogeton	*Scirpus*	*Typha*
Number of Species		53-62	42-58	49-49
Diversity (H')		2.76-3.65	3.36-3.45	3.52-3.69
Relative Dominance Index		61.2-45.2	44.9-46.6	46.4-40.2
Dominant Species				
	1980	*Tanypus punctipennis*	*Limnophyes immucronatus*	*Limnophyes prolongatus*
		Derotanypus alaskensis[1]	*Limnophyes prolongatus*	*Limnophyes immucronatus*
		Chironomus tentans	*Dicrotendipes nervosus*	*Chironomus tentans*
		Glyptotendipes barbipes	*Derotanypus alaskensis*	*Derotanypus alaskensis*
		Corynoneura cf. *scutellata*	*Paratanytarsus* sp. 1	*Tanypus punctipennis*
	1981	*Cricotopus sylvestris*	*Paratanytarsus* sp. 1	*Cricotopus sylvestris*
		Tanypus punctipennis	*Limnophyes prolongatus*	*Paratanytarsus* sp. 1
		Glyptotendipes barbipes	*Glyptotendipes lobiferus*	*Limnophyes prolongatus*
		Cladotanytarsus sp.	*Corynoneura* cf. *scutellata*	*Corynoneura* cf. *scutellata*
		Corynoneura cf. *scutellata*	*Cricotopus sylvestris*	*Tanypus punctipennis*

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[1] As *Psectrotanypus alaskensis*.

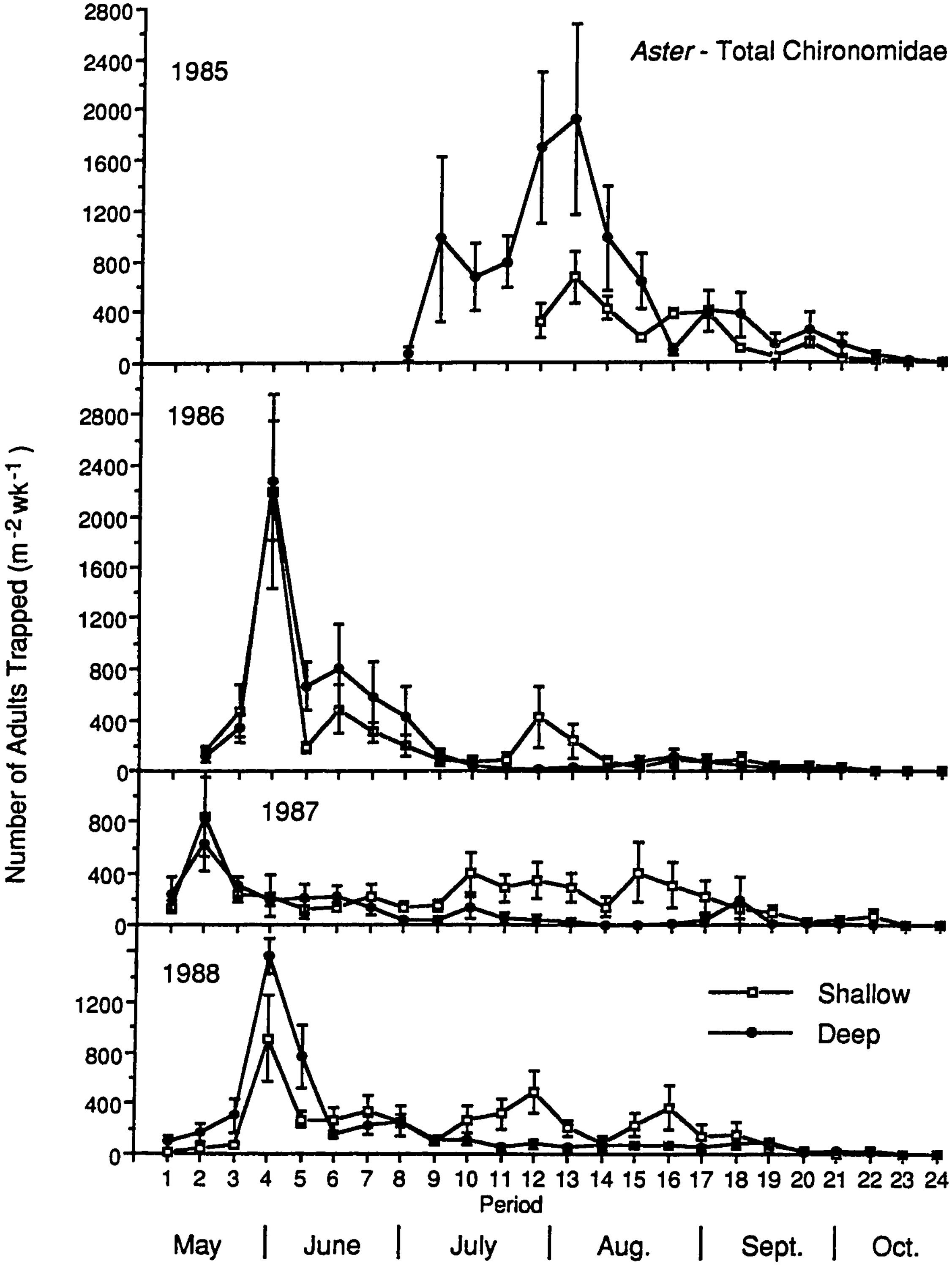


Figure 2.1. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Aster* habitat of the experimental cells.

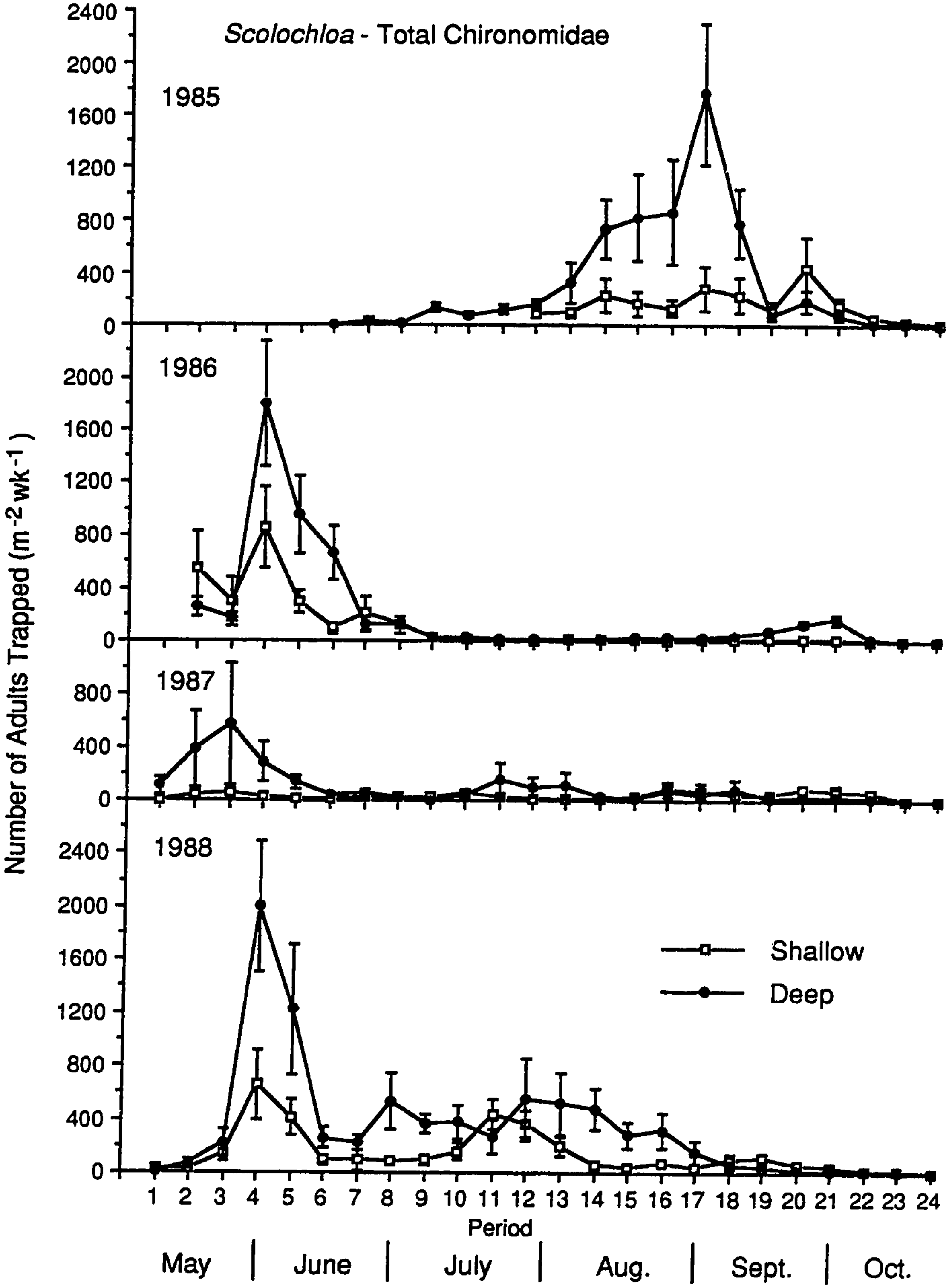


Figure 2.2. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Scolochloa* habitat of the experimental cells.

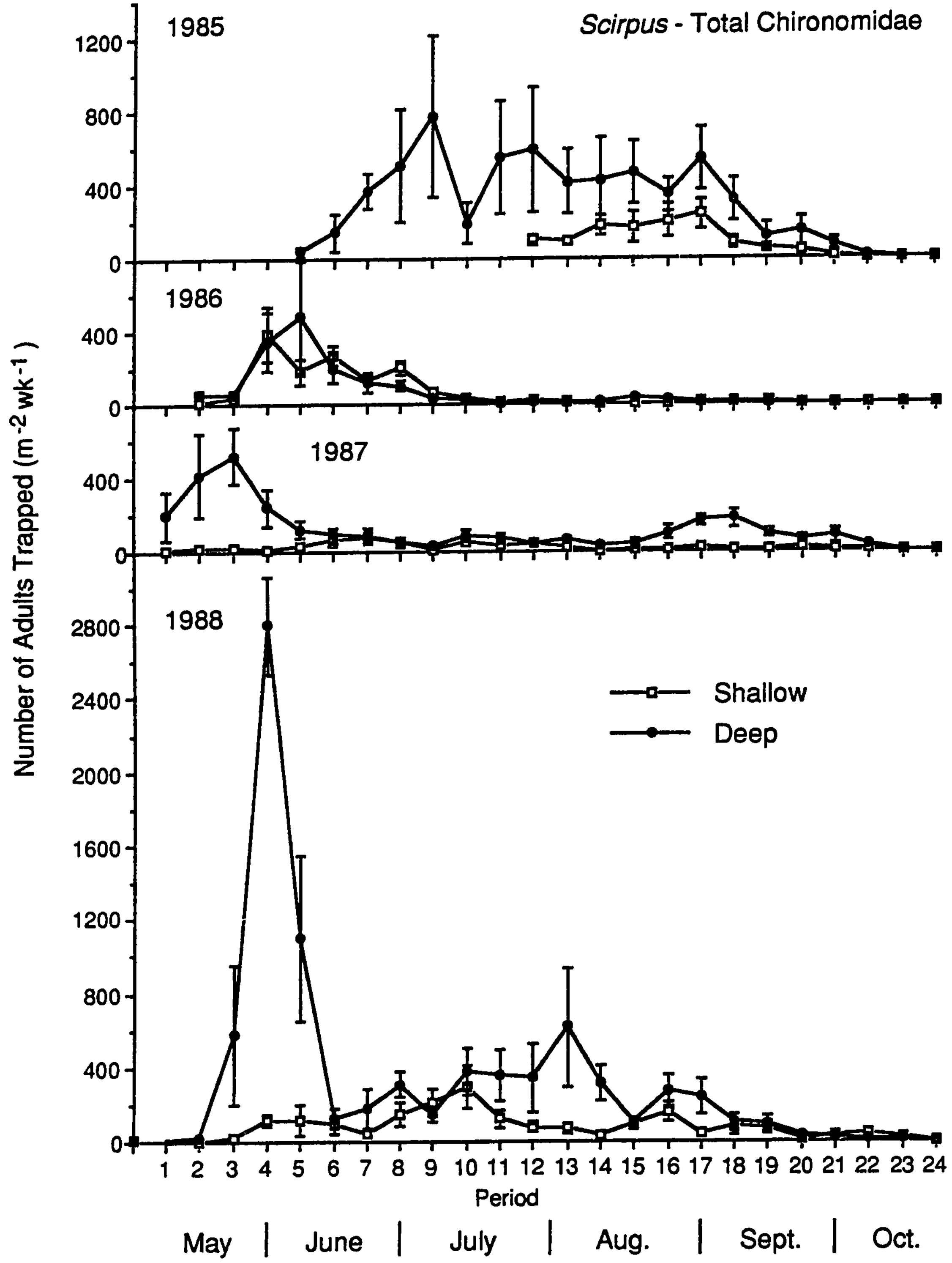


Figure 2.3. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Scirpus* habitat of the experimental cells.

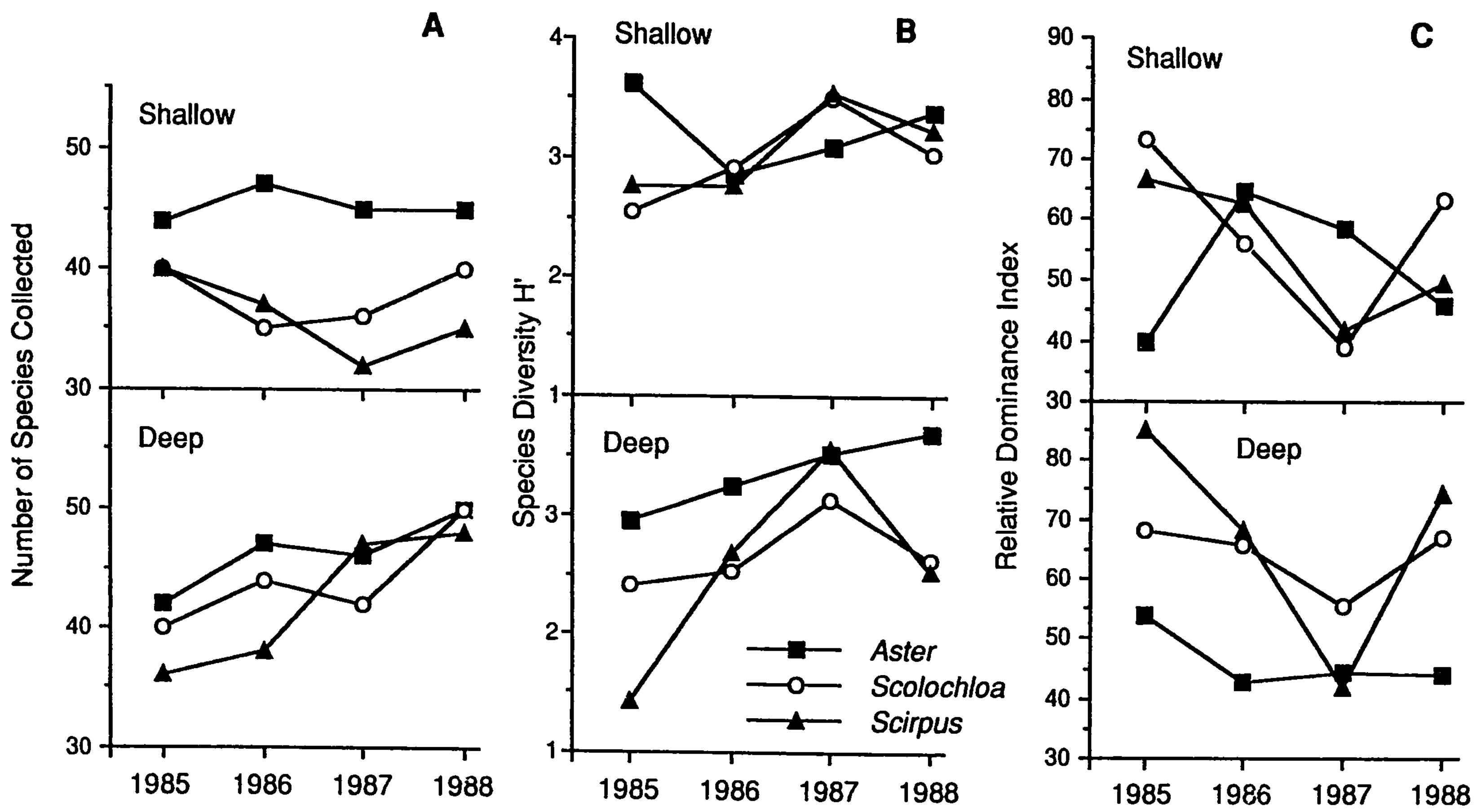


Figure 2.4. Numbers of species (A), species diversity (B) and the Relative Dominance Index (C) of Chironomidae collected from the three habitats and two water depths in the experimental cells.

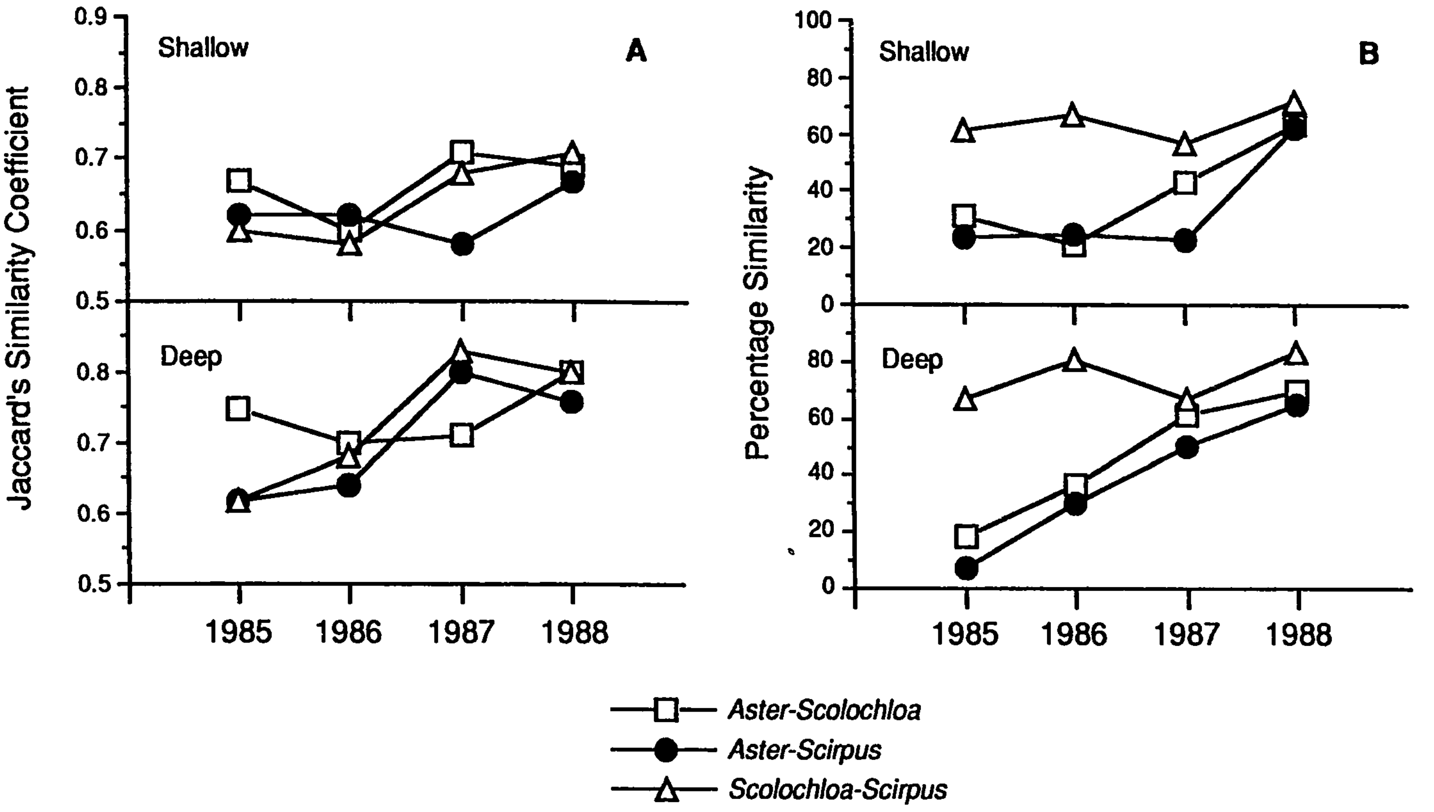


Figure 2.5. Jaccard's similarity coefficient (A) and percentage similarity values (B) for among habitat comparisons of chironomid emergence from the experimental cells.

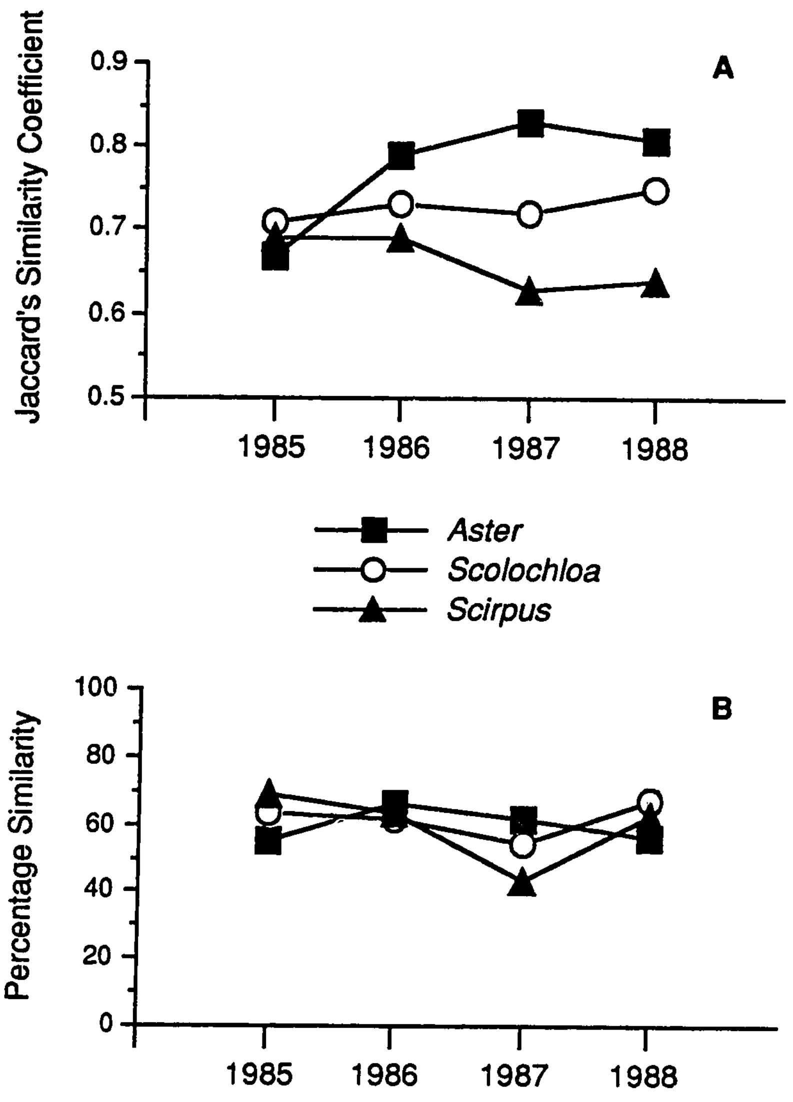


Figure 2.6. Jaccard's similarity coefficient (A) and percentage similarity values (B) for between depth comparisons of chironomid emergence from the experimental cells.

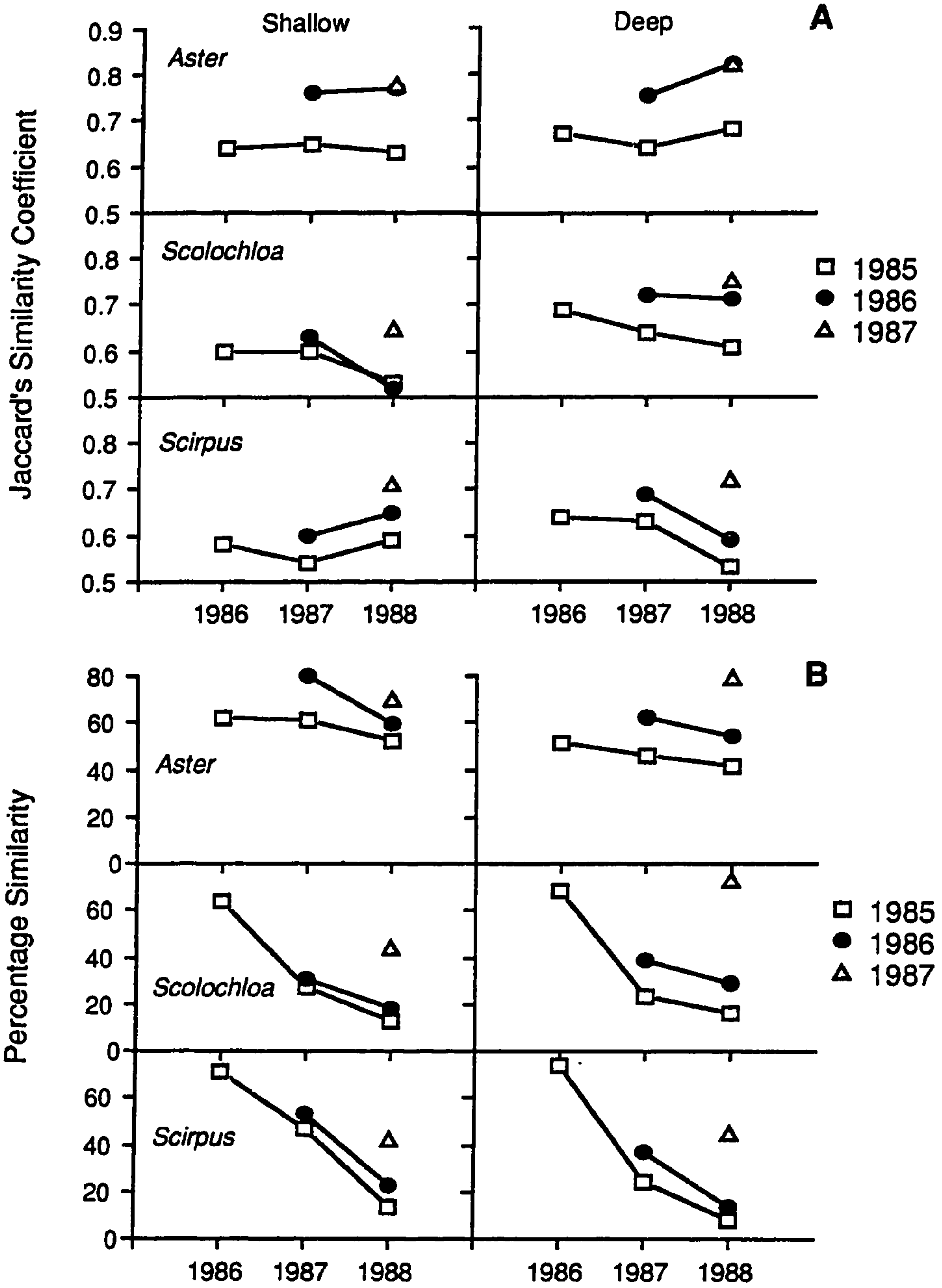
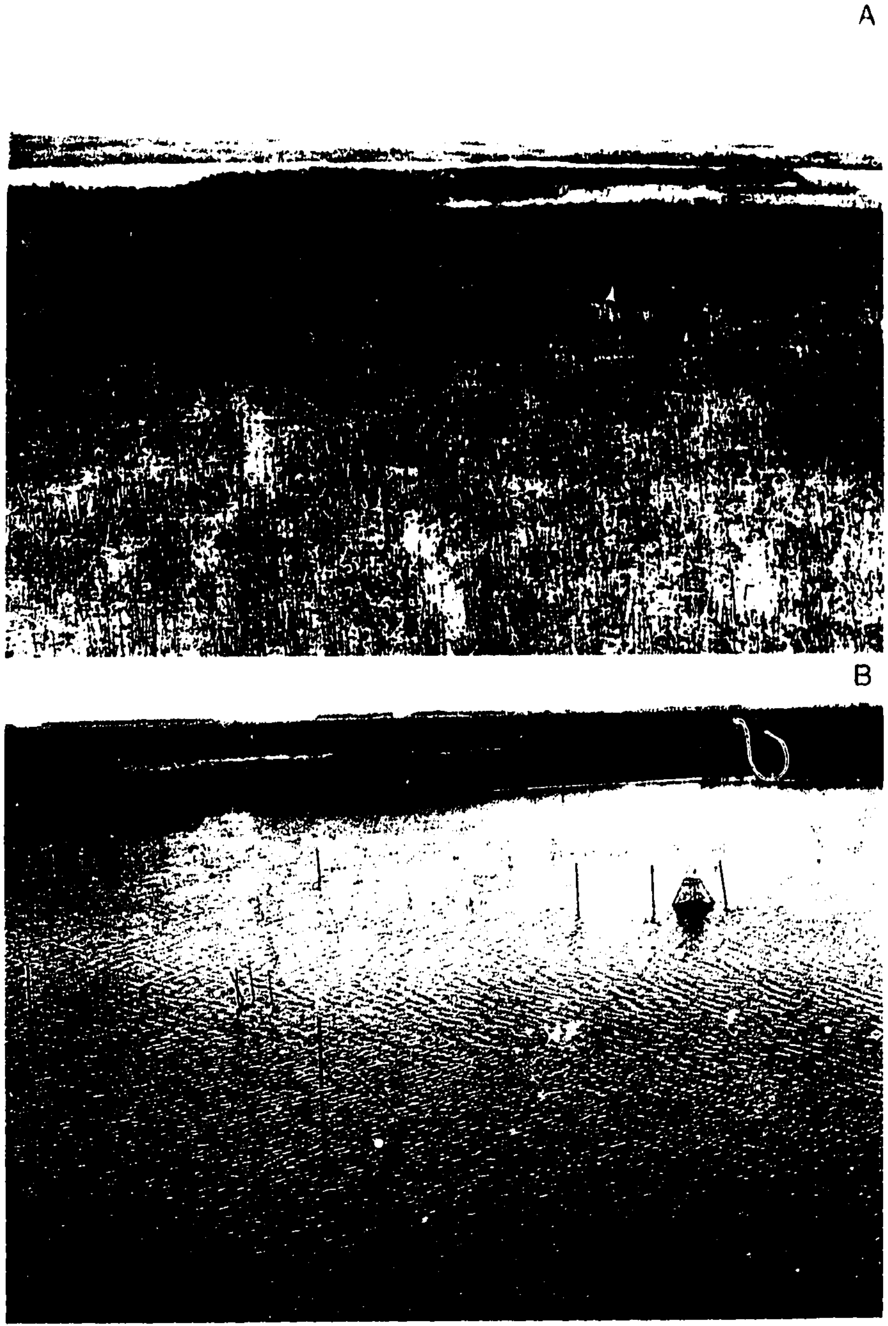


Figure 2.7. Jaccard's similarity coefficient (A) and percentage similarity values (B) for comparisons of chironomid emergence among years from the experimental cells.

Figure 2.8. The south end of cell 1 of the experimental cells showing loss of *Scirpus* at deep sites over a two year period. A. July, 1986. B. July, 1988.


A
B

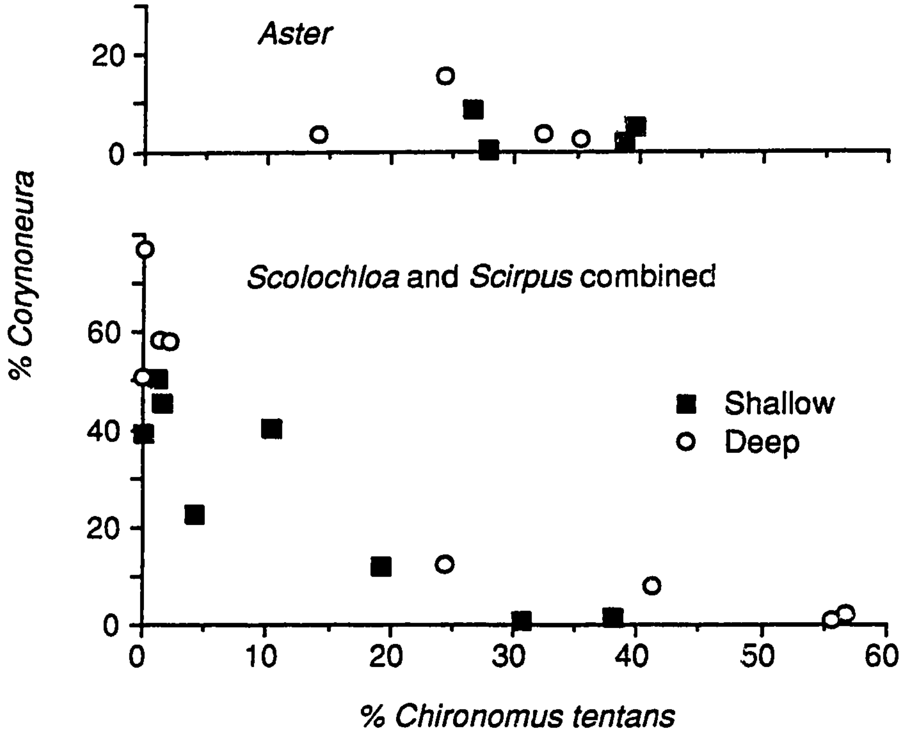


Figure 2.9. Proportion of chironomid emergence represented by *Chironomus tentans* and *Corynoneura* cf. *scutellata* from the three habitats sampled in the experimental cells.

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3. MANAGEMENT OF FRESHWATER WETLANDS: RESPONSES OF THE CHIRONOMIDAE (DIPTERA) TO THE EXPERIMENTAL FLOODING OF A SERIES OF DRAWDOWN MARSHES

3.1 SYNOPSIS

The Chironomidae (Diptera) are an important food resource for breeding waterfowl and their young. However, few attempts have been made to document their responses to wetland management. This study followed chironomid responses to the experimental flooding of ten diked areas in the Delta Marsh, Manitoba. Emergence traps were used to monitor chironomid emergence from three preflood vegetation types (the terrestrial annual *Aster laurentianus,* and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) flooded at two water depths (shallow: 20-40 cm, deep: 50-70 cm) over a four year period. The highest number of chironomids (9,168 m^{-2} yr^{-1}) emerged from the deep *Aster* sites in the first year of flooding. The highest biomass of chironomids (22,007 mg m^{-2} yr^{-1}) was from the deep *Scirpus* sites in the fourth year. Numbers, biomass and size classes of emerging chironomids were similar over the four years from the *Aster* habitat. However, the *Scolochloa* and *Scirpus* habitats were dominated initially by the smallest size-class, but shifted steadily toward production of much larger individuals over the four-year experiment. The potential of chironomids as a food resource for waterfowl was greatest from the *Aster* habitat during the first few years of flooding but as a consequence of shifts in species composition became greater in the *Scolochloa* and *Scirpus* habitats in the third and fourth years.

3.2 INTRODUCTION

Drawdown (artificial drainage) and reflooding have been increasingly used in marsh management in an effort to restore declining productivity of wetlands (Weller 1978). Stable water levels apparently are detrimental to long-term wetland productivity (Harris and Marshall 1963; Weller 1978). Drawdown enables many emergent macrophytes, as well as terrestrial annuals, to become established on the dry marsh bottom and reapplication of water floods this vegetation. The emergent macrophytes survive, depending upon the water depth, but the terrestrial plants drown and contribute to the detritus food chain.

Aquatic invertebrates of freshwater marshes are an extremely important food resource for waterfowl (e.g., Krapu 1981; Sugden 1973; Street 1977, 1978; Murkin and Batt 1987) and high use of new wetlands by waterfowl is believed to be a result, in part, of high invertebrate abundances in these new areas. McKnight and Low (1969) reported high densities of chironomids and corixids after reflooding of drawdown impoundments in Utah. Whitman (1974) reported that highest invertebrate densities occurred in impoundments less than four years old, and older impoundments had fewer invertebrates and less waterfowl use. Peak production of duck broods on a shallow Swedish lake was coincident with peak chironomid abundances, five years after flooding (Danell and Sjöberg 1982). However, not all studies have recorded large increases in invertebrates following drawdown and reflooding. Kadlec (1962) reported very low densities of invertebrates following reflooding of a large impoundment in Michigan and suggested that it may be harmful to invertebrate populations.

The vegetational changes that take place in wetlands have received intensive study (e.g., Weller and Fredrickson 1974; van der Valk and Davis 1978; van der Valk 1981, 1982, 1987 and references therein), but invertebrate responses to these changes are not well understood. Trends in development of invertebrate communities have been suggested from several studies which sampled wetlands of different ages (Whitman 1974) or vegetational structure (Voigts 1976). Danell and Sjöberg (1982) followed invertebrate responses in years 3-7 after creation of a shallow lake in northern Sweden, and Kenow and Rusch (1989) reported the responses of the nektonic invertebrate community to three years of continual flooding in several impoundments of the Horicon Marsh, Wisconsin. However, invertebrate community development from the time of reflooding has not been followed within a single wetland. In this study I describe the responses of the Chironomidae (numbers, biomass and size classes) to the reflooding of a series of experimental marshes during a four year period. Chironomids are one of the most abundant aquatic insect groups within these habitats and are also a valuable waterfowl food (Wrubleski 1987).

3.3 MATERIALS AND METHODS

3.3.1 Study area. This study was conducted within the experimental marshes (cells) of the Marsh Ecology Research Program (MERP) in the Delta Marsh, in south-central Manitoba (50° 11' N, 98° 19' W). A complex of 10 contiguous 4-6 ha diked marshes were built in 1979, of earth excavated from within each cell. Water levels were manipulated and maintained with electric pumps. Descriptions of the long-term experimental design and water-level manipulations within the cells are given in Batt et al. (1983), Murkin et al. (1984) and van der Valk et al. (1988). Vegetation and water chemistry in the cells have been described by Kadlec (1986a,b, 1989), van der Valk and Welling (1988) and van der Valk et al. (1989). During 1983 and 1984 the cells were drained (drawdown). Water was reapplied in June-August 1985.

3.3.2 Sampling. Floating emergence traps were used to sample adult chironomids at the water surface. Emergence traps have two main advantages over conventional bottom sampling; adults can be identified more readily to species than benthic larvae, and emergence samples require less effort per sample and thus more habitats can be sampled. The trap used was a modified version of the 'week' trap (basal area = 0.5 m^2) described by LeSage and Harrison (1979).

Emergence trap sites were established within the cells in the spring and summer of 1985. Sites were stratified according to pre-flood habitat and water depth. Three of the dominant habitat types, based on preflood vegetation surveys, were selected for sampling; these were *Aster laurentianus* Fern., *Scolochloa festucacea* (Willd.) Link (whitetop) and *Scirpus lacustris* L. ssp. *validus* (Wahl.) Koyama (softstem bulrush). Each habitat was sampled at two water depths, shallow (20-40 cm) and deep (50-70 cm). Six traps were used for each habitat-water depth combination for a total of 36 traps.

Traps were set out as soon as sufficient water was in place to float them. Deep water sites, which were at lower elevations, were flooded much earlier than shallow water sites at higher elevations. Consequently initiation of sampling varied between 16 May and 20 July. Within each habitat-water depth combination the six emergence trap sites were not flooded at the same time, but most were flooded within a few weeks of each other, except for two shallow *Scirpus* sites that were flooded 9 weeks before the other four sites (data from these 9 weeks were excluded from the analyses). In 1987 and 1988, traps were set out at the same sites in the last week of April and emptied weekly through the third week of October to provide data for 24 weeks or sample periods. In 1986, traps were not set out until the first week of May and data were collected over 23 weeks.

3.3.3 Data summation. All chironomids were identified to species (see Chapter 2). Numbers collected from each trap during every week were summed for the entire sampling season, multiplied by 2 to give no. m^{-2} and then used to determine mean annual emergence (no. $m^{-2} yr^{-1}$ ± SE, n=6) for each habitat-water depth combination. Procedures used to generate missing data for traps lost due to muskrat damage and wind storms are reported in Appendix 1. A length-weight regression (Wrubleski and Rosenberg 1990) was used to determine biomass (mg $m^{-2} yr^{-1}$) of emerging chironomids. Separate counts for each sex were not made during sorting, therefore sex ratios from a previous study in the Delta Marsh (Wrubleski 1984) were used to partition the numbers for each species between males and females before determination of biomass. In addition, a relative frequency distribution of size classes (1 mm) was determined for each habitat-water depth combination, based on body length (pronotum to penultimate abdominal segment).

3.3.4 Statistical analysis. Emergence numbers and biomass were compared using a split plot ANOVA with habitat, depth and depth × habitat as whole plot sources which were tested against traps nested within depth × habitat (Table 3.1). Year, year × depth, year × habitat and year × depth × habitat were split plot sources which were tested against the residual (year × trap (depth × habitat)). Analyses were conducted using the PROC GLM procedure of SAS (SAS Institute Inc. 1985). Data were $\log_{10}(x+1)$ transformed prior to analysis to stabilize the variances, but untransformed data are presented in the figures. Year comparisons were done within habitat and depths by one-way ANOVA followed by Tukey's HSD test [*P*<.05; as recommended by Day and Quinn (1989)] to compare individual year means Habitats were compared within years and depths with one-way ANOVA and Tukey's HSD test to compare individual habitats, and depths were compared within habitat and year by *t*-tests (*P*<.05). All one-way ANOVAs, Tukey's HSD tests and *t*-tests were done with SYSTAT (vers. 3.2) on a Macintosh computer.

3.4 RESULTS

The overall split plot ANOVA indicated that numbers and biomass of emerging chironomids differed significantly between depths, and among habitats and years (Table 3.1). The depth × habitat interaction was nearly significant for both numbers (F= 2.71, df=2,30, *P*=.08) and biomass (F=2.81, df=2,30, *P*=.08) suggesting that chironomids responded differently to preflood vegetation and depth of flooding. Numbers of chironomids emerging each year varied between depths (depth × year, F=2.87, df=3,90, *P*=.04) but biomass did not (F=1.19, df=3,90, *P*=.32). Data for both annual numbers and biomass showed significant interactions between habitat and year indicating that habitats had different outputs over the four years. The three-way depth × habitat × year interaction was significant for biomass and nearly so for numbers, indicating that chironomids responded differently to preflood vegetation and water depth and that these differences also varied annually.

One-way ANOVA for habitat comparisons within depths and years indicated that in 1986, *Scirpus*-deep had a significantly lower emergence than the other two habitats, and in 1987 *Aster*-shallow had a higher emergence than the other two shallow habitats (Figure 3.1). Differences among habitats in chironomid biomass were more striking than were those for numbers (Figure 3.2). Biomass of chironomids emerging from *Aster* was much higher than that from the other two habitats in 1985, 1986 and 1987 in the shallow depths and 1985 and 1986 in the deeper habitats. In 1986 all three habitats differed significantly from each other in the deep sites and in 1988 *Scirpus* had a much higher emergence than *Aster*.

In 1985, significantly more chironomids emerged from the deep sites than from shallow sites in *Aster* and *Scirpus*, and the same trend was marginally significant (*t*=2.211, *P*=0.051) in *Scolochloa* (Figure 3.1). These differences may reflect the fact that deep sites were flooded much earlier than shallow sites. Therefore, these data were reanalyzed using equal time periods (i.e., those weeks that both habitats were flooded together). Because these analyses indicate no differences between depths (*Aster*: numbers *t*=0.65, *P*=.53, biomass *t*=1.51, *P*=.16; *Scirpus*: numbers *t*=1.58, *P*=.14), I conclude that the significant differences found above were due simply to the deep sites being flooded for longer periods. In 1986, no differences were found between depths. In both 1987 and 1988 higher numbers and biomass of chironomids emerged from the deep sites in *Scirpus* compared to the shallow sites. In *Scolochloa,* there were marginally more chironomids emerging from deep water in 1988 (number: *t*=2.122, *P*=.06; biomass: *t*=1.958, *P*=.08).

In shallow water, similar numbers of chironomids emerged in all years, except for a significant increase in emergence in the *Scirpus* habitat between 1987 and 1988. In the deep water sites, I observed a trend for high emergence in 1985, followed by declining numbers during 1986 and 1987 and a subsequent increase in 1988 (Figure 3.1). In terms of biomass, a significant increase in emergence in 1988 was observed in both *Scolochloa* and *Scirpus* in the shallow waters. This increase was also observed in the deep sites but started in 1987 in the *Scirpus* habitat. Biomass of emerging chironomids did not differ over the four years in shallow or deep waters from *Aster*.

There were consp[illegible]anges in sizes of emerging chironomids in *Scolochloa* and *Scirp*[illegible] during the four years (Figure 3.3) which reflected changes in spe[illegible]osition (Chapter 2). In 1985, emergence was dominated by small indiv[illegible]ticularly in the 1-1.99 mm size class. Over the next four years there [illegible] a shift to much larger individuals. This was very apparent for the deep habitats where the 9.00 - 9.99 mm size class dominated emergence. The shallow habitats had a more bimodal distribution of sizes, similar to that observed in the *Aster* habitat. In *Aster*, the pattern present in all four years and both depths was similar with a bimodal distribution of sizes with peaks around 2-5 mm and 7-10 mm.

3.5 DISCUSSION

3.5.1 Reflooding of drawdown marshes and its effect on the chironomids.

Several studies have reported larger numbers of invertebrates in newly flooded marsh habitats than in nearby older wetlands (McKnight and Low 1969; Whitman 1974; Street and Titmus 1979). After the first four years of flooding, the highest number of chironomids recorded from the experimental cells (9,168 m^{-2} yr^{-1} from deep *Aster* sites in 1985) was only about two-thirds of the highest numbers that have been recorded from the unmanaged Delta Marsh (15,601.2 m^{-2} yr^{-1} from the pondweed habitat of Bone Pile Pond [BPP] [Wrubleski and Rosenberg 1990]). Deep *Scirpus* sites, however, had comparable emergence numbers (4,574.4 - 8,148 m^{-2} yr^{-1}) to that found in the *Scirpus* habitat of BPP (4,024.0 - 6,193.2 m^{-2} yr^{-1}). Numbers of chironomids emerging from shallow *Scolochloa* sites (841.0 - 3,340.4 m^{-2} yr^{-1}) tended to be similar to those from a seasonally flooded *Scolochloa* habitat in the Delta Marsh (2,500 m^{-2} yr^{-1} [Wrubleski 1987]), but numbers emerging from deep *Scolochloa* sites, particularly in the first (6,165.4 m^{-2} yr^{-1}) and fourth (7,983.6 m^{-2} yr^{-1}) years, were much higher.

Although highest numbers emerging from the MERP cells were not as high as from the unmanaged Delta Marsh, biomass was significantly greater. Highest biomass emerging from the experimental cells was from deep *Scirpus* sites in 1988 (22,007.22 mg m^{-2} yr^{-1}) and was more than 5 times that found in the *Scirpus* habitat of BPP (2,922 - 3,866.2 mg m^{-2} yr^{-1}) and almost twice that of the highest biomass estimated from the pondweed habitat (9,174.0 - 13,431.5

mg $m^{-2} yr^{-1}$), the most productive habitat in BPP (Wrubleski and Rosenberg 1990). Most of this higher biomass, particularly in years three and four in the *Scolochloa* and *Scirpus* habitats, was in the larger size classes. Figure 3.4 illustrates size class distributions for chironomids emerging from BPP. It is apparent that although numbers might be higher from the pondweed habitat of BPP, most individuals were of smaller size, explaining the lower total biomass compared to the experimental cells.

Trends in numbers and biomass of chironomids emerging over the four year period differed among the habitats and depths sampled. Numbers of chironomids emerging from the shallow water depths showed few significant changes over time, whereas the deep water sites showed a general trend for high numbers emerging in the first year, with a decline in numbers in the second and/or third years in all three habitats, and significant increases by the fourth year in *Scolochloa* and *Scirpus* habitats. Biomass of chironomids emerging from both water depths showed very little change over time in *Aster*, whereas in *Scolochloa* and *Scirpus* there was a significant increase in biomass emerging by the third or fourth years of flooding. Whitman (1974) reported highest numbers of larval chironomids in wetland impoundments less than one year old. Danell and Sjöberg (1982) found highest numbers of chironomids emerging in year five of a newly flooded lake managed for waterfowl, with a considerable decline in numbers in subsequent years (emergence was not sampled during the first three years). They also noted a decrease in mean larval chironomid size from the third to seventh years of flooding. My results suggest that little change in size occurred in *Aster*, whereas in *Scolochloa* and *Scirpus* a shift to larger-sized individuals, particularly in the deep waters, occurred over the four years.

Aquatic invertebrate populations in wetland habitats do respond to changes in vegetation and water depth (Voigts 1976; Murkin and Kadlec 1986; Kenow and Rusch 1989). In the experimental cells differences in chironomid emergence were found between the *Aster* and the two emergent macrophyte habitats sampled. *Aster laurentianus* is a terrestrial annual characteristic of mud-flats, and cannot survive flooding. Consequently, a large amount of plant litter was added to the bottom in one large pulse with no or very little standing emergent vegetation present. Metaphyton developed extensively in these open, sunny areas (Wrubleski, pers. observ.). This material provided a structurally complex habitat with abundant algal production. It was colonized by a variety of chironomid species, including larger benthic and mining species such as *Chironomus tentans, C. atrella* and *Glyptotendipes barbipes*, as well as smaller epiphytic species such *Paratanytarsus* sp. 1 and several *Cricotopus* species (Chapter 2).

In the *Scolochloa* and *Scirpus* habitats, not as much litter was added to the bottom due to their initial tolerance of flooding. These dense stands of live stems shaded the bottom in these habitats restricting benthic algal production. Gurney and Robinson (1988) reported a significant negative correlation between macrophyte stem density and the amount of metaphyton present within the experimental cells. The large amount of metaphyton-free surface area provided by the stems and leaves of these emergent macrophytes provided an excellent habitat for *Corynoneura* cf. *scutellata*, the most abundant species in these habitats during the first two years of flooding (Chapter 2). The members of this genus are small free-living grazers dependent upon submersed surfaces (Kesler 1981). However, after several years of flooding, these macrophytes began to die back (van der Valk, pers comm.; Figure 2.8), particularly at the deeper flooding depths, and a large input of plant litter was added to the bottom beginning in the second year of flooding. Consequently there was a marked increase in the same benthic and mining species observed in the *Aster* habitat and a dramatic decline in the epiphytic species (Chapter 2). Driver (1977) and Murkin and Kadlec (1986) both reported increases by *Chironomus tentans* following the death of emergent macrophytes due to excessive flooding.

3.5.2 Management implications. Aquatic macroinvertebrates are an important food resource for breeding waterfowl and their young (e.g., Krapu 1981, Sugden 1973, Street 1977, 1978, Murkin and Batt 1987) and the effects of marsh management on invertebrate populations must be considered. In this experiment, preflood vegetation and depth of flooding produced different abundances of chironomids as potential waterfowl food.

Although chironomids as a group are known to be an important food resource for waterfowl the relative importances of the different species is unknown. One important consideration is probably the size of the individual chironomids produced by each habitat. Data from the experimental cells show a wide range of sizes of chironomid adults were produced and this varied by habitat and depth and over the four years of this experiment. However, studies of waterfowl food habits have generally ignored the importance of invertebrate size (Nudds and Bowlby 1984) so it is not known which species are important waterfowl food. It is unlikely that the smallest size class reported in this study (1.0 - 1.99 mm) is valuable as food for waterfowl, but all other sizes are likely to be consumed.

The *Aster* habitat produced a variety of chironomids, with many in the larger size classes becoming established at the time of flooding. *Scolochloa* and *Scirpus* on the other hand, produced very small chironomids during their first two years of flooding, and not until the third and fourth years were large numbers of the larger-sized chironomids produced. Production was greater in the deep-water habitats, depths that are probably too deep for most dabbling duck species. However, during emergence periods these chironomids become a readily available food resource for waterfowl (Swanson and Sargeant 1972; Swanson 1977; Sjöberg and Danell 1982).

The presence of emergent vegetation and the abundance of plant litter on the bottom are the two most important features regulating the abundances of the larger-sized chironomids within experimental marshes. Dense stands of emergent vegetation were beneficial to the smallest-sized chironomids but had a negative effect on the larger benthic chironomids Several studies have reported low numbers of invertebrates in dense stands of emergent macrophytes compared to other more open habitats (Voigts 1976; Wrubleski and Rosenberg 1990).

In my study, the abundance of plant litter in the *Aster* habitat at the time of flooding, and in years three and four in the *Scolochloa* and *Scirpus* habitats, was probably an important contributor to the high numbers of large benthic chironomids. Thus my results concur with suggestions by McKnight and Low (1969), Whitman (1974), Kaminski and Prince (1981) and others that abundant plant litter from the preflood vegetation is responsible for high invertebrate production observed in new wetland habitats. However, other factors are undoubtedly also important. Andersson and Danell (1982) failed in an attempt to increase invertebrate production by adding terrestrial plant litter to an existing wetland. They attributed a lack of response to the existence of abundant predatory invertebrates already present, and suggested that one benefit of drawdown was the elimination of the more slowly colonizing predatory invertebrates. A similar experiment in flooded gravel pits in England was successful in producing larger numbers of invertebrates in a habitat that was structurally very simple (Street and Titmus 1982; Street 1982).

Whitman (1974) suggested that optimum conditions for invertebrate production in newly created wetlands occurred during the first 1.5 to 4 years of age, and recommended drawdown between the ages of 5 to 7 years to improve food and cover for waterfowl. In the present study, chironomid production was high from the first application of water and continued to be high through to the fourth year, first from the flooded terrestrial vegetation and then from the drowned emergent macrophyte habitats. In the experimental cells it is anticipated that this high chironomid production will decline as the coarse detritus inputs within these habitats disappear. Because of the flooding, new emergent macrophyte regrowth will not occur so no large inputs of detritus will take place. Invertebrate production will decline in subsequent years unless submersed vegetation is able to invade and provide additional habitat for invertebrates. It is apparent that the management of freshwater wetlands for the benefit of aquatic invertebrates and thus the waterfowl, must consider the production of plant litter during the drawdown phase (Murkin et al. 1989). An abundance of vegetation must be encouraged during drawdown to provide an abundant pool of litter when water is reapplied.

Table 3.1. Split-plot ANOVA table of numbers and biomass [log(x+1) transformed data]

Source of Variation (Numbers)	SS	df	MS	F	*P*
Depth	3.6054	1	3.6054	26.40	0.0001
Habitat	2.9844	2	1.4922	10.93	0.0003
Depth x Habitat	0.7406	2	0.3703	2.71	0.0827
Trap (Depth x Habitat)	4.0973	30	0.1366		
Year	3.2500	3	1.0833	9.48	0.0001
Depth x Year	0.9845	3	0.3282	2.87	0.0407
Habitat x Year	1.7678	6	0.2946	2.58	0.0238
Depth x Habitat x Year	1.4128	6	0.2355	2.06	0.0658
Error	10.2881	90	0.1143		

Source of Variation (Biomass)	SS	df	MS	F	*P*
Depth	4.0545	1	4.0545	17.95	0.0002
Habitat	18.3149	2	9.1575	40.54	0.0001
Depth x Habitat	1.2701	2	0.6351	2.81	0.0760
Trap (Depth x Habitat)	6.7773	30	0.2259		
Year	17.7876	3	5.9292	34.15	0.0001
Depth x Year	0.6189	3	0.2063	1.19	0.3188
Habitat x Year	9.2394	6	1.5399	8.87	0.0001
Depth x Habitat x Year	3.8754	6	0.6459	3.72	0.0024
Error	15.6249	90	0.1736		

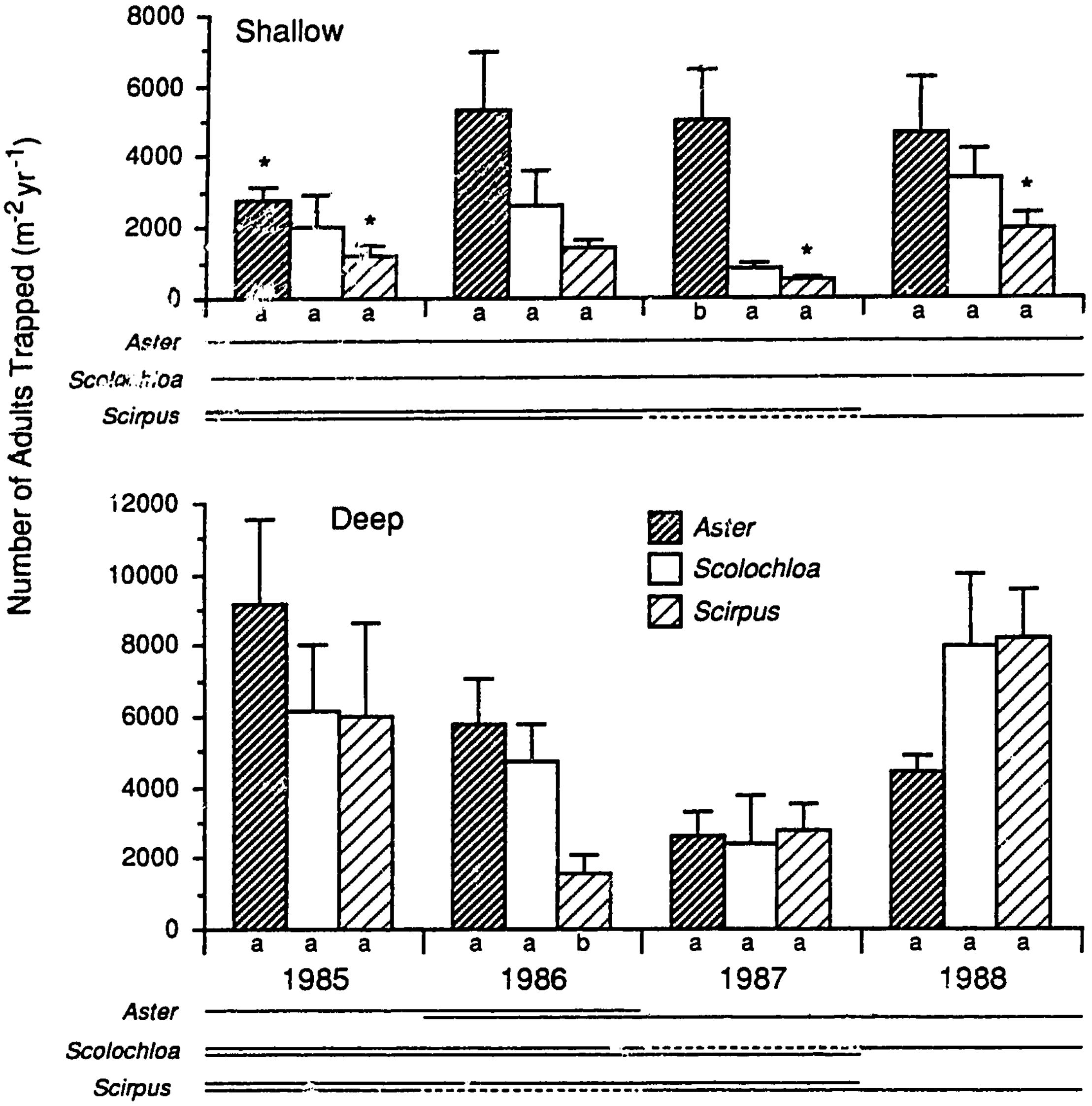

Figure 3.1. Mean (± SE, n=6) annual emergence of chironomids over a four year period from three habitats and two water depths in the experimental marshes. * indicates a significant difference between depths within habitat and year (*t*-test, *P*<.05). Habitat means with the same subscripts are not significantly different, within year and depth (Tukey's HSD test following significant ANOVA, *P*<.05). Lines below each graph indicate means that are not significantly different across years (Tukey's HSD test following significant ANOVA, *P*<.05). A dotted line is used to connect a solid line when the years that do not differ significantly are seperated by a year that does differ significantly from those underlined.

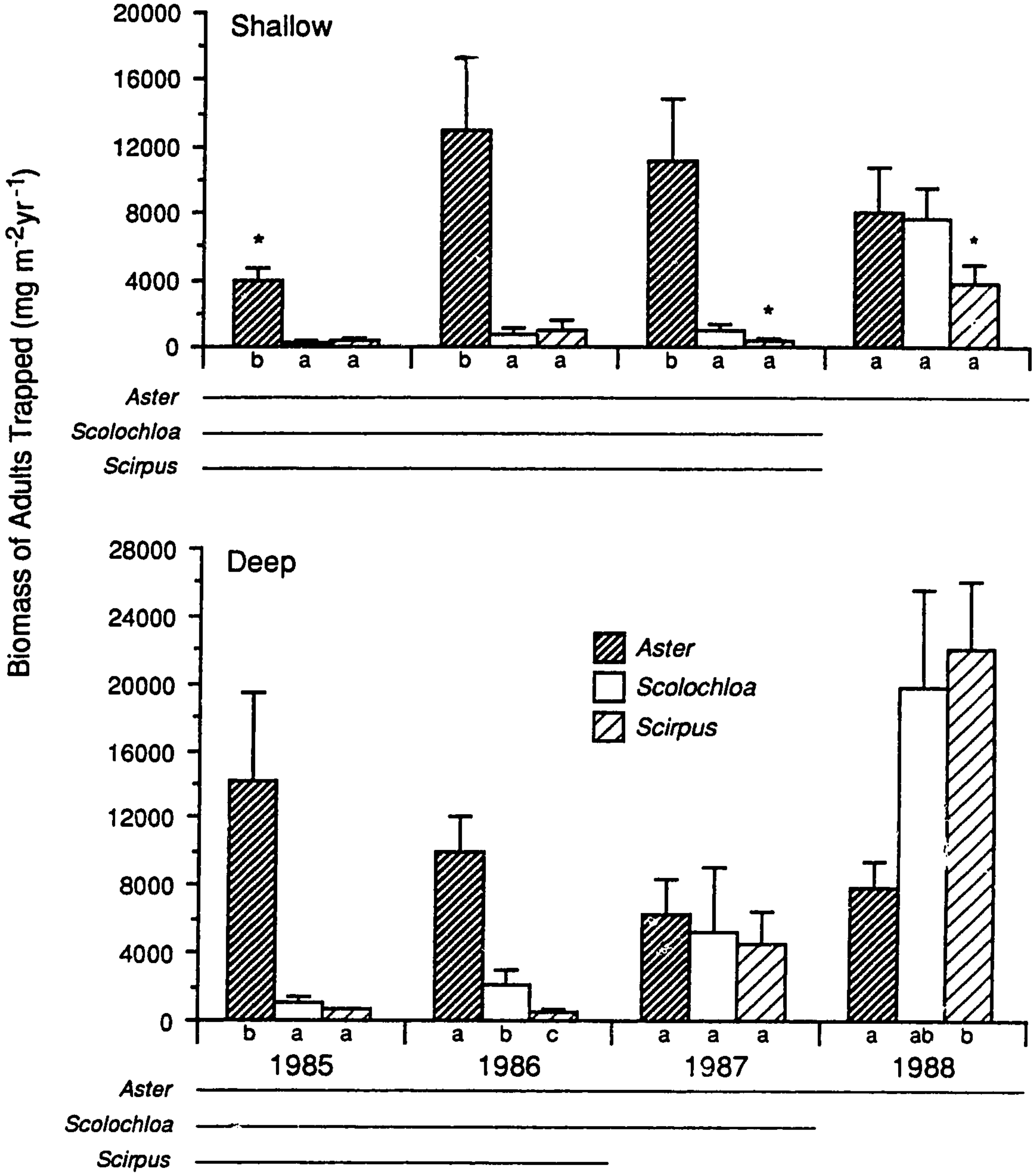

Figure 3.2. Mean (± SE, n=6) annual biomass of chironomids emerging over a four year period from three habitats and two water depths in the experimental marshes. (See Figure 3.1 for explanation of symbols).

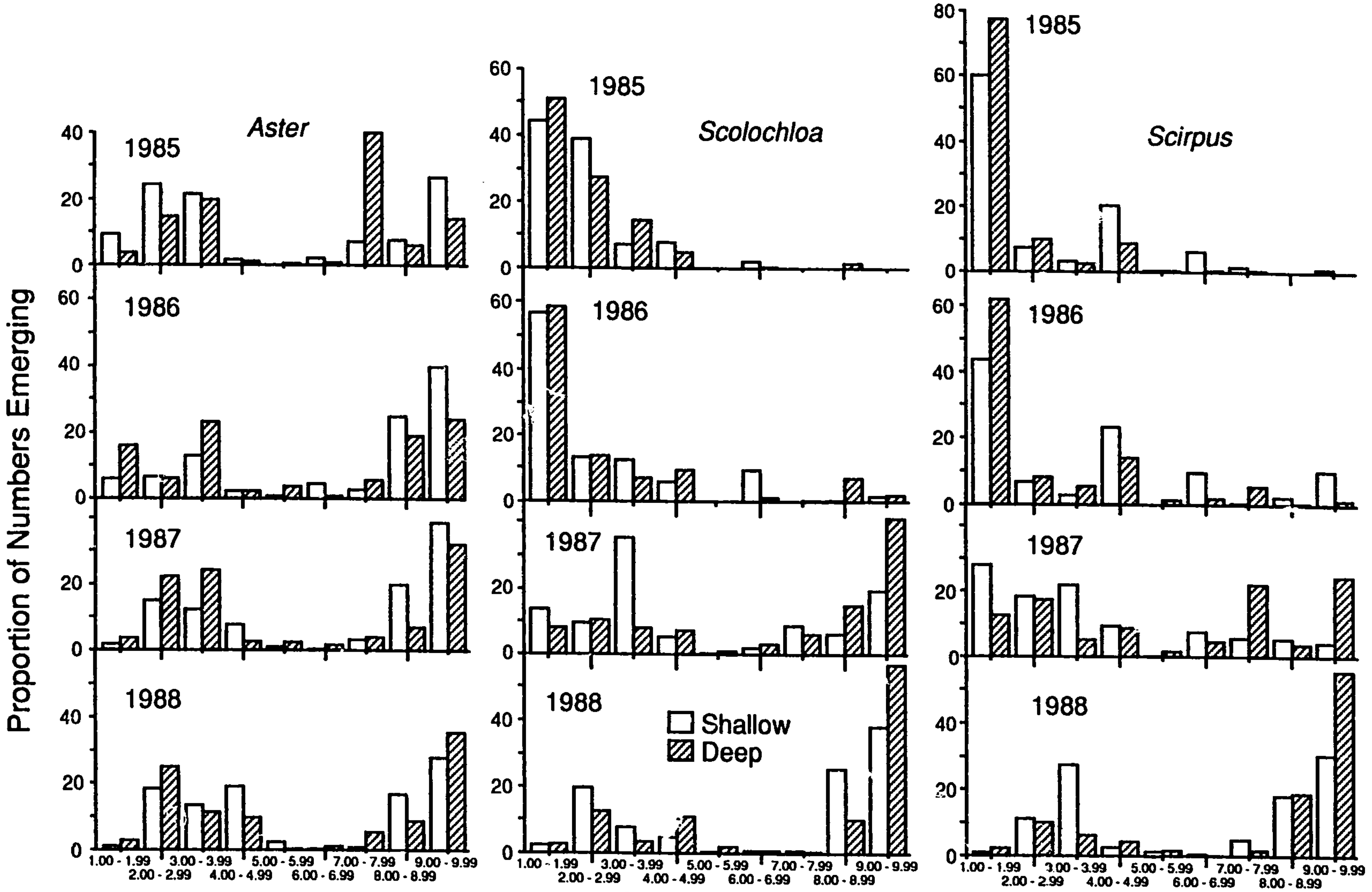

Figure 3.3. Proportion of annual chironomid emergence represented by each 1.00 mm size class over a four year period from the three habitats and two water depths sampled in the experimental marshes.

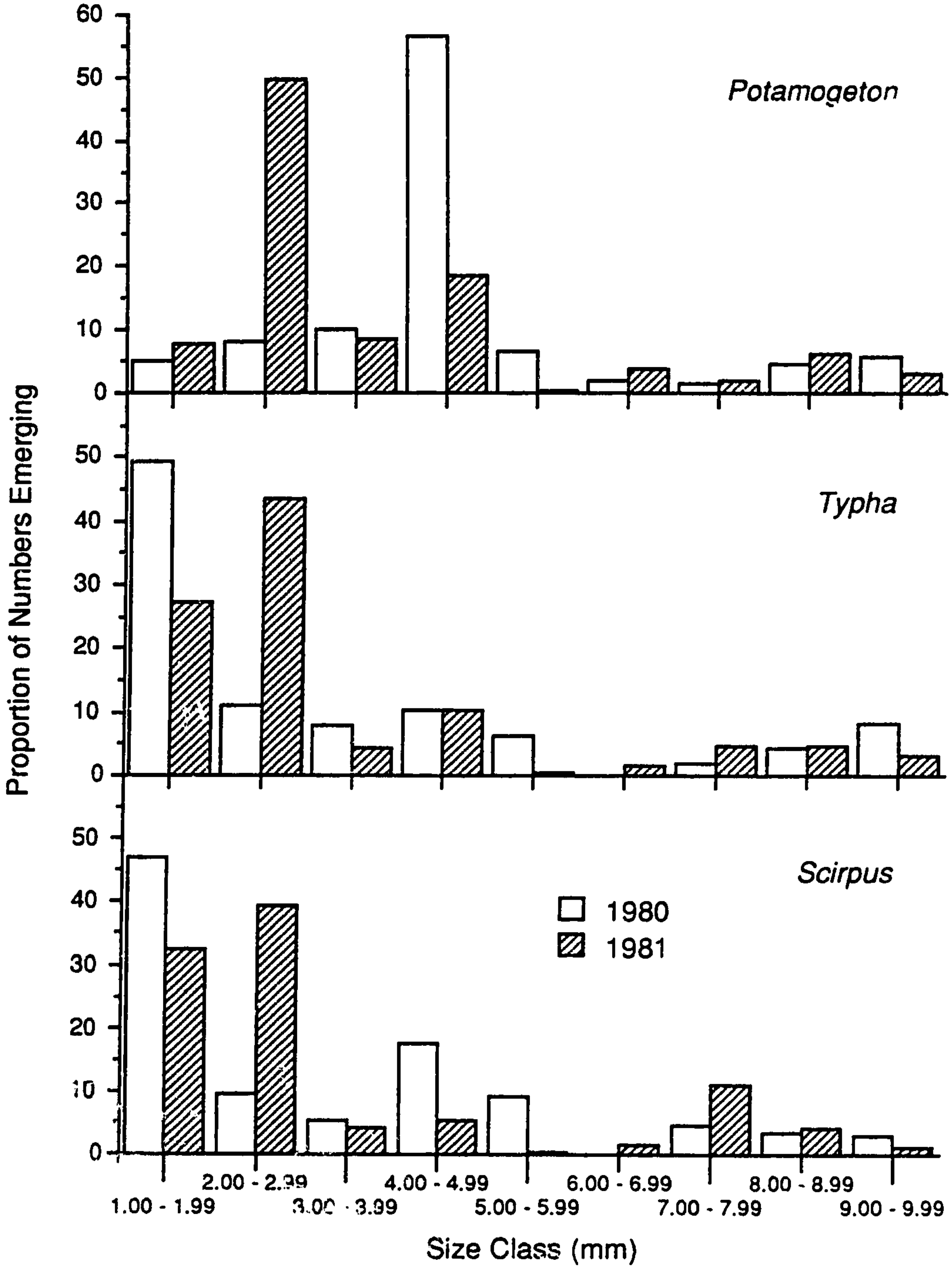

Figure 3.4. Proportion of annual chironomid emergence represented by each 1.00 mm size class over a two year period from three habitats sampled in Bone Pile Pond, Delta Marsh. Calculated from data in Wrubleski and Rosenberg (1990).

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4. THE EFFECT OF SUBMERSED MACROPHYTES ON THE BENTHIC INVERTEBRATE COMMUNITY OF A FRESHWATER MARSH

4.1 SYNOPSIS

A field experiment was undertaken in Delta Marsh, Manitoba, to examine the effect of seasonal development of submersed vegetation on benthic invertebrates. Sago pondweed (*Potamogeton pectinatus*) was either removed via clipping or permitted to grow in fenced 5 x 5 m plots. Aquatic invertebrates were sampled with emergence traps and bottom cores. Invertebrates (primarily copepods) were more abundant in the clipped plots than the pondweed plots at the end of the season. Total chironomid larvae and adult emergence did not differ between the two treatments, although *Polypedilum halterale* and *Cladotanytarsus* sp. were more abundant in the clipped plots, and *Corynoneura* cf. *scutellata* had a higher emergence from the pondweed plots. Algal biomass beneath pondweed tended to be lower than in plots where the plants had been removed suggesting that by shading the bottom, aquatic macrophytes reduce bottom algal biomass and indirectly influence benthic invertebrate communities.

4.2 INTRODUCTION

Shallow freshwater wetlands are frequently dominated by aquatic macrophytes. In northern latitudes, the seasonal development of submersed macrophytes has a major effect on the physical and biological processes within open-water areas. Submersed macrophytes alter their surrounding physico-chemical environment (e.g., Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983; Carpenter and Lodge 1986), and they influence aquatic invertebrate communities by increasing habitat structural complexity, and by providing additional food and living space within the water column for many species (e.g., Berg 1949, 1950; Krull 1970; Soszka 1975; Menzie 1980). Areas with submersed macrophytes have been reported to support higher densities of invertebrates than areas without vegetation (Wohlschlag 1950; Gerking 1957; Krull 1970), the general assumption being that these plants increase the amount of colonizable surface area for invertebrates in the water column. Recent evidence, however, suggests that invertebrate colonization of submersed macrophytes is not based solely on the amount of surface area available, but that each plant species differs in its ability to support invertebrate populations (Cyr and Downing 1988).

The habitat value of these plants has been well documented, but their negative effects on some members of the invertebrate community are not as well known. For example, Richard et al. (1985) found that the total number of zooplankton species was reduced following elimination of submersed vegetation, but that mean densities increased. The presence of submersed vegetation also can have a marked effect on zooplankton community composition (Rabe and Gibson 1984). Dense beds of submersed macrophytes also may have adverse affects on benthic invertebrates. Hall et al. (1970) and Danell and Sjöberg (1982) noted shifts in chironomid communities, from benthic to epiphytic species, when submersed vegetation invaded new areas. Johnson and Mulla (1983) reported lower densities of benthic chironomids in areas with Eurasian milfoil than in areas without, and Wrubleski (1989) suggested that *Chironomus* species were absent beneath a dense bed of sago pondweed. Changes in water circulation patterns, temperature, dissolved oxygen and benthic algal abundances may have caused the declines in benthic chironomid species reported above. However, there have been no experimental studies of the mechanism for this inhibition. In this paper I describe a field experiment designed to examine the interactions among submersed vegetation, the physico-chemical environment, and the benthic invertebrate community of a shallow prairie marsh.

4.3 STUDY AREA

This study was conducted in the Delta Marsh at the south end of Lake Manitoba, in south-central Manitoba (50° 11' N, 98° 19' W). Descriptions of the marsh vegetation and water chemistry are given in Löve and Löve (1954), Anderson and Jones (1976), Anderson (1978), Shay and Shay (1986), and Kadlec (1986).

Bone Pile Pond (BPP) is a long, narrow bay separated from the main marsh by a dense stand of hybrid cattail (*Typha glauca* Godr.) at its eastern end. Surface water pH ranged from 8.5-10.5 and conductivity ranged from 2350-3725 µS cm^{-1} at 25°C (Wrubleski, unpubl. data). The bottom is relatively flat and is composed of thick organic muck (~ 36.5% organic matter). Wind seiches on Lake Manitoba and the Delta Marsh result in continually fluctuating water levels within the pond (range 18 - 40 cm). The water column and much of the bottom sediments freeze in the winter (Wrubleski 1984).

The open-water area of the pond is dominated by sago pondweed (*Potamogeton pectinatus* L.), with some bladderwort (*Utricularia vulgaris* L.) also present early in the season. Waterfowl feeding removes much of the pondweed during July and August of most years (Wrubleski 1989). Two species of emergent plants, cattail and hardstem bulrush (*Scirpus lacustris* L. ssp. *glaucus* (Sm.) Hartm.), surround the open-water area. Carp (*Cyprinus carpio* L.) were present in the pond in 1986 and from 19 May to 8 June in 1987. Their activities within the pond disrupt development of the pondweed (Wrubleski, unpubl. observ.). A weir was constructed at the eastern end of the pond, at the beginning of June, to prevent more carp from entering the pond and to permit those already present to leave.

4.4 MATERIALS AND METHODS

4.4.1 Experimental treatments. Six experimental treatment plots, each 5 x 5 m, were established at random positions in the western end of BPP on 18-19 May, 1987, using a pre-existing grid system (Wrubleski 1984). Plots were assigned randomly to one of two treatments: (1) pondweed (pondweed permitted to grow) or (2) clipped (pondweed removed by clipping). Plots were enclosed by a fence of 5-cm mesh stucco wire, 0.5m high, to prevent access by waterfowl. To minimize exclosure effects, fences did not extend more than 10 cm below the water surface. A centre post within each plot was used to anchor one side of an emergence trap and to hold maximum-minimum thermometers. String and brightly colored flagging tape were strung across the tops of the exclosures to deter waterfowl from landing inside them, however waterfowl were observed within the pondweed plots on two occasions in late August.

Clipping of the pondweed began on 18 June and continued through the summer as regrowth occurred. No clipping was done during the week preceding algal and core sampling. Pondweed was clipped at the mud-water interface using small hand-held clippers. Clipped pondweed was collected and removed. All work within the exclosures was done from a canoe to minimize disturbance of the pond bottom.

4.4.2 Pondweed biomass. Pondweed biomass was determined at monthly intervals within exclosures. Three replicate pondweed foliage samples were removed from each plot using a cylindrical aluminium quadrat (314.2 cm^2). Above-ground, green plant material was sorted in the laboratory, dried and weighed.

4.4.3 Environmental variables. Surface and bottom water temperatures were recorded every 2 d, starting on 18 June, with maximum-minimum thermometers at the centre of each plot. Accumulated degree-days were calculated for each plot by summing the differences (in degrees) between each 2-d mean temperature and 0°C, and multiplying by 2.

Dissolved oxygen levels were determined weekly during the minimum-maximum periods of the diel cycle (i.e. 700-800 h and 1500-1600 h respectively; Wrubleski and Ross 1989). Measurements were made at the surface and approximately 5 cm above the bottom using a YSI model 57 oxygen meter with a self stirring probe. During these visits, water samples were collected from the surface and bottom of each plot and returned to the laboratory for determination of pH and conductivity.

4.4.4 Algal communities. Epiphytic algae (haptobenthic algae or periphyton colonizing solid substrates) were sampled using vertically-positioned acrylic rods as artificial substrates following Goldsborough et al. (1986). The rods were 80 cm long, 0.6 cm in diameter and precut (scored) at 5 cm intervals for subsampling. The first 25 cm of each rod extended into the substrate.

Eighteen rods were placed in each plot on 5 June. At approximately monthly intervals (3 and 31 July, 1 September), 5 rods were removed from each plot (three rods were spares). From four of the rods, the 5 cm section of rod immediately below the water surface and the 5 cm section above the pond bottom were removed and placed in labelled vials. These same sections were removed from the fifth rod but were preserved in Lugol's solution for later identification of the algal community.

On 31 July a second set of rods (6) was placed in each plot. This set was introduced when it became apparent that the rods were occasionally rubbed during pondweed clipping, and that this could introduce artificial differences among rods. This second set was added after pondweed regrowth slowed and the amount of clipping required in the plots was reduced.

Epipelic algae (herpobenthic algae) living on the sediments were sampled as described by Eaton and Moss (1966). Five, 500 ml samples of surface sediments, from an area of the bottom 22.9 cm^2, were collected from each plot using a hand-held vacuum pump. Samples were returned to the laboratory, washed into glass beakers and left in the dark for 24 h. Surface water was then removed and beakers were placed outside under ambient light. Lens tissue papers (traps) cut to the diameter of the beakers were placed on the sediment surfaces. These tissues were then removed the following morning at 1000 h, new tissues were replaced and removed at 1400 h and again at 1900 h. The three lens tissues from each sample were combined into a single vial. Four samples from each plot were analyzed for chlorophyll *a* and the fifth was preserved for algal identification.

Planktonic algae (phytoplankton) were sampled at monthly intervals (11 June, 9 July and 15 August). By 4 September the pondweed had already begun to senesce and settle to the bottom, so it was impossible to obtain samples. Five, 500 ml water samples were obtained from the surface and from immediately above the bottom in each plot. Samples were returned to the laboratory and vacuum filtered through Whatman GF/C filter papers. Four samples were frozen for chlorophyll *a* determinations and the fifth was preserved for identification of the algae. Samples from 9 July were later found to be unusable.

All algal samples used for chlorophyll *a* determination were frozen for at least 24 h to enhance pigment extraction. A known volume of 90% methanol was then added to each sample and vortexed 3 times over a 24-h dark period at 5°C (Gurney and Robinson 1989). Phaeophytin-corrected chlorophyll *a* levels were determined spectrophotometrically after Marker et al. (1980).

4.4.5 Invertebrates. Benthic invertebrates were sampled with a hand-held corer (17.35 cm^2). Three core samples were collected from each plot at monthly intervals: 8 June (preclipping), 6 July, 3 August and 2 September. Plants were moved to the side in an attempt to minimize contamination of core samples with epiphytic invertebrates. Immediately after collection, surface water was removed via a valve in the side of the corer and the samples were returned to the laboratory. Samples were then washed through a 250 µm sieve, preserved in 95% ethyl alcohol and stained with Rose Bengal to facilitate sorting. Samples were later sorted under a dissecting stereomicroscope at 60x magnification. Chironomid larvae were slide mounted in polyvinyl alcohol and identified to genera.

Emerging adult insects were sampled with a modified LeSage and Harrison (1979) model 'week' emergence trap (basal area 0.5 m^2). A single trap was placed in each plot on 27 May. Traps were emptied at 2-d intervals until 6 September (20 d preclipping and 82 d postclipping). Traps were anchored to the centre post and one of the fence posts, and repositioned within the plots at biweekly intervals to minimize shading of the pondweed.

All adult chironomids were identified to species. Nomenclature follows Oliver et al. (1990). A length-weight regression (Wrubleski and Rosenberg 1990) was used to calculate biomass of emerging chironomids. Because some species of Trichoptera are capable of ovipositing beneath the water surface and then re-emerging (Nielsen 1948; Badcock 1953), females that were nulliparous and gravid were considered newly emerged, as were all males. Parous females were treated as old (oviposited) females (Corbet 1966).

4.4.6 Statistical analysis. Nested ANOVA were used to test significance of differences in pondweed biomass, algal (epiphytic, epipelic and planktonic) biomass, and benthic invertebrate densities between treatments ($n = 3$ plots/treatments). *t*-tests were used to test significance of differences in insect emergence between the two treatments. Prior to statistical analyses data were transformed [$\log_{10}(x+1)$] to stabilize the variances, but untransformed data are presented in the tables and figures. All analyses were done on a Macintosh personal computer using SYSTAT (version 3.2).

4.5 RESULTS

4.5.1 Pondweed biomass. Prior to initiation of clipping, pondweed biomass was similar between the two areas (Table 4.1). Pondweed growth was rapid during June and July and clipping only reduced biomass by 60% in the July samples. However, after the middle of July, pondweed biomass in the clipped plots remained low. During the last two weeks of July, waterfowl began to increase in numbers within the pond and through August and September they consumed much of the pondweed outside of the exclosures (Wrubleski, unpubl. data).

4.5.2 Environmental variables. None of the four parameters measured showed strong effects of the pondweed or clipping treatments. No significant differences were detected for conductivity and pH. Dissolved oxygen levels differed significantly between treatments on only two dates (8 and 24 July), with pondweed plots showing higher levels of dissolved oxygen (Wrubleski, unpubl. data). Bottom temperatures within the clipped plots were slightly warmer than under the pondweed (Figure 4.1). These differences were most apparent during calm weather (e.g., 24-28 July) but disappeared during windy weather. Accumulated degree days did not differ significantly between treatments (*t*=2.114, df=4, *P*=.10).

4.5.3 Algal communities. Levels of epiphytic chlorophyll *a*, present at the surface and bottom in the two treatments, did not differ during July (Figure 4.2). By September, however, more epiphytic chlorophyll *a* was present in the clipped plots. Differences were significant for the one month samples but not for the samples in place for 3 months. Differences between the clipped and pondweed plots probably were accentuated at the water's surface due to abrasion of the rods by pondweed movement.

At no time did the amount of chlorophyll *a* present in the epipelon differ significantly between the two treatments (Figure 4.3). However, a distinct trend for greater biomass was evident in the clipped plots towards the end of the season, with a nearly significant difference in biomass in September.

Before the initiation of clipping, planktonic algal abundances were similar between the clipped and pondweed plots (Figure 4.4). The August samples showed a trend for higher abundances in the clipped plots at both the surface and the bottom but these differences were not significant.

4.5.4 Invertebrates. By 2 September significantly higher numbers of benthic invertebrates occurred in the clipped plots than in the pondweed plots (Table 4.2), due to higher numbers of copepods and ostracods in the clipped plots. The considerably higher numbers of copepods in the clipped plots was due mainly to the Harpacticoida. Cyclopoida was the most abundant group of copepods in the pondweed plots, although even they tended to be more abundant in clipped than in pondweed plots. Cladocera had higher numbers in the pondweed plots, and the difference was nearly significant in September (F=6.445, df=1,4, *P*=.06).

The overall abundances of Chironomidae did not differ between the two treatments (Table 4.2). *Corynoneura* sp. present in the core samples may have been due to larvae falling off the pondweed when taking cores in these plots. *Corynoneura* sp. are most often found on submersed vegetation (Kesler 1981). However, even if *Corynoneura* from the core samples are removed, there is no difference in total Chironomidae between treatments (F=0.032, df=1,4, *P*=.87). *Polypedilum* spp. and *Cladotanytarsus* sp. did show significantly higher numbers in the clipped plots in August and September.

Tanypus punctipennis Meig. had significantly higher emergence in the clipped plots than the pondweed plots (Table 4.3). However, the core samples showed no differences in larval abundance between treatments (Table 4.2), suggesting some kind of bias for this species in the emergence samples. Pupae of *Tanypus* species, as with other Tanypodinae, are highly mobile and it would seem that the pupae of this species congregated in the clipped plots prior to emergence. Therefore, data on *T. punctipennis* have been excluded from Total Chironomidae, Tanypodinae or emerging biomass estimates in Table 4.3. This presumed bias is not apparent for the other Tanypodinae.

During the 20-d period before clipping began, *Procladius bellus* (Loew) and *Parachironomus tenuicaudatus* (Mall.), had significantly different emergence rates between the two treatments (Table 4.3). With *P. bellus*, these differences are probably due to chance alone due to the low number of individuals collected. No explanation can be offered for *P. tenuicaudatus*.

Following clipping, there was no significant difference (*t*=2.078, df=4, *P*=.11) in the numbers of total Chironomidae emerging between the two treatments but the subfamily Orthocladiinae did have significantly greater numbers emerging from the pondweed plots (Table 4.3). The seasonal pattern showed a constant trend of higher emergence from the pondweed plots as the season progressed (Figure 4.5A). The increasing difference in emergence was due primarily to *Corynoneura* cf. *scutellata* Winn. (Figure 4.5B). Biomass of emerging chironomids was not significantly different (*t*=1.913, df=4, *P*=.13) between treatments (Table 4.3).

Three chironomid species showed significant differences between treatments (Table 4.3). Both *Tanypus punctipennis* and *Polypedilum halterale* (Coq.) had significantly higher numbers emerging from the clipped plots, showing emergence peaks not apparent in the pondweed plots (Figure 5C,D). Emergence results for *P. halterale*, unlike for *T. punctipennis*, agree with those of the core samples. *Cladotanytarsus* sp., which had a significantly higher number of larvae in the clipped plots (Table 4.2), had a nearly significant (*t*=2.513, df=4, *P*=.06) higher emergence from the clipped plots as well. *Corynoneura* cf. *scutellata* had a significantly higher emergence from the pondweed plots (Table 4.3).

Mayflies and caddisflies also were collected in the emergence traps. The mayfly *Callibaetis fluctuans* (Walsh) showed no difference in emergence between the two treatments (Table 4.3). *Agraylea multipunctata* Curtis was the most abundant trichopteran, representing 77.1% of all caddisflies collected. Emergence of this species (new females and males) showed no difference between treatments, but older females were significantly more abundant in the clipped plots, suggesting an ovipositional preference by the females for open-water areas.

4.6 DISCUSSION

4.6.1 Submersed vegetation and benthic invertebrates. Submersed vegetation may provide additional habitat for invertebrates within the water column, but their presence can also have a marked effect on those invertebrates living on the bottom. By September in BPP, total benthic invertebrate numbers were higher in the clipped plots, but individual invertebrate groups varied in their responses to the treatments. Copepods, particularly the Harpacticoida, were considerably more abundant in the areas without submersed macrophytes. Cladocera on the other hand, were more abundant under the plants. Total chironomids showed no differences between the two treatments but some differences in species abundances were found.

Only one other study, Johnson and Mulla (1983), has compared benthic invertebrate communities between vegetated and artificially created non-vegetated areas. They observed lower numbers of chironomid larvae under *Myriophyllum spicatum* than in areas where the plants were eliminated by herbicides. In BPP, total larval chironomid numbers were similar between treatments, but two genera (*Polypedilum* and *Cladotanytarsus*) did have significantly lower larval numbers under the pondweed.

Although the general assumption that benthos numbers are higher in areas with plants than areas without plants is widely held, only a few studies (e.g., Wohlschlag 1950; Krull 1970; Menzie 1980; Engel 1985,1988; Schramm and Jirka 1989) actually have compared the benthic fauna between vegetated and 'naturally occurring' non-vegetated areas, and these comparisons should be viewed with caution. The absence of submersed macrophytes may be due to sediment type, vertebrate activities, water depth or currents. These factors also affect occurrence of benthic invertebrates. For example, Thorp (1988) reported that open patches in dense beds of submersed vegetation, created by the spawning activities of male centrarchid fish, had significantly lower benthic invertebrate diversities and densities than areas occupied by vegetation, and that these differences were still apparent the following year. The experimental approach taken in the present study minimizes these problems.

The emergence trap collections permit a comparison of numbers and biomass of emerging chironomids (both epiphytic and benthic) between vegetated and non-vegetated habitats. My results indicate no differences in total numbers or biomass of emerging chironomids between these two habitats, although *Corynoneura* cf. *scutellata* did have a higher emergence from the pondweed plots. In BPP, the presence of *Potamogeton pectinatus* did benefit one small epiphytic species but otherwise did not contribute to any increase in chironomid numbers over what was present in the bare sediments. Because of the dominance of *C.* cf *scutellata* in the pondweed emergence collections, average individual size of chironomids was 144.0 µg as compared to 221.2 µg from the clipped plots. In a previous waterfowl exclosure study within BPP, Wrubleski (1989) found that chironomid emergence from pondweed was also dominated by smaller epiphytic species, whereas larger benthic *Chironomus* species dominated emergence from areas where the plants had been removed by waterfowl.

The development of submersed vegetation was beneficial to some benthic invertebrates in BPP. Cladocera, for example, had higher densities under the pondweed. In lake littoral zones, submersed macrophytes stabilize the bottom where high wave energies can make the bottom sediments very loose and unstable, thereby benefiting benthic invertebrates in these habitats (McLachlan 1969; Jónasson and Lindegaard 1979; Schramm and Jirka 1989).

4.6.2 Factors responsible for regulating benthic invertebrates. The seasonal development of dense beds of submersed macrophytes can have a major impact on physico-chemical parameters within the water column and on the bottom (e.g., Buscemi 1958; Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983; Wylie and Jones 1987), and several of these parameters have been suggested as potential factors limiting abundances of benthic invertebrates (Hall et al. 1970; Danell and Sjöberg 1982; Wrubleski 1989). Restriction of water circulation and shading of the bottom, along with high respiration rates of decomposing vegetation, can contribute to very low oxygen levels on the bottom (Buscemi 1958; Wylie and Jones 1987). Anoxic conditions beneath a dense bed of *Myriophyllum spicatum* may have explained a depauperate sediment fauna in a study by Learner et al. (1989). Fish (1966) reported that removal of a dense cover of *Lagarosiphon major* (Ridley) Moss. resulted in a large increase in chironomid larval numbers, and speculated that this was due to better oxygen conditions present on the bottom following removal of the plants. Temperatures on the bottom beneath vegetation are also lower due to stratification caused by vegetation impeding circulation (Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983)

These features were observed in Bone Pile Pond, but the extent of the differences between the two treatments were not great and were only readily apparent for short periods. Wind-induced mixing of the shallow water, facilitated by removal of pondweed from the rest of the pond by waterfowl, is probably responsible for the lack of stratification of temperatures, oxygen, pH and conductivities. Mixing of the water column would also preclude the effects of allelochemicals produced by pondweed as being responsible for influencing the invertebrate community beneath the vegetation, as has been found for *Myriophyllum spicatum* (Dhillon et al. 1982).

Evidence from this study suggests that algal abundances were associated with differences in benthic invertebrate communities between the two treatments. By shading of the bottom, pondweed restricted benthic algal production in BPP. Light levels were not measured during this study but readings of photosynthetically active radiation (μE m^{-2} s^{-1}) taken the previous year in BPP indicated that approximately 60.3% of surface light levels reached the bottom in areas free of vegetation as opposed to only 2.1% underneath the pondweed (water depth = 15 - 20 cm). Several studies have reported low algal production beneath submersed macrophytes. Brandl et al. (1970) reported a more than 50% reduction in phytoplankton production beneath weed beds, and Goulder (1969) measured no phytoplankton production beneath a dense bed of Ceratophyllum. O'Neill Morin and Kimball (1983) reported light levels declined with depth in a *Myriophyllum heterophyllum* Michx. bed and this restricted periphyton growth on the the lower plant stems.

Algae are an important food resource for many benthic invertebrates (see review in Lamberti and Moore 1984) and this may also be so for the invertebrates of freshwater wetlands, where traditionally invertebrate production has been thought to be dependent upon the processing of detritus (Mann 1988; Murkin 1989). Shading by emergent (Straskraba and Pieczynska 1970; Gurney and Robinson 1988; Hosseini and van der Valk 1989a,b) and submersed (studies cited above) vegetation in wetland habitats restricts algal communities and can thereby negatively impact invertebrate communities. An analogous situation occurs in lotic habitats where shading by riparian vegetation reduces algal abundances in streams, and this in turn results in lower aquatic invertebrate densities and secondary production (Murphy et al. 1981; Hawkins et al. 1982; Behmer and Hawkins 1986; Feminella et al. 1989).

Interactions among submersed macrophytes, the physico-chemical environment, and benthic invertebrates are complex. These plants greatly increase the physical complexity of open-water areas and provide additional habitat within the water column for many invertebrates, but at the same time they may benefit or inhibit different components of the benthic invertebrate community. Thus, dense beds of submersed vegetation are not benign environments as suggested by Nelson and Kadlec (1984). The value of *Potamogeton pectinatus* as habitat for chironomids and other invertebrates requires further investigation. The findings of the present study suggest that the seasonal development of this plant contributes to shading of the pond bottom and thereby restricts algal production, and thus indirectly has a negative impact on the food resources of some benthic invertebrates. The relative importance of algae as a food resource for the invertebrates of freshwater wetlands remains unknown but the results of the present study point to a need for a further examination of the relationship between the invertebrate and algal communities of freshwater marshes.

Table 4.1. Sago pondweed biomass (g dry weight m^{-2}; mean ± SE, n=3; df=1,4 in all nested ANOVA) before clipping (15 June) and after clipping in Bone Pile Pond, 1987.

Sample Date	Clipped	Pondweed	F	*P*
15 June	3.43 ± 1.54	6.47 ± 2.45	0.295	0.616
13 July	50.16 ± 11.30	123.98 ± 15.95	12.060	0.025
11 August	2.57 ± 0.79	141.91 ± 20.64	227.649	0.000
4 September	3.03 ± 0.56	97.52 ± 50.44	15.100	0.018

Table 4.2. Numbers of chironomids and other invertebrates from core samples in clipped and pondweed plots, Bone Pile Pond, 1987 (mean number core^{-1} ± SE; n=3). * $P<0.05$; ** $P<0.01$; ***$P<0.001$; nested ANOVA, df=1,4. (multiply by 576.4 to get no. m^{-2})

Species	8 June (preclipping)		3 August		2 September	
	Clipped	Pondweed	Clipped	Pondweed	Clipped	Pondweed
Tanypus sp.	0.9 ± 0.7	1.1 ± 0.3	3.8 ± 1.9	3.4 ± 3.3	7.4 ± 2.8	6.8 ± 2.1
Procladius spp.	3.4 ± 1.0	2.1 ± 0.8	2.9 ± 1.2	1.9 ± 0.2	1.1 ± 0.5	1.7 ± 0.3
Corynoneura sp.	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.2 ± 0.4	1.3 ± 0.2	6.9 ± 4.8
Chironomus spp.	0.0 ± 0.0	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.2	0.3 ± 0.3	2.8 ± 2.0
Cladopelma sp.	0.1 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.0	0.0 ± 0.0
Dicrotendipes sp.	0.3 ± 0.3	0.1 ± 0.1	0.7 ± 0.5	0.0 ± 0.0	1.6 ± 0.8	4.3 ± 1.0
Glyptotendipes spp.	0.3 ± 0.3	0.7 ± 0.4	1.4 ± 0.4	1.1 ± 0.7	1.9 ± 0.4	3.1 ± 1.4
Polypedilum spp.	2.1 ± 1.6	0.4 ± 0.3	2.0 ± 0.6	0.0 ± 0.0 *	2.1 ± 0.7	0.2 ± 0.3 *
Cladotanytarsus sp.	3.0 ± 1.0	1.7 ± 0.8	1.9 ± 0.5	0.2 ± 0.2 **	1.9 ± 0.5	0.1 ± 0.2 *
Total Chironomidae	13.8 ± 5.1	9.0 ± 2.0	14.2 ± 3.9	8.1 ± 4.0	19.7 ± 4.1	27.8 ± 2.5
Cladocera	26.4 ± 9.8	30.2 ± 15.6	29.9 ± 10.3	92.1 ± 30.4	99.4 ± 35.8	305.4 ± 53.5
Ostracoda	86.2 ± 16.7	50.6 ± 10.1	172.8 ± 35.8	109.3 ± 11.4	190.0 ± 81.2	106.3 ± 13.2
Cyclopoida	90.6 ± 21.0	104.7 ± 17.0	97.7 ± 36.2	74.0 ± 4.2	81.0 ± 19.0	42.1 ± 7.6
Harpacticoida	11.0 ± 6.4	5.3 ± 1.8	155.9 ± 83.6	11.2 ± 7.3 *	361.0 ± 73.2	4.6 ± 1.8 ***
Total Copepoda	106.0 ± 27.1	111.9 ± 17.3	255.1 ± 87.9	88.6 ± 9.5	442.0 ± 91.9	46.7 ± 6.6 ***
Hyalella azteca	2.1 ± 1.8	0.7 ± 0.7	0.8 ± 0.5	0.0 ± 0.0	1.0 ± 0.6	0.2 ± 0.2
Total Invertebrates	238.0 ± 58.2	204.11 ± 24.0	475.2 ± 137.8	299.3 ± 49.7	758.0 ± 79.4	489.1 ± 72.8 *

Table 4.3. Aquatic insect emergence before (27 May - 16 June) and after (18 June - 6 September) clipping of pondweed in Bone Pile Pond (mean no. trap^{-1} ± SE; n=3). Total Chironomidae, Tanypodinae and chironomid biomass do not include *Tanypus punctipennis* (see text for explanation). * indicates a significant difference (*t*-test, $P<0.05$) between treatments.

Species	Pre - Clipping		Post - Clipping	
	Clipped	Pondweed	Clipped	Pondweed
Procladius bellus	0.0 ± 0.0	1.3 ± 0.3 *	3.7 ± 1.8	7.3 ± 1.8
P. denticulatus	0.3 ± 0.3	0.0 ± 0.0	77.3 ± 23.8	81.0 ± 7.8
P. freemani	0.3 ± 0.3	0.7 ± 0.3	4.7 ± 1.2	3.0 ± 1.6
Tanypus punctipennis	168.3 ± 86.4	199.3 ± 54.3	277.7 ± 38.3	45.3 ± 6.9 *
Corynoneura cf. *scutellata*	0.7 ± 0.7	0.7 ± 0.7	200.3 ± 61.4	1305.3 ± 396.2 *
Cricotopus sylvestris	128.7 ± 8.4	76.7 ± 35.2	118.7 ± 12.2	110.7 ± 32.9
C. cf. *flavipes*	3.3 ± 1.5	1.3 ± 0.9	28.3 ± 8.9	109.7 ± 49.3
C. intersectus	4.3 ± 0.9	2.7 ± 1.5	23.3 ± 5.5	8.3 ± 5.5
Cladopelma viridula	6.7 ± 1.8	5.7 ± [illegible]	24.4 ± 5.8	15.3 ± 3.3
Dicrotendipes nervosus	437.3 ± 277.6	338.0 ± [illegible]	41.0 ± 9.6	50.7 ± 14.0
Endochironomus nigricans	0.0 ± 0.0	0.3 ± 0.3	10.3 ± 3.3	10.7 ± 6.7
Glyptotendipes barbipes	18.0 ± 15.6	9.0 ± 5.0	8.3 ± 2.9	17.0 ± 8.4
G. lobiferus	0.0 ± 0.0	0.3 ± 0.3	13.3 ± 2.3	9.3 ± 4.1
Parachironomus tenuicaudatus	52.3 ± 5.6	31.7 ± 3.7 *	19.3 ± 2.7	29.3 ± 4.1
Polypedilum halterale	36.3 ± 24.1	28.3 ± 13.6	63.7 ± 0.9	9.7 ± 6.2 *
Cladotanytarsus sp.	0.7 ± 0.3	2.7 ± 2.7	104.3 ± 20.0	40.0 ± 15.9
Paratanytarsus sp. 3	45.7 ± 14.8	50.3 ± 14.1	19.7 ± 8.2	53.0 ± 26.0
Tanypodinae	1.7 ± 0.7	3.7 ± 0.9	86.0 ± 24.6	91.7 ± 8.4
Orthocladiinae	150.3 ± 10.5	97.0 ± 38.3	403.0 ± 59.4	1541.[illegible] ± 453.0 *
Chironomini	572.0 ± 267.2	433.7 ± 272.3	199.7 ± 12.4	156.3 ± 25.5
Tanytarsini	117.7 ± 38.7	87.3 ± 16.4	154.7 ± 16.2	119.3 ± 44.2
TOTAL CHIRONOMIDAE	841.7 ± 309.4	618.0 ± 270.5	837.7 ± 92.2	1908.3 ± 487.4
Chironomid Biomass (mg dry weight)	338.7 ± 171.8	246.4 ± 134.4	218.2 ± 5.1	272.4 ± 27.7
Callibaetis fluctuans	0.0 ± 0.0	0.0 ± 0.0	7.7 ± 4.2	7.7 ± 2.4
Agraylea multipunctata (new ♀ and ♂)	3.0 ± 1.0	0.7 ± 0.7	38.7 ± 3.7	22.7 ± 5.8
A. multipunctata (old ♀)	0.7 ± 0.7	1.3 ± 0.9	78.0 ± 9.5	30.0 ± 4.0 *
Other Trichoptera	4.0 ± 1.7	4.0 ± 1.2	19.0 ± 7.2	25.0 ± 6.0

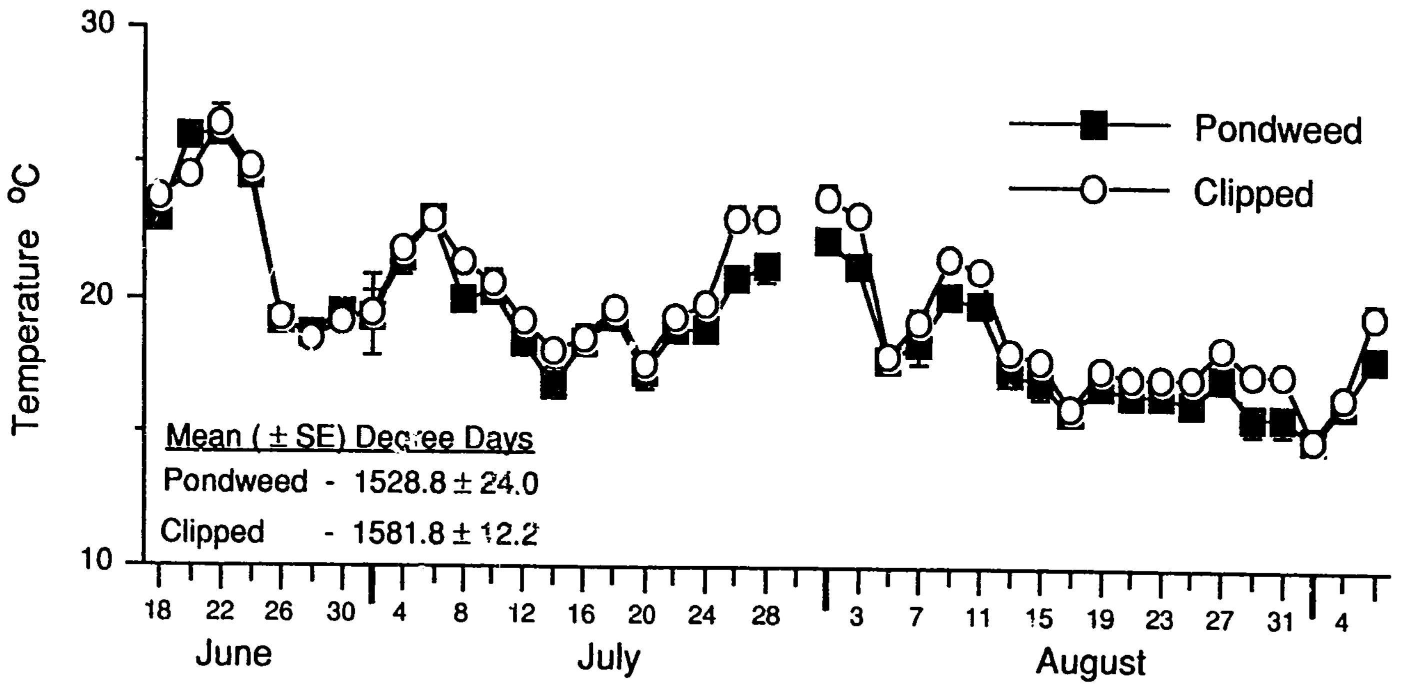

Figure 4.1. Mean (± SE; n=3) bottom temperatures in the clipped and pondweed plots in Bone Pile Pond, 1987. Thermometers were removed for cleaning and calibration on 28 July.

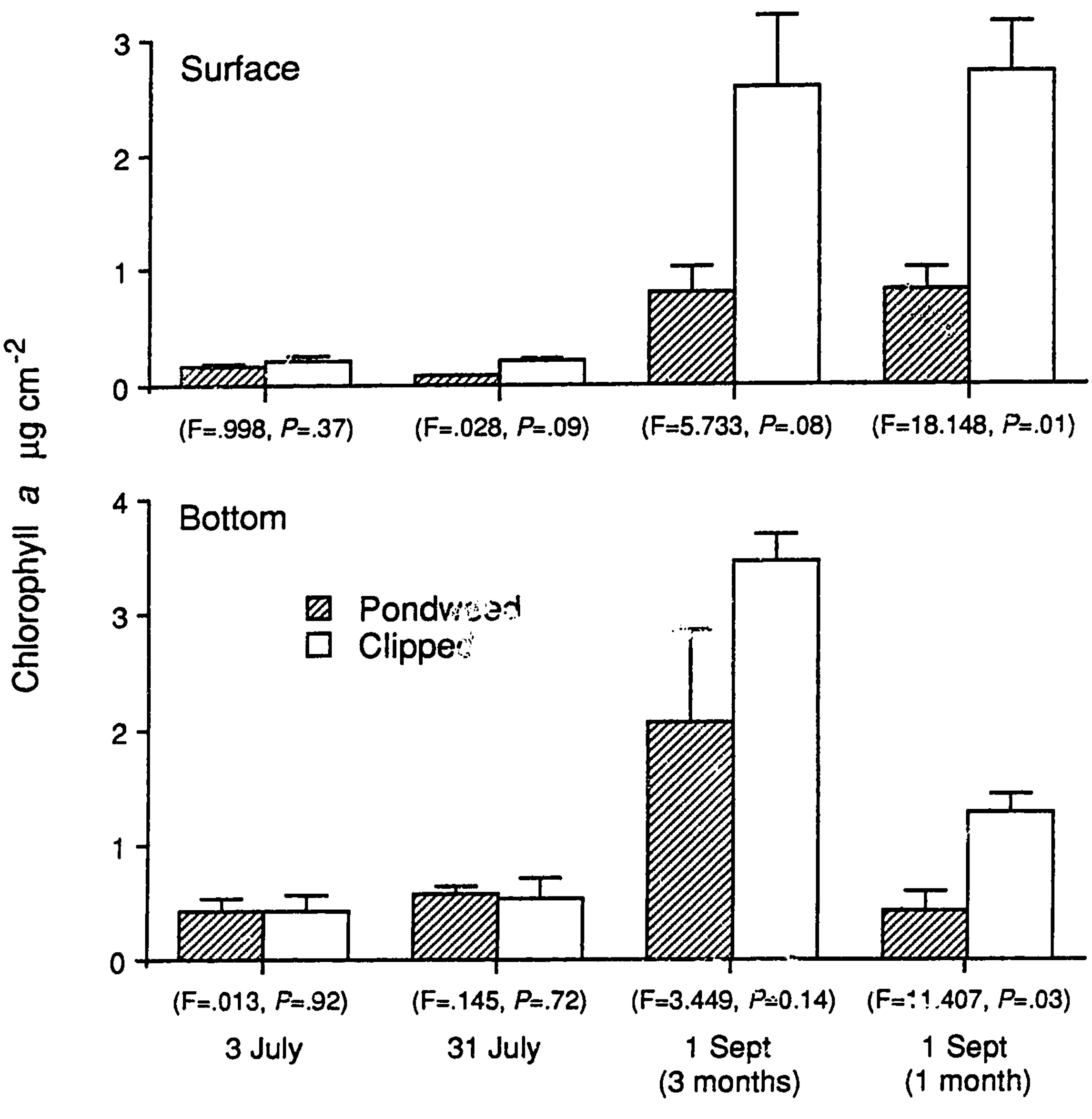

Figure 4.2. Mean (± SE; n=3; df=1,4 in all nested ANOVA) epiphytic algal biomass (as chlorophyll *a*) on artificial substrates in clipped and pondweed plots in Bone Pile Pond, 1987. Samples were collected at the surface and bottom of the water column. 1 September samples were obtained from substrates in place for three months and one month.

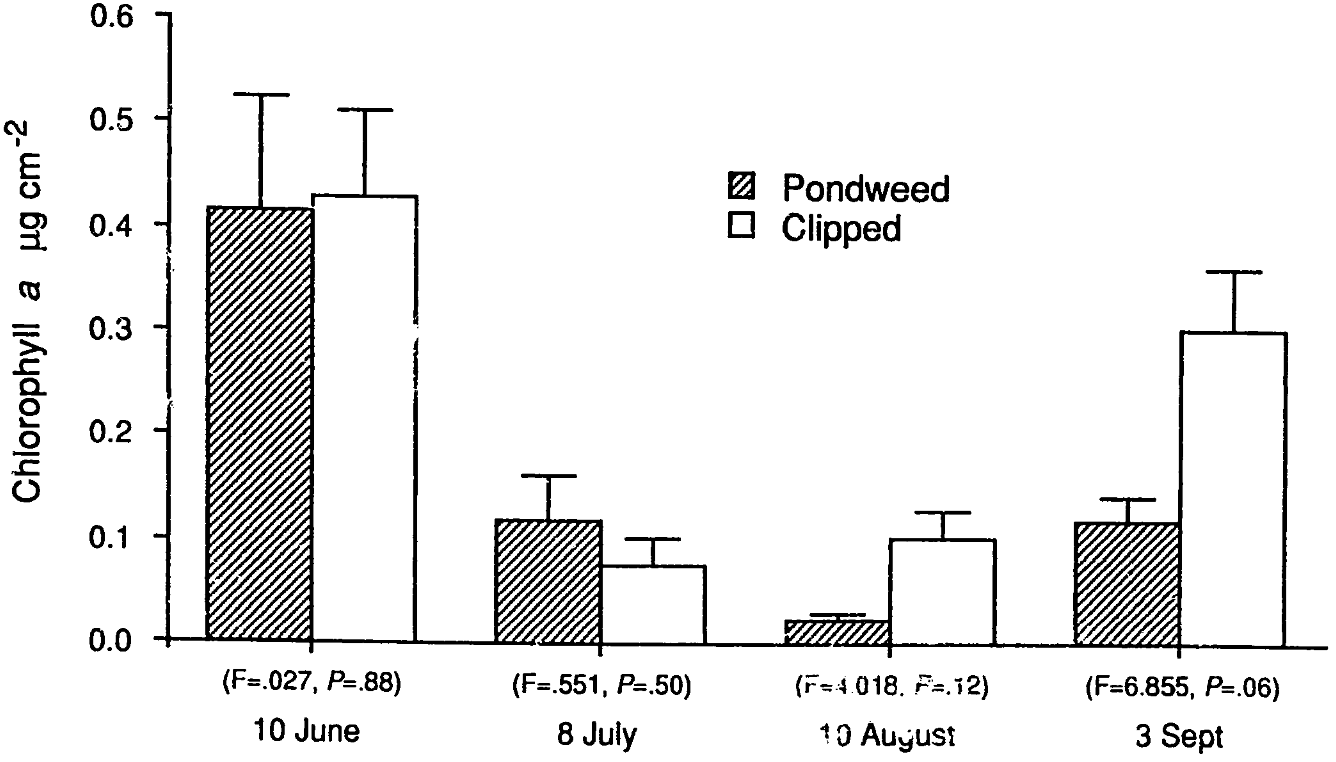

Figure 4.3. Mean (± SE; n=3; df=1,4 in all nested ANOVA) epipelic algal biomass (as chlorophyll *a*) collected from the bottom sediments of clipped and pondweed plots in BonePile Pond, 1987.

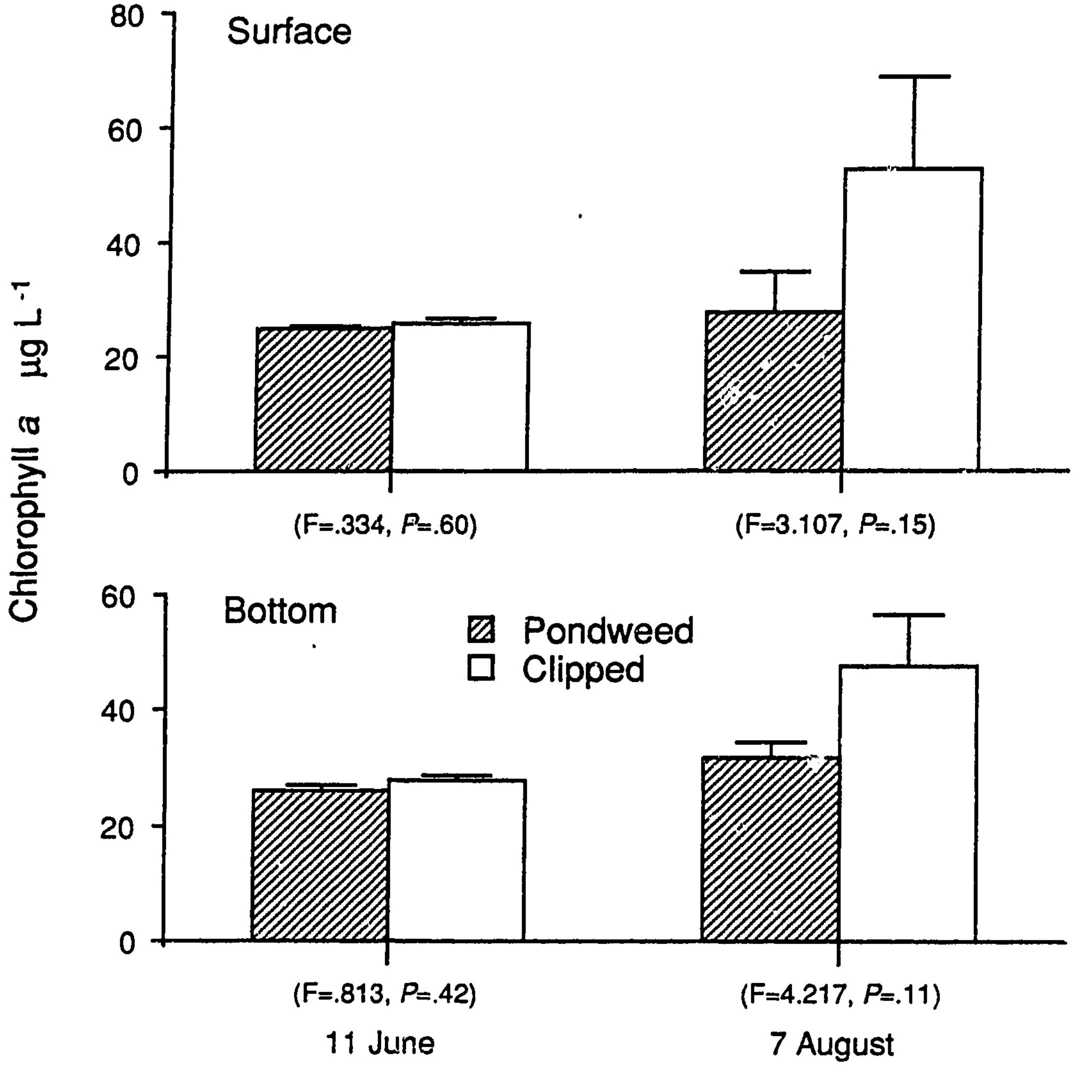

Figure 4.4. Mean (± SE; n=3; df=1,4 in all nested ANOVA) planktonic algal biomass (as chlorophyll *a*) in clipped and pondweed plots in Bone Pile Pond, 1987.

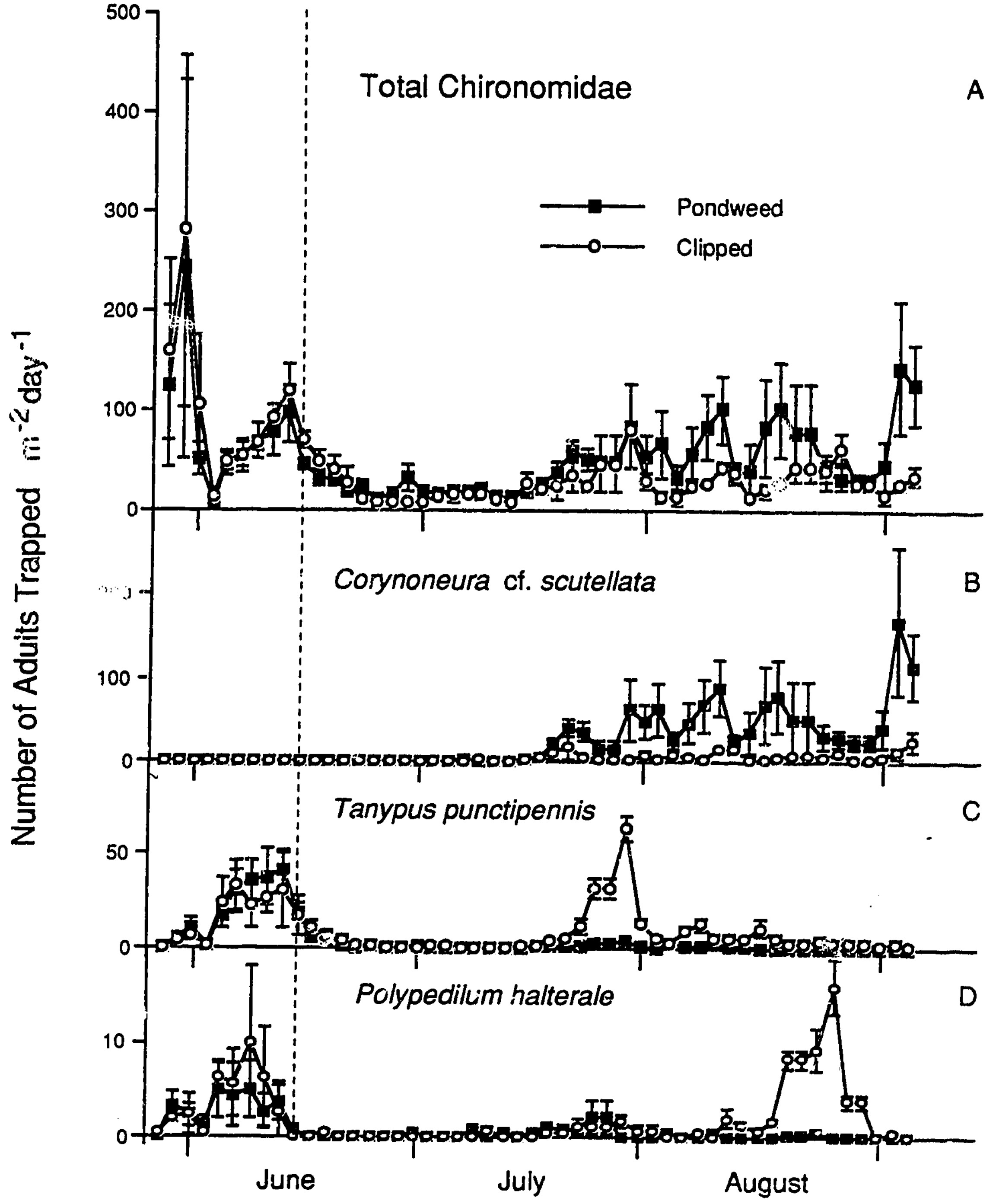

Figure 4.5. Mean (±SE; n=3) number of chironomid adults emerging from clipped and pondweed plots in Bone Pile Pond, 1987. Dashed line indicates when clipping of the pondweed began.

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UNIVERSITY OF ALBERTA

CHIRONOMIDAE (DIPTERA) COMMUNITY DEVELOPMENT FOLLOWING EXPERIMENTAL MANIPULATION OF WATER LEVELS AND AQUATIC VEGETATION

BY

Dale A. Wrubleski

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

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SUBMITTED BY DALE A. WRUBLESKI

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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Date: 12 April 1991

DEDICATION

I dedicate this thesis to Anita, Kristin and Amanda
for their patience, encouragement and love.

ABSTRACT

The importance of aquatic vegetation in structuring invertebrate communities of a northern prairie marsh are investigated in two field experiments.

In the first experiment, responses by the Chironomidae (Diptera) to the experimental flooding of ten diked marshes in the Delta Marsh, Manitoba were followed over four years. Emergence traps were used in three 'preflood' vegetation types (the terrestrial annual *Aster laurentianus*, and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) flooded at two water depths (shallow: 20-40 cm, deep: 50-70 cm). Highest number of chironomids (9,168 m^{-2} yr^{-1}) emerged from the deep *Aster* sites in the first year. The highest biomass of chironomids (22,007 mg m^{-2} yr^{-1}) was from the deep *Scirpus* sites in the fourth year. In *Aster*, a diverse group of chironomids, including epiphytic and bottom-dwelling species, were present from the first application of water. Numbers, biomass and size classes were similar over the four years. In the two emergent macrophyte habitats, small epiphytic species, particularly *Corynoneura* cf. *scutellata*, dominated emergence during the first two years. Prolonged flooding contributed to the death of the emergent macrophytes, epiphytic species declined in abundance and benthic species, particularly *Chironomus tentans* and *Glyptotendipes barbipes*, increased in numbers. The potential of chironomids as a food resource for waterfowl was initially greatest from the *Aster* habitat but became greater from the *Scolochloa* and *Scirpus* habitats in the third and fourth years. Comparisons are made with developmental sequences reported for reservoirs, and the unmanaged Delta Marsh.

A second field experiment examined how the seasonal development of submersed vegetation affects benthic invertebrates. *Potamogeton pectinatus* was either removed via clipping or permitted to grow in fenced plots. Invertebrates (primarily copepods) were more abundant in the clipped plots. Chironomid larval numbers and adult emergence did not differ between treatments, although *Polypedilum halterale* and *Cladotanytarsus* sp. were more abundant in clipped plots, and more *Corynoneura* cf. *scutellata* emerged from pondweed plots. Algal biomass beneath the pondweed tended to be lower than in the clipped plots suggesting that by shading the bottom, submersed macrophytes reduced algal biomass and indirectly affected benthic invertebrate abundances.

ACKNOWLEDGEMENTS

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I would like to give special recognition to Bruce Batt and Henry Murkin. Their continued support of myself and this type of intensive, time-consumming research is greatly appreciated.

John Spence provided advice and constant support as my supervisor. He always encouraged me to take my results that one step further. I would also like to thank my supervisory committee members, George Ball, Doug Craig, John Holmes and Richard Palmer, for their constructive council and guidance during my thesis program. George Ball acted as my supervisor during John Spence's sabbatical leave and provided additional funds for the sorting of core samples during a preliminary attempt at the pondweed manipulation experiment.

I would like to thank Lisette Ross and Karen Tome for supervising the field crews during the collection of emergence trap samples in the MERP cells. Field assistants were provided through the MacMillan and Webster Fellowship Programs. Colleen Barber, Rosie Bolen and Bruce Pollard helped in the field with the pondweed manipulation experiment. Sharon Gurney advised on the collection and analysis of algal samples and Lorie Shortreed sorted many of the core samples from the pondweed manipulation experiment. Ray Weingardt graciously offered his time and expertise with statistical matters. Don Oliver verified many of my chironomid determinations.

Finally, I would to thank my fellow graduate students at Delta and the University of Alberta for their lively discussions and warm friendship.

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1. INTRODUCTION

Agriculture, urban expansion and other human activities contribute to a continuing loss of North American wetlands. Interest in wetland preservation is increasing, although the rate of loss is still very high (Millar 1989; Wilen 1989). Wetlands are important for many reasons including water storage and purification, protection of shorelines from erosion, recreation and wildlife habitat (Brande 1980). However, much of the concern for wetland preservation comes from recognition that these habitats are crucial to migratory waterfowl populations. Wetlands of the prairie pothole region for example, produce between 50 and 75% of North American waterfowl (Batt et al. 1989). Along with the increasing demand to protect and conserve remaining wetlands, there is also pressure to manage intensively many of the protected areas to maintain high waterfowl productivity in the face of continued habitat loss.

Recent studies of waterfowl feeding have revealed that aquatic invertebrates are a crucial food resource for waterfowl, especially during reproduction and early growth of broods (Murkin and Batt 1987; Swanson and Duebbert 1989). These organisms also are involved in a number of important ecosystem functions such as food chain support, decomposition and nutrient cycling within wetlands (Murkin and Wrubleski 1988). For these reasons the study of the aquatic invertebrate fauna of wetlands is extremely important, and consideration must be given to the effects of wetland management practices on invertebrate communities.

1.1 Previous studies of wetland invertebrates. Most work on the invertebrates of North American freshwater marshes[1] has been descriptive faunal surveys (e.g., Judd 1949, 1953; Watts 1970; Smith 1968; Hanson and Swanson 1989; Wrubleski and Rosenberg 1990). Because of the taxonomic challenges with important groups and the perceived lack of importance of wetland invertebrates, other than pestiferous species, very little process-level work has been undertaken (Rosenberg and Danks 1987b). However, before detailed ecological work can proceed a basic knowledge of the fauna present is required. The Biological Survey of Canada recognized the need for more information on the taxonomy and ecology of aquatic insects of Canadian wetland habitats and established a project to coordinate interest in this area and to summarize existing knowledge. The culmination of this effort was the publication of a conference proceedings "Aquatic Insects of Peatlands and Marshes in Canada" (Rosenberg and Danks 1987a) which summarizes our present knowledge of the insect fauna of Canadian wetlands. This thorough and informative publication provides a much needed basis for future work on the aquatic insects of wetland habitats.

Ecological studies within freshwater wetlands have concentrated on the role of habitat features such as aquatic vegetation and water levels, and their

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[1] For the purposes of this review the term marsh is used in a very general sense to include most shallow freshwater habitats but not peatland or swamp type habitats (Zoltai 1987).

effects on invertebrate communities. Krull (1970), Voigts (1976), Henson (1988), and Wrubleski and Rosenberg (1990) have examined invertebrate abundances and community composition in different aquatic plant communities. Driver (1977) attempted to correlate chironomid community composition with permanence of prairie potholes. Murkin and Kadlec (1986b) reported on the effects of prolonged flooding on the invertebrate communities of a series of experimental marshes in the Delta Marsh, Manitoba, and Neckles et al. (1990) examined the role of water levels on the invertebrate community of seasonal marshes. Corkum (1984) and Wrubleski and Ross (1989) have reported on diel activities of the invertebrate fauna of marshes. Unfortunately, almost no autecological studies have been done (but see Corkum 1985).

A number of investigations of aquatic invertebrate communities of wetland habitats have been done in conjunction with waterfowl studies. Waterfowl production and habitat use have been correlated with invertebrate abundances by McKnight and Low (1969), Kaminski and Prince (1981), Murkin et al. (1982), Talent et al. (1982), and Murkin and Kadlec (1986a), and the effects of waterfowl feeding and disturbance on invertebrate populations have been examined by Collins and Resh (1985), Smith et al. (1986), Peterson et al. (1989), and Wrubleski (1989).

Field experiments are only recently being undertaken within wetland habitats. Smith et al. (1986), Peterson et al. (1989) and Wrubleski (1989) used exclosures to determine impacts of waterfowl feeding on invertebrate communities. Campeau (1990) examined the roles of detritus and algae in supporting invertebrate populations in wetlands. Morrill and Neal (1990) investigated the impact of an experimental application of the insecticide deltamethrin on the Chironomidae of prairie ponds.

Descriptive studies still are needed to provide basic information about the aquatic invertebrate fauna of wetland habitats. However, field experiments provide a greater understanding of their ecological and functional relationships in this habitat, and this approach should be encouraged.

1.2 Wetland management and aquatic invertebrates. Much of the interest in the aquatic invertebrates of North American wetlands has been generated by studies of waterfowl food habits which have revealed that breeding hens and their young are dependent upon invertebrates as a primary source of protein (Murkin and Batt 1987; Swanson and Duebbert 1989). As noted above, waterfowl habitat use is often correlated with availability of invertebrates. The now widely recognized importance of aquatic invertebrates to waterfowl has provided evidence needed to justify study of the effects of wetland management techniques on aquatic invertebrate communities.

Wetland management, however, is still in its infancy and much of its practice is based on trial and error rather than sound scientific principles (Weller 1978). Most management practices are designed to provide food and cover for waterfowl through manipulation of plant communities (Fredrickson and Taylor 1982), and it is the effects of management on vegetation that has received the greatest emphasis. Nevertheless, several investigations have considered aquatic invertebrate responses to wetland management practices, and in particular the impacts of drawdown (artificial drainage and reflooding). The first such study was by Kadlec (1962) who concluded that drawdown of waterfowl impoundments in Michigan was detrimental to invertebrate populations. McKnight and Low (1969) provided qualitative evidence that drawdown of salt marshes in Utah actually enhanced aquatic invertebrate numbers. Whitman (1974), studying impoundments within the Tintamarre and Missaquash Marshes of Nova Scotia, found that those less than four years old provided the highest numbers of invertebrates as food for waterfowl. Danell and Sjöberg (1982) reported that in a Swedish lake highest numbers of chironomids occurred in the fifth year of flooding, coincident with peak production of waterfowl broods. Kenow and Rusch (1989) reported that nektonic invertebrates increased in numbers over a three year period following flooding of impoundments within the Horicon Marsh, in Wisconsin. Except for the study of Kadlec (1962), drawdown has generally been reported to increase invertebrate numbers over those found in nearby mature (older) areas.

However, with the exception of Kenow and Rusch (1989), none of the studies listed above have followed invertebrate responses within a single wetland from the first application of water, and except for Danell and Sjöberg (1982) none of these studies have attempted to identify invertebrates further than the order or family level. Interpretation of management effects at these higher taxonomic levels can be problematic (e.g., Resh and Unzicker 1975; Rosenberg et al. 1986). Therefore, additional work is necessary to understand responses of the aquatic invertebrates to drawdown and other wetland management practices.

1.3 Marsh ecology research program. To understand further the effects of wetland management practices, and in particular drawdown, the Delta Waterfowl and Wetlands Research Station and Ducks Unlimited Canada established the Marsh Ecology Research Program (MERP) in 1979. This was a long-term (10 years), interdisciplinary program, centred around a series of ten experimental marshes situated within the Delta Marsh in south-central Manitoba (Figure 1.1). Its stated purpose was to develop a clearer understanding of ecological processes in northern prairie marshes and how these processes influence the distribution and abundance of the flora and fauna within marshes. The aquatic invertebrates were identified as one of seven specific research interests within the program (Batt et al. 1983; Murkin et al. 1984).

1.4. Objectives of this thesis. In Chapter 2, I describe the development of the chironomid community following reflooding of these experimental marshes which had undergone a drawdown. The Chironomidae were selected for intensive study for several reasons: 1) they are one of the most abundant and diverse invertebrate groups in the Delta Marsh, as well as other freshwater marshes (Wrubleski 1987), 2) they perform a number of important ecological functions within wetlands and are also an important waterfowl food resource (Wrubleski 1987), 3) emergence traps can be used to sample adults which can then be identified to species much more readily than immature stages, and 4) a previous study of chironomids within the unmanaged Delta Marsh provides information for comparative purposes (Wrubleski and Rosenberg 1990). The present study describes the most intensively sampled and longest running data set for any specific invertebrate group within a wetland habitat to date. Biological requirements of dominant species, derived from the published literature, are used to help explain observed patterns of overall chironomid community development. The effects of aquatic plant communities and water depth on community development are also discussed.

In Chapter 3, I use a condensed data set from Chapter 2 to provide information for wetland managers as to the observed responses of the chironomids to drawdown in a northern prairie marsh. Because of the known importance of these insects, their responses to this management technique are important. Numbers, biomass and size class information are used to evaluate chironomid production from different plant communities and water depths within the experimental cells.

In Chapter 4, I describe a field experiment which examined the effects of submersed vegetation on the benthic community of a shallow marsh. Hall et al. (1970), Danell and Sjöberg (1982), Johnson and Mulla (1983) and Wrubleski (1989) have noted differences between benthic invertebrate communities when submersed vegetation is present or absent. Aquatic macrophytes are known to alter their physical environment (e.g., Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983), but the effects of these modifications on invertebrate communities of wetlands and other aquatic habitats has not been well documented.

In Chapter 5, I summarize my findings and make suggestions as to future research needs. I also comment on the present state of invertebrate research in wetlands. Problems with sampling and identification greatly hamper our understanding of aquatic invertebrates in these habitats. Increased effort will be required if we are to progress in our understanding of invertebrate community dynamics in these habitats.

Figure removed for copyright reasons.

Figure 1.1. Location of the experimental cells of the Marsh Ecology Research Program in the Delta Marsh, Manitoba. Cells are numbered 1 to 10 from west to east (from Murkin et al. 1984).

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2. CHIRONOMID (DIPTERA: CHIRONOMIDAE) COMMUNITY DEVELOPMENT FOLLOWING EXPERIMENTAL WATER-LEVEL MANIPULATIONS IN A NORTHERN PRAIRIE MARSH, DELTA MARSH, MANITOBA, CANADA

2.1 SYNOPSIS

This study describes the development of the chironomid community in a series of newly flooded marshes. Emergence traps were used to compare chironomid communities among three 'preflood' vegetation types (the terrestrial annual *Aster laurentianus* and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) and two water depths, over a four year period. Chironomids colonized the marshes rapidly with high numbers of individuals and species found in the first year of flooding. Patterns of community development differed between the *Aster* habitat and the two emergent macrophytes. In *Aster*, a diverse group of chironomids, including epiphytic and bottom-dwelling species, were present from the first application of water. In the two habitats with emergent macrophytes, epiphytic species, particularly *Corynoneura* cf. *scutellata*, dominated chironomid emergence during the first two years. Prolonged flooding resulted in the death of the macrophytes, epiphytic species declined in abundance and benthic species, particularly *Chironomus tentans* and *Glyptotendipes barbipes*, increased in numbers. Comparisons are made with developmental sequences reported for chironomid communities in reservoirs, and an area of the unmanaged Delta Marsh.

2.2 INTRODUCTION

Chironomids are an abundant and diverse family of aquatic insects. They dominate benthic assemblages of many freshwater habitats and are one of the first groups to colonize newly created water bodies. Chironomid colonization and succession have been studied in a variety of new reservoirs (e.g., Armitage 1977, 1983; Sephton et al. 1983; Brown and Oldham 1984; Rosenberg et al. 1984) and other shallow water habitats (e.g., Clement et al. 1977; Street and Titmus 1979; Titmus 1979; Danell and Sjöberg 1982; Barnes 1983), but the dynamics of chironomid assemblages have not been examined in newly created wetland habitats.

The flooding of a series of experimental marshes in southern Manitoba enabled me to study chironomid colonization and succession within these structurally complex habitats. During the drawdown phase, marsh bottoms were colonized by a variety of terrestrial and aquatic macrophytes (van der Valk et al. 1989; van der Valk and Welling 1988; Welling et al. 1988). Flooding of this 'preflood' vegetation provided a diverse array of habitats for chironomid colonization. Marsh vegetation does influence chironomid community composition (Wrubleski 1987; Wrubleski and Rosenberg 1990), but how these effects are manifested is not well understood. In the experimental cells, terrestrial plants were drowned and aquatic macrophytes survived for varying periods of time, depending upon depth of flooding (van der Valk, unpubl. data). Death of these plants contributed to an abundance of plant litter on the bottom and additional habitat for chironomids. Thus, within these experimental cells, habitats available for colonization by the chironomids varied in form, abundance and duration.

In this paper, I describe changes in the abundance, diversity and species composition of the chironomid community within these experimentally flooded marshes. Observations were made over a period of four years to evaluate changes in the chironomid community and their relationship to changes in the plant communities. Information about habitat requirements of the dominant species are used to explain underlying patterns of chironomid community development. Comparisons are made with sequences of community development reported for reservoir habitats (e.g., McLachlan 1974). Comparisons are also made with an unmanaged area of the Delta Marsh (Wrubleski and Rosenberg 1990) to determine the effects of this disturbance on chironomid community parameters such as diversity and dominance.

2.3 STUDY AREA

A complex of 10 contiguous, rectangular, 4-6 ha experimental marshes (cells) were established in 1979 by the Marsh Ecology Research Program (MERP) in the Delta Marsh, in south-central Manitoba (50° 11' N, 98° 19' W). The dikes were built of earth excavated from within each cell. Water levels were manipulated and maintained by electric pumps. In 1980-1982 the cells were flooded to a depth 1 m above average Delta Marsh water levels (Batt et al. 1983; Murkin et al. 1984). The cells were drained (drawdown) during 1983 and 1984, and then reflooded in June-August of 1985. Vegetation and water chemistry in the cells have been described by Kadlec (1986a,b, 1989), van der Valk (1986), van der Valk and Welling (1988), Gurney and Robinson (1988) and van der Valk et al. (1989).

2.4 MATERIALS AND METHODS

2.4.1 Sampling. The design of the reflooding experiment for the Marsh Ecology Research Program (MERP) called for three cells to be flooded at the long-term average of the Delta Marsh ('low' treatment), three flooded to a depth 60 cm above average ('high' treatment), and four to be flooded to a depth 30 cm above average ('medium' treatment) (Batt et al. 1983; Murkin et al. 1984). The experimental cells varied widely in the development of plant communities on the drawdown surfaces (van der Valk et al. 1989; van der Valk and Welling 1988; Welling et al. 1988), and water depths following reflooding increased from north to south within the cells. This variation rendered the cells unsuitable as 'replicates' for the study of chironomid community responses, and therefore I selected the following habitats, based on preflood vegetation, as treatments rather than the cells: *Aster*, *Scolochloa* and *Scirpus*. These plant species formed extensive stands on the drawdown surfaces of the experimental cells (van der Valk, unpubl. data). Each habitat was sampled at two water depths, shallow (20-40 cm) and deep (50-70 cm). The deep flooding sites were anticipated to lose their emergent macrophyte cover faster than the shallow sites.

Aster laurentianus Fern. was one of the dominant terrestrial annuals to grow on the dry marsh bottoms (van der Valk 1986, as *A. brachyactis* Blake) and was drowned following flooding. *Scolochloa festucacea* (Willd.) Link (whitetop) and *Scirpus lacustris* L. ssp. *validus* (Wahl.) Koyama (softstem bulrush) were selected to represent emergent macrophyte habitats from the five species that dominated the drawdown surfaces of the cells (Welling et al. 1988; van der Valk and Welling 1988). *Scolochloa festucacea* is tolerant to seasonal flooding but not to prolonged flooding (Millar 1973; Neckles et al. 1985). *Scirpus lacustris validus* is more tolerant to flooding than *S. festucacea,* but intolerant to long periods of flooding (Harris and Marshall 1963; Shay and Shay 1986).

Each vegetation-water depth combination was sampled with six emergence traps, for a total of 36 traps. I used a modified LeSage and Harrison (1979) model 'week' trap (basal area = 0.5 m^2). Traps were set out when there was sufficient water at a site to float them. The same trap sites were used for each of the four years of this study (1985-88). At each site, three stakes, 2 m apart and in a line, were driven into the substrate. The emergence trap was anchored to the centre stake and one of the outside stakes, and switched to the opposite outside stake at approximately monthly intervals to reduce trap and disturbance effects below the trap.

Deep water sites, which were at lower elevations, were flooded earlier than shallow water sites at higher elevations. Initiation of sampling varied between 16 May and 20 July, 1985. Within each habitat-water depth combination the six emergence trap sites were not flooded at the same time, but all were flooded within two weeks of each other, except for two shallow *Scirpus* sites that were flooded 9 weeks before the other four sites (data from these 9 weeks were excluded from the analyses). In 1987 and 1988 traps were set out in the last week of April and emptied weekly through the third week of October, providing data for 24 weekly sample periods. In 1986, traps were not set out until the first week of May and data were collected over 23 weeks.

2.4.2 Identification of Chironomidae. All adults were identified to species. Nomenclature follows Oliver et al. (1990). Determinations were verified by Dr. Don Oliver, Biosystematics Research Centre, Ottawa, and representative specimens have been deposited in the Canadian National Collection, Ottawa.

2.4.3 Lost traps, missing data and data summation. Samples were lost in the fall of each year, particularly in 1985, because traps were sunk or damaged by muskrats. Other traps were occasionally upset by strong winds throughout the year. In some instances when a trap was damaged or upset it was replaced immediately. For these samples, the number of individuals present in the sample was adjusted proportionately to estimate the catch as if the trap had been in place for the full 7 days (e.g., a sample from a trap in place for 3 days was multiplied by 2.3 to equal a 7 day sampling period). Most traps, however, were not replaced until their next regularly scheduled visit. Highest number of complete sample losses was 23 of 138 samples (16.7%) for shallow *Scolochloa* sites in 1986. Total sample losses in the shallow sites were 0.7% and 5.8% in the deep sites over the four years.

Numbers collected from each trap during every week were summed for the entire sampling season, multiplied by 2 to give no. m^{-2} and then used to determine mean annual emergence (no. $m^{-2} yr^{-1}$ ± SE, n=6) for each habitat-water depth combination. To determine the chironomid emergence from each trap over the entire season the data lost during each week that a trap was not operating were estimated using the procedure outlined in Appendix 1.

2.4.4 Community parameters. The chironomid assemblages collected within each habitat-depth combination were compared by several methods. Number of species (species richness) collected within each was determined. Species diversity was estimated using the Shannon-Wiener (H') function (Krebs 1989, p. 361). The relative dominance index (RDI) of McNaughton (1967, after Driver 1977), the proportion of emergence represented by the two most abundant species, was also determined for each habitat-depth combination. Two similarity indices were used to compare communities and changes within and among communities over time. Jaccard's similarity coefficient is a binary index based on presence-absence and therefore gives equal weight to all species (Krebs 1989, p. 295). The percentage similarity index of Renkonen (1938, from Krebs 1989, p. 304) uses relative abundances and is influenced heavily by dominant species. Non-transformed data were used for the determination of all similarity and dominance indices.

2.4.5 Statistical analysis. Emergence data were $\log_{10}(x+1)$ transformed prior to analysis to stabilize the variances. Year comparisons were done within habitat and depths by one-way ANOVA followed by Tukey's test ($P<.05$) to compare individual year means as recommended by Day and Quinn (1989). Habitats were compared within years and depths with one-way ANOVA and Tukey's test to compare individual habitats, and depths were compared within habitat and year by *t*-tests ($P<.05$). All analyses were done with SYSTAT (vers. 3.2) on a Macintosh computer.

2.5 RESULTS

2.5.1 Total Chironomidae. Chironomids colonized the marsh cells rapidly and large populations were found during the first year of flooding (Table 2.1). The highest number of total chironomids collected in any one year was during the first year of flooding in the deep *Aster* sites (Table 2.1). *Scolochloa* and *Scirpus* sites had their highest numbers emerging during the fourth year but these numbers were not significantly different from numbers observed in the first year.

The trends for total numbers emerging over the four years did not differ among habitats but did differ between depths. In the shallow sites little change was found among years, except for a significant increase in numbers emerging from the *Scirpus* sites between the third and fourth years of flooding. In the deep sites there was a trend for high numbers emerging in the first year of flooding followed by a decline in the second and/or third years and a subsequent increase in the fourth year of flooding.

Comparisons of total chironomid numbers emerging among the three habitats showed few differences (Table 2.1). Among shallow sites *Aster* tended to have higher numbers emerging than the two emergent vegetation habitats but these differences were only significant in 1987. Among the deep sites *Aster* tended to be higher during the first two years but then numbers of emerging chironomids increased from the two emergent habitats, particularly in the fourth year. The only significant difference, however, was a very low number emerging from the *Scirpus* habitat in 1986.

Few differences were found between numbers of total chironomids emerging between depths within each habitat (Table 2.1). In 1985, deep *Aster* and *Scirpus* sites had higher emergence than their corresponding shallow sites, however this was a function of the longer flooding times in the deeper sites (Chapter 3). In 1987 and 1988, deep *Scirpus* sites had higher numbers emerging than the shallow sites.

Seasonal trends in emergence for total chironomids varied among years (Figures 2.1-3). In 1985, patterns of emergence differed among the three habitats. Emergence peaked in period 13 (early August) for both depths in the *Aster* habitat. In the *Scolochloa* habitat emergence peaked in late August - early September (period 17) in the deep sites but showed a low continuous emergence in the shallow sites. Weekly numbers emerging rose much more slowly in deep *Scolochloa* sites than the other two habitats. In the *Scirpus* habitat no readily obvious peaks were observed at either depth. Emergence in all three habitats shifted to a primarily early spring emergence in subsequent years (Figures 2.1-3). The large July-August peaks in emergence from the deep sites in 1985, were not observed in subsequent years. *Aster* continued to have a low continuous emergence throughout the summer in 1986, 1987 and 1988, particularly from the shallow sites, whereas *Scolochloa* and *Scirpus* had very low emergence after the end of June in 1986 and 1987, but in 1988 a greater proportion of emergence was found later in the summer, but from the deep sites rather than the shallow sites as found in *Aster.*

2.5.2 Species composition. Underlying the changes in the numbers of Chironomidae are changes in the abundances of the subfamilies, tribes and species. Although patterns in total numbers were similar among habitats over the four years (Table 2.1), species composition differed among habitats and varied over the duration of this experiment, as outlined below.

2.5.2.1 Chironomini. *Aster* sites were dominated by the Chironomini during all four years (Table 2.1). In the first year of flooding, the deep *Aster* sites were dominated by *Chironomus atrella* (Townes), which represented 39.7% of the chironomids collected (Table 2.2). This species represented only 6.7% of emergence from shallow *Aster* sites in the first year, where another member of this tribe, *Chironomus tentans* Fab., was the most abundant species. *Chironomus tentans* was the most abundant species from this habitat at both depths during the next three years, whereas *Chironomus atrella* had much lower emergence in subsequent years (Table 2.2; Appendix 2A). *Glyptotendipes barbipes* (Staeg.) was also very abundant in this habitat over the four years (Table 2.2).

During the first two years of flooding, members of the Chironomini were a much smaller proportion of the emergence from the two emergent vegetation habitats (Table 2.1). *Dicrotendipes nervosus* (Staeg.) was abundant during these first two years (Tables 2.3,2.4). However, by the fourth year in the shallow sites (66.0 - 76.7%) and the third year in the deep sites (66.2 - 75.2%), Chironomini represented a much greater proportion of the emergence from these two habitats (Table 2.1). This increase in abundance was due primarily to *Chironomus tentans* and *Glyptotendipes barbipes* (Tables 2.3,2.4).

2.5.2.2 Orthocladiinae. During the first few years in the *Scolochloa* and *Scirpus* habitats the Orthocladiinae, and specifically *Corynoneura* cf. *scutellata* Winn., dominated emergence numbers (Tables. 2.1,2.3,2.4). However, by the third year this species declined considerably in number and proportion of emergence in these two habitats and was not among the five most abundant species in the fourth year (Tables 2.3,2.4). Orthocladiinae represented a small but constant proportion of chironomid emergence from the *Aster* habitat (Table 2.1). *Corynoneura* cf. *scutellata* was present in this habitat (Table 2.2; Appendix 2A) but did not dominate emergence as it had in the two emergent vegetation habitats.

Other orthoclads were also important components of emergence from the experimental cells. *Cricotopus sylvestris* (Fab.) and/or *C. ornatus* (Meig.) were consistently among the five most abundant species in *Aster* and *Scolochloa* sites but were not as abundant in the *Scirpus* habitat (Tables 2.2-4). *Limnophyes prolongatus* (Kieff.), a semi-terrestrial species, had very low abundances in the *Aster* sites (Appendix 2A) but was abundant in *Scolochloa* and *Scirpus* sites in the first two years of flooding and then declined in abundance (Tables 2.3,2.4; Appendix 2B,C).

2.5.2.3 Tanytarsini. The Tanytarsini showed almost no significant changes in total numbers over the four year period (Table 2.1). In the shallow sites, it was significantly less abundant in *Scirpus* than in *Aster* during the first three years. The most abundant species was *Paratanytarsus* sp. 1 which was particularly numerous in the first few years of flooding (Tables 2.2-4). *Tanytarsus* sp. 1 was the most abundant species in shallow *Scolochloa* sites in 1987, and the second most abundant species in deep *Aster* sites in the same year (Table 2.2). Numbers were considerably greater in deep *Aster* sites in the first year but it was third in abundance after *Chironomus tentans* and *C. atrella* (Table 2.2).

2.5.2.4 Tanypodinae. This group had very low numbers in the first years of flooding but showed significant increases by the fourth year in shallow *Aster*, deep *Scolochloa*, and both *Scirpus* sites (Table 2.1). Much of the increase over the four years was due to *Tanypus punctipennis* Meig (Tables 2.2-3), but almost all species showed some increase in numbers over the four year period (Appendix 2).

2.5.2.5 Pseudochironomini. This tribe was represented by one species, *Pseudochironomus middlekauffi* Town. (Appendix 2). It showed consistent increases in abundance in all three habitats and at both depths during the four years, and was the third most abundant species in shallow *Scolochloa* in the fourth year (Table 2.3).

2.5.3 Chironomid community parameters. As with the number of chironomids collected, high numbers of species were present within the experimental cells in the first year of flooding (Figure 2.4A). *Aster* had higher numbers in the first year at both depths and maintained this higher number of species in the shallow sites over the four year period. In the deep sites however, *Scolochloa* and *Scirpus* reached comparable numbers by the third or fourth years of flooding (Figure 2.4A). Numbers of species collected increased steadily in the deep sites over the four years and by the fourth year were higher than in the shallow sites.

Aster had the highest species diversity in the first year of flooding (Figure 2.4B) and the lowest relative dominance (Figure 2.4C), whereas the deep *Scirpus* sites had very low diversity in the first year of flooding (Figure 2.4B) due to the dominance of emergence by *Corynoneura* cf. *scutellata* and *Paratanytarsus* sp. 1 (Table 2.4; Figure 2.4C). In the shallow *Aster* sites diversity dropped in the second year and then increased steadily in the third and fourth years (Figure 2.4B) and relative dominance showed the opposite pattern (Figure 2.4C). The deep *Aster* sites exhibited a steady increase in diversity from the first year onwards whereas the dominance of the two most abundant species declined in the second year and then remained stable. Both *Scolochloa* and *Scirpus* had increasing diversities up to the the third year of flooding but then exhibited a decrease in diversity with a concurrent increase in dominance due to a large increase in the emergence of *Chironomus tentans* and *Glyptotendipes barbipes* in both habitats and at both depths (Tables 2.3,2.4). Diversity was highest and dominance lowest about the time that some emergent vegetation still remained and large amounts of plant litter had been deposited on the bottom. The greatest amount of microhabitat, both in terms of emergent vegetation and plant litter, was available at this time. With the subsequent elimination of the emergent macrophytes, diversity dropped and dominance by benthic species increased.

The two similarity indices displayed different patterns (Figures 2.5-2.7). Jaccard's coefficient revealed *Aster* and *Scolochloa* habitats to be more similar in species composition in the first year of flooding, but the percentage similarity coefficient indicated *Scolochloa* and *Scirpus* as the most similar habitats over the entire four years (Figure 2.5). The percentage similarity values were heavily influenced by the dominance of emergence by *Corynoneura* cf. *scutellata* during the first few years in *Scolochloa* and *Scirpus*, and by the subsequent shift to *Chironomus tentans* by the fourth year, which was also the dominant species in the *Aster* habitat (Tables 2.2,3,4). This explains the increasing percentage similarity between *Aster* and the two emergent vegetation habitats over the four years (Figure 2.5B).

When comparing the chironomid communities between depths within each habitat, Jaccard's coefficient revealed very similar communities in the first year of flooding (Figure 2.6A). *Aster* increased in similarity over the four years and *Scirpus* declined slightly to have the least similar communities in its shallow and deep sites by the fourth year of flooding. The percentage similarity index indicated relatively similar communities between the two depths within each of the three habitats (Figure 2.6B).

When comparing changes in the chironomid communities over the four years the percentage similarity index indicated much less change within the *Aster* habitat than in the two emergent vegetation habitats (Figure 2.7B). The dramatic changes in percentage similarity within the two emergent vegetation habitats is a reflection of the domination of emergence by *Corynoneura* cf. *scutellata* during the first two years and the subsequent shift to *Chironomus tentans*. In the two emergent vegetation habitats greatest percentage similarity among years was between 1985-1986 whereas Jaccard's coefficient revealed greatest similarity in species composition among years to be between 1987-1988 (Figure 2.7).

2.6 DISCUSSION

2.6.1 Chironomid habitat and species biology. The chironomid assemblage within the experimental cells was dramatically influenced by changes in the aquatic macrophyte community following water level manipulations. Two very different patterns of chironomid community development were observed in the *Aster* and the emergent macrophyte habitats.

Aster was drowned following flooding and little live vegetation remained. The large input of plant litter contributed to a highly structured habitat, and along with the abundant metaphyton that developed in this habitat (Wrubleski, pers. observ.), a wide range of microhabitats became available for chironomid colonization. *Aster* had a varied community with both small epiphytic chironomids (e.g., *Corynoneura*, *Cricotopus*, *Paratanytarsus*) and larger benthic or mining species (*Chironomus, Glyptotendipes*) abundant over the four years. *Aster* litter seems to resist decay and can persist within the cells for many years (Murkin, pers. comm.), thereby providing a relatively stable habitat. This may explain the lack of significant changes within this community over the four year period.

Scolochloa and *Scirpus* habitats showed more dynamic changes in chironomid community composition over time. During the first two years these habitats were dominated by *Corynoneura* cf. *scutellata*. Larvae of *Corynoneura* are very small free-living grazers dependent upon submersed surfaces (Table 2.5). The live stems and leaves of *Scolochloa* and *Scirpus* provided ideal habitat for this species, as well as other epiphytic species such as *Paratanytarsus* sp.1 and several *Cricotopus* species (Table 2.5). The survival of these plants during the initial flooding delayed deposition of plant litter at that time (Wrubleski, pers. observ.) and this may have prevented large populations of mining species such as *Chironomus tentans* and *Glyptotendipes barbipes* from becoming established in the first few years. Although both of these species have been reported to mine plant litter or other soft materials, they are more often reported to live in soft highly organic bottom sediments (Table 2.5) which would have been present in these two habitats. Their absence in the two emergent vegetation habitats could indicate that factors other than availability of plant litter were responsible for the absence of bottom-dwelling species. Emergent macrophytes can produce unfavourable conditions on the bottom. They restrict algal growth, an important food resource for these species (Table 2.5), through shading (Straskraba and Pieczynska 1970; Gurney and Robinson 1988). They can also prevent mixing of the water column and contribute to low oxygen conditions on the bottom (Dvorak 1969; Suthers and Gee 1986).

Prolonged flooding, particularly at the deeper depths, eliminated emergent macrophytes by the fourth year (van der Valk, pers. comm.; Figure 2.8). The death of these plants contributed to a large deposition of plant litter and reduced shading of the bottom. Epiphytic species declined in numbers and benthic species dominated the chironomid assemblage. *Corynoneura* cf. *scutellata* declined to levels similar to that found in the *Aster* habitat. *Chironomus tentans* and *Glyptotendipes barbipes*, species that were abundant in the *Aster* habitat from the time of initial flooding, also became abundant in both the *Scolochloa* and *Scirpus* habitats after the death of the emergent plants. Driver (1977) reported that *C. tentans* increased in abundance following increased water levels on a prairie pond. He suggested that the increase in this species was attributed to its ability to use not only the dead stems and roots of *Scirpus americanus* Pers. but also the open areas created by the loss of vegetation. My results concur with Driver's observation that *Chironomus tentans* increases in abundance when emergent vegetation was flooded, but without information on larval distributions the basis for this response is unclear.

The death of *Aster*, *Scolochloa* and *Scirpus* due to flooding resulted in the deposition of abundant plant litter to the bottom. In wetland habitats, plant litter has been thought to be an important food resource for invertebrate production (Mann 1988), but recent developments have indicated that algae may be a more important food resource for invertebrates in freshwater wetlands (Murkin 1989; Campeau 1990; Chapter 4). A review of food habits of the dominant chironomid species present in the experimental cells indicates that algae are indeed important (Table 2.5). Street and Titmus (1982) were able to separate the effects of food and habitat provided by straw additions to a gravel-pit lake. Their findings indicated that habitat structure was a more important determinant of animal distributions than the availability of plant litter as food. Aquatic macrophytes and their resultant plant litter provide an important habitat for chironomids, but it may be the highly productive algal communities of wetlands (Crumpton 1989) that are the most important food resource for chironomids.

Changes in the chironomid community of the experimental cells can be related to observed changes in habitat structure. However, interactions between individual species are unknown in this habitat and cannot be ruled out as unimportant. Cantrell and McLachlan (1977), for example, found that competition between two benthic chironomids determined habitat distribution in a newly created reservoir. In the *Scolochloa* and *Scirpus* habitats of the experimental cells, a striking shift from an assemblage dominated by *Corynoneura* cf. *scutellata* to one dominated by *Chironomus tentans* was observed (Figure 2.9). In Aster, *Corynoneura* did not contribute significantly to emergence so no relationship is apparent, but in the *Scolochloa* and *Scirpus* habitats there was a clear negative relationship of abundance between these two species. Published information indicates that neither species use the same microhabitat (Table 2.5) and so a negative relationship between them is more likely to be explained by changes in habitat structure over time and the requirements of these two species than by competitive effects. Interactions between other species pairs, however, must be studied by direct experiments before conclusions about possible interactions may be drawn.

2.6.2. Comparisons with reservoir studies. Studies of aquatic invertebrate colonization and succession have been done primarily in man-made reservoirs (e.g., Nursall 1952; Paterson and Fernando 1970; Sephton et al. 1983; Brown and Oldman 1984; Voshell and Simmons 1984). Invertebrate community development in reservoirs has been characterized by four phases (McLachlan 1974, after Morduchai-Boltovskoi 1961). 1) The first phase is short and occurs during the initial filling of impoundments when river fauna and terrestrial invertebrates are present within the reservoir. 2) A second productive phase coincides with the final filling of the reservoir. This high productivity has been attributed to the release of nutrients from the flooded vegetation and surface soils. The length of time needed to reach peak abundances (often reported to be between 1 to 4 years) is determined by such factors as basin morphology, climate, water chemistry and invertebrate population structure (Armitage 1977; Sephton et al. 1983). This peak in invertebrate numbers is often dominated by chironomids, particularly *Chironomus plumosus*-type larvae (McLachlan 1974). 3) A subsequent decline in invertebrate abundances has been attributed to loss of the flooded terrestrial vegetation through decomposition, consumption by invertebrates and sedimentation. Increasing populations of fish and predatory invertebrates (e.g. leeches, odonates) have also been suggested as contributing to the decline in invertebrate densities (Andersson and Danell 1982). 4) Eventually invertebrate abundances reach an equilibrium which is determined by prevailing conditions within and outside the water body. Although this general pattern of invertebrate community development has been reported often (now considered part of the 'reservoir paradigm'; Hecky et al. 1984), Wiens and Rosenberg (1984) found little evidence of McLachlan's (1974) four phases in the responses of benthic invertebrates to reservoir formation in Southern Indian Lake, Manitoba.

The generalized pattern observed in reservoirs can be compared with development of the chironomid community in the diked marshes of the present study. The first phase of reservoir fauna development can be seen in the experimental cells in the abundance of semi-terrestrial chironomids, such as *Limnophyes prolongatus,* in *Scolochloa* and *Scirpus* during the first few years following flooding. However, with continued flooding this species declined in abundance. A similar response was also noted when these experimental cells were flooded as part of an earlier water level manipulation (Murkin and Kadlec 1986; Wrubleski, unpubl. data).

The second or 'productive' phase in reservoirs varies in duration and timing and is generally the result of high production by a single species. In the *Aster* habitat numbers were highest in the second year in the shallow sites and in the first year in the deep sites, but these numbers were not significantly different from most other years. Biomass of emerging chironomids showed much the same pattern (Chapter 3). The composition of the chironomid community did not show great differences over time as indicated by the high similarity values among years (Figure 2.7), and the community was not dominated by one or two species as was the case in the two emergent vegetation habitats (Figure 2.4C).

In the *Scolochloa* and *Scirpus* habitats, few differences in total numbers were observed in the shallow sites over the four years, but in the deep sites numbers were high in the first and fourth years of flooding. Biomass was highest in the fourth year (Chapter 3). *Corynoneura* cf. *scutellata* dominated during the first two years and *Chironomus tentans* dominated in the fourth year. The high abundances of *Chironomus tentans*, following the death of the emergent macrophytes and the addition of litter to the bottom, are consistent with reservoir studies where *Chironomus* species often dominate following flooding of the terrestrial vegetation (McLachlan 1974).

Few reservoir studies have reported high numbers of Orthocladiinae during reservoir formation. This is probably due to several factors; 1) orthoclads prefer vegetated habitats and most reservoir studies tend to focus on the deeper open-water or profundal habitats where few aquatic macrophytes are found. Paterson and Fernando (1970), Armitage (1977, 1983) and Ertlová (1980) sampled littoral habitats during reservoir formation and reported high numbers of orthoclads. 2) In reservoir studies bottom sediments are usually sampled rather than submersed or emergent vegetation, and 3) *Corynoneura* larvae, in particular, are extremely small and easily overlooked in any benthic sampling program. Street and Titmus (1979) reported that very different results were obtained when larval sampling and emergence trap sampling programs were used to describe the colonization of several small gravel-pit ponds by chironomids, and suggested that the importance of larger benthic species as pioneers may have been overestimated in previous colonization studies where larval sampling alone had been done. If a benthic sampling program had been used in the experimental cells this phase in the development of the chironomid community would have been missed entirely.

Whether it serves as food or habitat, the eventual loss of the plant litter to consumption, decomposition or siltation results in a decline in invertebrate numbers in reservoirs. In the experimental cells, chironomid abundances within the *Scolochloa* and *Scirpus* habitat, and probably *Aster* as well, can be expected to decline over the next few years. Decomposition of *Scirpus* and *Scolochloa* litter is rapid (Murkin et al. 1989) and little of it will remain as habitat for invertebrates. As more flood-tolerant emergent macrophytes or submersed macrophytes develop within the cells and provide new habitat, numbers of chironomids and other invertebrates can be expected to recover.

As in reservoir studies, my results suggest that the contribution of plant litter following flooding was the principal factor regulating the development of the chironomid community of the experimental cells. In the experimental cells however, chironomid responses to the additions of litter took place in two phases. First was the death of the terrestrial annuals which provide an immediate pulse of coarse detritus to the bottom. Prolonged flooding caused the death of emergent macrophytes and a second pulse of plant litter was added to the marsh bottom, resulting in a second pulse of chironomid production.

2.6.3 Comparisons with the unmanaged Delta Marsh. Data presented in Wrubleski and Rosenberg (1990) permit a comparison of the chironomid assemblages within the experimental cells with Bone Pile Pond (BPP, see Chapter 4 for a description), an unmanipulated area of the Delta Marsh. Although many newly created water bodies are reported to produce higher numbers of chironomids than older, mature areas (see Chapter 3 for references), this was not so for the experimental cells. Numbers emerging from the cells were comparable to those found in emergent vegetation habitats of BPP, but did not match the high numbers found in the *Potamogeton* habitat (Chapter 3). Numbers of species were higher in the *Potamogeton* habitat of BPP than in the experimental cells, but by year four species richness from the experimental cells was similar to that found in the *Scirpus* and *Typha* habitats of BPP (Table 2.6, Figure 2.4).

Chironomid species diversity in the two emergent vegetation habitats of the experimental cells was related to habitat structural diversity. In the first few years chironomid habitat was principally the emergent vegetation and by the fourth year it was the litter on the bottom. In year three, both emergent vegetation and litter were present and provided a greater variety of habitats and consequently chironomid diversity was greatest at this time. Diversity was greater in the *Aster* habitat than the two emergent vegetation habitats and probably this was related also to higher habitat diversity in *Aster* sites. Species diversities in the experimental cells in the third year of flooding were comparable to values for BPP. Diversity was lower in the *Potamogeton* habitat of BPP in 1980 due to a large number of *Tanypus punctipennis* (Wrubleski and Rosenberg 1990). Relative dominance values tended to be lower in BPP, somewhat comparable to those in the deep *Aster* sites in the second to fourth years of flooding.

The *Scirpus* and *Typha* habitats in BPP had an abundance of semi-terrestrial chironomid species, including *Limnophyes immucronatus* and *L. prolongatus* (Table 2.6; Wrubleski and Rosenberg 1990). This was not so in the two emergent vegetation habitats of the experimental cells. *Limnophyes prolongatus* was abundant initially in *Scolochloa* and *Scirpus* habitats but then declined in abundance with prolonged flooding (Tables 2.3,2.4). Water levels within BPP fluctuated greatly and occasionally there was no surface water present in the *Scirpus* and *Typha* habitats. This would explain the abundances of semi-terrestrial species in these habitats. Flooding to depths of 20-40 cm greatly reduced the abundances of these species in the experimental cells.

Tanypus punctipennis was a dominant species in the *Potamogeton* habitat of BPP (Table 2.6). *Tanypus* species prefer soft mud substrates through which they can move easily (e.g., Parkin and Stahl 1981; Titmus and Badcock 1981). Their gradual increase in numbers in the experimental cells (Tables 2.2-4, Appendix 2) may be an indication of changing substrate conditions within the cells, however, the exact reason remains unknown.

2.6.4 Conclusions. Freshwater wetlands are dynamic habitats. Vegetation and water chemistry vary with water levels which fluctuate within and among years. The aquatic macrophytes, which typify wetlands, provide structurally complex habitats for aquatic invertebrates such as chironomids. Species composition and abundances of the chironomid assemblages within these habitats can change considerably among years (e.g., Morrill and Neal 1990; Wrubleski and Rosenberg 1990) but the factors responsible are not known. The results of the present study indicate that habitat changes, and specifically changes in vegetation, are important factors regulating chironomid communities in northern prairie wetlands.

The exact mechanisms of this regulation remain unknown. We do know that aquatic macrophytes provide habitat for many species. For example, in this study the two emergent macrophytes provided habitat for *Corynoneura* cf. *scutellata* and other epiphytic species. Death of the these plants due to excessive flooding benefited larger benthic species. This benefit may be in one or all of the following forms. 1) Plant litter provides a soft material in which these species could burrow. 2) Algae and bacteria would colonize the abundant surface area provided by the litter and in turn provide an excellent food resource for chironomids. 3) The absence of emergent macrophytes would contribute to increased mixing of the water column and greater algal production on the bottom. Further studies are needed to determine how dense stands of emergent macrophytes inhibit benthic chironomids. Field experiments, such as those described in Chapter 4 and Straskraba and Pieczynska (1970), are needed to tease apart the interactions between emergent macrophytes and chironomids. Much of this effort must use information about larvae. Emergence trap samples provide detailed descriptions of patterns, but are not capable of providing the information necessary to evaluate larval responses, the life cycle stage at which habitat manipulations have their true effects.

Table 2.1. Mean annual emergence [no. m^{-2} (±SE), n=6] of the four major chironomid taxa[1] and total Chironomidae from the three habitats and two water depths in the experimental cells. Means underlined with the same line are not significantly different (Tukey's HSD test following a significant one-way ANOVA, $P<.05$). A dashed line is used to connect a solid line when the habitats that do not differ significantly are separated by a habitat that does differ significantly from those underlined. * indicates a significant difference between depths within years (*t*-test, $P<.05$). Habitat means with the same subscripts do not differ significantly within year and depth (Tukey's HSD test following a significant one-way ANOVA, $P<.05$).

		Shallow				Deep			
		1985	1986	1987	1988	1985	1986	1987	1988
Tanypodinae									
	Aster	20.0_a	85.0_a	433.3_b	1078.3_b	66.7_a	247.3_a	148.7_a	263.7_a
		(6.3)	(30.0)	(215.6)	(489.9)	(21.9)	(116.8)	(76.0)	(142.2)
	Scolochloa	20.4_a	25.6_{ab}	7.4_a	161.0_a	17.4_a	44.6_a	50.6_a	566.4_a
		(6.8)	(9.6)	(1.4)	(103.0)	(5.6)	(11.4)	(28.2)	(169.2)
	Scirpus	24.3^*_a	6.0^*_b	5.7^*_a	65.3^*_a	39.7_a	38.3_a	48.0_a	444.0_a
		(6.6)	(3.1)	(2.7)	(18.8)	(3.2)	(15.8)	(15.6)	(129.2)
Orthocladiinae									
	Aster	736.7_a	706.3_a	718.3_a	626.7_a	1425.7_a	1309.7_{ab}	263.0_a	638.3_a
		(177.5)	(300.9)	(206.6)	(235.3)	(292.1)	(224.1)	(49.4)	(86.1)
	Scolochloa	961.4^*_a	1852.6_a	251.0_a	400.0^*_a	4952.0_a	3559.4_a	422.4_a	912.6_a
		(381.8)	(626.8)	(74.4)	(99.4)	(1640.8)	(932.4)	(157.6)	(169.8)
	Scirpus	724.7^*_a	634.3_a	262.0^*_a	414.0_a	4744.3_a	1065.3_b	775.7_b	866.0_a
		(353.1)	(118.1)	(67.4)	(95.6)	(2425.0)	(471.0)	(81.5)	(293.5)

Table 2.1. continued...

	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
Chironomini								
Aster	1295.7$^{*}{}_{b}$	3962.7$_{b}$	3219.3$_{b}$	2292.0$_{a}$	5726.0$_{b}$	3173.0$_{a}$	1568.0$_{a}$	2909.3$_{a}$
	(229.3)	(1308.5)	(1012.9)	(740.7)	(1838.4)	(641.3)	(542.2)	(516.0)
Scolochloa	295.0$_{a}$	407.4$_{a}$	357.7$_{a}$	2322.3$_{a}$	580.4$_{a}$	1001.3$_{ab}$	1784.3$_{a}$	6247.3$_{a}$
	(154.4)	(186.2)	(102.0)	(551.5)	(174.8)	(312.0)	(1219.8)	(1755.7)
Scirpus	358.7$^{*}{}_{a}$	673.3$_{a}$	178.0$^{*}{}_{a}$	1193.3$^{*}{}_{a}$	700.0$_{a}$	385.3$_{b}$	1841.6$_{a}$	6695.0$_{a}$
	(156.8)	(271.2)	(64.8)	(351.7)	(145.2)	(128.3)	(686.7)	(1182.4)
Tanytarsini								
Aster	683.0$_{a}$	547.7$_{a}$	666.3$_{a}$	599.3$_{a}$	1949.3$_{a}$	1028.7$_{a}$	659.7$_{b}$	561.0$_{a}$
	(101.9)	(177.6)	(184.9)	(256.5)	(664.2)	(802.2)	(232.1)	(117.1)
Scolochloa	724.6$_{ab}$	300.0$_{ab}$	223.0$_{ab}$	215.6$_{a}$	615.6$_{a}$	107.0$_{a}$	115.4$_{a}$	192.6$_{ab}$
	(459.8)	(186.2)	(93.2)	(71.4)	(204.8)	(20.0)	(53.8)	(64.4)
Scirpus	71.7$^{*}{}_{b}$	86.3$_{b}$	82.7$_{b}$	169.7$_{a}$	513.0$_{a}$	48.7$_{a}$	120.7$_{a}$	114.0$_{b}$
	(22.6)	(39.4)	(27.7)	(81.2)	(162.4)	(25.3)	(22.9)	(31.3)

Table 2.1. continued...

	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
Total Chironomidae								
Aster	2735.3^*_a	5302.0_a	5038.7_b	4650.7_a	9168.0_a	5758.7_a	2643.3_a	4438.7_a
	(422.1)	(1673.8)	(1356.4)	(1562.5)	(2406.7)	(1282.6)	(650.3)	(447.8)
Scolochloa	2003.4_a	2585.6_a	841.0_a	3340.4_a	6165.4_a	4713.4_a	2373.6_a	7983.6_a
	(917.6)	(967.8)	(164.0)	(820.4)	(1860.4)	(1049.6)	(1406.6)	(2005.2)
Scirpus	1179.7^*_a	1400.0_a	529.3^*_a	1910.0^*_a	5997.0_a	1537.7_b	2789.3_a	8148.0_a
	(333.9)	(275.9)	(67.3)	(459.2)	(2663.5)	(599.6)	(725.8)	(1355.0)

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[1] The tribe Pseudochironomini was represented by one species, *Pseudochironomus middlekauffi Town.*, and is included in the Total Chironomidae but not listed separately in this table.

Table 2.2. The five most abundant species (mean $m^{-2} \pm$ SE, n=6) collected from the *Aster* habitat for each year and depth, listed in decreasing order of abundance.

Aster	1985	1986	1987	1988
Shallow	*Chironomus tentans* 725.0 ± 144.1	*Chironomus tentans* 2106.0 ± 684.0	*Chironomus tentans* 1954.3 ± 827.7	*Chironomus tentans* 1292.3 ± 414.5
	Paratanytarsus sp. 1 357.7 ± 96.6	*Glyptotendipes barbipes* 1322.7 ± 533.8	*Glyptotendipes barbipes* 999.3 ± 276.4	*Tanypus punctipennis* 847.0 ± 408.6
	Corynoneura cf. *scutellata* 232.7 ± 127.7	*Tanytarsus* sp. 1 344.0 ± 186.3	*Tanypus punctipennis* 338.7 ± 200.5	*Glyptotendipes barbipes* 782.3 ± 444.8
	Cricotopus ornatus 231.3 ± 64.8	*Corynoneura* cf. *scutellata* 273.3 ± 134.7	*Cricotopus sylvestris* 290.7 ± 92.2	*Cladotanytarsus* sp. 405.3 ± 270.1
	Glyptotendipes barbipes 206.0 ± 56.7	*Cricotopus ornatus* 248.3 ± 157.7	*Cricotopus ornatus* 278.0 ± 93.6	*Cricotopus ornatus* 267.3 ± 173.2
Deep	*Chironomus atrella* 3637.3 ± 972.6	*Chironomus tentans* 1391.7 ± 493.6	*Chironomus tentans* 850.7 ± 286.0	*Chironomus tentans* 1568.3 ± 303.2
	Chironomus tentans 1292.3 ± 809.6	*Glyptotendipes barbipes* 1077.3 ± 544.7	*Tanytarsus* sp. 1 324.0 ± 185.5	*Glyptotendipes barbipes* 387.3 ± 183.0
	Tanytarsus sp. 1 1152.0 ± 655.9	*Tanytarsus* sp. 1 948.0 ± 750.6	*Paratanytarsus* sp. 3 297.7 ± 211.8	*Dicrotendipes nervosus* 357.3 ± 191.4
	Tanytarsus sp. 4 701.0 ± 441.9	*Corynoneura* cf. *scutellata* 883.0 ± 197.4	*Cladopelma viridula* 271.7 ± 165.7	*Cricotopus sylvestris* 238.7 ± 60.5
	Glyptotendipes barbipes 547.3 ± 235.7	*Chironomus atrella* 313.3 ± 146.6	*Glyptotendipes barbipes* 190.0 ± 104.1	*Paratanytarsus* sp. 3 226.3 ± 119.0

Table 2.3. The five most abundant species (mean m^{-2}± SE, n=6) collected from the *Scolochloa* habitat for each year and depth, listed in decreasing order of abundance.

Scolochloa	1985	1986	1987	1988
Shallow	*Corynoneura* cf. *scutellata* 782.3 ± 344.1	*Corynoneura* cf. *scutellata* 1175.3 ± 433.5	*Tanytarsus* sp. 1 163.7 ± 92.6	*Chironomus tentans* 1266.0 ± 317.9
	Paratanytarsus sp. 1 686.3 ± 446.1	*Limnophyes prolongatus* 275.3 ± 150.4	*Chironomus tentans* 162.3 ± 89.4	*Glyptotendipes barbipes* 849.7 ± 274.1
	Dicrotendipes nervosus 125.3 ± 74.9	*Paratanytarsus* sp. 1 257.0 ± 171.6	*Acricotopus nitidellus* 119.3 ± 85.9	*Pseudochiron. middlekauffi* 241.3 ± 105.9
	Limnophyes prolongatus 93.3 ± 37.2	*Chironomus riparius* 206.0 ± 111.7	*Corynoneura* cf. *scutellata* 99.7 ± 34.8	*Cricotopus sylvestris* 171.0 ± 65.0
	Parachironomus tenuicaudatus 78.7 ± 47.9	*Cricotopus ornatus* 186.0 ± 104.9	*Chironomus atrella* 68.0 ± 26.3	*Dicrotendipes nervosus* 114.0 ± 43.1
Deep	*Corynoneura* cf. *scutellata* 3128.3 ± 1778.1	*Corynoneura* cf. *scutellata* 2739.3 ± 945.4	*Chironomus tentans* 978.3 ± 762.5	*Chironomus tentans* 4525.0 ± 1252.8
	Cricotopus sylvestris 1074.3 ± 452.5	*Dicrotendipes nervosus* 366.0 ± 79.7	*Glyptotendipes barbipes* 340.3 ± 266.2	Glyptotendipes barbipes 820.3 ± 367.5
	Paratanytarsus sp. 1 586.3 ± 198.6	*Glyptotendipes barbipes* 340.3 ± 208.9	*Corynoneura* cf. *scutellata* 187.7 ± 117.0	*Dicrotendipes nervosus* 549.3 ± 328.6
	Cricotopus ornatus 584.0 ± 312.0	*Cricotopus sylvestris* 282.3 ± 82.9	*Dicrotendipes nervosus* 166.3 ± 66.1	*Cricotopus sylvestris* 445.7 ± 178.2
	Dicrotendipes nervosus 218.3 ± 72.3	*Psectrocladius edwardsi* 272.3 ± 32.4	*Cricotopus sylvestris* 148.3 ± 35.9	*Tanypus punctipennis* 279.3 ± 174.3

Table 2.4. The five most abundant species (mean m^{-2} ± SE, n=6) collected from the *Scirpus* habitat for each year and depth, listed in decreasing order of abundance.

Scirpus	1985	1986	1987	1988
Shallow	*Corynoneura* cf. *scutellata* 596.0 ± 322.6	*Corynoneura* cf. *scutellata* 565.3 ± 123.9	*Corynoneura* cf. *scutellata* 120.7 ± 78.7	*Chironomus tentans* 582.0 ± 180.8
	Dicrotendipes nervosus 187.0 ± 88.1	*Dicrotendipes nervosus* 310.0 ± 90.5	*Acricotopus nitidellus* 101.0 ± 47.2	*Glyptotendipes barbipes* 361.7 ± 186.5
	Limnophyes prolongatus 94.0 ± 34.1	*Chironomus tentans* 143.3 ± 108.8	*Paratanytarsus* sp. 1 71.0 ± 25.0	*Acricotopus nitidellus* 307.3 ± 88.6
	Chironomus staegeri 56.7 ± 38.6	*Chironomus riparius* 117.3 ± 66.0	*Dicrotendipes nervosus* 44.7 ± 11.9	*Cladopelma viridula* 100.3 ± 74.9
	Paratanytarsus sp. 1 54.0 ± 22.5	*Paratanytarsus* sp. 1 83.3 ± 38.2	*Chironomus atrella* 28.7 ± 13.1	*Chironomus atrella* 85.7 ± 24.2
Deep	*Corynoneura* cf. *scutellata* 4600.0 ± 2415.6	*Corynoneura* cf. *scutellata* 895.0 ± 424.3	*Chironomus tentans* 678.0 ± 324.9	*Chironomus tentans* 4522.0 ± 575.2
	Paratanytarsus sp. 1 504.3 ± 162.0	*Dicrotendipes nervosus* 155.3 ± 67.8	*Chironomus atrella* 491.0 ± 289.2	*Glyptotendipes barbipes* 1523.3 ± 636.7
	Dicrotendipes nervosus 417.3 ± 90.0	*Chironomus atrella* 64.0 ± 27.4	*Corynoneura* cf. *scutellata* 341.3 ± 54.2	*Cricotopus sylvestris* 352.3 ± 175.3
	Parachironomus sp. 3 102.3 ± 25.8	*Limnophyes prolongatus* 48.7 ± 24.8	*Cricotopus sylvestris* 336.3 ± 66.8	*Dicrotendipes nervosus* 223.7 ± 55.9
	Parachironomus tenuicaudatus 101.7 ± 28.5	*Paratanytarsus* sp. 1 44.7 ± 25.0	*Dicrotendipes nervosus* 220.3 ± 31.7	*Cricotopus ornatus* 212.0 ± 144.0

Table 2.5. Literature references for habitat and food habits of dominant chironomid species collected from the experimental cells.

Reference	Habitat	Food Habits
Tanypus punctipennis		
Fellton (1940)	- lake bottom	- predacious; feeding on newly hatched and older chironomid larvae
Oláh (1976)	- lake; open water sediments	- fed mainly on diatoms
Titmus and Badcock (1981)	- gravel pit-lake bottom	- fed mainly on unicellular algae
Corynoneura scutellata		
Kesler (1981)	- free-living on submerged surfaces	- grazers of periphyton
Cricotopus sylvestris		
Darby (1962)	- tubes on the surface of the mud, bottom debris or submersed vegetation	- fed on diatoms, algal debris, and green algae
Menzie (1981)	- on submersed plants when present or on the bottom	
Cricotopus ornatus		
Swanson and Hammer (1983)	- tubes on the sediment, algal mats and submersed vegetation	- not reported
Chironomus tentans		
Sadler (1935)	- tubes in the sediment or algae	- will eat whatever is offered, but where algae are present in sufficient quantities they comprise the main bulk of the diet
Palmén and Aho (1966)	- shallow water with large amounts of detritus as substratum	- not reported

Table 2.5. continued...

Reference	Habitat	Food Habits
Hall et al. (1970)	- tubes in the sediment	- filters plankton during the day and searches the sediment surface at night for larger food items
Topping (1971)	- soft ooze and detritus	- not reported
Mason and Bryant (1975)	- within dead *Typha* stems	- brown detrital material of rotting *Typha* and no living algae
Dicrotendipes nervosus		
Fellton (1940)	- restricted to green algal mats	- not reported
Moore (1980)	- organically rich lake sediments	- detritus, very little algae
Glyptotendipes barbipes		
Kimerle and Anderson (1971)	- tubes in the sediments	- irrigation of the tube supplies sestonic food particles, primarily algal cells
Driver (1977)	- axiles of *Scolochloa*	- not reported
Wrubleski and Rosenberg (1984)	- miner of polystyrene foam	- not reported
Paratanytarsus sp. 1		
Wrubleski (unpubl. observ.)	- tubes on flooded vegetation	- grazing algae

Table 2.6. Species richness, diversity, relative dominance and the most abundant species of Chironomidae collected from Bone Pile Pond, Delta Marsh in 1980 and 1981 (calculated from data in Wrubleski and Rosenberg 1990). Abundant species are listed in decreasing order of abundance.

		Potamogeton	*Scirpus*	*Typha*
Number of Species		53-62	42-58	49-49
Diversity (H')		2.76-3.65	3.36-3.45	3.52-3.69
Relative Dominance Index		61.2-45.2	44.9-46.6	46.4-40.2
Dominant Species				
	1980	*Tanypus punctipennis*	*Limnophyes immucronatus*	*Limnophyes prolongatus*
		Derotanypus alaskensis[1]	*Limnophyes prolongatus*	*Limnophyes immucronatus*
		Chironomus tentans	*Dicrotendipes nervosus*	*Chironomus tentans*
		Glyptotendipes barbipes	*Derotanypus alaskensis*	*Derotanypus alaskensis*
		Corynoneura cf. *scutellata*	*Paratanytarsus* sp. 1	*Tanypus punctipennis*
	1981	*Cricotopus sylvestris*	*Paratanytarsus* sp. 1	*Cricotopus sylvestris*
		Tanypus punctipennis	*Limnophyes prolongatus*	*Paratanytarsus* sp. 1
		Glyptotendipes barbipes	*Glyptotendipes lobiferus*	*Limnophyes prolongatus*
		Cladotanytarsus sp.	*Corynoneura* cf. *scutellata*	*Corynoneura* cf. *scutellata*
		Corynoneura cf. *scutellata*	*Cricotopus sylvestris*	*Tanypus punctipennis*

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[1] As *Psectrotanypus alaskensis*.

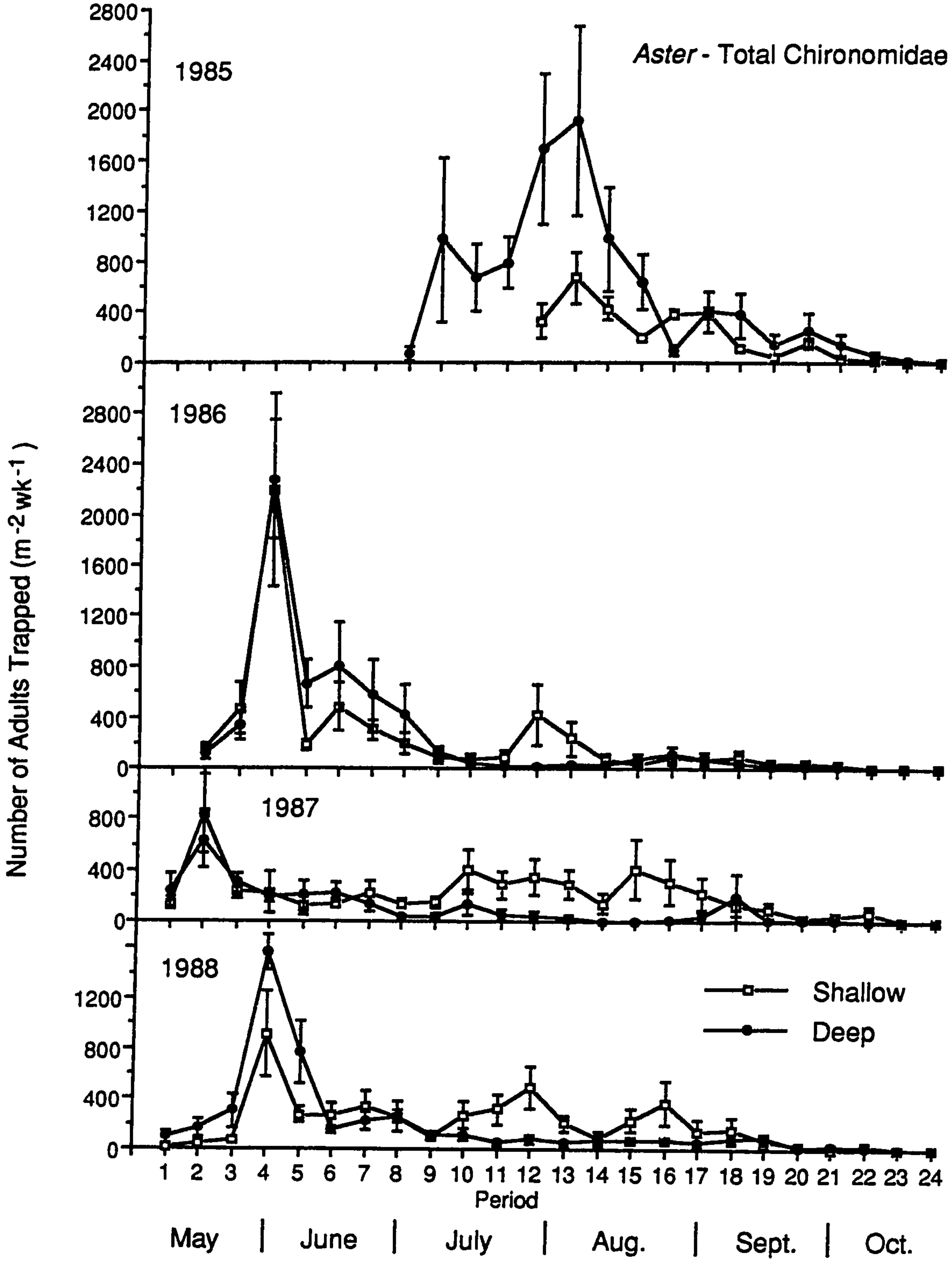


Figure 2.1. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Aster* habitat of the experimental cells.

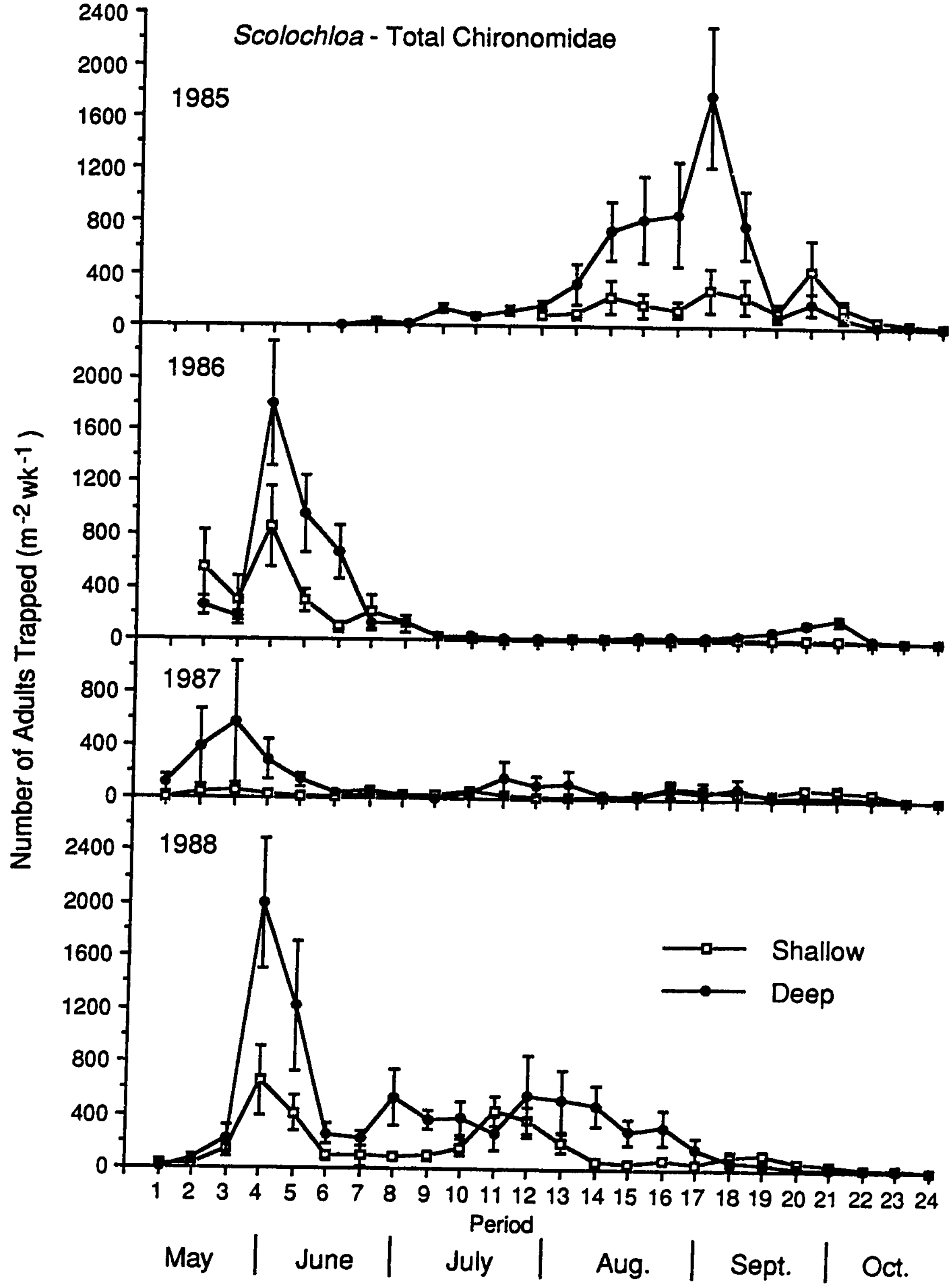


Figure 2.2. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Scolochloa* habitat of the experimental cells.

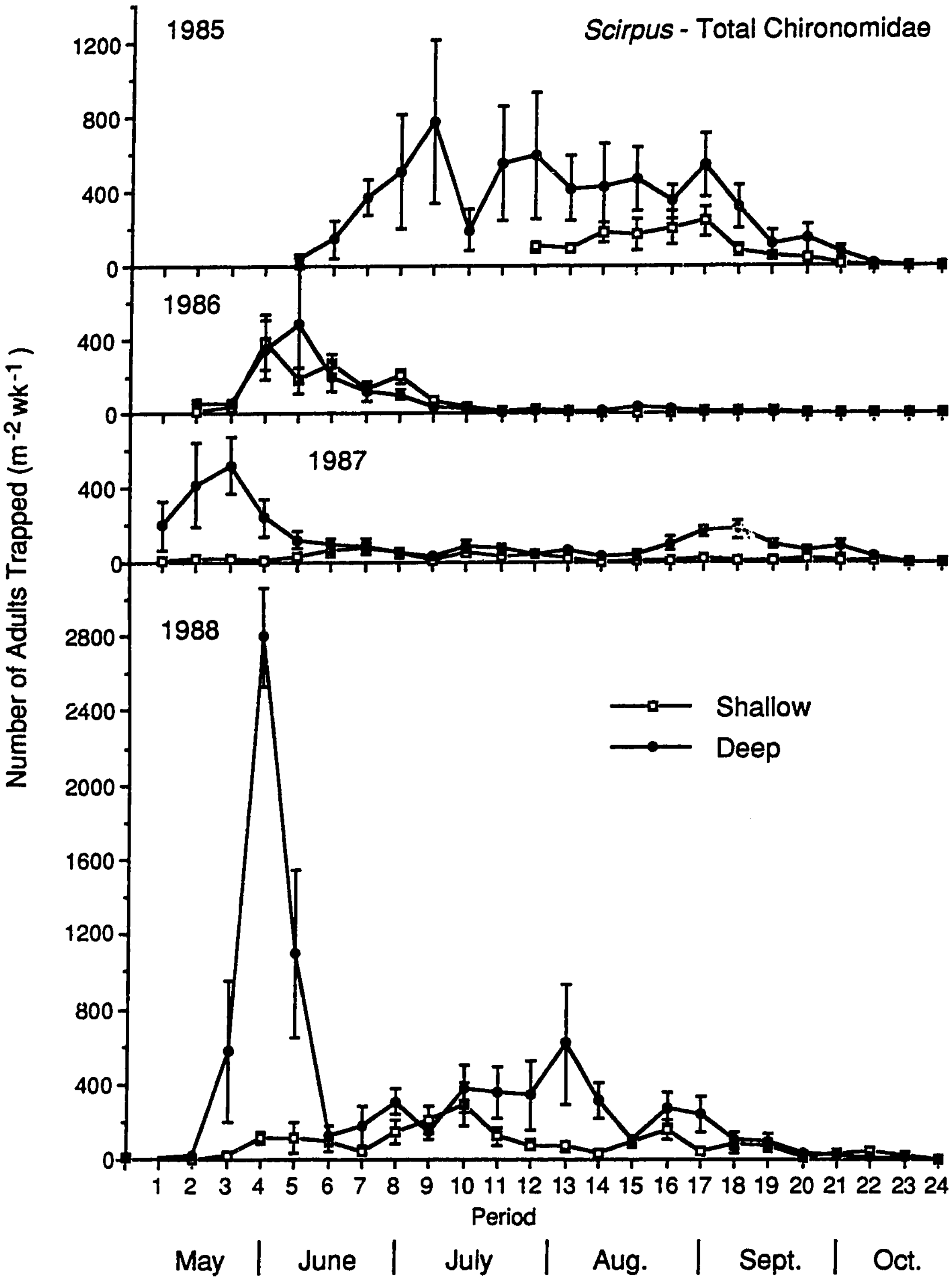


Figure 2.3. Seasonal trends in mean (± SE, n=6) weekly emergence for Chironomidae from the *Scirpus* habitat of the experimental cells.

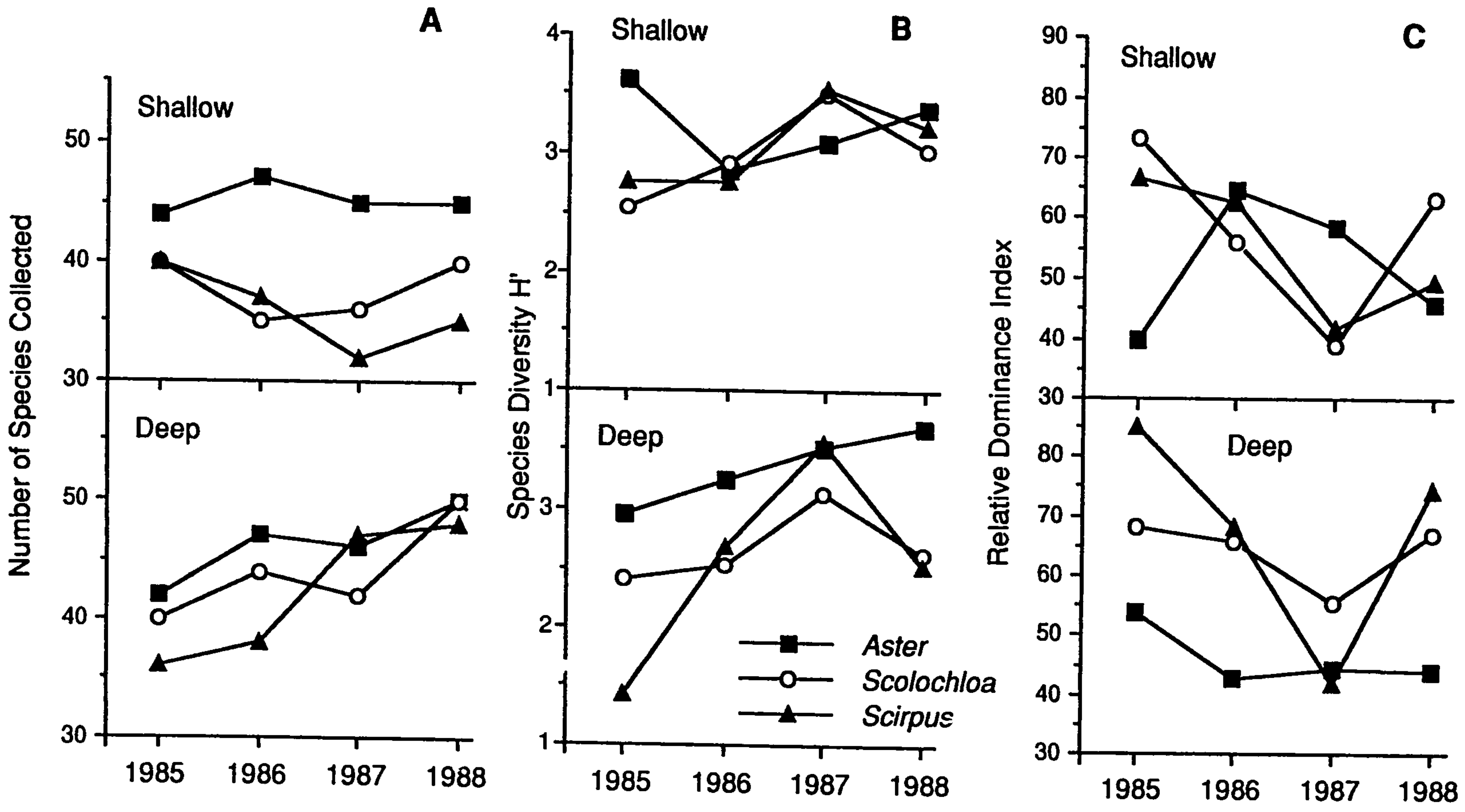


Figure 2.4. Numbers of species (A), species diversity (B) and the Relative Dominance Index (C) of Chironomidae collected from the three habitats and two water depths in the experimental cells.

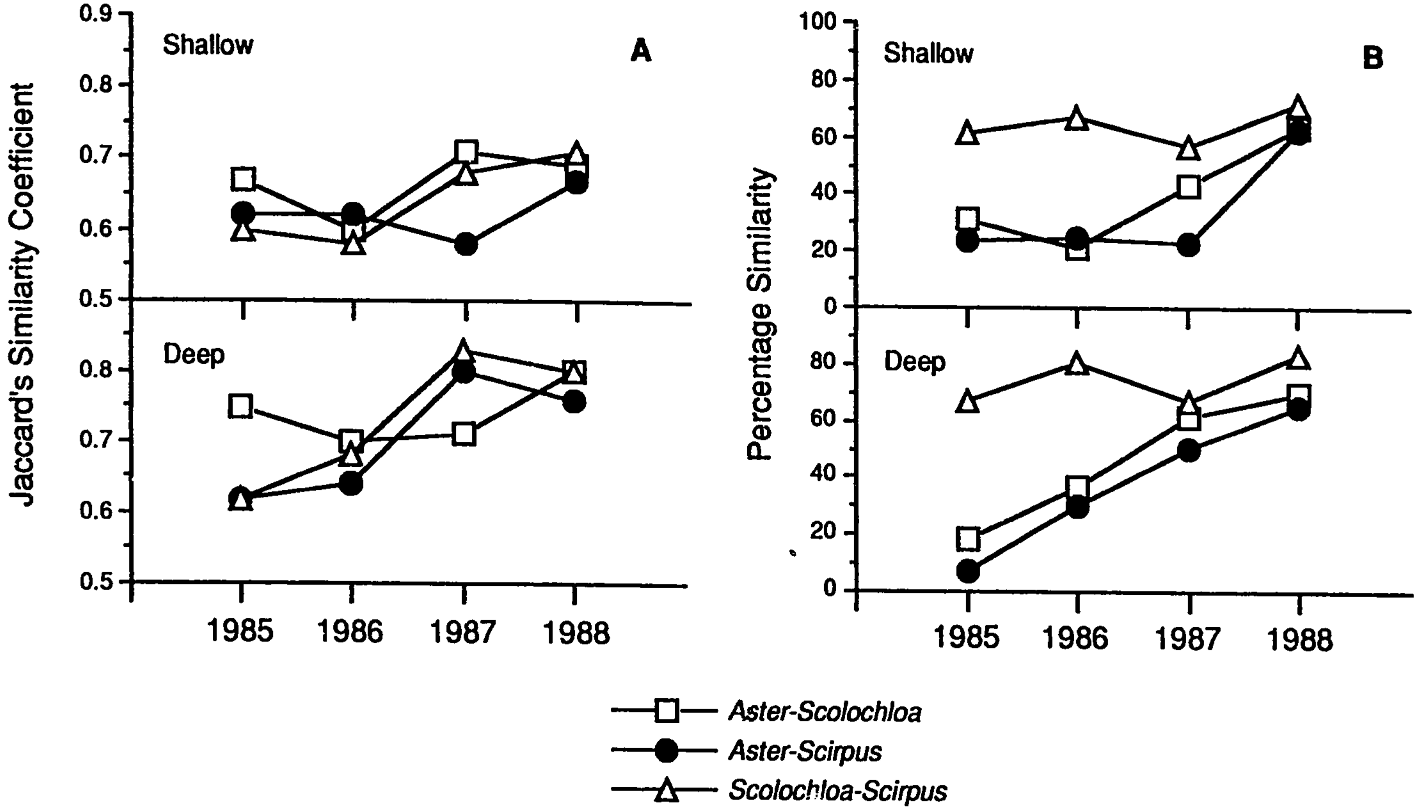


Figure 2.5. Jaccard's similarity coefficient (A) and percentage similarity values (B) for among habitat comparisons of chironomid emergence from the experimental cells.

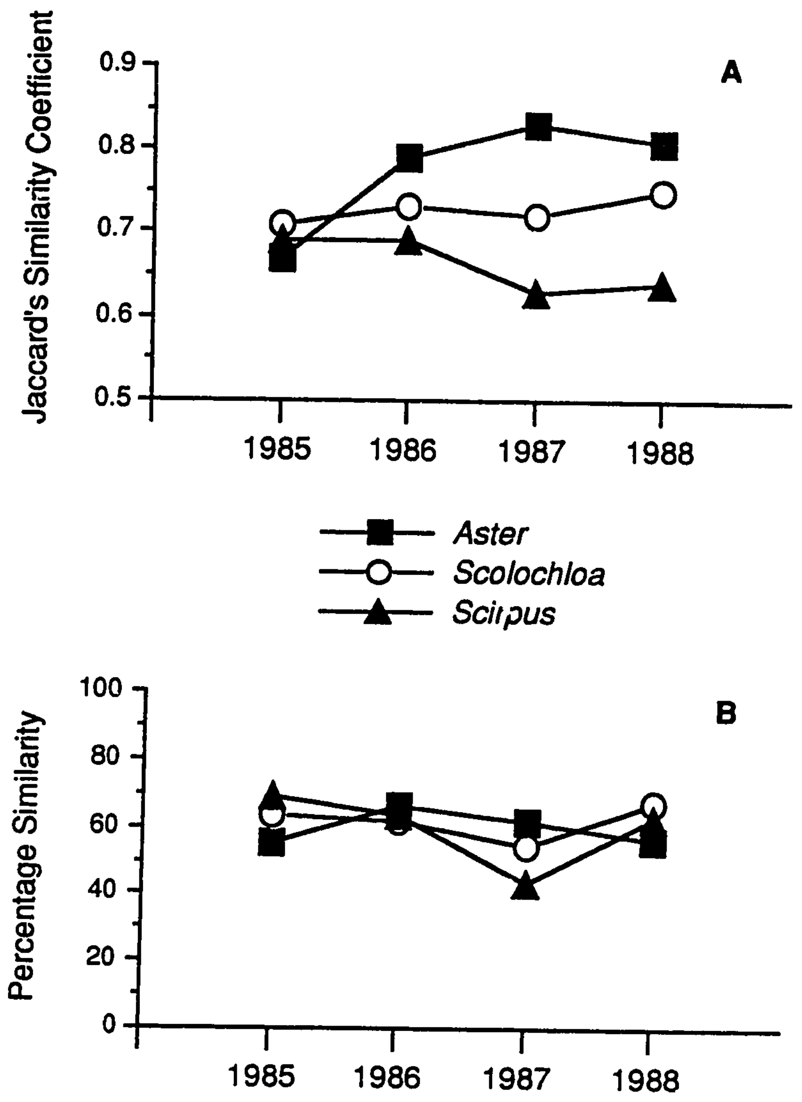


Figure 2.6. Jaccard's similarity coefficient (A) and percentage similarity values (B) for between depth comparisons of chironomid emergence from the experimental cells.

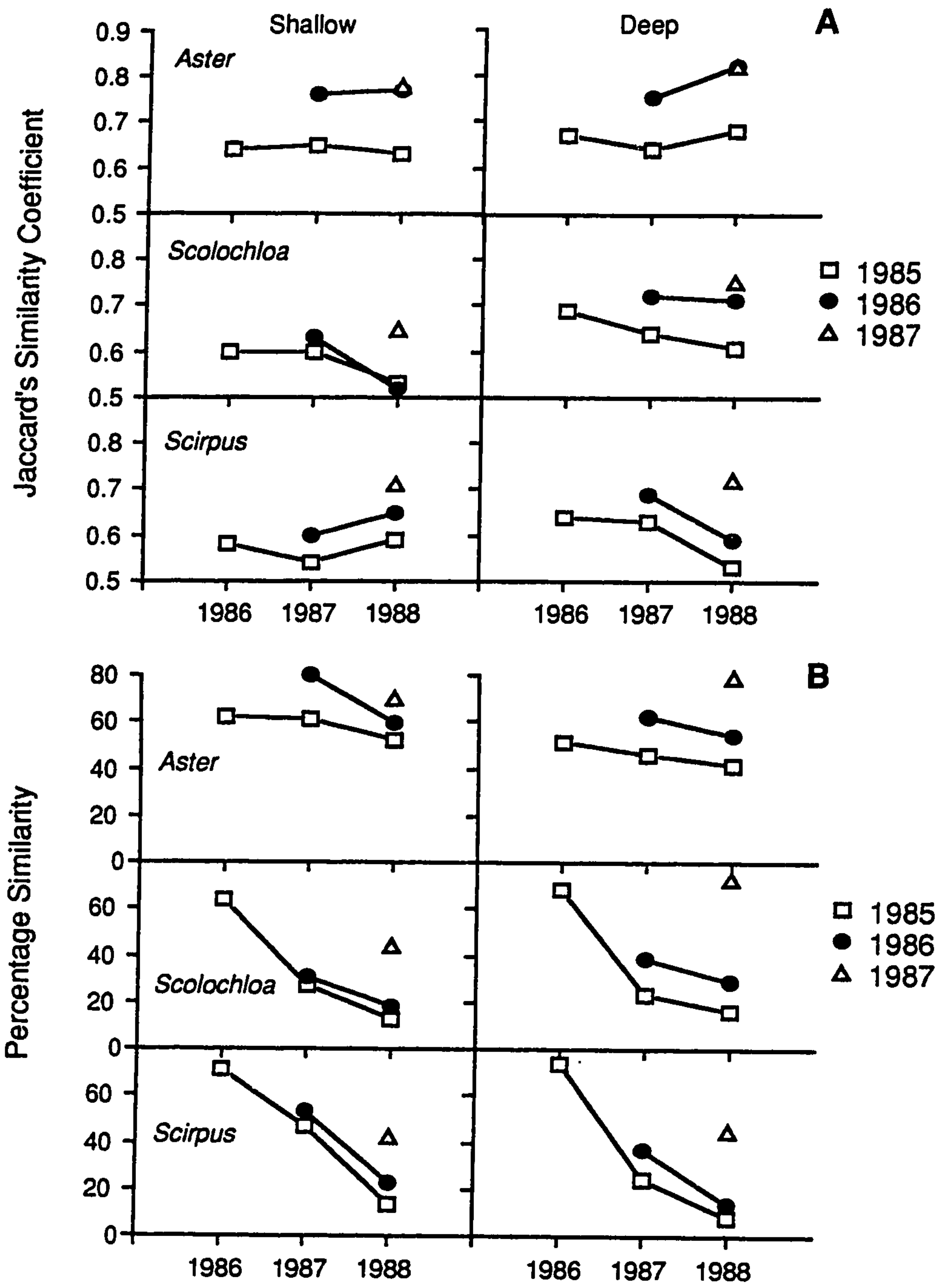
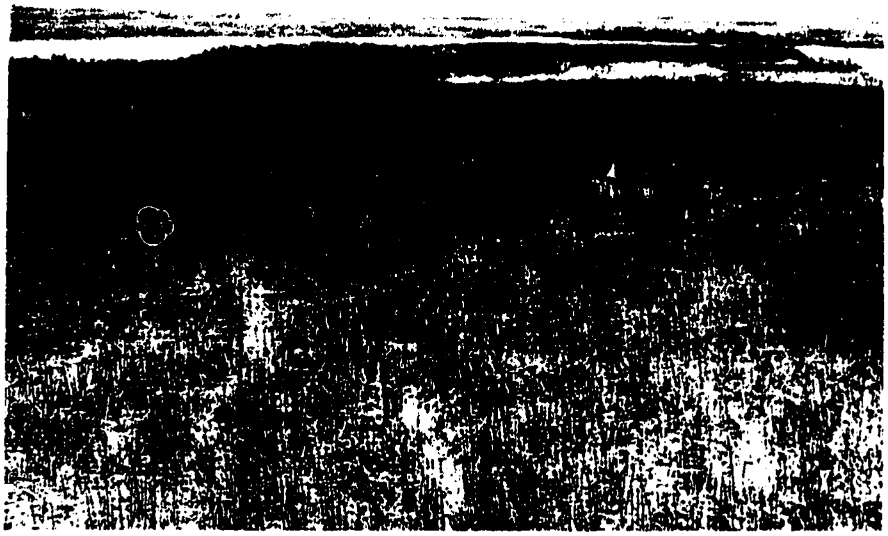


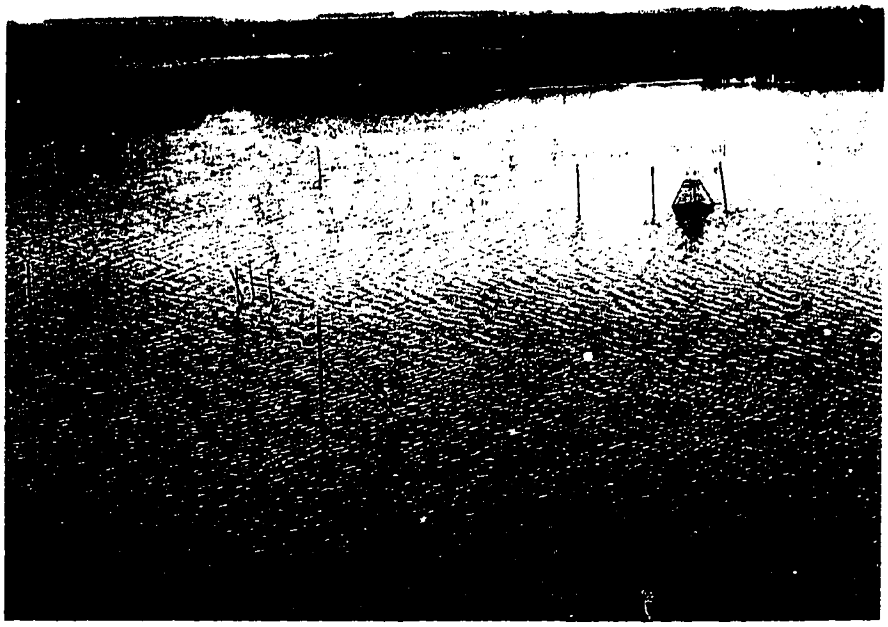
Figure 2.7. Jaccard's similarity coefficient (A) and percentage similarity values (B) for comparisons of chironomid emergence among years from the experimental cells.

Figure 2.8. The south end of cell 1 of the experimental cells showing loss of *Scirpus* at deep sites over a two year period. A. July, 1986. B. July, 1988.

A



B



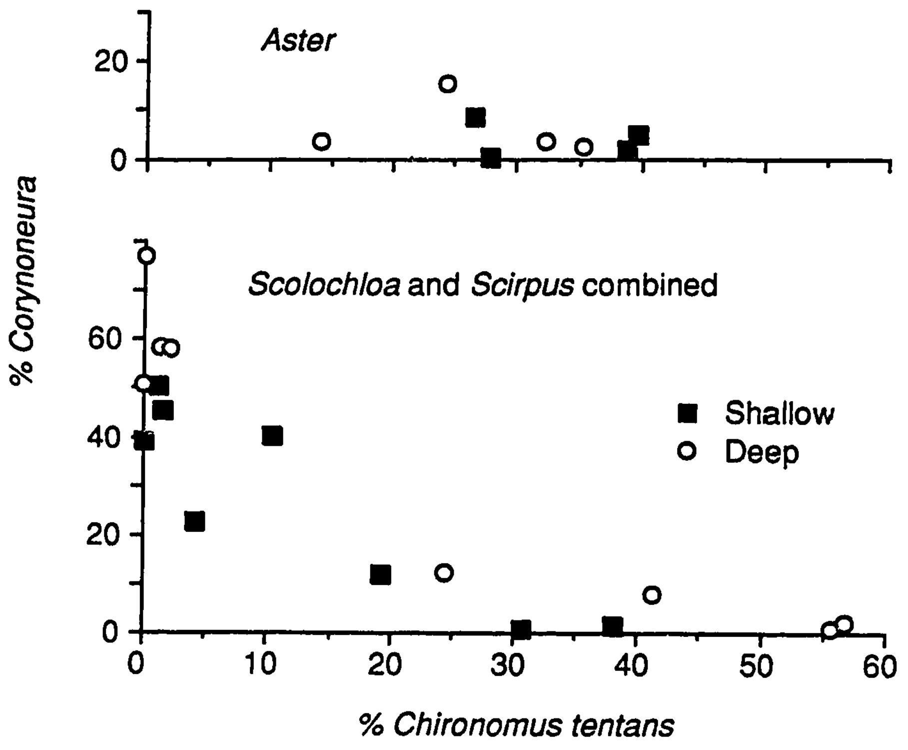


Figure 2.9. Proportion of chironomid emergence represented by *Chironomus tentans* and *Corynoneura* cf. *scutellata* from the three habitats sampled in the experimental cells.

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3. MANAGEMENT OF FRESHWATER WETLANDS: RESPONSES OF THE CHIRONOMIDAE (DIPTERA) TO THE EXPERIMENTAL FLOODING OF A SERIES OF DRAWDOWN MARSHES

3.1 SYNOPSIS

The Chironomidae (Diptera) are an important food resource for breeding waterfowl and their young. However, few attempts have been made to document their responses to wetland management. This study followed chironomid responses to the experimental flooding of ten diked areas in the Delta Marsh, Manitoba. Emergence traps were used to monitor chironomid emergence from three preflood vegetation types (the terrestrial annual *Aster laurentianus,* and two emergent macrophytes, *Scolochloa festucacea* and *Scirpus lacustris validus*) flooded at two water depths (shallow: 20-40 cm, deep: 50-70 cm) over a four year period. The highest number of chironomids (9,168 m^{-2} yr^{-1}) emerged from the deep *Aster* sites in the first year of flooding. The highest biomass of chironomids (22,007 mg m^{-2} yr^{-1}) was from the deep *Scirpus* sites in the fourth year. Numbers, biomass and size classes of emerging chironomids were similar over the four years from the *Aster* habitat. However, the *Scolochloa* and *Scirpus* habitats were dominated initially by the smallest size-class, but shifted steadily toward production of much larger individuals over the four-year experiment. The potential of chironomids as a food resource for waterfowl was greatest from the *Aster* habitat during the first few years of flooding but as a consequence of shifts in species composition became greater in the *Scolochloa* and *Scirpus* habitats in the third and fourth years.

3.2 INTRODUCTION

Drawdown (artificial drainage) and reflooding have been increasingly used in marsh management in an effort to restore declining productivity of wetlands (Weller 1978). Stable water levels apparently are detrimental to long-term wetland productivity (Harris and Marshall 1963; Weller 1978). Drawdown enables many emergent macrophytes, as well as terrestrial annuals, to become established on the dry marsh bottom and reapplication of water floods this vegetation. The emergent macrophytes survive, depending upon the water depth, but the terrestrial plants drown and contribute to the detritus food chain.

Aquatic invertebrates of freshwater marshes are an extremely important food resource for waterfowl (e.g., Krapu 1981; Sugden 1973; Street 1977, 1978; Murkin and Batt 1987) and high use of new wetlands by waterfowl is believed to be a result, in part, of high invertebrate abundances in these new areas. McKnight and Low (1969) reported high densities of chironomids and corixids after reflooding of drawdown impoundments in Utah. Whitman (1974) reported that highest invertebrate densities occurred in impoundments less than four years old, and older impoundments had fewer invertebrates and less waterfowl use. Peak production of duck broods on a shallow Swedish lake was coincident with peak chironomid abundances, five years after flooding (Danell and Sjöberg 1982). However, not all studies have recorded large increases in invertebrates following drawdown and reflooding. Kadlec (1962) reported very low densities of invertebrates following reflooding of a large impoundment in Michigan and suggested that it may be harmful to invertebrate populations.

The vegetational changes that take place in wetlands have received intensive study (e.g., Weller and Fredrickson 1974; van der Valk and Davis 1978; van der Valk 1981, 1982, 1987 and references therein), but invertebrate responses to these changes are not well understood. Trends in development of invertebrate communities have been suggested from several studies which sampled wetlands of different ages (Whitman 1974) or vegetational structure (Voigts 1976). Danell and Sjöberg (1982) followed invertebrate responses in years 3-7 after creation of a shallow lake in northern Sweden, and Kenow and Rusch (1989) reported the responses of the nektonic invertebrate community to three years of continual flooding in several impoundments of the Horicon Marsh, Wisconsin. However, invertebrate community development from the time of reflooding has not been followed within a single wetland. In this study I describe the responses of the Chironomidae (numbers, biomass and size classes) to the reflooding of a series of experimental marshes during a four year period. Chironomids are one of the most abundant aquatic insect groups within these habitats and are also a valuable waterfowl food (Wrubleski 1987).

3.3 MATERIALS AND METHODS

3.3.1 Study area. This study was conducted within the experimental marshes (cells) of the Marsh Ecology Research Program (MERP) in the Delta Marsh, in south-central Manitoba (50° 11' N, 98° 19' W). A complex of 10 contiguous 4-6 ha diked marshes were built in 1979, of earth excavated from within each cell. Water levels were manipulated and maintained with electric pumps. Descriptions of the long-term experimental design and water-level manipulations within the cells are given in Batt et al. (1983), Murkin et al. (1984) and van der Valk et al. (1988). Vegetation and water chemistry in the cells have been described by Kadlec (1986a,b, 1989), van der Valk and Welling (1988) and van der Valk et al. (1989). During 1983 and 1984 the cells were drained (drawdown). Water was reapplied in June-August 1985.

3.3.2 Sampling. Floating emergence traps were used to sample adult chironomids at the water surface. Emergence traps have two main advantages over conventional bottom sampling; adults can be identified more readily to species than benthic larvae, and emergence samples require less effort per sample and thus more habitats can be sampled. The trap used was a modified version of the 'week' trap (basal area = 0.5 m^2) described by LeSage and Harrison (1979).

Emergence trap sites were established within the cells in the spring and summer of 1985. Sites were stratified according to pre-flood habitat and water depth. Three of the dominant habitat types, based on preflood vegetation surveys, were selected for sampling; these were *Aster laurentianus* Fern., *Scolochloa festucacea* (Willd.) Link (whitetop) and *Scirpus lacustris* L. ssp. *validus* (Wahl.) Koyama (softstem bulrush). Each habitat was sampled at two water depths, shallow (20-40 cm) and deep (50-70 cm). Six traps were used for each habitat-water depth combination for a total of 36 traps.

Traps were set out as soon as sufficient water was in place to float them. Deep water sites, which were at lower elevations, were flooded much earlier than shallow water sites at higher elevations. Consequently initiation of sampling varied between 16 May and 20 July. Within each habitat-water depth combination the six emergence trap sites were not flooded at the same time, but most were flooded within a few weeks of each other, except for two shallow *Scirpus* sites that were flooded 9 weeks before the other four sites (data from these 9 weeks were excluded from the analyses). In 1987 and 1988, traps were set out at the same sites in the last week of April and emptied weekly through the third week of October to provide data for 24 weeks or sample periods. In 1986, traps were not set out until the first week of May and data were collected over 23 weeks.

3.3.3 Data summation. All chironomids were identified to species (see Chapter 2). Numbers collected from each trap during every week were summed for the entire sampling season, multiplied by 2 to give no. m^{-2} and then used to determine mean annual emergence (no. $m^{-2} yr^{-1}$ ± SE, n=6) for each habitat-water depth combination. Procedures used to generate missing data for traps lost due to muskrat damage and wind storms are reported in Appendix 1. A length-weight regression (Wrubleski and Rosenberg 1990) was used to determine biomass (mg m^{-2} yr^{-1}) of emerging chironomids. Separate counts for each sex were not made during sorting, therefore sex ratios from a previous study in the Delta Marsh (Wrubleski 1984) were used to partition the numbers for each species between males and females before determination of biomass. In addition, a relative frequency distribution of size classes (1 mm) was determined for each habitat-water depth combination, based on body length (pronotum to penultimate abdominal segment).

3.3.4 Statistical analysis. Emergence numbers and biomass were compared using a split plot ANOVA with habitat, depth and depth × habitat as whole plot sources which were tested against traps nested within depth × habitat (Table 3.1). Year, year × depth, year × habitat and year × depth × habitat were split plot sources which were tested against the residual (year × trap (depth × habitat)). Analyses were conducted using the PROC GLM procedure of SAS (SAS Institute Inc. 1985). Data were $\log_{10}(x+1)$ transformed prior to analysis to stabilize the variances, but untransformed data are presented in the figures. Year comparisons were done within habitat and depths by one-way ANOVA followed by Tukey's HSD test [$P<.05$; as recommended by Day and Quinn (1989)] to compare individual year means Habitats were compared within years and depths with one-way ANOVA and Tukey's HSD test to compare individual habitats, and depths were compared within habitat and year by *t*-tests (*P*<.05). All one-way ANOVAs, Tukey's HSD tests and *t*-tests were done with SYSTAT (vers. 3.2) on a Macintosh computer.

3.4 RESULTS

The overall split plot ANOVA indicated that numbers and biomass of emerging chironomids differed significantly between depths, and among habitats and years (Table 3.1). The depth × habitat interaction was nearly significant for both numbers (F= 2.71, df=2,30, *P*=.08) and biomass (F=2.81, df=2,30, *P*=.08) suggesting that chironomids responded differently to preflood vegetation and depth of flooding. Numbers of chironomids emerging each year varied between depths (depth × year, F=2.87, df=3,90, *P*=.04) but biomass did not (F=1.19, df=3,90, *P*=.32). Data for both annual numbers and biomass showed significant interactions between habitat and year indicating that habitats had different outputs over the four years. The three-way depth × habitat × year interaction was significant for biomass and nearly so for numbers, indicating that chironomids responded differently to preflood vegetation and water depth and that these differences also varied annually.

One-way ANOVA for habitat comparisons within depths and years indicated that in 1986, *Scirpus*-deep had a significantly lower emergence than the other two habitats, and in 1987 *Aster*-shallow had a higher emergence than the other two shallow habitats (Figure 3.1). Differences among habitats in chironomid biomass were more striking than were those for numbers (Figure 3.2). Biomass of chironomids emerging from *Aster* was much higher than that from the other two habitats in 1985, 1986 and 1987 in the shallow depths and 1985 and 1986 in the deeper habitats. In 1986 all three habitats differed significantly from each other in the deep sites and in 1988 *Scirpus* had a much higher emergence than *Aster*.

In 1985, significantly more chironomids emerged from the deep sites than from shallow sites in *Aster* and *Scirpus*, and the same trend was marginally significant (*t*=2.211, *P*=0.051) in *Scolochloa* (Figure 3.1). These differences may reflect the fact that deep sites were flooded much earlier than shallow sites. Therefore, these data were reanalyzed using equal time periods (i.e., those weeks that both habitats were flooded together). Because these analyses indicate no differences between depths (*Aster*: numbers *t*=0.65, *P*=.53, biomass *t*=1.51, *P*=.16; *Scirpus*: numbers *t*=1.58, *P*=.14), I conclude that the significant differences found above were due simply to the deep sites being flooded for longer periods. In 1986, no differences were found between depths. In both 1987 and 1988 higher numbers and biomass of chironomids emerged from the deep sites in *Scirpus* compared to the shallow sites. In *Scolochloa*, there were marginally more chironomids emerging from deep water in 1988 (number: *t*=2.122, *P*=.06; biomass: *t*=1.958, *P*=.08).

In shallow water, similar numbers of chironomids emerged in all years, except for a significant increase in emergence in the *Scirpus* habitat between 1987 and 1988. In the deep water sites, I observed a trend for high emergence in 1985, followed by declining numbers during 1986 and 1987 and a subsequent increase in 1988 (Figure 3.1). In terms of biomass, a significant increase in emergence in 1988 was observed in both *Scolochloa* and *Scirpus* in the shallow waters. This increase was also observed in the deep sites but started in 1987 in the *Scirpus* habitat. Biomass of emerging chironomids did not differ over the four years in shallow or [illegible] from *Aster*.

There were conspicuous changes [illegible] of emerging chironomids in *Scolochloa* and *Scirpus* habitats during [illegible] four years (Figure 3.3) which reflected changes in species composition (Chapter 2). In 1985, emergence was dominated by small individuals, particularly in the 1-1.99 mm size class. Over the next four years there was a shift to much larger individuals. This was very apparent for the deep habitats where the 9.00 - 9.99 mm size class dominated emergence. The shallow habitats had a more bimodal distribution of sizes, similar to that observed in the *Aster* habitat. In *Aster*, the pattern present in all four years and both depths was similar with a bimodal distribution of sizes with peaks around 2-5 mm and 7-10 mm.

3.5 DISCUSSION

3.5.1 Reflooding of drawdown marshes and its effect on the chironomids. Several studies have reported larger numbers of invertebrates in newly flooded marsh habitats than in nearby older wetlands (McKnight and Low 1969; Whitman 1974; Street and Titmus 1979). After the first four years of flooding, the highest number of chironomids recorded from the experimental cells (9,168 m^{-2} yr^{-1} from deep *Aster* sites in 1985) was only about two-thirds of the highest numbers that have been recorded from the unmanaged Delta Marsh (15,601.2 m^{-2} yr^{-1} from the pondweed habitat of Bone Pile Pond [BPP] [Wrubleski and Rosenberg 1990]). Deep *Scirpus* sites, however, had comparable emergence numbers (4,574.4 - 8,148 m^{-2} yr^{-1}) to that found in the *Scirpus* habitat of BPP (4,024.0 - 6,193.2 m^{-2} yr^{-1}). Numbers of chironomids emerging from shallow *Scolochloa* sites (841.0 - 3,340.4 m^{-2} yr^{-1}) tended to be similar to those from a seasonally flooded *Scolochloa* habitat in the Delta Marsh (2,500 m^{-2} yr^{-1} [Wrubleski 1987]), but numbers emerging from deep *Scolochloa* sites, particularly in the first (6,165.4 m^{-2} yr^{-1}) and fourth (7,983.6 m^{-2} yr^{-1}) years, were much higher.

Although highest numbers emerging from the MERP cells were not as high as from the unmanaged Delta Marsh, biomass was significantly greater. Highest biomass emerging from the experimental cells was from deep *Scirpus* sites in 1988 (22,007.22 mg m^{-2} yr^{-1}) and was more than 5 times that found in the *Scirpus* habitat of BPP (2,922 - 3,866.2 mg m^{-2} yr^{-1}) and almost twice that of the highest biomass estimated from the pondweed habitat (9,174.0 - 13,431.5

mg $m^{-2} yr^{-1}$), the most productive habitat in BPP (Wrubleski and Rosenberg 1990). Most of this higher biomass, particularly in years three and four in the *Scolochloa* and *Scirpus* habitats, was in the larger size classes. Figure 3.4 illustrates size class distributions for chironomids emerging from BPP. It is apparent that although numbers might be higher from the pondweed habitat of BPP, most individuals were of smaller size, explaining the lower total biomass compared to the experimental cells.

Trends in numbers and biomass of chironomids emerging over the four year period differed among the habitats and depths sampled. Numbers of chironomids emerging from the shallow water depths showed few significant changes over time, whereas the deep water sites showed a general trend for high numbers emerging in the first year, with a decline in numbers in the second and/or third years in all three habitats, and significant increases by the fourth year in *Scolochloa* and *Scirpus* habitats. Biomass of chironomids emerging from both water depths showed very little change over time in *Aster*, whereas in *Scolochloa* and *Scirpus* there was a significant increase in biomass emerging by the third or fourth years of flooding. Whitman (1974) reported highest numbers of larval chironomids in wetland impoundments less than one year old. Danell and Sjöberg (1982) found highest numbers of chironomids emerging in year five of a newly flooded lake managed for waterfowl, with a considerable decline in numbers in subsequent years (emergence was not sampled during the first three years). They also noted a decrease in mean larval chironomid size from the third to seventh years of flooding. My results suggest that little change in size occurred in *Aster*, whereas in *Scolochloa* and *Scirpus* a shift to larger-sized individuals, particularly in the deep waters, occurred over the four years.

Aquatic invertebrate populations in wetland habitats do respond to changes in vegetation and water depth (Voigts 1976; Murkin and Kadlec 1986; Kenow and Rusch 1989). In the experimental cells differences in chironomid emergence were found between the *Aster* and the two emergent macrophyte habitats sampled. *Aster laurentianus* is a terrestrial annual characteristic of mud-flats, and cannot survive flooding. Consequently, a large amount of plant litter was added to the bottom in one large pulse with no or very little standing emergent vegetation present. Metaphyton developed extensively in these open, sunny areas (Wrubleski, pers. observ.). This material provided a structurally complex habitat with abundant algal production. It was colonized by a variety of chironomid species, including larger benthic and mining species such as *Chironomus tentans, C. atrella* and *Glyptotendipes barbipes*, as well as smaller epiphytic species such *Paratanytarsus* sp. 1 and several *Cricotopus* species (Chapter 2).

In the *Scolochloa* and *Scirpus* habitats, not as much litter was added to the bottom due to their initial tolerance of flooding. These dense stands of live stems shaded the bottom in these habitats restricting benthic algal production. Gurney and Robinson (1988) reported a significant negative correlation between macrophyte stem density and the amount of metaphyton present within the experimental cells. The large amount of metaphyton-free surface area provided by the stems and leaves of these emergent macrophytes provided an excellent habitat for *Corynoneura* cf. *scutellata*, the most abundant species in these habitats during the first two years of flooding (Chapter 2). The members of this genus are small free-living grazers dependent upon submersed surfaces (Kesler 1981). However, after several years of flooding, these macrophytes began to die back (van der Valk, pers comm.; Figure 2.8), particularly at the deeper flooding depths, and a large input of plant litter was added to the bottom beginning in the second year of flooding. Consequently there was a marked increase in the same benthic and mining species observed in the *Aster* habitat and a dramatic decline in the epiphytic species (Chapter 2). Driver (1977) and Murkin and Kadlec (1986) both reported increases by *Chironomus tentans* following the death of emergent macrophytes due to excessive flooding.

3.5.2 Management implications. Aquatic macroinvertebrates are an important food resource for breeding waterfowl and their young (e.g., Krapu 1981, Sugden 1973, Street 1977, 1978, Murkin and Batt 1987) and the effects of marsh management on invertebrate populations must be considered. In this experiment, preflood vegetation and depth of flooding produced different abundances of chironomids as potential waterfowl food.

Although chironomids as a group are known to be an important food resource for waterfowl the relative importances of the different species is unknown. One important consideration is probably the size of the individual chironomids produced by each habitat. Data from the experimental cells show a wide range of sizes of chironomid adults were produced and this varied by habitat and depth and over the four years of this experiment. However, studies of waterfowl food habits have generally ignored the importance of invertebrate size (Nudds and Bowlby 1984) so it is not known which species are important waterfowl food. It is unlikely that the smallest size class reported in this study (1.0 - 1.99 mm) is valuable as food for waterfowl, but all other sizes are likely to be consumed.

The *Aster* habitat produced a variety of chironomids, with many in the larger size classes becoming established at the time of flooding. *Scolochloa* and *Scirpus* on the other hand, produced very small chironomids during their first two years of flooding, and not until the third and fourth years were large numbers of the larger-sized chironomids produced. Production was greater in the deep-water habitats, depths that are probably too deep for most dabbling duck species. However, during emergence periods these chironomids become a readily available food resource for waterfowl (Swanson and Sargeant 1972; Swanson 1977; Sjöberg and Danell 1982).

The presence of emergent vegetation and the abundance of plant litter on the bottom are the two most important features regulating the abundances of the larger-sized chironomids within experimental marshes. Dense stands of emergent vegetation were beneficial to the smallest-sized chironomids but had a negative effect on the larger benthic chironomids Several studies have reported low numbers of invertebrates in dense stands of emergent macrophytes compared to other more open habitats (Voigts 1976; Wrubleski and Rosenberg 1990).

In my study, the abundance of plant litter in the *Aster* habitat at the time of flooding, and in years three and four in the *Scolochloa* and *Scirpus* habitats, was probably an important contributor to the high numbers of large benthic chironomids. Thus my results concur with suggestions by McKnight and Low (1969), Whitman (1974), Kaminski and Prince (1981) and others that abundant plant litter from the preflood vegetation is responsible for high invertebrate production observed in new wetland habitats. However, other factors are undoubtedly also important. Andersson and Danell (1982) failed in an attempt to increase invertebrate production by adding terrestrial plant litter to an existing wetland. They attributed a lack of response to the existence of abundant predatory invertebrates already present, and suggested that one benefit of drawdown was the elimination of the more slowly colonizing predatory invertebrates. A similar experiment in flooded gravel pits in England was successful in producing larger numbers of invertebrates in a habitat that was structurally very simple (Street and Titmus 1982; Street 1982).

Whitman (1974) suggested that optimum conditions for invertebrate production in newly created wetlands occurred during the first 1.5 to 4 years of age, and recommended drawdown between the ages of 5 to 7 years to improve food and cover for waterfowl. In the present study, chironomid production was high from the first application of water and continued to be high through to the fourth year, first from the flooded terrestrial vegetation and then from the drowned emergent macrophyte habitats. In the experimental cells it is anticipated that this high chironomid production will decline as the coarse detritus inputs within these habitats disappear. Because of the flooding, new emergent macrophyte regrowth will not occur so no large inputs of detritus will take place. Invertebrate production will decline in subsequent years unless submersed vegetation is able to invade and provide additional habitat for invertebrates. It is apparent that the management of freshwater wetlands for the benefit of aquatic invertebrates and thus the waterfowl, must consider the production of plant litter during the drawdown phase (Murkin et al. 1989). An abundance of vegetation must be encouraged during drawdown to provide an abundant pool of litter when water is reapplied.

Table 3.1. Split-plot ANOVA table of numbers and biomass [log(x+1) transformed data]

Source of Variation (Numbers)	SS	df	MS	F	*P*
Depth	3.6054	1	3.6054	26.40	0.0001
Habitat	2.9844	2	1.4922	10.93	0.0003
Depth x Habitat	0.7406	2	0.3703	2.71	0.0827
Trap (Depth x Habitat)	4.0973	30	0.1366		
Year	3.2500	3	1.0833	9.48	0.0001
Depth x Year	0.9845	3	0.3282	2.87	0.0407
Habitat x Year	1.7678	6	0.2946	2.58	0.0236
Depth x Habitat x Year	1.4128	6	0.2355	2.06	0.0658
Error	10.2881	90	0.1143		

Source of Variation (Biomass)	SS	df	MS	F	*P*
Depth	4.0545	1	4.0545	17.95	0.0002
Habitat	18.3149	2	9.1575	40.54	0.0001
Depth x Habitat	1.2701	2	0.6351	2.81	0.0760
Trap (Depth x Habitat)	6.7773	30	0.2259		
Year	17.7876	3	5.9292	34.15	0.0001
Depth x Year	0.6189	3	0.2063	1.19	0.3188
Habitat x Year	9.2394	6	1.5399	8.87	0.0001
Depth x Habitat x Year	3.8754	6	0.6459	3.72	0.0024
Error	15.6249	90	0.1736		

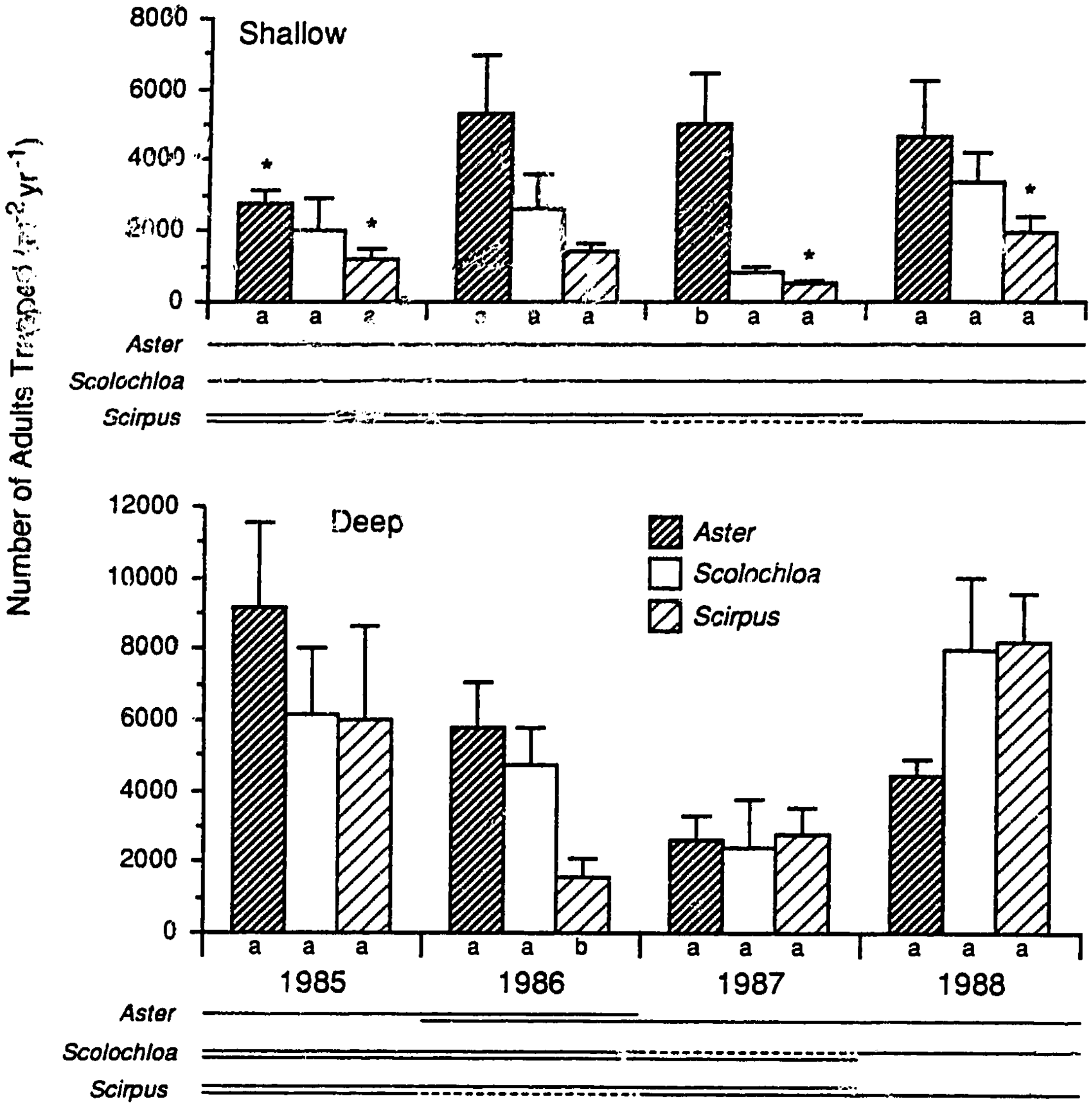

Figure 3.1. Mean (± SE, n=6) annual emergence of chironomids over a four year period from three habitats and two water depths in the experimental marshes. * indicates a significant difference between depths within habitat and year (*t*-test, *P*<.05). Habitat means with the same subscripts are not significantly different, within year and depth (Tukey's HSD test following significant ANOVA, *P*<.05). Lines below each graph indicate means that are not significantly different across years (Tukey's HSD test following significant ANOVA, *P*<.05). A dotted line is used to connect a solid line when the years that do not differ significantly are seperated by a year that does differ significantly from those underlined.

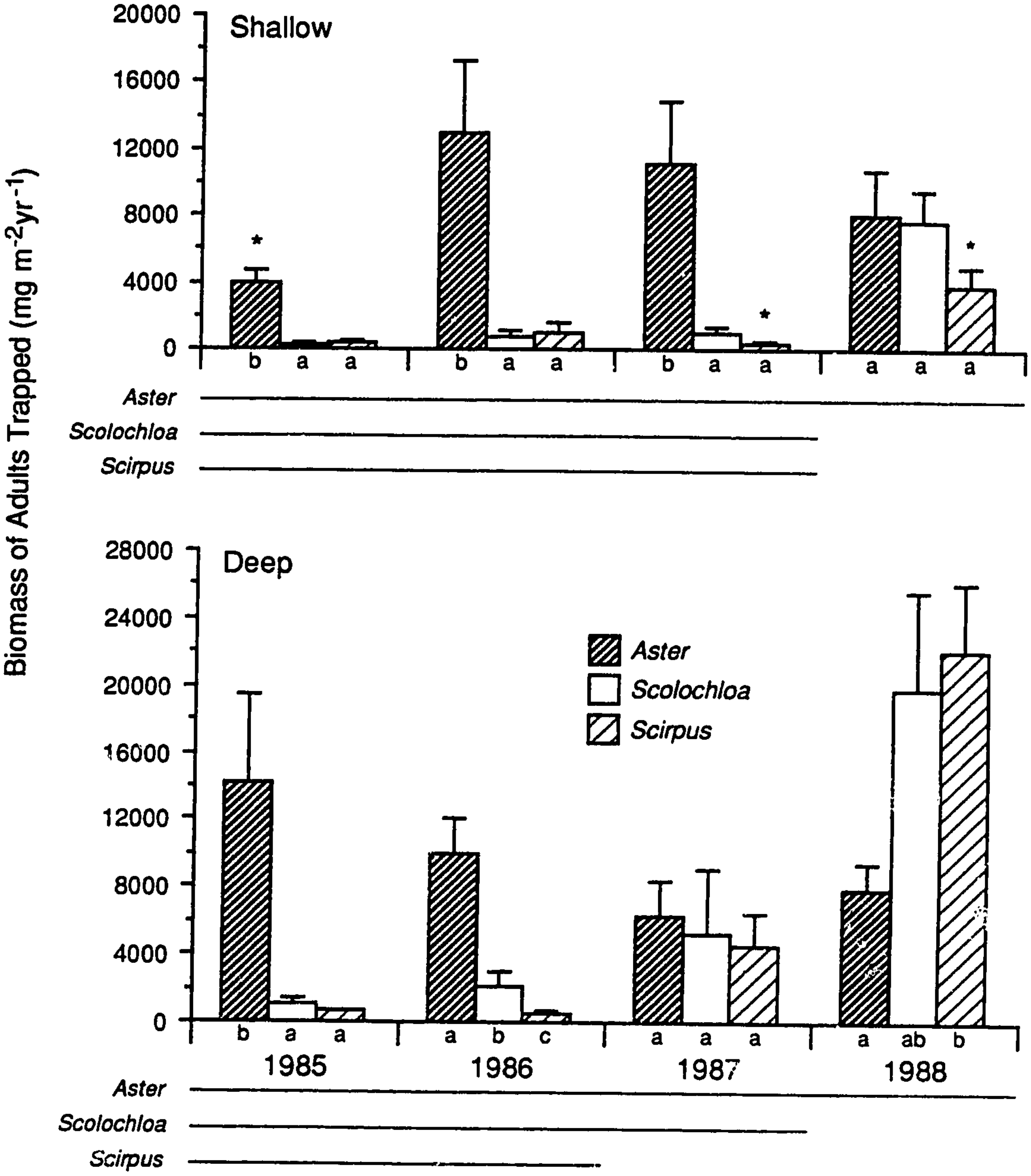

Figure 3.2. Mean (± SE, n=6) annual biomass of chironomids emerging over a four year period from three habitats and two water depths in the experimental marshes. (See Figure 3.1 for explanation of symbols).

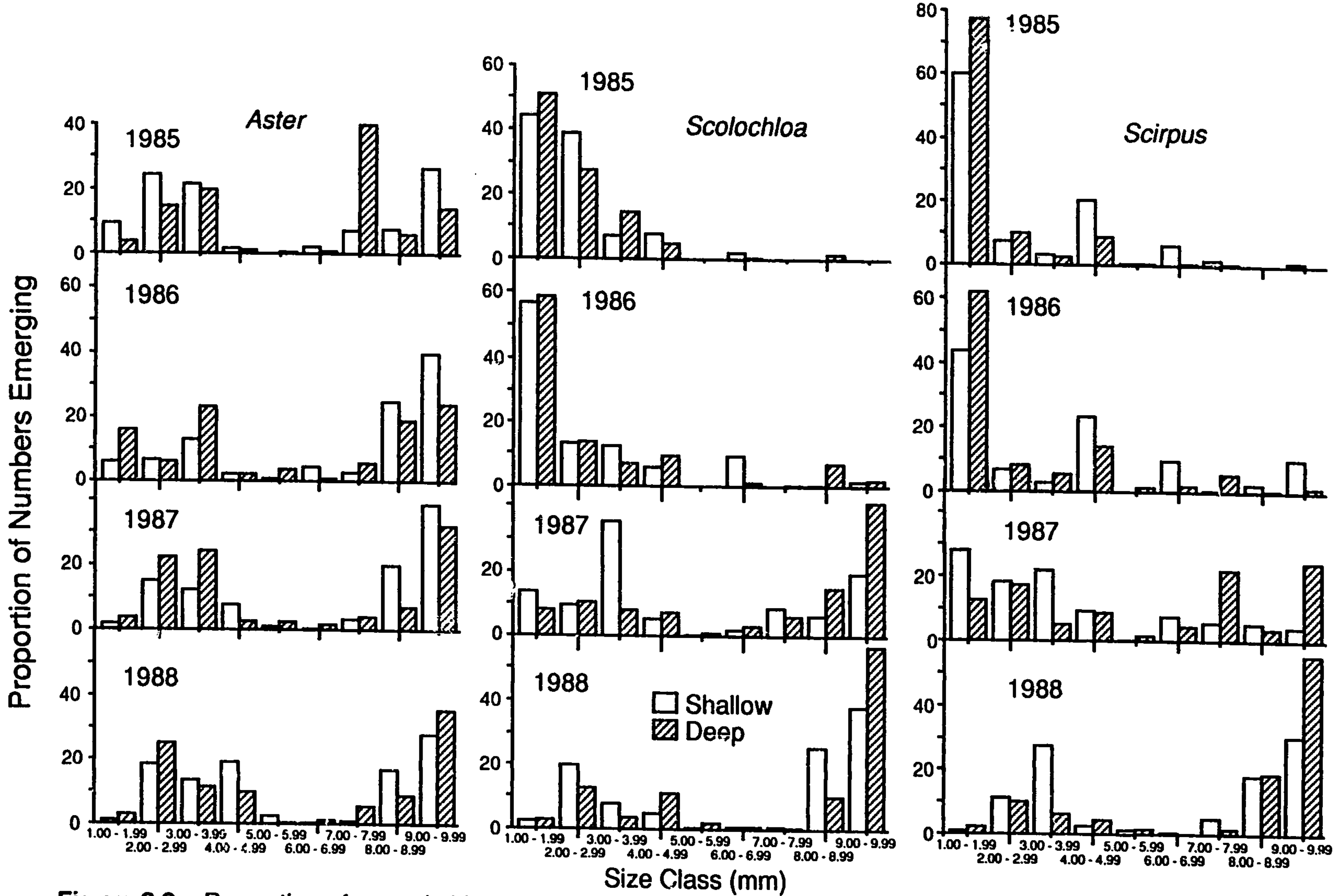

Figure 3.3. Proportion of annual chironomid emergence represented by each 1.00 mm size class over a four year period from the three habitats and two water depths sampled in the experimental marshes.

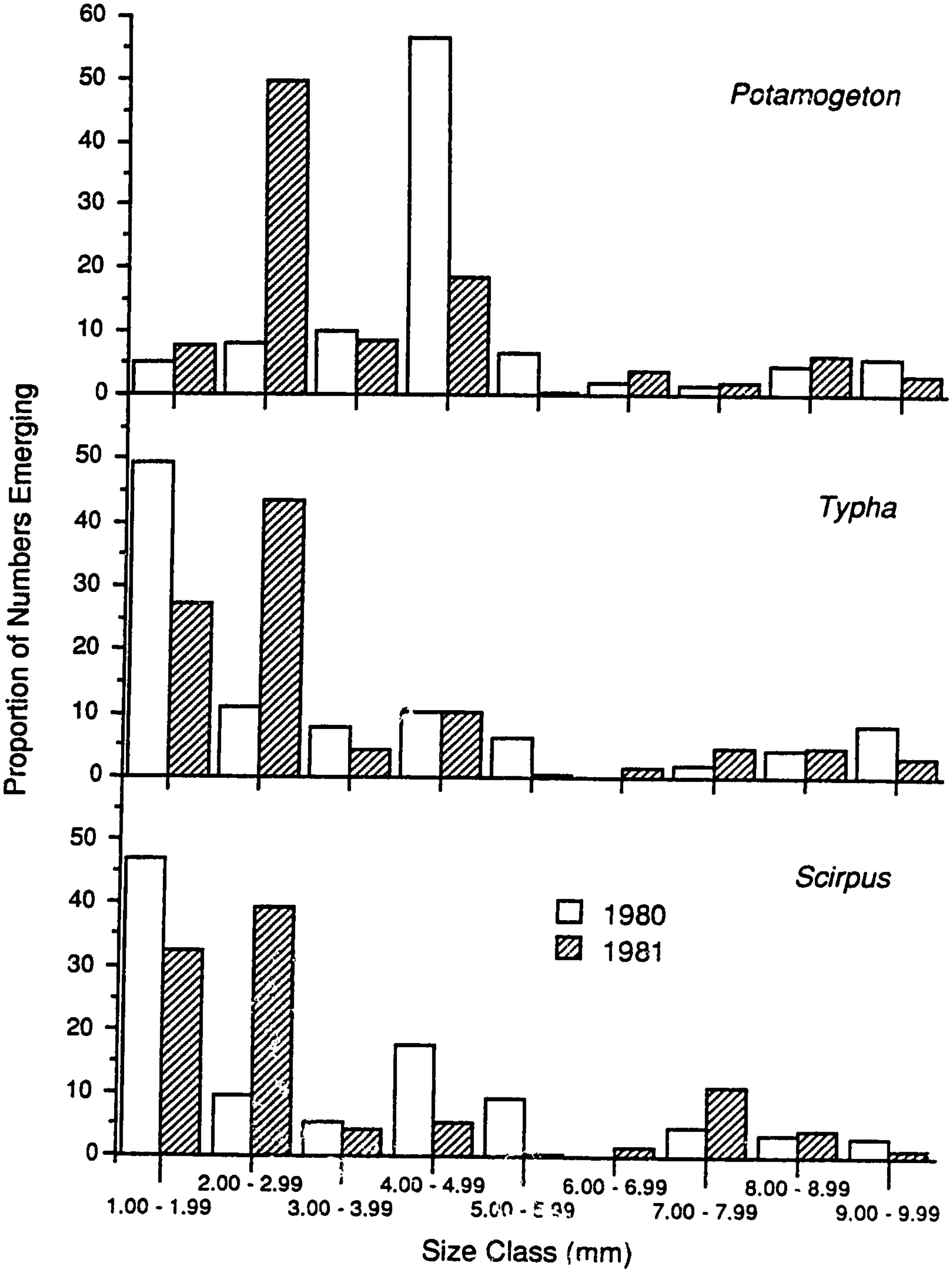

Figure 3.4. Proportion of annual chironomid emergence represented by each 1.00 mm size class over a two year period from three habitats sampled in Bone Pile Pond, Delta Marsh. Calculated from data in Wrubleski and Rosenberg (1990).

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4. THE EFFECT OF SUBMERSED MACROPHYTES ON THE BENTHIC INVERTEBRATE COMMUNITY OF A FRESHWATER MARSH

4.1 SYNOPSIS

A field experiment was undertaken in Delta Marsh, Manitoba, to examine the effect of seasonal development of submersed vegetation on benthic invertebrates. Sago pondweed (*Potamogeton pectinatus*) was either removed via clipping or permitted to grow in fenced 5 x 5 m plots. Aquatic invertebrates were sampled with emergence traps and bottom cores. Invertebrates (primarily copepods) were more abundant in the clipped plots than the pondweed plots at the end of the season. Total chironomid larvae and adult emergence did not differ between the two treatments, although *Polypedilum halterale* and *Cladotanytarsus* sp. were more abundant in the clipped plots, and *Corynoneura* cf. *scutellata* had a higher emergence from the pondweed plots. Algal biomass beneath pondweed tended to be lower than in plots where the plants had been removed suggesting that by shading the bottom, aquatic macrophytes reduce bottom algal biomass and indirectly influence benthic invertebrate communities.

4.2 INTRODUCTION

Shallow freshwater wetlands are frequently dominated by aquatic macrophytes. In northern latitudes, the seasonal development of submersed macrophytes has a major effect on the physical and biological processes within open-water areas. Submersed macrophytes alter their surrounding physico-chemical environment (e.g., Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983; Carpenter and Lodge 1986), and they influence aquatic invertebrate communities by increasing habitat structural complexity, and by providing additional food and living space within the water column for many species (e.g., Berg 1949, 1950; Krull 1970; Soszka 1975; Menzie 1980). Areas with submersed macrophytes have been reported to support higher densities of invertebrates than areas without vegetation (Wohlschlag 1950; Gerking 1957; Krull 1970), the general assumption being that these plants increase the amount of colonizable surface area for invertebrates in the water column. Recent evidence, however, suggests that invertebrate colonization of submersed macrophytes is not based solely on the amount of surface area available, but that each plant species differs in its ability to support invertebrate populations (Cyr and Downing 1988).

The habitat value of these plants has been well documented, but their negative effects on some members of the invertebrate community are not as well known. For example, Richard et al. (1985) found that the total number of zooplankton species was reduced following elimination of submersed vegetation, but that mean densities increased. The presence of submersed vegetation also can have a marked effect on zooplankton community composition (Rabe and Gibson 1984). Dense beds of submersed macrophytes also may have adverse affects on benthic invertebrates. Hall et al. (1970) and Danell and Sjöberg (1982) noted shifts in chironomid communities, from benthic to epiphytic species, when submersed vegetation invaded new areas. Johnson and Mulla (1983) reported lower densities of benthic chironomids in areas with Eurasian milfoil than in areas without, and Wrubleski (1989) suggested that *Chironomus* species were absent beneath a dense bed of sago pondweed. Changes in water circulation patterns, temperature, dissolved oxygen and benthic algal abundances may have caused the declines in benthic chironomid species reported above. However, there have been no experimental studies of the mechanism for this inhibition. In this paper I describe a field experiment designed to examine the interactions among submersed vegetation, the physico-chemical environment, and the benthic invertebrate community of a shallow prairie marsh.

4.3 STUDY AREA

This study was conducted in the Delta Marsh at the south end of Lake Manitoba, in south-central Manitoba (50° 11' N, 98° 19' W). Descriptions of the marsh vegetation and water chemistry are given in Löve and Löve (1954), Anderson and Jones (1976), Anderson (1978), Shay and Shay (1986), and Kadlec (1986).

Bone Pile Pond (BPP) is a long, narrow bay separated from the main marsh by a dense stand of hybrid cattail (*Typha glauca* Godr.) at its eastern end. Surface water pH ranged from 8.5-10.5 and conductivity ranged from 2350-3725 μS cm^{-1} at 25°C (Wrubleski, unpubl. data). The bottom is relatively flat and is composed of thick organic muck (~ 36.5% organic matter). Wind seiches on Lake Manitoba and the Delta Marsh result in continually fluctuating water levels within the pond (range 18 - 40 cm). The water column and much of the bottom sediments freeze in the winter (Wrubleski 1984).

The open-water area of the pond is dominated by sago pondweed (*Potamogeton pectinatus* L.), with some bladderwort (*Utricularia vulgaris* L.) also present early in the season. Waterfowl feeding removes much of the pondweed during July and August of most years (Wrubleski 1989). Two species of emergent plants, cattail and hardstem bulrush (*Scirpus lacustris* L. ssp. *glaucus* (Sm.) Hartm.), surround the open-water area. Carp (*Cyprinus carpio* L.) were present in the pond in 1986 and from 19 May to 8 June in 1987. Their activities within the pond disrupt development of the pondweed (Wrubleski, unpubl. observ.). A weir was constructed at the eastern end of the pond, at the beginning of June, to prevent more carp from entering the pond and to permit those already present to leave.

4.4 MATERIALS AND METHODS

4.4.1 Experimental treatments. Six experimental treatment plots, each 5 x 5 m, were established at random positions in the western end of BPP on 18-19 May, 1987, using a pre-existing grid system (Wrubleski 1984). Plots were assigned randomly to one of two treatments: (1) pondweed (pondweed permitted to grow) or (2) clipped (pondweed removed by clipping). Plots were enclosed by a fence of 5-cm mesh stucco wire, 0.5m high, to prevent access by waterfowl. To minimize exclosure effects, fences did not extend more than 10 cm below the water surface. A centre post within each plot was used to anchor one side of an emergence trap and to hold maximum-minimum thermometers. String and brightly colored flagging tape were strung across the tops of the exclosures to deter waterfowl from landing inside them, however waterfowl were observed within the pondweed plots on two occasions in late August.

Clipping of the pondweed began on 18 June and continued through the summer as regrowth occurred. No clipping was done during the week preceding algal and core sampling. Pondweed was clipped at the mud-water interface using small hand-held clippers. Clipped pondweed was collected and removed. All work within the exclosures was done from a canoe to minimize disturbance of the pond bottom.

4.4.2 Pondweed biomass. Pondweed biomass was determined at monthly intervals within exclosures. Three replicate pondweed foliage samples were removed from each plot using a cylindrical aluminium quadrat (314.2 cm^2). Above-ground, green plant material was sorted in the laboratory, dried and weighed.

4.4.3 Environmental variables. Surface and bottom water temperatures were recorded every 2 d, starting on 18 June, with maximum-minimum thermometers at the centre of each plot. Accumulated degree-days were calculated for each plot by summing the differences (in degrees) between each 2-d mean temperature and 0°C, and multiplying by 2.

Dissolved oxygen levels were determined weekly during the minimum-maximum periods of the diel cycle (i.e. 700-800 h and 1500-1600 h respectively; Wrubleski and Ross 1989). Measurements were made at the surface and approximately 5 cm above the bottom using a YSI model 57 oxygen meter with a self stirring probe. During these visits, water samples were collected from the surface and bottom of each plot and returned to the laboratory for determination of pH and conductivity.

4.4.4 Algal communities. Epiphytic algae (haptobenthic algae or periphyton colonizing solid substrates) were sampled using vertically-positioned acrylic rods as artificial substrates following Goldsborough et al. (1986). The rods were 80 cm long, 0.6 cm in diameter and precut (scored) at 5 cm intervals for subsampling. The first 25 cm of each rod extended into the substrate.

Eighteen rods were placed in each plot on 5 June. At approximately monthly intervals (3 and 31 July, 1 September), 5 rods were removed from each plot (three rods were spares). From four of the rods, the 5 cm section of rod immediately below the water surface and the 5 cm section above the pond bottom were removed and placed in labelled vials. These same sections were removed from the fifth rod but were preserved in Lugol's solution for later identification of the algal community.

On 31 July a second set of rods (6) was placed in each plot. This set was introduced when it became apparent that the rods were occasionally rubbed during pondweed clipping, and that this could introduce artificial differences among rods. This second set was added after pondweed regrowth slowed and the amount of clipping required in the plots was reduced.

Epipelic algae (herpobenthic algae) living on the sediments were sampled as described by Eaton and Moss (1966). Five, 500 ml samples of surface sediments, from an area of the bottom 22.9 cm^2, were collected from each plot using a hand-held vacuum pump. Samples were returned to the laboratory, washed into glass beakers and left in the dark for 24 h. Surface water was then removed and beakers were placed outside under ambient light. Lens tissue papers (traps) cut to the diameter of the beakers were placed on the sediment surfaces. These tissues were then removed the following morning at 1000 h, new tissues were replaced and removed at 1400 h and again at 1900 h. The three lens tissues from each sample were combined into a single vial. Four samples from each plot were analyzed for chlorophyll *a* and the fifth was preserved for algal identification.

Planktonic algae (phytoplankton) were sampled at monthly intervals (11 June, 9 July and 15 August). By 4 September the pondweed had already begun to senesce and settle to the bottom, so it was impossible to obtain samples. Five, 500 ml water samples were obtained from the surface and from immediately above the bottom in each plot. Samples were returned to the laboratory and vacuum filtered through Whatman GF/C filter papers. Four samples were frozen for chlorophyll *a* determinations and the fifth was preserved for identification of the algae. Samples from 9 July were later found to be unusable.

All algal samples used for chlorophyll *a* determination were frozen for at least 24 h to enhance pigment extraction. A known volume of 90% methanol was then added to each sample and vortexed 3 times over a 24-h dark period at 5°C (Gurney and Robinson 1989). Phaeophytin-corrected chlorophyll *a* levels were determined spectrophotometrically after Marker et al. (1980).

4.4.5 Invertebrates. Benthic invertebrates were sampled with a hand-held corer (17.35 cm^2). Three core samples were collected from each plot at monthly intervals: 8 June (preclipping), 6 July, 3 August and 2 September. Plants were moved to the side in an attempt to minimize contamination of core samples with epiphytic invertebrates. Immediately after collection, surface water was removed via a valve in the side of the corer and the samples were returned to the laboratory. Samples were then washed through a 250 µm sieve, preserved in 95% ethyl alcohol and stained with Rose Bengal to facilitate sorting. Samples were later sorted under a dissecting stereomicroscope at 60× magnification. Chironomid larvae were slide mounted in polyvinyl alcohol and identified to genera.

Emerging adult insects were sampled with a modified LeSage and Harrison (1979) model 'week' emergence trap (basal area 0.5 m^2). A single trap was placed in each plot on 27 May. Traps were emptied at 2-d intervals until 6 September (20 d preclipping and 82 d postclipping). Traps were anchored to the centre post and one of the fence posts, and repositioned within the plots at biweekly intervals to minimize shading of the pondweed.

All adult chironomids were identified to species. Nomenclature follows Oliver et al. (1990). A length-weight regression (Wrubleski and Rosenberg 1990) was used to calculate biomass of emerging chironomids. Because some species of Trichoptera are capable of ovipositing beneath the water surface and then re-emerging (Nielsen 1948; Badcock 1953), females that were nulliparous and gravid were considered newly emerged, as were all males. Parous females were treated as old (oviposited) females (Corbet 1966).

4.4.6 Statistical analysis. Nested ANOVA were used to test significance of differences in pondweed biomass, algal (epiphytic, epipelic and planktonic) biomass, and benthic invertebrate densities between treatments (n = 3 plots/treatments). *t*-tests were used to test significance of differences in insect emergence between the two treatments. Prior to statistical analyses data were transformed [$\log_{10}$ (x+1)] to stabilize the variances, but untransformed data are presented in the tables and figures. All analyses were done on a Macintosh personal computer using SYSTAT (version 3.2).

4.5 RESULTS

4.5.1 Pondweed biomass. Prior to initiation of clipping, pondweed biomass was similar between the two areas (Table 4.1). Pondweed growth was rapid during June and July and clipping only reduced biomass by 60% in the July samples. However, after the middle of July, pondweed biomass in the clipped plots remained low. During the last two weeks of July, waterfowl began to increase in numbers within the pond and through August and September they consumed much of the pondweed outside of the exclosures (Wrubleski, unpubl. data).

4.5.2 Environmental variables. None of the four parameters measured showed strong effects of the pondweed or clipping treatments. No significant [illegible] were detected for conductivity and pH. Dissolved oxygen levels differed significantly between treatments on only two dates (8 and 24 July), with pondweed plots showing higher levels of dissolved oxygen (Wrubleski, unpubl. data). Bottom temperatures within the clipped plots were slightly warmer than under the pondweed (Figure 4.1). These differences were most apparent during calm weather (e.g., 24-28 July) but disappeared during windy weather. Accumulated degree days did not differ significantly between treatments (*t*=2.114, df=4, *P*=.10).

4.5.3 Algal communities. Levels of epiphytic chlorophyll *a*, present at the surface and bottom in the two treatments, did not differ during July (Figure 4.2). By September, however, more epiphytic chlorophyll *a* was present in the clipped plots. Differences were significant for the one month samples but not for the samples in place for 3 months. Differences between the clipped and pondweed plots probably were accentuated at the water's surface due to abrasion of the rods by pondweed movement.

At no time did the amount of chlorophyll *a* present in the epipelon differ significantly between the two treatments (Figure 4.3). However, a distinct trend for greater biomass was evident in the clipped plots towards the end of the season, with a nearly significant difference in biomass in September.

Before the initiation of clipping, planktonic algal abundances were similar between the clipped and pondweed plots (Figure 4.4). The August samples showed a trend for higher abundances in the clipped plots at both the surface and the bottom but these differences were not significant.

4.5.4 Invertebrates. By 2 September significantly higher numbers of benthic invertebrates occurred in the clipped plots than in the pondweed plots (Table 4.2), due to higher numbers of copepods and ostracods in the clipped plots. The considerably higher numbers of copepods in the clipped plots was due mainly to the Harpacticoida. Cyclopoida was the most abundant group of copepods in the pondweed plots, although even they tended to be more abundant in clipped than in pondweed plots. Cladocera had higher numbers in the pondweed plots, and the difference was nearly significant in September (F=6.445, df=1,4, *P*=.06).

The overall abundances of Chironomidae did not differ between the two treatments (Table 4.2). *Corynoneura* sp. present in the core samples may have been due to larvae falling off the pondweed when taking cores in these plots. *Corynoneura* sp. are most often found on submersed vegetation (Kesler 1981). However, even if *Corynoneura* from the core samples are removed, there is no difference in total Chironomidae between treatments (F=0.032, df=1,4, *P*=.87). *Polypedilum* spp. and *Cladotanytarsus* sp. did show significantly higher numbers in the clipped plots in August and September.

Tanypus punctipennis Meig. had significantly higher emergence in the clipped plots than the pondweed plots (Table 4.3). However, the core samples showed no differences in larval abundance between treatments (Table 4.2), suggesting some kind of bias for this species in the emergence samples. Pupae of *Tanypus* species, as with other Tanypodinae, are highly mobile and it would seem that the pupae of this species congregated in the clipped plots prior to emergence. Therefore, data on *T. punctipennis* have been excluded from Total Chironomidae, Tanypodinae or emerging biomass estimates in Table 4.3. This presumed bias is not apparent for the other Tanypodinae.

During the 20-d period before clipping began, *Procladius bellus* (Loew) and *Parachironomus tenuicaudatus* (Mall.), had significantly different emergence rates between the two treatments (Table 4.3). With *P. bellus*, these differences are probably due to chance alone due to the low number of individuals collected. No explanation can be offered for *P. tenuicaudatus*.

Following clipping, there was no significant difference (*t*=2.078, df=4, *P*=.11) in the numbers of total Chironomidae emerging between the two treatments, but the subfamily Orthocladiinae did have significantly greater numbers emerging from the pondweed plots (Table 4.3). The seasonal pattern showed a constant trend of higher emergence from the pondweed plots as the season progressed (Figure 4.5A). The increasing difference in emergence was due primarily to *Corynoneura* cf. *scutellata* Winn. (Figure 4.5B). Biomass of emerging chironomids was not significantly different (*t*=1.913, df=4, *P*=.13) between treatments (Table 4.3).

Three chironomid species showed significant differences between treatments (Table 4.3). Both *Tanypus punctipennis* and *Polypedilum halterale* (Coq.) had significantly higher numbers emerging from the clipped plots, showing emergence peaks not apparent in the pondweed plots (Figure 5C,D). Emergence results for *P. halterale*, unlike for *T. punctipennis*, agree with those of the core samples. *Cladotanytarsus* sp., which had a significantly higher number of larvae in the clipped plots (Table 4.2), had a nearly significant (*t*=2.513, df=4, *P*=.06) higher emergence from the clipped plots as well. *Corynoneura* cf. *scutellata* had a significantly higher emergence from the pondweed plots (Table 4.3).

Mayflies and caddisflies also were collected in the emergence traps. The mayfly *Callibaetis fluctuans* (Walsh) showed no difference in emergence between the two treatments (Table 4.3). *Agraylea multipunctata* Curtis was the most abundant trichopteran, representing 77.1% of all caddisflies collected. Emergence of this species (new females and males) showed no difference between treatments, but older females were significantly more abundant in the clipped plots, suggesting an ovipositional preference by the females for open-water areas.

4.6 DISCUSSION

4.6.1 Submersed vegetation and benthic invertebrates. Submersed vegetation may provide additional habitat for invertebrates within the water column, but their presence can also have a marked effect on those invertebrates living on the bottom. By September in BPP, total benthic invertebrate numbers were higher in the clipped plots, but individual invertebrate groups varied in their responses to the treatments. Copepods, particularly the Harpacticoida, were considerably more abundant in the areas without submersed macrophytes. Cladocera on the other hand, were more abundant under the plants. Total chironomids showed no differences between the two treatments but some differences in species abundances were found.

Only one other study, Johnson and Mulla (1983), has compared benthic invertebrate communities between vegetated and artificially created non-vegetated areas. They observed lower numbers of chironomid larvae under *Myriophyllum spicatum* than in areas where the plants were eliminated by herbicides. In BPP, total larval chironomid numbers were similar between treatments, but two genera (*Polypedilum* and *Cladotanytarsus*) did have significantly lower larval numbers under the pondweed.

Although the general assumption that benthos numbers are higher in areas with plants than areas without plants is widely held, only a few studies (e.g., Wohlschlag 1950; Krull 1970; Menzie 1980; Engel 1985,1988; Schramm and Jirka 1989) actually have compared the benthic fauna between vegetated and 'naturally occurring' non-vegetated areas, and these comparisons should be viewed with caution. The absence of submersed macrophytes may be due to sediment type, vertebrate activities, water depth or currents. These factors also affect occurrence of benthic invertebrates. For example, Thorp (1988) reported that open patches in dense beds of submersed vegetation, created by the spawning activities of male centrarchid fish, had significantly lower benthic invertebrate diversities and densities than areas occupied by vegetation, and that these differences were still apparent the following year. The experimental approach taken in the present study minimizes these problems.

The emergence trap collections permit a comparison of numbers and biomass of emerging chironomids (both epiphytic and benthic) between vegetated and non-vegetated habitats. My results indicate no differences in total numbers or biomass of emerging chironomids between these two habitats, although *Corynoneura* cf. *scutellata* did have a higher emergence from the pondweed plots. In BPP, the presence of *Potamogeton pectinatus* did benefit one small epiphytic species but otherwise did not contribute to any increase in chironomid numbers over what was present in the bare sediments. Because of the dominance of *C.* cf *scutellata* in the pondweed emergence collections, average individual size of chironomids was 144.0 µg as compared to 221.2 µg from the clipped plots. In a previous waterfowl exclosure study within BPP, Wrubleski (1989) found that chironomid emergence from pondweed was also dominated by smaller epiphytic species, whereas larger benthic *Chironomus* species dominated emergence from areas where the plants had been removed by waterfowl.

The development of submersed vegetation was beneficial to some benthic invertebrates in BPP. Cladocera, for example, had higher densities under the pondweed. In lake littoral zones, submersed macrophytes stabilize the bottom where high wave energies can make the bottom sediments very loose and unstable, thereby benefiting benthic invertebrates in these habitats (McLachlan 1969; Jónasson and Lindegaard 1979; Schramm and Jirka 1989).

4.6.2 Factors responsible for regulating benthic invertebrates. The seasonal development of dense beds of submersed macrophytes can have a major impact on physico-chemical parameters within the water column and on the bottom (e.g., Buscemi 1958; Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983; Wylie and Jones 1987), and several of these parameters have been suggested as potential factors limiting abundances of benthic invertebrates (Hall et al. 1970; Danell and Sjöberg 1982; Wrubleski 1989). Restriction of water circulation and shading of the bottom, along with high respiration rates of decomposing vegetation, can contribute to very low oxygen levels on the bottom (Buscemi 1958; Wylie and Jones 1987). Anoxic conditions beneath a dense bed of *Myriophyllum spicatum* may have explained a depauperate sediment fauna in a study by Learner et al. (1989). Fish (1966) reported that removal of a dense cover of *Lagarosiphon major* (Ridley) Moss. resulted in a large increase in chironomid larval numbers, and speculated that this was due to better oxygen conditions present on the bottom following removal of the plants. Temperatures on the bottom beneath vegetation are also lower due to stratification caused by vegetation impeding circulation (Kollman and Wali 1976; Dale and Gillespie 1977; O'Neill Morin and Kimball 1983)

These features were observed in Bone Pile Pond, but the extent of the differences between the two treatments were not great and were only readily apparent for short periods. Wind-induced mixing of the shallow water, facilitated by removal of pondweed from the rest of the pond by waterfowl, is probably responsible for the lack of stratification of temperatures, oxygen, pH and conductivities. Mixing of the water column would also preclude the effects of allelochemicals produced by pondweed as being responsible for influencing the invertebrate community beneath the vegetation, as has been found for *Myriophyllum spicatum* (Dhillon et al. 1982).

Evidence from this study suggests that algal abundances were associated with differences in benthic invertebrate communities between the two treatments. By shading of the bottom, pondweed restricted benthic algal production in BPP. Light levels were not measured during this study but readings of photosynthetically active radiation ($\mu E\ m^{-2}\ s^{-1}$) taken the previous year in BPP indicated that approximately 60.3% of surface light levels reached the bottom in areas free of vegetation as opposed to only 2.1% underneath the pondweed (water depth = 15 - 20 cm). Several studies have reported low algal production beneath submersed macrophytes. Brandi et al. (1970) reported a more than 50% reduction in phytoplankton production beneath weed beds, and Goulder (1969) measured no phytoplankton production beneath a dense bed of Ceratophyllum. O'Neill Morin and Kimball (1983) reported light levels declined with depth in a *Myriophyllum heterophyllum* Michx. bed and this restricted periphyton growth on the the lower plant stems.

Algae are an important food resource for many benthic invertebrates (see review in Lamberti and Moore 1984) and this may also be so for the invertebrates of freshwater wetlands, where traditionally invertebrate production has been thought to be dependent upon the processing of detritus (Mann 1988; Murkin 1989). Shading by emergent (Straskraba and Pieczynska 1970; Gurney and Robinson 1988; Hosseini and van der Valk 1989a,b) and submersed (studies cited above) vegetation in wetland habitats restricts algal communities and can thereby negatively impact invertebrate communities. An analogous situation occurs in lotic habitats where shading by riparian vegetation reduces algal abundances in streams, and this in turn results in lower aquatic invertebrate densities and secondary production (Murphy et al. 1981; Hawkins et al. 1982; Behmer and Hawkins 1986; Feminella et al. 1989).

Interactions among submersed macrophytes, the physico-chemical environment, and benthic invertebrates are complex. These plants greatly increase the physical complexity of open-water areas and provide additional habitat within the water column for many invertebrates, but at the same time they may benefit or inhibit different components of the benthic invertebrate community. Thus, dense beds of submersed vegetation are not benign environments as suggested by Nelson and Kadlec (1984). The value of *Potamogeton pectinatus* as habitat for chironomids and other invertebrates requires further investigation. The findings of the present study suggest that the seasonal development of this plant contributes to shading of the pond bottom and thereby restricts algal production, and thus indirectly has a negative impact on the food resources of some benthic invertebrates. The relative importance of algae as a food resource for the invertebrates of freshwater wetlands remains unknown but the results of the present study point to a need for a further examination of the relationship between the invertebrate and algal communities of freshwater marshes.

Table 4.1. Sago pondweed biomass (g dry weight m^{-2}; mean ± SE, n=3; df=1,4 in all nested ANOVA) before clipping (15 June) and after clipping in Bone Pile Pond, 1987.

Sample Date	Clipped	Pondweed	F	*P*
15 June	3.43 ± 1.54	6.47 ± 2.45	0.295	0.616
13 July	50.16 ± 11.30	123.98 ± 15.95	12.080	0.025
11 August	2.57 ± 0.79	141.91 ± 20.64	227.649	0.000
4 September	3.03 ± 0.56	97.52 ± 50.44	15.100	0.018

Table 4.2. Numbers of chironomids and other invertebrates from core samples in clipped and pondweed plots, Bone Pile Pond, 1987 (mean number core^{-1} ± SE; n=3). * $P<0.05$; ** $P<0.01$; *** $P<0.001$; nested [illegible] df=1,4. (multiply by 576.4 to get no. m^{-2})

Species	8 June (preclipping) Clipped	8 June (preclipping) Pondweed	3 Au[illegible] Clipped	[illegible]d	2 September Clipped	2 September Pondweed
Tanypus sp.	0.9 ± 0.7	1.1 ± 0.3	3.8 ± 1.9	3.[illegible]	7.4 ± 2.8	6.8 ± 2.1
Procladius spp.	3.4 ± 1.0	2.1 ± 0.8	2.9 ± 1.2	1.9 ± 0.2	1.1 ± 0.5	1.7 ± 0.3
Corynoneura sp.	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.2 ± 0.4	1.3 ± 0.2	6.9 ± 4.8
Chironomus spp.	0.0 ± 0.0	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.2	0.3 ± 0.3	2.8 ± 2.0
Cladopelma sp.	0.1 ± 0.1	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.0	0.0 ± 0.0
Dicrotendipes sp.	0.3 ± 0.3	0.1 ± 0.1	0.7 ± 0.5	0.0 ± 0.0	1.6 ± 0.8	4.3 ± 1.0
Glyptotendipes spp.	0.3 ± 0.3	0.7 ± 0.4	1.4 ± 0.4	1.1 ± 0.7	1.9 ± 0.4	3.1 ± 1.4
Polypedilum spp.	2.1 ± 1.6	0.4 ± 0.3	2.0 ± 0.6	0.0 ± 0.0 *	2.1 ± 0.7	0.2 ± 0.3 *
Cladotanytarsus sp.	3.0 ± 1.0	1.7 ± 0.8	1.9 ± 0.5	0.2 ± 0.2 **	1.9 ± 0.5	0.1 ± 0.2 *
Total Chironomidae	13.8 ± 5.1	9.0 ± 2.0	14.2 ± 3.9	8.1 ± 4.0	19.7 ± 4.1	27.8 ± 2.5
Cladocera	26.4 ± 9.8	30.2 ± 15.6	29.9 ± 10.3	92.1 ± 30.4	99.4 ± 35.8	305.4 ± 53.5
Ostracoda	86.2 ± 16.7	50.6 ± 10.1	172.8 ± 35.8	109.3 ± 11.4	190.0 ± 81.2	106.3 ± 13.2
Cyclopoida	90.6 ± 21.0	104.7 ± 17.0	97.7 ± 36.2	74.0 ± 4.2	81.0 ± 19.0	42.1 ± 7.6
Harpacticoida	11.0 ± 6.4	5.3 ± 1.8	155.9 ± 83.6	11.2 ± 7.3 *	361.0 ± 73.2	4.6 ± 1.8 ***
Total Copepoda	106.0 ± 27.1	111.9 ± 17.3	255.1 ± 87.9	88.6 ± 9.5	442.0 ± 91.9	46.7 ± 6.6 ***
Hyalella azteca	2.1 ± 1.8	0.7 ± 0.7	0.8 ± 0.5	0.0 ± 0.0	1.0 ± 0.6	0.2 ± 0.2
Total Invertebrates	238.0 ± 58.2	204.11 ± 24.0	475.2 ± 137.8	299.3 ± 49.7	758.0 ± 79.4	489.1 ± 72.8 *

Table 4.3. Aquatic insect emergence before (27 May - 16 June) and after (18 June - 6 September) clipping of pondweed in Bone Pile Pond (mean no. trap^{-1} ± SE; n=3). Total Chironomidae, Tanypodinae and chironomid biomass do not include *Tanypus punctipennis* (see text for explanation). * indicates a significant difference (*t*-test, $P<0.05$) between treatments.

Species	Pre - Clipping Clipped	Pre - Clipping Pondweed	Post - Clipping Clipped	Post - Clipping Pondweed
Procladius bellus	0.0 ± 0.0	1.3 ± 0.3 *	3.7 ± 1.8	7.3 ± 1.8
P. denticulatus	0.3 ± 0.3	0.0 ± 0.0	77.3 ± 23.8	81.0 ± 7.8
P. freemani	0.3 ± 0.3	0.7 ± 0.3	4.7 ± 1.2	3.0 ± 1.6
Tanypus punctipennis	168.3 ± 86.4	199.3 ± 54.3	277.7 ± 38.3	45.3 ± 6.9 *
Corynoneura cf. *scutellata*	0.7 ± 0.7	0.7 ± 0.7	200.3 ± 61.4	1305.3 ± 396.2 *
Cricotopus sylvestris	128.7 ± 8.4	76.7 ± 35.2	118.7 ± 12.2	110.7 ± 32.9
C. cf. *flavipes*	3.3 ± 1.5	1.3 ± 0.9	28.3 ± 8.9	109.7 ± 49.3
C. intersectus	4.3 ± 0.9	2.7 ± 1.5	23.3 ± 5.5	8.3 ± 5.5
Cladopelma viridula	6.7 ± 1.8	5.7 ± 3.3	24.4 ± 5.8	15.3 ± 3.3
Dicrotendipes nervosus	437.3 ± 277.6	338.0 ± 284.8	41.0 ± 9.6	50.7 ± 14.0
Endochironomus nigricans	0.0 ± 0.0	0.3 ± 0.3	10.3 ± 3.3	10.7 ± 6.7
Glyptotendipes barbipes	18.0 ± 15.6	9.0 ± 5.0	8.3 ± 2.9	17.0 ± 8.4
G. lobiferus	0.0 ± 0.0	0.3 ± 0.3	13.3 ± 2.3	9.3 ± 4.1
Parachironomus tenuicaudatus	52.3 ± 5.6	31.7 ± 3.7 *	19.3 ± 2.7	29.3 ± 4.1
Polypedilum halterale	36.3 ± 24.1	28.3 ± 13.6	63.7 ± 0.9	9.7 ± 6.2 *
Cladotanytarsus sp.	0.7 ± 0.3	2.7 ± 2.7	104.3 ± 20.0	40.0 ± 15.9
Paratanytarsus sp. 3	45.7 ± 14.8	50.3 ± 14.7	19.7 ± 8.2	53.0 ± 26.0
Tanypodinae	1.7 ± 0.7	3.7 ± 0.9	86.0 ± 24.6	91.7 ± 8.4
Orthocladiinae	150.3 ± 10.5	97.0 ± 38.3	403.0 ± 59.4	1541.0 ± 453.0 *
Chironomini	572.0 ± 267.2	433.7 ± 272.3	199.7 ± 12.4	156.3 ± 25.5
Tanytarsini	117.7 ± 38.7	87.3 ± 16.4	154.7 ± 16.2	119.3 ± 44.2
TOTAL CHIRONOMIDAE	841.7 ± 309.4	618.0 ± 270.5	837.7 ± 92.2	1908.3 ± 487.4
Chironomid Biomass (mg dry weight)	338.7 ± 171.8	246.4 ± 134.4	218.2 ± 5.1	272.4 ± 27.7
Callibaetis fluctuans	0.0 ± 0.0	0.0 ± 0.0	7.7 ± 4.2	7.7 ± 2.4
Agraylea multipunctata (new ♀ and ♂)	3.0 ± 1.0	0.7 ± 0.7	38.7 ± 3.7	22.7 ± 5.8
A. multipunctata (old ♀)	0.7 ± 0.7	1.3 ± 0.9	78.0 ± 9.5	30.0 ± 4.0 *
Other Trichoptera	4.0 ± 1.7	4.0 ± 1.2	19.0 ± 7.2	25.0 ± 6.0

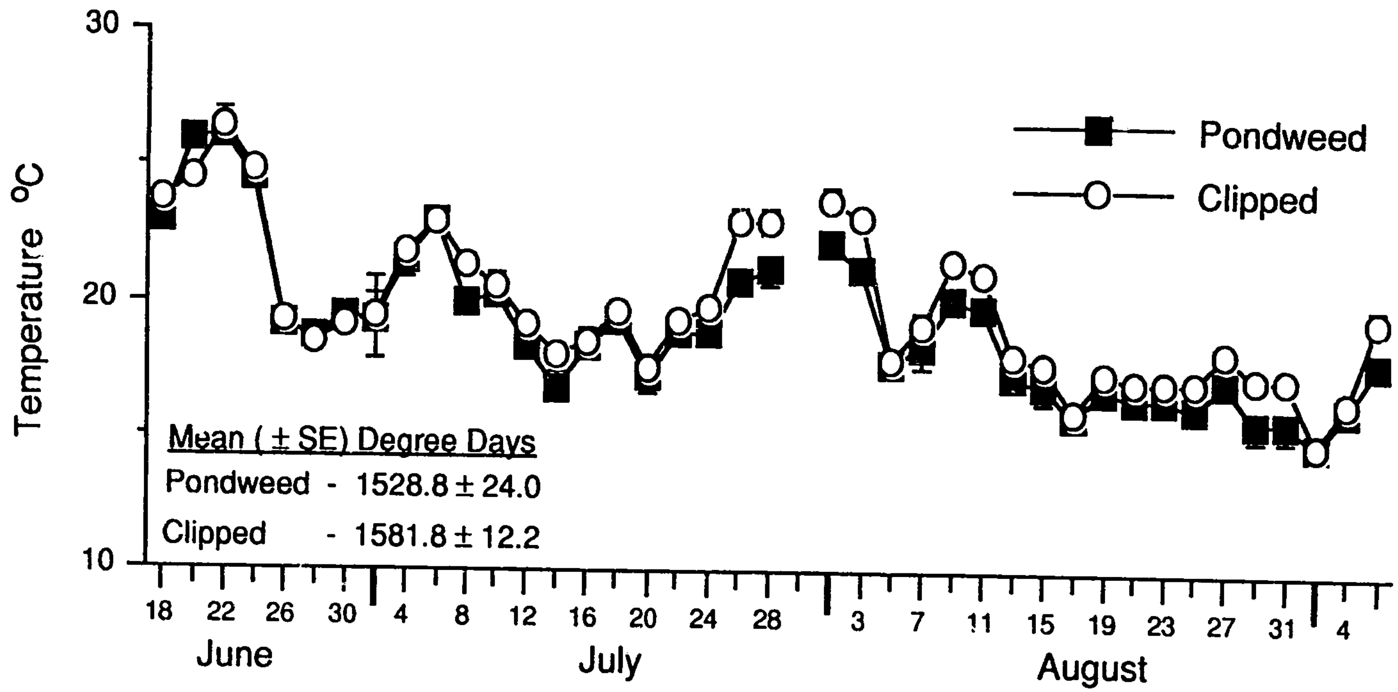

Figure 4.1. Mean (± SE; n=3) bottom temperatures in the clipped and pondweed plots in Bone Pile Pond, 1987. Thermometers were removed for cleaning and calibration on 28 July.

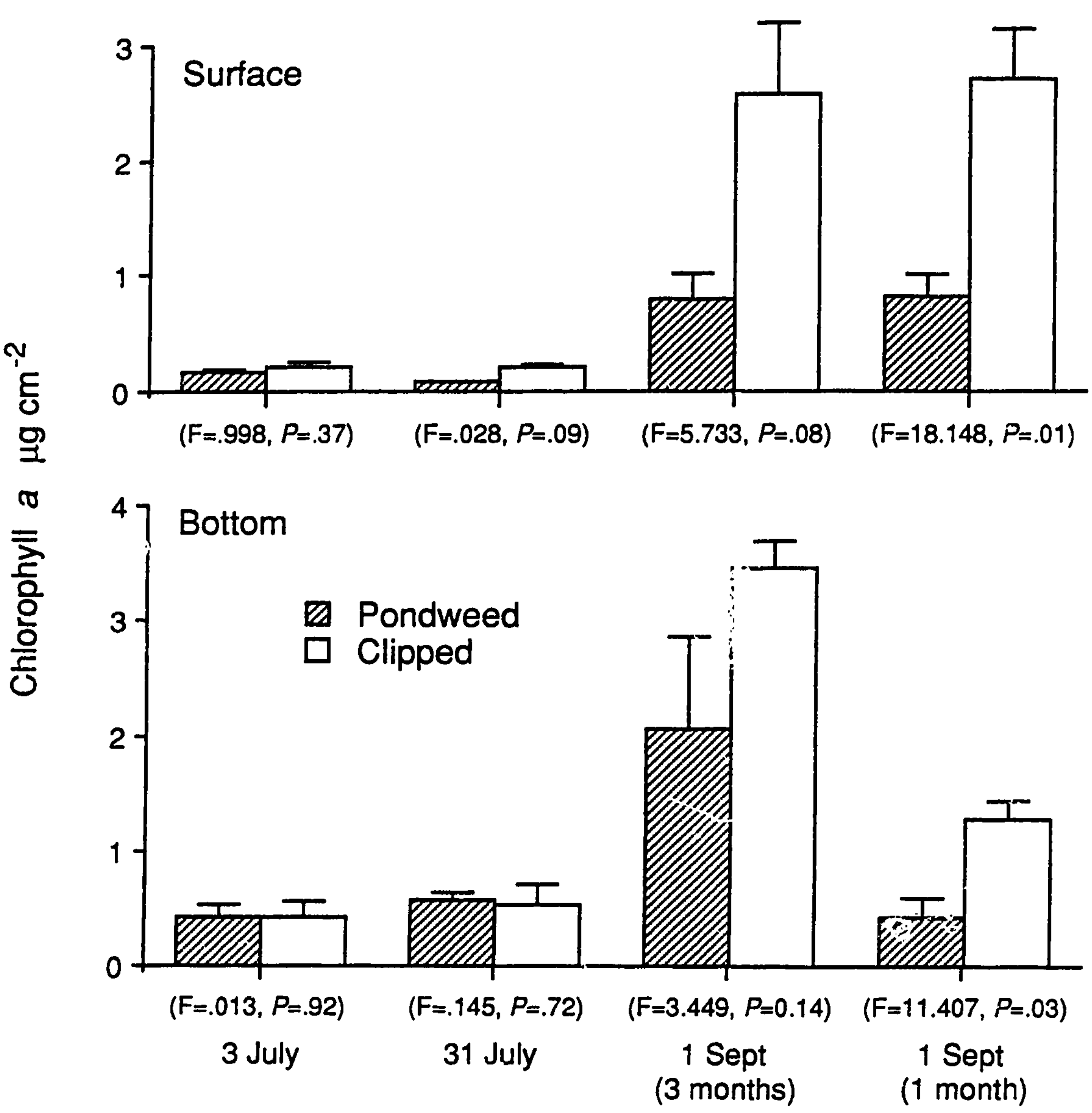

Figure 4.2. Mean (± SE; n=3; df=1,4 in all nested ANOVA) epiphytic algal biomass (as chlorophyll *a*) on artificial substrates in clipped and pondweed plots in Bone Pile Pond, 1987. Samples were collected at the surface and bottom of the water column. 1 September samples were obtained from substrates in place for three months and one month.

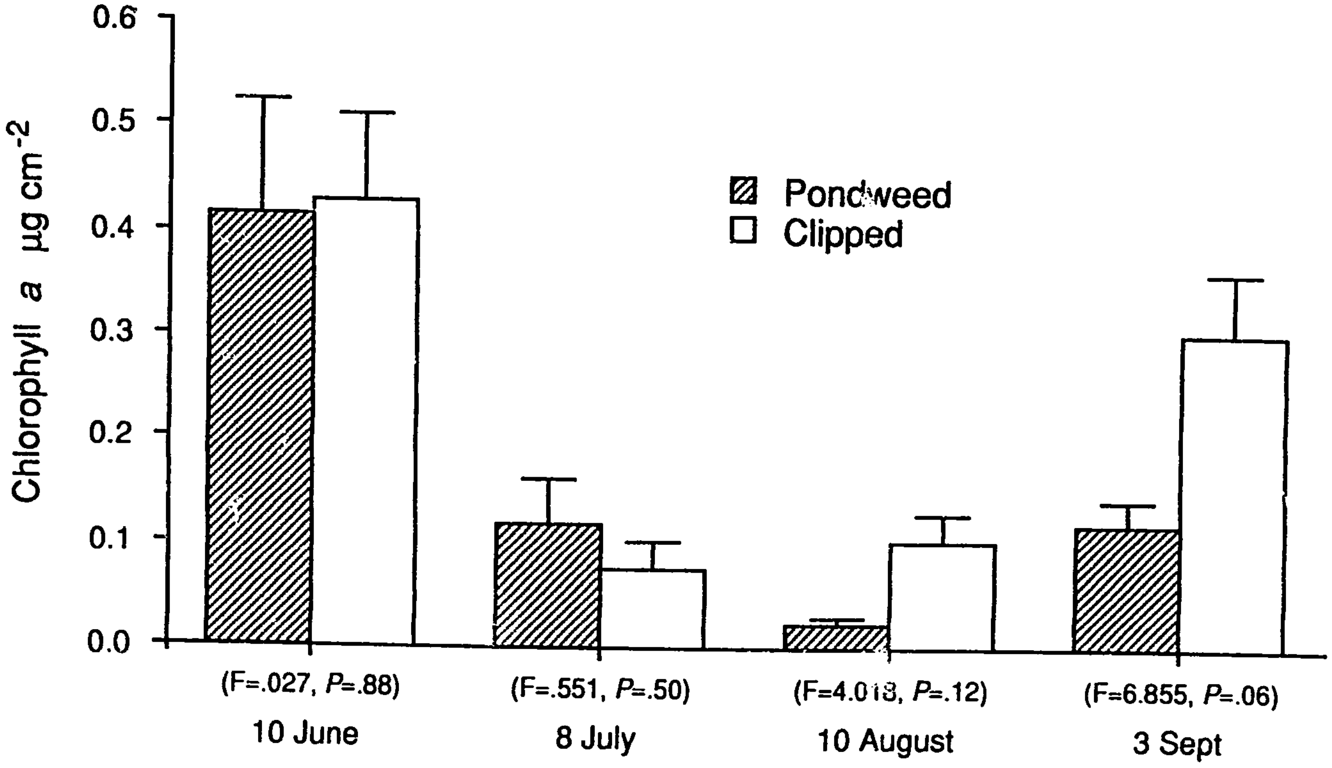

Figure 4.3. Mean (± SE; n=3; df=1,4 in all nested ANOVA) epipelic algal biomass (as chlorophyll *a*) collected from the bottom sediments of clipped and pondweed plots in BonePile Pond, 1987.

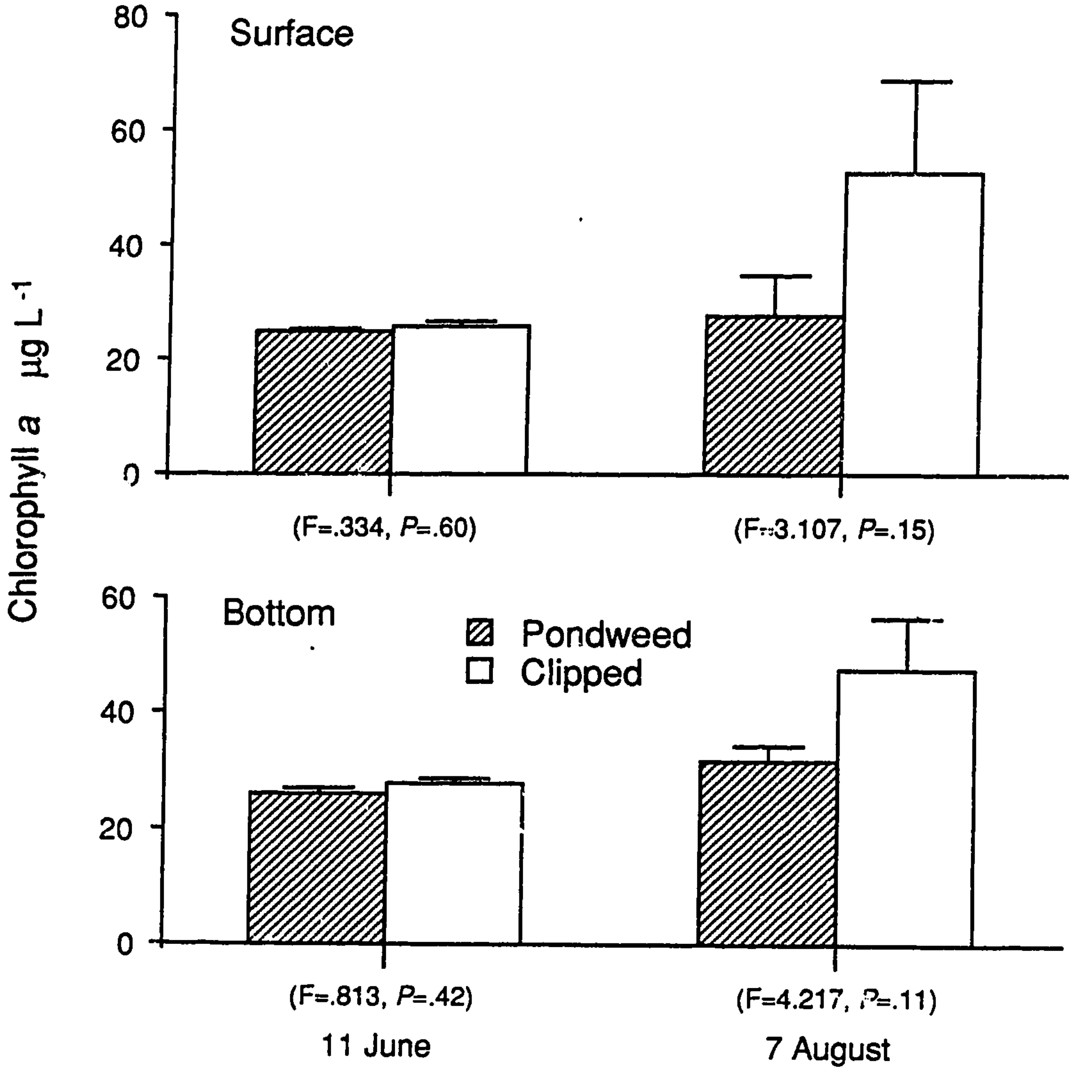

Figure 4.4. Mean (± SE; n=3; df=1,4 in all nested ANOVA) planktonic algal biomass (as chlorophyll *a*) in clipped and pondweed plots in Bone Pile Pond, 1987.

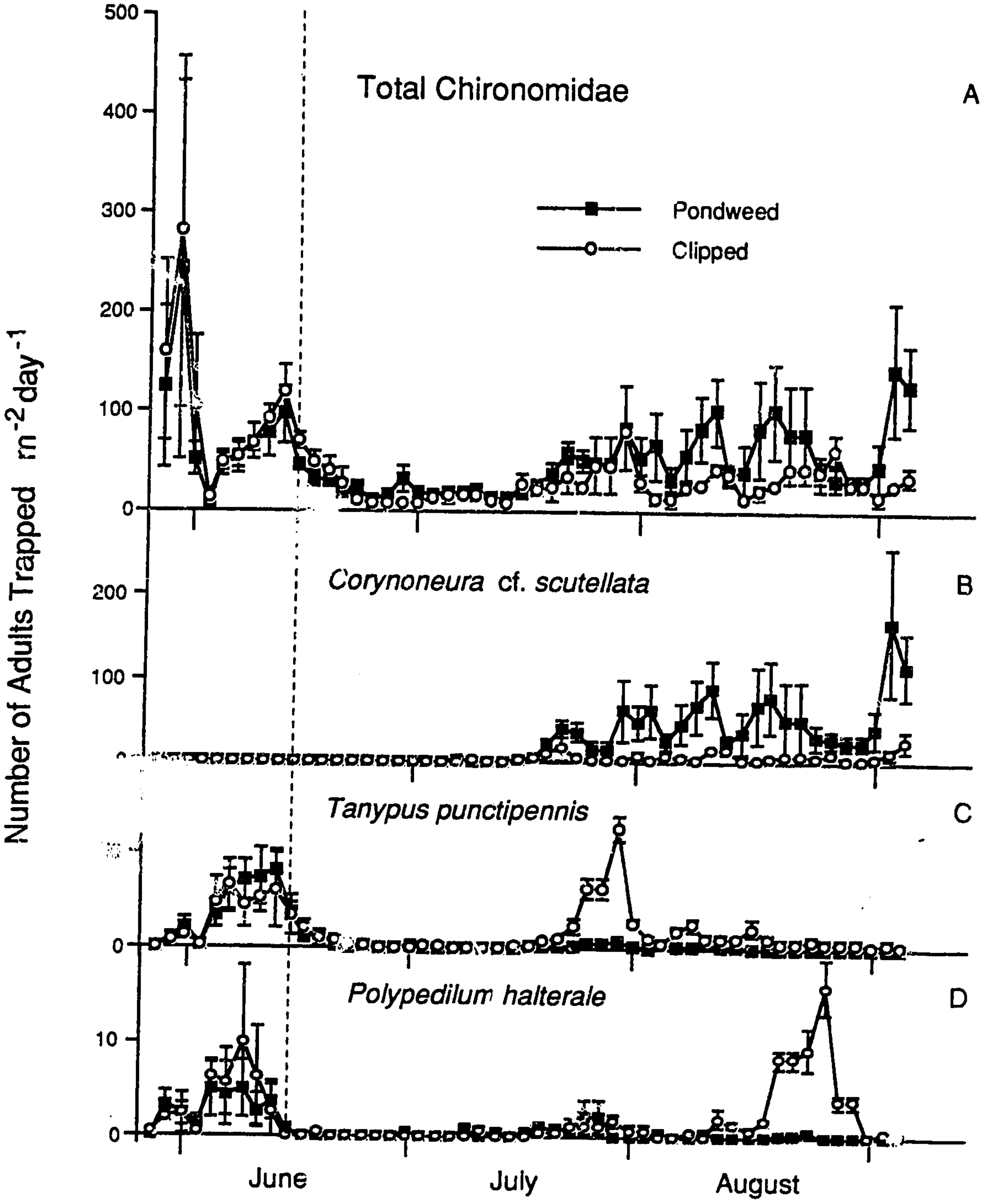

Figure 4.5. Mean (±SE; n=3) number of chironomid adults emerging from clipped and pondweed plots in Bone Pile Pond, 1987. Dashed line indicates when clipping of the pondweed began.

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5. CONCLUSIONS

5.1 Summary. Aquatic macrophytes are a dominant feature of wetland habitats. The results of the present studies demonstrate that they are also important determinants of invertebrate communities in these habitats.

In Chapter 2, chironomid production differed among the habitats (plant communities) and water depths sampled and these differences varied over the four years of the study. Two distinct patterns of chironomid community development were found and these patterns were related to macrophyte responses to the flooding, the structure of the plants, and the amount of litter present on the bottom. Terrestrial plants such as *Aster* were drowned following flooding, creating a habitat with ample plant litter and metaphyton. An abundant chironomid fauna developed from the first application of water with both epiphytic and benthic species present. A different pattern was found in the two emergent vegetation habitats. Initially, small epiphytic species (primarily *Corynoneura* cf. *scutellata*) dominated and benthic species were absent. The abundance of live and dead standing stems provided excellent habitat for epiphytic chironomids. However, prolonged flooding gradually reduced the abundances of emergent vegetation, epiphytic chironomids declined in abundance and benthic species increased substantially.

Two possible explanations could account for responses of the benthic species in the emergent vegetation habitats. 1) Dense stands of emergent macrophytes may have produced unfavourable conditions on the bottom that restricted benthic chironomids. These plants have been shown to influence algal communities through shading, and physico-chemical parameters by preventing mixing of the water column (Straskraba and Pieczynska 1970). Such conditions may have restricted the development of a benthic chironomid community while the emergent macrophytes were present. 2) An alternative explanation may be a lack of plant litter in these habitats. Both *Scolochloa* and *Scirpus* initially survived the flooding so no large input of litter occurred at that time. Not until the second year did these plants begin to die due to flooding and large inputs of litter occur (Figure 2.8). Both of the dominant benthic species, *Chironomus tentans* and *Glyptotendipes barbipes*, have been reported to mine plant litter, but also are known to live in the sediments. Whether the availability of decayed water-soaked vegetation is important to these species in wetland habitats remains unknown.

From a management standpoint, production of chironomids as potential waterfowl food varied among habitats, depths and over time (Chapter 3). Initially, the *Aster* habitat was more productive, at least in terms of larger chironomids that might be consumed by waterfowl. But by years three and four, the two emergent vegetation habitats were more productive, particularly in deeper water. It is apparent from this study that consideration must be given to the types of vegetation that colonize the drawdown surfaces of marshes and their subsequent responses to flooding, when attempting to increase invertebrate production following drawdown.

Submersed macrophytes are known for their ability to support epiphytic invertebrate populations, however, their potential influence on benthic invertebrates has not been as well recognized. In Chapter 4, I demonstrated that dense beds of submersed vegetation can have a negative impact on some members of the benthic community and that this impact appears to operate through shading of the algal communities. The algae of wetland habitats are only now being recognized as an important food resource for the aquatic invertebrates in these habitats (Murkin 1989; Campeau 1990).

5.2 Aquatic invertebrate research in wetland habitats. The study of aquatic invertebrate communities in wetland habitats lags behind that of studies in other aquatic habitats (Danks and Rosenberg 1987). One important reason for this has been the generally perceived lack of importance of the invertebrates in wetland habitats (Rosenberg and Danks 1987a). But recent findings have demonstrated their importance in a number of ecological processes within these habitats (Murkin and Wrubleski 1988; Rosenberg and Danks 1987b and the papers therein). Even with this increased awareness, efforts to study the invertebrate communities in wetlands are surprisingly few and rather cursory when compared to current research activities in lotic habitats.

Why are studies of wetland invertebrates so few and of such poor quality when compared to other aquatic habitats? First, as noted above, the fact that aquatic invertebrates perform important ecological functions within wetland habitats has been recognized only recently (Murkin and Wrubleski 1988). Second, many of the studies have been done in conjunction with other activities, and are more or less efforts to explain things like waterfowl feeding ecology or to develop wetland management practices. Therefore, not enough time or effort are allocated for detailed study of invertebrates. These two reasons may reflect the newness of this area of research and one can hope that more time and effort will be expended.

Now that interest is increasing, difficulties with sample collection and processing pose the greatest problem for aquatic invertebrate study in wetland habitats. Sampling devices are gradually improving and now include methods of obtaining samples that eliminate or reduce the amount of extraneous material collected, such as activity traps (Murkin et al. 1983) and emergence traps. However these same techniques are not without their shortcomings as demonstrated in Chapter 4 for emergence traps.

The aquatic invertebrates of wetlands, as well as of most other aquatic habitats, are numerous, small and diverse. A great deal of time and effort is required to sort, identify and count samples. The production of large numbers of samples often constrains the amount and kind of effort that can be put into sample processing, and this can have a marked effect on the results obtained. For example, Murkin and Kadlec (1986) reported benthic densities in the Delta Marsh averaged 1,200 m^{-2}, and that these numbers were low compared to some lakes and reservoir studies cited. They suggested that these low densities were a function of conditions common to wetland habitats, such as anoxic conditions in summer and complete freezing in winter. Benthic densities in Bone Pile Pond (BPP) of the Delta Marsh, which does not go anoxic but does freeze solidly in winter (Wrubleski 1984), ranged from 115,000 to 440,000 m^{-2} (Chapter 4). These widely divergent numbers taken from the same marsh are probably not due to actual differences between the experimental cells and BPP, but to differences in sample processing (both studies used similarly sized corers to sample the benthos). In the Murkin and Kadlec (1986) study, samples were sieved through a 500 µm mesh and live sorted shortly after collection. Samples from BPP were sieved through a smaller mesh (250 µm), stained with Rose Bengal and preserved in alcohol, and later sorted under a stereomicroscope at 60× magnification. This greater effort in processing benthic samples from BPP has resulted in benthic density estimates that are 100 to 400 times greater.

It could be argued that very small invertebrates (such as the harpacticoid copepods in Chapter 4), that would have been overlooked by cruder sorting methods, are not important duck food and therefore insignificant. However, size is not necessarily a good indicator of the importance of an organism to the environment in which it lives, and its direct importance to waterfowl should not be used as criteria for determining its apparent value in wetlands. These smaller animals are food for larger secondary consumers and their importance on up the food chain can be significant.

Another area in need of greater effort is the level of identification of the invertebrates collected. Few attempts have been made to identify wetland invertebrates to the species level. Many groups have individuals that are small and require slide mounting for proper identification. Keys are not available for many groups. A considerable amount of time is needed to acquire adequate taxonomic expertise, and this is outside the time constraints of many studies. However, species are the basic biological units. It is only at this level that changes within invertebrate communities can be properly documented and explained. In Chapters 2 and 3, for example, changes in the chironomids as a whole could not be interpreted without some knowledge of the species involved and information on their ecology. In Chapter 4, further identification of the Crustacea might have provided more useful insights into the interactions between submersed vegetation and benthic invertebrates.

5.3 Future directions and needs. Considerable time and effort went into the invertebrate sampling and identification in the present thesis. Differences in individual species responses were observed and these were used to help explain overall invertebrate community responses to the reflooding of the experimental cells and the seasonal development of submersed vegetation in a shallow bay of the Delta Marsh. However, I am still limited by the lack of information for many of the species. Even for the dominant chironomids in the experimental cells, little information on ecological requirements is available and almost all of it comes from habitats other than wetlands. An important area for future research are detailed ecological studies of dominant species within wetlands, such as *Chironomus tentans* and *Glyptotendipes barbipes* for example. Better information on their ecology in wetland habitats would help explain observed patterns within the experimental cells.

The role of aquatic vegetation in determining invertebrate communities in wetland habitats needs further study. Their ability to support epiphytic species is well documented but their apparent inhibitory effects on benthic species as demonstrated in the present studies requires further investigation. Are these effects manifested through alterations of physico-chemical parameters or through the shading of algae as suggested in Chapter 4? The role of algae as a food resource for aquatic invertebrates in wetland habitats needs examination.

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APPENDIX 1. MISSING DATA CALCULATIONS

Emergence trap samples were occasionally lost due to muskrat activity and wind storms. Mean annual emergence (no. m^{-2} yr^{-1} ± SE) for each habitat-water depth combination is determined from the collections of the six traps used for each combination. Numbers collected from each trap during every week (period) were summed for the entire sampling season. However, if a trap was not operating for a week then part of the annual total for that particular trap was missing. Therefore, an estimate of the missing value must be determined. This was done by determining trends between the missing trap and the remaining five traps within the same habitat-water depth combination. Data for a five week period (three weeks before the trap loss, the week of the trap loss and one week after the loss) were used.

The table below presents data for species sp30A (*Paratanytarsus* sp. 1) during periods 13 to 17 from the deep *Scirpus* habitat in 1985. Trap 2 was lost during week 16.

	Trap					
Week	1	2	3	4	5	6
13	43	26	11	1	7	5
14	81	42	7	34	23	1
15	47	36	68	69	1	3
16	21		37	93	2	0
17	137	46	109	98	2	0

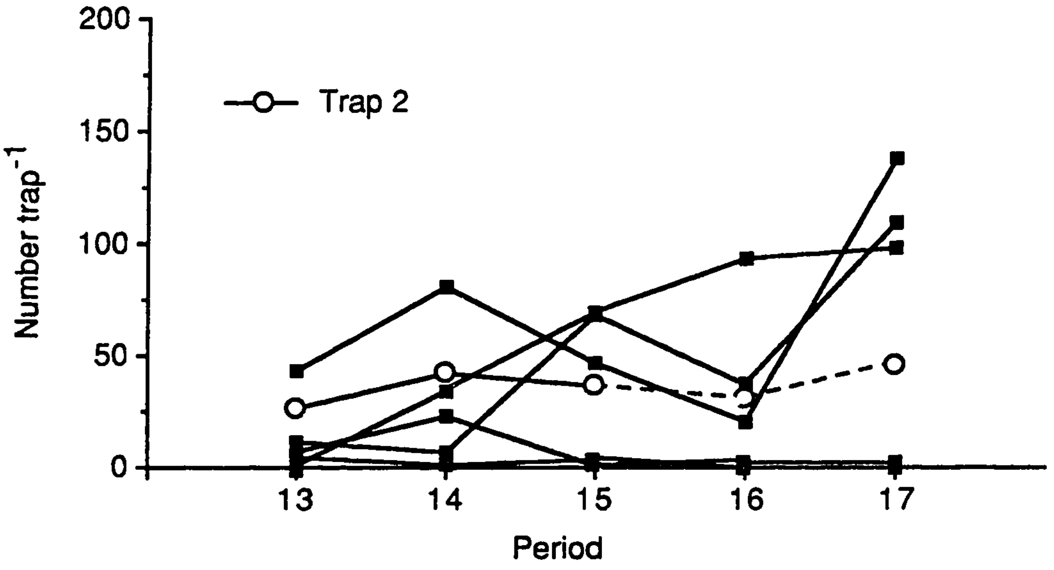
To estimate the missing value, these data were subjected to a regression analysis using PROC GLM of SAS with the SOLUTION option in the MODEL statement (Freund and Littell 1981). The program commands for the above data in a file called 85svd3 are as follows:

```
CMS F  DEF AAA DISK 85SVD30A data20 A!;
DATA numbers;
INFILE AAA;
INPUT period trap sp30A;
TITLE 'lsq means for data set 85SVD30A';
PROC GLM;
CLASS period trap;
MODEL sp30A=period trap/solution;
LSMEANS period trap;
```

Table 6.1 is the SAS output for this analysis. It provides the intercept (absolute value of the overall least squares mean with the effect of the last row (week) and column (trap) means removed (|36.0 - (1.8 + 65.3)| = 31.1). The mean for each row (week) and column (trap) are determined and then standardized with the last row and column which have been set to zero (see below).

Week	Trap 1	2	3	4	5	6	Week x̄	Week Effect
13	43	26	11	1	7	5	15.5	*-49.8*
14	81	42	7	34	23	1	31.3	*-34.0*
15	47	36	68	69	1	3	37.3	*-28.0*
16	21		37	93	2	0	30.6	*-34.7*
17	137	46	109	98	2	0	65.3	*0.0*
Trap x̄	65.8	36.2	46.4	59.0	7.0	1.8	***36.0***	
Trap Effect	*64.0*	*34.4*	*44.6*	*57.2*	*5.2*	*0.0*		

Using the intercept or corrected mean (31.1) and the effect for week 16 (-34.7) and the effect for trap 2 (34.4), an estimate for the missing trap value is obtained (30.8 rounded off to 31). This number is then inserted into the raw data tables for *Paratanytarsus* sp. 1 for week 16, trap 2 in the deep *Scirpus* habitat for 1985. The figure below illustrates the estimated value for trap 2 in week 16 in relation to the patterns observed for the five other traps.



These analyses were run for each species that might be expected to be in the missing sample. This was inferred by the presence of a species in samples from the missing trap the week before or the week after the trap sample was lost. If a species had not been recorded before or after the missing sample then it was assumed to not have been present at all. This procedure would underestimate rare species that might have been sporadically present in the samples from a particular habitat-water depth combination. Because this method of estimating the missing value standardizes the each week and trap effect to the last row and column by setting these to zero, the missing sample cannot be in the last period or in trap 6. If a sample from trap 6 were missing it was simply switched with trap 5.

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able 6.1. SAS output for the estimation of missing data for species sp30A.

```
                                         1985 Scirpus Deep 85SVD30a                    15:25 FRIDAY, JUNE 22, 1990    2

                                        GENERAL LINEAR MODELS PROCEDURE

DEPENDENT VARIABLE: SP30A

SOURCE                      DF        SUM OF SQUARES          MEAN SQUARE         F VALUE          PR > F        R-SQUARE          C.V.

MODEL                        9        25649.33362069        2849.92595785            3.65          0.0084        0.633305       77.2175

ERROR                       19        14851.42500000         781.65394737                        ROOT MSE                   SP30A MEAN

CORRECTED TOTAL             28        40500.75862069                                          27.95807482                 36.20689655

SOURCE                      DF             TYPE I SS       F VALUE       PR > F          DF         TYPE III SS        F VALUE       PR > F

PERIOD                       4         7970.05862069          2.55       0.0729           4       7962.37500000           2.55       0.0731
TRAP                         5        17679.27500000          4.52       0.0059           5      17679.27500000           4.52       0.0059

                                                     T FOR HO:       PR > |T|             STD ERROR OF
PARAMETER                          ESTIMATE        PARAMETER=0                              ESTIMATE

INTERCEPT                       31.10833333 B              1.92         0.0697             16.18180571
PERIOD          13             -49.83333333 B             -3.09         0.0061             16.14160202
                14             -34.00000000 B             -2.11         0.0487             16.14160202
                15             -28.00000000 B             -1.73         0.0990             16.14160202
                16             -34.70833333 B             -2.03         0.0568             17.12076437
                17               0.00000000 B              .             .                  .
TRAP             1              64.00000000 B              3.62         0.0018             17.68223808
                 2              34.35000000 B              1.81         0.0859             18.98208891
                 3              44.60000000 B              2.52         0.0207             17.68223808
                 4              57.20000000 B              3.23         0.0044             17.68223808
                 5               5.20000000 B              0.29         0.7718             17.68223808
                 6               0.00000000 B              .             .                  .

NOTE: THE X'X MATRIX HAS BEEN DEEMED SINGULAR AND A GENERALIZED INVERSE HAS BEEN EMPLOYED TO SOLVE THE NORMAL EQUATIONS.
      THE ABOVE ESTIMATES REPRESENT ONLY ONE OF MANY POSSIBLE SOLUTIONS TO THE NORMAL EQUATIONS. ESTIMATES FOLLOWED BY
      THE LETTER B ARE BIASED AND DO NOT ESTIMATE THE PARAMETER BUT ARE BLUE FOR SOME LINEAR COMBINATION OF PARAMETERS
      (OR ARE ZERO). THE EXPECTED VALUE OF THE BIASED ESTIMATORS MAY BE OBTAINED FROM THE GENERAL FORM OF ESTIMABLE
      FUNCTIONS. FOR THE BIASED ESTIMATORS, THE STD ERR IS THAT OF THE BIASED ESTIMATOR AND THE T VALUE TESTS
      HO: E(BIASED ESTIMATOR) = 0. ESTIMATES NOT FOLLOWED BY THE LETTER B ARE BLUE FOR THE PARAMETER.
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endix 2A. Species composition and mean annual emergence [no. m^{-2} (±SE), n=6] for the Chironomidae
cted from the *Aster* habitat of the experimental cells.

	Shallow				Deep			
ies	1985	1986	1987	1988	1985	1986	1987	1988
podinae								
esmyia pulchripennis (Lund.)	0.0	14.7	0.7	3.3	0.0	1.7	0.3	2.0
	(0.0)	(9.6)	(0.7)	(2.2)	(0.0)	(0.6)	(0.3)	(0.7)
anypus alaskensis (Mall.)	1.3	25.7	54.3	108.7	46.3	202.7	27.3	4.3
	(0.4)	(9.1)	(26.4)	(58.3)	(21.9)	(103.4)	(17.3)	(1.9)
adius bellus (Loew)	1.3	0.3	2.3	2.7	0.0	0.0	2.3	4.7
	(0.7)	(0.3)	(1.3)	(2.0)	(0.0)	(0.0)	(1.0)	(2.6)
ltaensis Roback	0.0	1.0	24.7	75.3	0.0	1.0	30.3	147.0
	(0.0)	(0.7)	(10.8)	(30.9)	(0.0)	(0.4)	(13.4)	(96.0)
nticulatus Subl.	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.4)	(0.0)
emani Subl.	9.0	2.3	0.7	3.7	1.0	3.7	3.3	5.0
	(2.7)	(1.2)	(0.4)	(1.7)	(0.4)	(2.3)	(1.1)	(1.7)
tus Roback	0.0	1.3	6.7	36.0	0.0	0.0	64.7	67.0
	(0.0)	(1.0)	(4.0)	(13.4)	(0.0)	(0.0)	(41.0)	(26.5)
trotanypus dyari (Coq.)	7.3	20.0	5.3	1.0	11.7	6.7	0.7	1.0
	(4.0)	(13.8)	(2.8)	(0.7)	(3.2)	(2.2)	(0.4)	(0.4)
pus punctipennis Meig.	0.0	7.0	338.7	847.0	0.3	18.0	10.3	30.7
	(0.0)	(3.5)	(200.5)	(408.6)	(0.3)	(11.9)	(5.0)	(22.5)
ndinia sp.?	0.3	0.0	0.0	0.3	0.0	0.0	2.7	0.7
	(0.3)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(1.8)	(0.7)
ntified Tanypodinae	0.7	12.7	0.0	0.3	7.3	13.7	6.0	1.3
	(0.4)	(8.6)	(0.0)	(0.3)	(4.4)	(5.1)	(2.4)	(0.7)
ocladiinae								
otopus nitidellus (Mall.)	87.7	3.7	29.3	148.7	80.3	2.0	5.0	30.0
	(35.5)	(1.2)	(14.8)	(90.6)	(58.8)	(0.9)	(2.6)	(11.3)

endix 2A. continued...

cies	Shallow 1985	1986	1987	1988	Deep 1985	1986	1987	1988
noneura cf. *scutellata* Winn.	232.7	273.3	90.7	17.0	332.0	883.0	90.0	114.7
	(127.7)	(134.7)	(43.8)	(4.9)	(153.2)	(197.4)	(22.8)	(35.5)
.1	2.0	3.0	0.0	15.7	0.0	4.7	0.0	6.7
	(2.0)	(2.0)	(0.0)	(12.7)	(0.0)	(1.3)	(0.0)	(2.6)
topus cf. *flavipes* Joh.	0.3	0.7	0.7	0.7	0.3	0.0	1.7	0.0
	(0.3)	(0.4)	(0.4)	(0.4)	(0.3)	(0.0)	(1.7)	(0.0)
tersectus (Staeg.)	0.0	0.3	4.3	35.3	2.0	1.0	11.3	27.0
	(0.0)	(0.3)	(2.7)	(20.4)	(1.0)	(0.7)	(7.2)	(11.0)
rnatus (Meig.)	231.3	248.3	278.0	267.3	291.3	62.0	5.0	139.3
	(64.8)	(157.7)	(93.6)	(173.2)	(60.6)	(32.0)	(2.7)	(72.1)
lvestris (Fab.)	149.3	133.0	290.7	101.7	537.3	245.7	89.7	238.7
	(24.3)	(28.9)	(92.2)	(36.5)	(145.2)	(98.2)	(42.0)	(60.5)
fasciatus (Meig.)	0.0	0.0	0.0	1.0	0.0	0.7	2.3	18.7
	(0.0)	(0.0)	(0.0)	(0.4)	(0.0)	(0.4)	(2.3)	(10.2)
ophyes immucronatus Saeth.	5.0	4.0	2.7	2.3	2.3	8.7	7.3	2.0
	(1.3)	(1.5)	(1.6)	(1.0)	(1.3)	(3.6)	(3.1)	(0.7)
rolongatus (Kieff.)	13.3	25.0	3.7	18.3	5.3	28.3	2.0	6.0
	(2.8)	(5.6)	(1.4)	(6.7)	(1.5)	(9.1)	(0.5)	(3.4)
phaenocladius nasthecus Saeth.	0.0	0.7	0.0	0.0	0.0	0.3	0.0	0.3
	(0.0)	(0.4)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.3)
ctrocladius barbimanus (Edw.)	6.3	7.7	5.0	16.7	152.0	31.7	3.0	29.7
	(2.8)	(4.8)	(3.5)	(15.1)	(73.5)	(12.1)	(1.4)	(6.2)
dwardsi Brund.	0.3	0.3	5.0	0.0	7.7	12.3	11.7	11.0
	(0.3)	(0.3)	(1.1)	(0.0)	(7.3)	(6.2)	(5.6)	(5.1)
p.3	1.3	4.7	0.0	0.0	11.3	25.3	0.0	6.3
	(0.7)	(2.2)	(0.0)	(0.0)	(8.3)	(16.4)	(0.0)	(3.5)
udosmittia nanseni (Kieff.)	6.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0
	(4.3)	(0.0)	(5.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
p.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	1.3
	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(1.3)
entified Orthocladiinae	1.0	1.7	3.0	1.7	3.7	4.0	34.0	6.7
	(0.4)	(1.0)	(1.1)	(0.8)	(3.3)	(1.5)	(24.4)	(3.6)

)pendix 2A. continued...

ecies	Shallow 1985	1986	1987	1988	Deep 1985	1986	1987	1988
ironomini								
ironomus atrella (Town.)	183.3	133.7	141.7	19.7	3637.3	313.3	88.3	220.3
	(21.1)	(62.1)	(83.7)	(11.7)	(972.6)	(146.6)	(37.7)	(78.1)
nr. *atroviridis* (Town.)	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0
	(0.0)	(0.3)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
pallidivittatus Mall.	42.3	213.3	3.3	3.3	21.7	27.0	14.7	10.0
	(13.2)	(70.1)	(1.5)	(1.1)	(13.4)	(8.3)	(8.4)	(3.3)
riparius Meig.	5.7	25.3	0.3	0.3	16.7	3.7	0.3	4.7
	(2.9)	(16.7)	(0.3)	(0.3)	(5.1)	(2.4)	(0.3)	(3.5)
staegeri Lund.	8.0	0.0	0.0	0.0	35.0	1.7	0.0	0.3
	(3.6)	(0.0)	(0.0)	(0.0)	(26.9)	(1.7)	(0.0)	(0.3)
tentans Fab.	725.0	2106.0	1954.3	1292.3	1292.3	1391.7	850.7	1568.3
	(144.1)	(684.0)	(827.7)	(414.5)	(809.6)	(493.6)	(286.0)	(303.2)
utahensis Mall.	4.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
	(2.4)	(0.0)	(0.0)	(2.0)	(0.0)	(0.0)	(0.0)	(0.0)
ıdopelma viridula (Linn.)	6.3	15.0	18.7	47.3	26.7	168.7	271.7	68.7
	(4.0)	(8.5)	(9.2)	(19.5)	(16.9)	(78.7)	(165.7)	(36.7)
yptochironomus psittacinus (Meig.)	0.3	5.7	1.3	14.0	0.0	8.3	0.7	0.0
	(0.3)	(5.7)	(1.3)	(9.0)	(0.0)	(5.8)	(0.4)	(0.0)
yptotendipes cf. *darbyi* (Subl.)	12.7	1.3	2.0	4.0	1.3	17.0	7.0	8.7
	(9.1)	(0.8)	(2.0)	(2.4)	(0.4)	(16.6)	(3.0)	(7.9)
meijerea brachialis Coq.)	0.0	0.0	0.0	0.0	0.0	1.7	1.3	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.3)	(0.8)	(1.0)
rotendipes modestus (Say)	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)
nervosus (Staeg.)	20.7	81.0	37.3	37.3	47.7	59.3	57.0	357.3
	(7.1)	(32.4)	(13.1)	(10.4)	(14.8)	(10.8)	(19.4)	(191.4)
ıfeldia pagana (Meig.)	0.0	1.0	3.0	2.3	0.0	6.3	7.7	9.7
	(0.0)	(0.7)	(1.6)	(2.0)	(0.0)	(3.7)	(3.9)	(2.3)

)pendix 2A. continued...

ecies	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
lochironomus nigricans (Joh.)	0.0	2.0	5.3	0.7	0.3	1.3	21.0	21.3
	(0.0)	(1.3)	(1.8)	(0.4)	(0.3)	(1.0)	(10.4)	(14.1)
subtendens (Town.)	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)
ptotendipes barbipes (Staeg.)	206.0	1322.7	999.3	782.3	547.3	1077.3	190.0	387.3
	(56.7)	(533.8)	(276.4)	(444.8)	(235.7)	(544.7)	(104.1)	(183.0)
lobiferus (Say)	7.3	0.3	17.0	3.7	1.7	0.7	12.3	20.7
	(3.6)	(0.3)	(12.0)	(1.7)	(0.8)	(0.4)	(7.3)	(15.9)
sp.	1.3	2.7	3.7	0.7	0.0	0.3	31.7	4.0
	(1.0)	(1.4)	(2.7)	(0.4)	(0.0)	(0.3)	(21.6)	(3.3)
rachironomus potamogeti (Town.)	31.7	45.0	24.0	35.3	45.3	73.3	5.3	175.7
	(14.5)	(12.9)	(8.0)	(14.1)	(8.7)	(19.0)	(1.9)	(67.6)
tenuicaudatus (Mall.)	22.7	2.0	2.7	0.3	29.3	1.0	5.0	4.0
	(10.9)	(1.3)	(1.1)	(0.3)	(17.1)	(0.4)	(1.8)	(2.5)
sp. 3	14.3	4.0	0.0	2.3	19.7	17.3	2.0	42.7
	(8.9)	(2.4)	(0.0)	(0.8)	(5.5)	(6.7)	(1.0)	(17.3)
sp. 4	0.0	0.3	0.0	0.0	1.3	0.7	0.0	0.3
	(0.0)	(0.3)	(0.0)	(0.0)	(1.3)	(0.4)	(0.0)	(0.3)
aenopsectra punctipes (Wied.)	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
lypedilum halterale (Coq.)	0.0	0.0	3.3	42.0	0.0	0.7	0.3	1.7
	(0.0)	(0.0)	(1.3)	(26.6)	(0.0)	(0.7)	(0.3)	(1.1)
illinoense (Mall.)	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.7)	(0.0)	(0.0)	(0.0)
tritum (Walk.)	2.0	0.0	0.3	0.0	0.7	0.0	0.0	2.0
	(1.6)	(0.0)	(0.3)	(0.0)	(0.4)	(0.0)	(0.0)	(2.0)
sp. 4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
identified Chironomini	1.7	1.0	1.7	1.3	0.3	1.0	1.0	0.7
	(0.8)	(1.0)	(0.6)	(0.4)	(0.3)	(0.7)	(0.7)	(0.4)

ppendix 2A. continued...

pecies	Shallow 1985	1986	1987	1988	Deep 1985	1986	1987	1988
seudochironomini								
seudochironomus middlekauffi Town.	0.0	0.3	1.3	54.3	0.3	0.0	4.0	66.3
	(0.0)	(0.3)	(1.0)	(31.9)	(0.3)	(0.0)	(1.5)	(17.9)
anytarsini								
ladotanytarsus sp.	7.7	13.7	94.3	405.3	2.3	27.3	3.0	1.0
	(6.5)	(7.6)	(67.9)	(270.1)	(1.3)	(21.5)	(1.9)	(0.7)
icropsectra sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
aratanytarsus sp. 1	357.7	32.0	115.7	15.7	63.3	19.0	4.0	14.7
	(96.6)	(9.1)	(66.1)	(7.8)	(16.6)	(10.9)	(1.4)	(4.2)
. sp.3	9.0	1.0	160.3	27.3	17.7	5.0	297.7	226.3
	(7.4)	(1.0)	(78.4)	(13.2)	(8.8)	(3.3)	(211.8)	(119.0)
anytarsus sp. 1	176.7	344.0	259.7	96.7	1152.0	948.0	324.0	39.7
	(48.3)	(186.3)	(198.8)	(45.4)	(655.9)	(750.6)	(185.5)	(9.7)
. sp.2	0.7	0.0	2.0	0.0	0.0	0.0	0.0	0.0
	(0.7)	(0.0)	(1.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
. sp.3	7.0	152.3	25.0	21.3	11.3	4.7	17.0	72.3
	(3.9)	(91.0)	(15.2)	(6.8)	(3.2)	(1.0)	(13.5)	(26.8)
. sp.4	123.3	0.0	0.0	0.0	701.0	0.0	0.0	0.0
	(88.0)	(0.0)	(0.0)	(0.0)	(441.9)	(0.0)	(0.0)	(0.0)
. sp.6	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
. sp.7	0.7	4.3	4.0	0.0	1.7	24.7	11.0	1.3
	(0.7)	(2.8)	(2.3)	(0.0)	(1.0)	(18.2)	(6.7)	(1.3)
nidentified Tanytarsini	0.0	0.0	5.3	33.0	0.0	0.0	3.0	205.7
	(0.0)	(0.0)	(1.3)	(12.8)	(0.0)	(0.0)	(0.9)	(128.6)

ppendix 2B. Species composition and mean annual emergence [no. m^{-2} (±SE), n=6] for the Chironomidae ollected from the *Scolochloa* habitat of the experimental cells.

pecies	Shallow 1985	Shallow 1986	Shallow 1987	Shallow 1988	Deep 1985	Deep 1986	Deep 1987	Deep 1988
anypodinae								
babesmyia illinoensis (Mall.)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.7)
. *pulchripennis* (Lund.)	0.3	0.0	1.3	2.0	0.7	0.3	10.0	132.0
	(0.3)	(0.0)	(1.3)	(1.3)	(0.4)	(0.3)	(6.3)	(80.0)
erotanypus alaskensis (Mall.)	0.0	0.7	0.0	10.7	1.3	0.3	5.0	25.0
	(0.0)	(0.4)	(0.0)	(5.7)	(1.3)	(0.3)	(4.6)	(13.8)
rocladius bellus (Loew)	5.7	0.0	1.0	3.7	0.0	0.7	3.0	7.7
	(2.0)	(0.0)	(0.7)	(2.7)	(0.0)	(0.4)	(1.2)	(3.2)
. *deltaensis* Roback	0.0	0.0	0.0	73.7	0.0	0.0	13.0	43.3
	(0.0)	(0.0)	(0.0)	(58.3)	(0.0)	(0.0)	(9.5)	(11.5)
. *denticulatus* Subl.	0.0	0.0	0.3	0.7	0.0	0.0	0.0	1.0
	(0.0)	(0.0)	(0.3)	(0.7)	(0.0)	(0.0)	(0.0)	(1.0)
. *freemani* Subl.	7.3	0.3	1.0	2.0	1.7	3.3	4.0	1.7
	(1.9)	(0.3)	(0.4)	(0.9)	(1.7)	(1.5)	(2.4)	(1.1)
. *nietus* Roback	0.0	0.0	0.3	27.0	0.0	0.0	3.3	67.3
	(0.0)	(0.0)	(0.3)	(20.8)	(0.0)	(0.0)	(1.8)	(31.8)
sectrotanypus dyari (Coq.)	1.3	8.3	0.3	0.3	4.0	3.7	0.0	1.0
	(1.0)	(3.5)	(0.3)	(0.3)	(2.4)	(1.9)	(0.0)	(1.0)
anypus punctipennis Meig.	0.0	0.0	2.0	41.0	0.0	0.3	0.3	279.3
	(0.0)	(0.0)	(0.7)	(18.2)	(0.0)	(0.3)	(0.3)	(174.3)
abrundinia sp.?	0.3	0.3	0.0	0.0	0.3	5.0	0.0	4.3
	(0.3)	(0.3)	(0.0)	(0.0)	(0.3)	(1.9)	(0.0)	(1.7)
nidentified Tanypodinae	5.3	16.0	1.0	0.0	9.3	31.0	12.0	3.0
	(4.2)	(9.6)	(0.7)	(0.0)	(3.8)	(9.2)	(7.2)	(2.3)

Appendix 2B. continued...

Species	Shallow 1985	1986	1987	1988	Deep 1985	1986	1987	1988
Orthocladiinae								
Acricotopus nitidellus (Mall.)	9.0	57.0	119.3	85.0	116.0	21.3	5.7	10.3
	(4.8)	(22.1)	(85.9)	(28.3)	(62.8)	(7.6)	(2.3)	(6.4)
Corynoneura cf. *scutellata* Winn.	782.3	1175.3	99.7	57.0	3128.3	2739.3	187.7	164.0
	(344.1)	(433.5)	(34.8)	(26.1)	(1778.1)	(945.4)	(117.0)	(52.0)
C. sp.1	0.0	1.0	0.0	6.0	0.0	7.0	2.7	44.0
	(0.0)	(0.7)	(0.0)	(4.5)	(0.0)	(4.7)	(2.0)	(24.6)
Cricotopus cf. *elegans* Joh.	0.0	0.0	0.0	2.0	0.0	0.0	0.0	1.3
	(0.0)	(0.0)	(0.0)	(1.6)	(0.0)	(0.0)	(0.0)	(0.7)
C. cf. *flavipes* Joh.	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.7)	(0.4)	(0.0)	(0.0)
C. intersectus (Staeg.)	0.3	0.3	0.0	0.3	0.3	4.3	1.7	179.3
	(0.3)	(0.3)	(0.0)	(0.3)	(0.3)	(4.3)	(0.8)	(64.1)
C. ornatus (Meig.)	5.7	186.0	1.0	53.0	584.0	52.3	12.3	18.7
	(1.7)	(104.9)	(1.0)	(30.7)	(312.0)	(21.5)	(8.5)	(13.5)
C. sylvestris (Fab.)	53.7	45.7	8.7	171.0	1074.3	282.3	148.3	445.7
	(19.1)	(13.5)	(3.5)	(65.0)	(452.5)	(82.9)	(35.9)	(178.2)
C. trifasciatus (Meig.)	0.0	0.0	0.0	0.0	0.0	2.0	0.0	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.3)	(0.0)	(1.0)
Limnophyes immucronatus Saeth.	11.3	18.3	4.3	1.0	6.7	5.0	0.0	2.3
	(4.5)	(8.4)	(2.1)	(0.4)	(3.1)	(2.1)	(0.0)	(2.3)
L. prolongatus (Kieff.)	93.3	275.3	9.3	17.3	9.7	16.0	1.0	5.3
	(37.2)	(150.4)	(3.0)	(7.3)	(2.6)	(3.7)	(0.4)	(2.4)
Nanocladius anderseni Saeth.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(2.0)
Psectrocladius barbimanus Edw.	1.3	3.3	0.3	5.7	8.3	85.3	21.7	25.0
	(1.3)	(2.2)	(0.3)	(1.8)	(2.8)	(43.9)	(12.5)	(6.5)
P. edwardsi Brund.	0.0	30.0	5.0	0.0	2.0	272.3	28.7	4.3
	(0.0)	(24.4)	(1.8)	(0.0)	(1.3)	(32.4)	(4.7)	(2.5)
P. sp.3	3.7	57.3	0.0	0.7	20.0	67.0	2.7	8.3
	(2.4)	(28.0)	(0.0)	(0.7)	(7.7)	(29.4)	(1.7)	(3.6)

Appendix 2B. continued...

Species	Shallow 1985	Shallow 1986	Shallow 1987	Shallow 1988	Deep 1985	Deep 1986	Deep 1987	Deep 1988
Pseudosmittia nanseni (Kieff.)	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
Unidentified Orthocladiinae	0.3	3.0	3.3	1.0	1.3	4.3	10.0	1.0
	(0.3)	(1.6)	(1.0)	(0.7)	(0.7)	(1.0)	(4.3)	(0.7)
Chironomini								
Chironomus atrella (Town.)	0.3	2.7	68.0	11.3	11.0	15.0	143.7	24.7
	(0.3)	(1.2)	(26.3)	(3.0)	(7.2)	(9.2)	(81.7)	(12.3)
C. nr. *atroviridis* (Town.)	3.7	0.0	0.0	0.0	0.7	0.0	0.0	0.0
	(2.7)	(0.0)	(0.0)	(0.0)	(0.4)	(0.0)	(0.0)	(0.0)
C. pallidivittatus Mall.	6.0	36.7	10.3	23.0	5.7	39.3	73.3	20.0
	(2.7)	(19.5)	(2.9)	(11.2)	(3.7)	(16.1)	(55.9)	(6.6)
C. riparius Meig.	30.7	206.0	0.7	0.0	19.3	3.3	0.0	0.0
	(11.7)	(111.7)	(0.7)	(0.0)	(11.0)	(1.4)	(0.0)	(0.0)
C. staegeri Lund.	0.3	0.0	0.0	0.0	1.0	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(1.0)	(0.0)	(0.0)	(0.0)
C. tentans Fab.	0.0	39.3	162.3	1266.0	5.7	97.3	978.3	4525.0
	(0.0)	(16.0)	(89.4)	(317.9)	(3.4)	(56.4)	(762.5)	(1252.8)
Cladopelma viridula (Linn.)	0.3	0.0	0.7	9.7	1.3	0.0	1.3	11.0
	(0.3)	(0.0)	(0.4)	(6.7)	(1.3)	(0.0)	(0.7)	(5.7)
Cryptochironomus psittacinus (Meig.)	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Cryptotendipes cf. *darbyi* (Subl.)	7.3	1.0	4.0	0.0	0.3	5.7	17.7	2.0
	(2.8)	(1.0)	(1.7)	(0.0)	(0.3)	(2.7)	(11.1)	(1.3)
C. emorsus (Town.)	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(1.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Demeijera brachialis (Coq.)	0.0	0.0	0.7	0.0	0.3	0.0	1.0	0.3
	(0.0)	(0.0)	(0.7)	(0.0)	(0.3)	(0.0)	(0.7)	(0.3)
Dicrotendipes modestus (Say)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(2.7)

Appendix 2B. continued...

Species	Shallow 1985	Shallow 1986	Shallow 1987	Shallow 1988	Deep 1985	Deep 1986	Deep 1987	Deep 1988
D. nervosus (Staeg.)	125.3	78.0	40.7	114.0	218.3	366.0	166.3	549.3
	(74.9)	(28.8)	(17.9)	(43.1)	(72.3)	(79.7)	(66.1)	(328.6)
Einfeldia pagana (Meig.)	0.0	0.0	0.0	1.3	0.0	0.0	5.7	25.7
	(0.0)	(0.0)	(0.0)	(0.7)	(0.0)	(0.0)	(1.6)	(4.0)
Endochironomus nigricans (Joh.)	0.0	4.3	4.3	0.3	5.3	18.7	2.7	9.3
	(0.0)	(1.7)	(2.9)	(0.3)	(2.3)	(7.4)	(2.7)	(4.2)
E. subtendens (Town.)	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)
Glyptotendipes barbipes (Staeg.)	0.3	8.0	52.0	849.7	88.7	340.3	340.3	820.3
	(0.3)	(6.4)	(25.2)	(274.1)	(43.7)	(208.9)	(266.2)	(367.5)
G. lobiferus (Say)	0.0	0.0	4.0	13.0	1.0	7.0	3.7	19.3
	(0.0)	(0.0)	(1.7)	(7.7)	(0.7)	(4.6)	(2.3)	(7.7)
G. n. sp.	2.0	0.0	0.0	0.0	1.3	0.7	1.3	2.3
	(1.0)	(0.0)	(0.0)	(0.0)	(0.8)	(0.4)	(0.7)	(1.6)
Kiefferulus dux (Joh.)	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Parachironomus potamogeti (Town.)	5.0	16.7	0.7	29.7	78.0	88.7	36.7	184.3
	(1.5)	(6.2)	(0.7)	(5.4)	(25.6)	(26.1)	(20.1)	(48.1)
P. tenuicaudatus (Mall.)	78.7	3.3	3.0	1.0	88.7	10.0	3.0	4.0
	(47.9)	(1.3)	(3.0)	(0.7)	(31.0)	(5.4)	(1.9)	(2.9)
P. sp. 3	24.3	0.3	0.7	1.0	47.3	4.0	3.7	38.0
	(15.4)	(0.3)	(0.7)	(0.7)	(13.2)	(2.6)	(1.7)	(10.5)
P. sp. 4	0.0	0.0	0.0	0.0	0.0	1.3	0.3	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.0)	(0.3)	(0.0)
Phaenopsectra punctipes (Wied.)	1.3	1.0	0.0	0.0	0.3	0.0	0.0	0.0
	(0.8)	(1.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
Polypedilum halterale (Coq.)	0.0	0.0	0.0	0.0	0.0	0.3	0.0	5.7
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(4.5)
P. illinoense (Mall.)	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0
	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)

Appendix 2B. continued...

	Shallow				Deep			
Species	1985	1986	1987	1988	1985	1986	1987	1988
P. tritum (Walk.)	4.7	0.3	4.7	0.0	2.0	0.7	1.7	0.0
	(3.1)	(0.3)	(3.0)	(0.0)	(1.6)	(0.4)	(1.1)	(0.0)
P. sp. 4	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)
Unidentified Chironomini	1.7	9.3	1.0	1.7	4.0	2.7	3.7	1.3
	(0.6)	(4.8)	(0.7)	(1.3)	(1.0)	(2.0)	(1.2)	(0.7)
Pseudochironomini								
Pseudochironomus middlekauffi (Town.)	2.0	0.0	2.0	241.3	0.0	1.0	1.0	64.7
	(1.0)	(0.0)	(0.9)	(105.9)	(0.0)	(0.4)	(0.7)	(23.3)
Tanytarsini								
Cladotanytarsus sp.	3.3	0.0	0.0	1.7	0.0	0.0	0.0	1.7
	(1.3)	(0.0)	(0.0)	(1.3)	(0.0)	(0.0)	(0.0)	(0.6)
Micropsectra sp.	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
	(0.0)	(2.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Paratanytarsus sp. 1	686.3	257.0	34.0	52.7	586.3	58.7	2.7	4.0
	(446.1)	(171.6)	(12.2)	(25.9)	(198.6)	(12.4)	(0.8)	(1.2)
P. sp.3	4.7	3.7	9.3	34.7	0.7	4.7	23.0	113.3
	(3.9)	(2.6)	(4.1)	(9.5)	(0.4)	(1.8)	(16.4)	(52.5)
Tanytarsus sp. 1	10.7	36.3	163.7	76.0	8.3	37.0	74.3	22.0
	(2.6)	(13.2)	(92.6)	(23.1)	(1.9)	(11.7)	(36.4)	(5.2)
T. sp.2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.0)	(0.0)
T. sp.3	7.0	0.3	13.0	38.7	0.0	5.0	5.0	38.7
	(4.8)	(0.3)	(3.8)	(16.8)	(0.0)	(2.5)	(2.1)	(18.2)
T. sp.4	11.3	0.0	0.0	1.0	3.3	1.3	0.3	0.7
	(9.8)	(0.0)	(0.0)	(1.0)	(2.3)	(1.3)	(0.3)	(0.7)
T. sp.7	1.0	0.3	0.3	0.0	0.0	0.3	5.3	2.3
	(1.0)	(0.3)	(0.3)	(0.0)	(0.0)	(0.3)	(4.2)	(1.3)

Appendix 2B. continued...

Species	Shallow 1985	Shallow 1986	Shallow 1987	Shallow 1988	Deep 1985	Deep 1986	Deep 1987	Deep 1988
Unidentified Tanytarsini	0.3 (0.3)	0.0 (0.0)	2.7 (0.7)	11.0 (6.7)	17.0 (5.9)	0.0 (0.0)	3.7 (2.3)	10.0 (3.8)

Appendix 2C. Species composition and mean annual emergence [no. m^{-2} (±SE), n=6] for the Chironomidae collected from the *Scirpus* habitat of the experimental cells.

Species	Shallow 1985	Shallow 1986	Shallow 1987	Shallow 1988	Deep 1985	Deep 1986	Deep 1987	Deep 1988
Tanypodinae								
Ablabesmyia illinoensis (Mall.)	0.3	0.0	0.0	0.0	8.3	0.0	0.0	0.3
	(0.3)	(0.0)	(0.0)	(0.0)	(2.6)	(0.0)	(0.0)	(0.3)
A. monilis (Linn.)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)
A. pulchripennis (Lund.)	2.7	0.3	0.7	1.7	7.7	0.7	11.0	65.3
	(0.8)	(0.3)	(0.4)	(1.7)	(1.9)	(0.4)	(7.1)	(38.7)
Derotanypus alaskensis (Mall.)	0.0	0.0	0.0	23.3	0.0	0.0	2.3	47.7
	(0.0)	(0.0)	(0.0)	(14.3)	(0.0)	(0.0)	(1.5)	(18.7)
Procladius bellus (Loew)	3.7	0.3	0.3	2.7	4.3	0.7	1.0	6.3
	(2.0)	(0.3)	(0.3)	(1.5)	(2.3)	(0.7)	(0.7)	(3.2)
P. culiciformis (Linn.)	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)
P. deltaensis Roback	0.0	0.3	0.3	5.0	0.0	0.0	5.0	83.3
	(0.0)	(0.3)	(0.3)	(2.2)	(0.0)	(0.0)	(2.4)	(17.8)
P. denticulatus Subl.	1.0	0.3	0.0	0.0	0.7	0.0	0.3	0.0
	(0.7)	(0.3)	(0.0)	(0.0)	(0.7)	(0.0)	(0.3)	(0.0)
P. freemani Subl.	1.0	3.3	4.0	2.7	0.7	2.0	1.7	19.0
	(1.0)	(1.5)	(2.5)	(1.1)	(0.4)	(0.7)	(0.8)	(9.3)
P. nietus Roback	0.0	0.0	0.0	0.0	0.0	0.0	3.3	152.3
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(2.2)	(80.8)
Psectrotanypus dyari (Coq.)	15.7	0.0	0.3	0.3	4.7	0.3	1.0	0.0
	(6.9)	(0.0)	(0.3)	(0.3)	(2.2)	(0.3)	(0.7)	(0.0)
Tanypus punctipennis Meig.	0.0	0.0	0.0	29.7	0.0	4.7	15.0	67.3
	(0.0)	(0.0)	(0.0)	(11.2)	(0.0)	(3.0)	(9.8)	(35.5)
Labrundinia sp.?	0.0	0.0	0.0	0.0	0.0	1.3	0.0	1.3
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.0)	(0.0)	(0.7)

Appendix 2C. continued...

	Shallow				Deep			
Species	1985	1986	1987	1988	1985	1986	1987	1988
Unidentified Tanypodinae	0.0	1.3	0.0	0.0	13.3	28.3	7.3	0.7
	(0.0)	(1.0)	(0.0)	(0.0)	(4.1)	(12.6)	(3.7)	(0.4)
Orthocladiinae								
Acricotopus nitidellus (Mall.)	1.3	2.0	101.0	307.3	4.3	4.0	6.0	0.3
	(0.7)	(1.0)	(47.2)	(88.6)	(1.7)	(2.4)	(1.3)	(0.3)
Corynoneura cf. *scutellata* Winn.	596.0	565.3	120.7	22.3	4600.0	895.0	341.3	77.3
	(322.6)	(123.9)	(78.7)	(5.3)	(2415.6)	(424.3)	(54.2)	(39.6)
C. sp.1	0.0	0.0	0.3	1.0	0.0	0.0	5.3	102.3
	(0.0)	(0.0)	(0.3)	(1.0)	(0.0)	(0.0)	(2.6)	(39.1)
C. sp.2	0.0	0.0	10.7	0.0	0.0	0.0	0.0	0.0
	(0.0)	(0.0)	(8.7)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Cricotopus cf. *elegans* Joh.	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
C. cf. *flavipes* Joh.	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(2.0)	(0.0)
C. intersectus (Staeg.)	0.3	0.0	0.0	0.0	1.7	0.3	26.7	85.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.6)	(0.3)	(16.9)	(33.8)
C. ornatus (Meig.)	2.3	1.7	0.0	9.3	11.3	6.3	19.0	212.0
	(1.0)	(0.8)	(0.0)	(7.7)	(6.4)	(2.9)	(6.6)	(144.0)
C. sylvestris (Fab.)	13.7	5.7	13.0	62.3	64.3	40.7	336.3	352.3
	(3.6)	(2.2)	(3.8)	(27.3)	(11.6)	(14.7)	(66.8)	(175.3)
Limnophyes immucronatus Saeth.	15.3	2.0	10.7	0.3	9.0	8.3	1.0	1.3
	(3.6)	(1.0)	(3.6)	(0.3)	(2.1)	(4.4)	(0.4)	(0.7)
L. prolongatus (Kieff.)	94.0	50.7	5.3	6.3	44.0	48.7	1.3	3.7
	(34.1)	(13.2)	(2.6)	(1.5)	(13.4)	(24.8)	(0.7)	(1.7)
Nanocladius anderseni Saeth.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.7
	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.6)
Paraphaenocladius nasthecus Saeth.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.0)

lix 2C. continued...

	Shallow				Deep			
	1985	1986	1987	1988	1985	1986	1987	1988
dius barbimanus Edw.	0.0	1.0	0.0	3.3	2.3	2.7	13.7	14.3
	(0.0)	(0.7)	(0.0)	(1.3)	(1.7)	(1.6)	(10.1)	(5.5)
si Brund.	0.0	0.3	0.3	0.0	7.0	35.7	8.0	0.3
	(0.0)	(0.3)	(0.3)	(0.0)	(4.4)	(20.9)	(2.7)	(0.3)
	0.0	2.0	0.0	0.3	0.0	22.3	2.3	9.0
	(0.0)	(1.6)	(0.0)	(0.3)	(0.0)	(7.8)	(1.5)	(4.2)
ittia nanseni (Kieff.)	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.4)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
d Orthocladiinae	0.7	3.7	0.0	1.3	0.0	1.3	12.7	5.3
	(0.7)	(1.4)	(0.0)	(1.0)	(0.0)	(0.7)	(6.7)	(4.0)
nini								
us atrella (Town.)	18.7	4.0	28.7	85.7	0.7	64.0	491.0	64.7
	(9.9)	(2.7)	(13.1)	(24.2)	(0.7)	(27.4)	(289.2)	(31.3)
ittatus Mall.	11.0	14.7	16.7	10.7	0.0	6.3	92.0	4.0
	(6.5)	(7.9)	(7.9)	(6.9)	(0.0)	(3.2)	(49.5)	(2.0)
Meig.	0.0	117.3	21.3	2.0	1.0	12.7	0.3	0.0
	(0.0)	(66.0)	(9.4)	(2.0)	(0.4)	(6.8)	(0.3)	(0.0)
ri Lund.	56.7	0.0	0.3	1.0	5.0	0.0	0.3	0.0
	(38.6)	(0.0)	(0.3)	(1.0)	(3.9)	(0.0)	(0.3)	(0.0)
s Fab.	11.7	143.3	22.0	582.0	0.3	20.0	678.0	4522.0
	(6.2)	(108.8)	(11.9)	(180.8)	(0.3)	(9.9)	(324.9)	(575.2)
sis Mall.	4.3	0.0	0.0	0.0	0.7	0.0	0.0	0.3
	(2.0)	(0.0)	(0.0)	(0.0)	(0.7)	(0.0)	(0.0)	(0.3)
na viridula (Linn.)	2.3	1.0	1.0	100.3	0.3	0.7	18.7	99.0
	(1.1)	(0.7)	(0.7)	(74.9)	(0.3)	(0.7)	(16.7)	(52.3)
ronomus psittacinus (Meig.)	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
	(1.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.3)
dipes cf. *darbyi* (Subl.)	0.0	5.7	0.7	0.3	0.0	0.0	0.7	4.7
	(0.0)	(2.4)	(0.7)	(0.3)	(0.0)	(0.0)	(0.7)	(3.5)

dix 2C. continued...

s	Shallow 1985	1986	1987	1988	Deep 1985	1986	1987	1988
rea brachialis (Coq.)	0.0	0.0	0.3	0.0	0.0	1.0	7.3	0.3
	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(1.0)	(6.5)	(0.3)
dipes modestus (Say)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(4.3)
osus (Staeg.)	187.0	310.0	44.7	25.7	417.3	155.3	220.3	223.7
	(88.1)	(90.5)	(11.9)	(8.0)	(90.0)	(67.8)	(31.7)	(55.9)
pagana (Meig.)	0.0	0.0	0.0	0.0	0.0	0.0	13.3	2.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(4.2)	(0.9)
ronomus nigricans (Joh.)	1.0	3.3	1.3	0.7	15.0	8.7	22.3	4.0
	(0.7)	(1.6)	(1.0)	(0.4)	(5.4)	(2.8)	(9.3)	(2.6)
ndipes barbipes (Staeg.)	3.0	33.0	28.0	361.7	1.7	6.0	105.0	1523.3
	(1.6)	(17.6)	(17.0)	(186.5)	(1.1)	(2.5)	(21.3)	(636.7)
rus (Say)	1.3	1.7	1.7	2.3	17.7	21.7	124.0	55.0
	(0.7)	(0.6)	(1.1)	(0.8)	(11.0)	(9.9)	(22.5)	(13.7)
.	3.3	1.7	0.0	0.0	8.7	21.0	23.3	0.7
	(3.0)	(1.1)	(0.0)	(0.0)	(4.8)	(13.9)	(16.7)	(0.4)
hia curtilamellata (Mall.)	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
	(0.0)	(0.7)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
ronomus potamogeti (Town.)	8.0	9.0	1.0	19.0	11.0	25.0	34.0	133.7
	(5.0)	(2.5)	(0.7)	(2.7)	(3.0)	(10.0)	(14.5)	(22.1)
caudatus (Mall.)	10.0	9.0	0.3	0.0	101.7	6.3	4.7	0.0
	(4.8)	(3.1)	(0.3)	(0.0)	(28.5)	(2.3)	(2.3)	(0.0)
	20.3	2.3	0.0	0.3	102.3	18.7	2.0	5.7
	(9.3)	(1.1)	(0.0)	(0.3)	(25.8)	(8.3)	(1.0)	(2.2)
	0.0	0.0	0.0	0.0	0.3	1.0	2.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(0.7)	(1.4)	(0.0)
psectra punctipes (Wied.)	0.0	0.3	0.0	0.0	0.0	2.7	0.0	0.0
	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)	(1.0)	(0.0)	(0.0)
lilum illinoense (Mall.)	0.7	0.0	0.0	0.0	1.0	0.0	0.0	0.0
	(0.7)	(0.0)	(0.0)	(0.0)	(0.7)	(0.0)	(0.0)	(0.0)

ıdix 2C. continued...

	Shallow				Deep			
s	1985	1986	1987	1988	1985	1986	1987	1988
ı (Walk.)	3.7	3.0	6.0	0.3	9.3	0.0	0.3	0.7
	(2.7)	(2.2)	(4.8)	(0.3)	(6.2)	(0.0)	(0.3)	(0.4)
	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0
	(0.7)	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
atrum (Town.)	0.0	8.0	0.0	0.0	0.0	0.3	0.0	0.0
	(0.0)	(1.8)	(0.0)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)
ified Chironomini	14.0	5.0	4.0	1.3	6.0	14.0	2.0	45.3
	(6.8)	(2.0)	(2.1)	(1.0)	(2.3)	(4.3)	(0.9)	(36.2)
ochironomini								
chironomus middlekauffi Town.	0.3	0.0	1.0	67.7	0.0	0.0	3.3	29.0
	(0.3)	(0.0)	(0.7)	(38.2)	(0.0)	(0.0)	(1.8)	(18.9)
ırsini								
ınytarsus sp.	4.0	1.0	0.0	0.0	0.3	0.0	0.0	4.0
	(1.7)	(0.7)	(0.0)	(0.0)	(0.3)	(0.0)	(0.0)	(2.5)
ıectra sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
ıytarsus sp. 1	54.0	83.3	71.0	72.0	504.3	44.7	26.0	10.7
	(22.5)	(38.2)	(25.0)	(28.6)	(162.0)	(25.0)	(4.9)	(4.8)
	5.7	0.7	3.7	4.3	2.7	0.3	39.7	36.3
	(3.4)	(0.7)	(2.1)	(2.9)	(1.1)	(0.3)	(18.6)	(18.3)
rsus sp. 1	4.0	0.7	1.7	84.7	1.7	2.0	36.3	15.0
	(1.4)	(0.4)	(1.3)	(54.4)	(1.0)	(1.0)	(11.2)	(5.1)
	0.3	0.0	0.0	5.3	0.0	0.3	7.7	42.3
	(0.3)	(0.0)	(0.0)	(1.6)	(0.0)	(0.3)	(3.8)	(18.1)
	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.7)	(0.0)
	0.0	0.0	0.0	0.0	0.0	0.0	0.3	3.7
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.3)	(2.7)

ndix 2C. continued...

	Shallow				Deep			
es	1985	1986	1987	1988	1985	1986	1987	1988
tified Tanytarsini	3.3 (1.1)	0.7 (0.4)	6.3 (2.7)	3.3 (1.1)	4.0 (0.9)	1.3 (0.4)	9.7 (5.5)	2.0 (0.9)

VITA

I was born in Moose Jaw, Saskatchewan on February 21, 1955. We initially lived in Gull Lake, Saskatchewan but then moved to Estevan where I attended school. I spent a great deal of time playing in the prairies and this is where I developed my interest in prairie sloughs, which were always so full of life. After completing high school in 1973 I went on to do an undergraduate degree in biology at the University of Regina. Larry Bogdan and Alina Walther, two very special people, encouraged my interests in prairie marshes. Dr Walther was my supervisor for an undergraduate thesis that I did on the aquatic invertebrate populations of a marsh near Regina. This thesis was instrumental in getting me a summer job with Ducks Unlimited Canada. During that summer I visited the Delta Waterfowl Research Station in Manitoba. Encouraged to develop my interests in the invertebrates of prairie marshes by people at Ducks Unlimited and Delta, I entered a M.Sc. program with David Rosenberg at the University of Manitoba in 1979. Bruce Batt and Henry Murkin actively encouraged my studies at Delta and provided the support necessary for me to continue my studies at the University of Alberta with John Spence in 1984. Having completed my dissertation I am now employed at Ducks Unlimited in Winnipeg where I am continuing my studies of prairie marshes.