

CHIRONOMIDAE (DIPTERA) RESPONSES TO THE EXPERIMENTAL FLOODING OF PRAIRIE MARSHES

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Abstract: This study examined chironomid responses to the flooding of ten drained experimental marshes in Delta Marsh, Manitoba, Canada. Emergence traps were used to monitor chironomid emergence from three vegetation types (*Symphyotrichum ciliatum*, *Scolochloa festucacea*, and *Schoenoplectus tabernaemontani*) flooded at two water depths (shallow: 20–40 cm, deep: 50–70 cm) over a four-year period. The greatest number (7,651 m⁻² yr⁻¹) and biomass (20.3 g m⁻² yr⁻¹) of chironomids emerged from *Schoenoplectus*-deep sites in the fourth year of flooding. Numbers, biomass, and size classes of emerging chironomids were similar over the four years from the *Symphyotrichum* habitat. However, chironomid emergence from *Scolochloa* and *Schoenoplectus* habitats was dominated initially by the smallest size class but shifted steadily toward production of much larger species over the four-year experiment. The production of chironomids as a potential food resource for waterfowl was high from the *Symphyotrichum* habitat during all four years of flooding, but emergence from the *Scolochloa* and *Schoenoplectus* habitats did not reach comparable levels until the third or fourth year.

Key Words: Chironomidae, Delta Marsh, emergence, marsh, marsh management, drawdown, prairie wetlands

INTRODUCTION

Stable water levels are detrimental to long-term productivity of prairie wetlands (Harris and Marshall 1963, Weller and Fredrickson 1974, Weller 1978). Hence, drawdown (artificial drainage) and reflooding are used increasingly to restore productivity of managed marshes (Weller 1978, Kadlec and Smith 1992, Murkin et al. 2000a). Drawdown enables many emergent macrophytes and mudflat annuals to establish on the dry marsh bottom. Emergent macrophytes may survive shallow flooding, but mudflat annuals are eliminated and contribute to the detritus food web.

The vegetational changes that occur in managed prairie marshes have been studied intensively (e.g., Weller and Fredrickson 1974, van der Valk and Davis 1978, van der Valk 1981, 1982, 1987, 1994, 2000, de Swart et al. 1994, van der Valk et al. 1994), but invertebrate responses to these changes are not understood well. Aquatic invertebrates of freshwater marshes are an extremely important food resource for waterfowl (Murkin and Batt 1987, Krapu and Reinecke 1992, Cox et al. 1998), and several studies have indicated that wetland use by waterfowl may be related to invertebrate abundances (McKnight and Low 1969, Danell and Sjöberg 1982, Murkin et al. 1982, Talent et al. 1982, Murkin and Kadlec 1986, Sedinger 1992).

Invertebrate responses to wetland management practices have been studied most intensively on waterfowl and shorebird migration and wintering grounds (e.g., Batzer and Resh 1992, Batzer et al. 1993, 1997, de Szalay and Resh 1997, 2000, de Szalay et al. 1996, 1999, Gray et al. 1999, Anderson and Smith 2000). However, the effects of wetland management practices on invertebrate populations in the northern breeding grounds have not been studied as intensively. Kaminiski and Prince (1981), Murkin et al. (1982), and Ball and Nudds (1989) have examined invertebrate responses to manipulations of aquatic macrophyte vegetation and litter. Only Murkin and Ross (1999) have reported on invertebrate responses to the reflooding of managed prairie marshes. They describe responses of nektonic and substrate-associated invertebrates to changing conditions within a series of experimental marshes. In this study, I describe the responses of Chironomidae (Diptera) to the reflooding of these same experimental marshes during a four-year period. Changes in numbers, biomass, and size classes are examined in three vegetation types and two water depths. A previous paper reported the changes in species composition of the chironomid community (Wrubleski 1999).

MATERIALS AND METHODS

Study Area

This study was conducted during 1985–88 within the experimental marshes of the Marsh Ecology Research Program (MERP) in the Delta Marsh, south-central Manitoba (50°11'N, 98°19'W). A complex of 10 adjoining 4- to 6-ha diked marshes was built in 1979 (Murkin et al. 2000b). Water levels in the marshes were manipulated and maintained by electric pumps. Vegetation and water chemistry in the marshes are described by Kadlec (1986a,b, 1989), van der Valk and Welling (1988), Welling et al. (1988a,b), van der Valk et al. (1989, 1994, 2000), and van der Valk (1994, 2000). During 1983 and 1984, the marshes were drawn down (artificial drainage). Water was re-applied in June–August 1985 and maintained at stable levels through 1989 (Murkin et al. 2000b).

Sampling

Floating emergence traps were used to sample adult chironomids emerging from the water surface. Emergence traps have two main advantages over conventional benthic sampling: adults can be identified to species more readily than larvae, and processing emergence samples requires less effort per sample compared to benthic samples. The trap used was a modified version of the “week” trap (basal area = 0.5 m²) described by LeSage and Harrison (1979).

Emergence trap sites were established within the marshes in the spring and summer of 1985. Sites were stratified according to habitat and water depth. Three habitat types, based on pre-flood vegetation, were selected for sampling: the mudflat annual *Symphyotrichum ciliatum* (Ledeb.) Nesom (rayless alkali aster) (*Aster laurentianus* Fern. in previous MERP publications), and two emergent macrophytes, *Scolochloa festucacea* (Willd.) Link (whitetop or rivergrass) and *Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla (softstem bulrush). These three plant communities formed extensive stands on the drawdown surfaces of the experimental marshes (Welling et al. 1988a,b, van der Valk 2000). Each habitat was sampled at shallow (20–40 cm) and deep (50–70 cm) water depths. I anticipated that the deep-water sites would lose their emergent macrophyte cover faster than the shallow sites. Because sufficiently large patches representing combinations of the three habitats and two depths were not available in each marsh, the marshes were not used as a blocking factor in the experimental design. Rather, suitable sites for each habitat and water-depth combination were identified across all marshes, and then sampling locations were randomly selected from the entire pool available. To distribute disturbance across

marshes and facilitate collection of samples, a restriction was placed on the randomization such that at least two traps were located in each qualifying marsh. Six traps were used for each habitat and water-depth combination, for a total of 36 traps.

Traps were set out when sufficient water was in place to float them. Deep-water sites, which were at lower elevations, were flooded about 40 days earlier than shallow water sites at higher elevations. Consequently, initiation of sampling varied between 16 May and 20 July in 1985. In 1986, traps were set out in the first week of May and emptied weekly through to the third week of October for 23 weeks or sample periods. In 1987 and 1988, traps were set in the last week of April and data were collected for 24 weeks. The same sample sites were used in all years.

Data Summation

All chironomids were identified to species (Wrubleski 1991, 1999). Numbers collected weekly from each trap were summed for the entire sampling season for each habitat water-depth combination (number trap⁻¹ yr⁻¹). Some weekly samples were lost to strong winds and muskrat damage each year. When possible, traps were replaced immediately, and 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 seven days (e.g., a sample from a trap in place for three days was multiplied by 2.3 to equal a seven-day sampling period). Most traps, however, were not replaced until their next regularly scheduled visit. I used the relationship between the missing trap and the five other traps within that habitat water-depth combination for the three previous sample periods, to estimate the species and numbers of chironomids that would have been anticipated in the lost sample. Imputation procedures used to generate missing data for trap-weeks are reported in Wrubleski (1991). The greatest number of weekly sample losses was 23 of 138 samples (16.7%) for *Scolochloa*-shallow sites in 1986. The total number of weekly samples lost over the four-year period was 0.7% in the shallow sites and 5.8% in the deep sites.

A length-mass regression (Wrubleski and Rosenberg 1990) was used to estimate biomass (g trap⁻¹ yr⁻¹) of emerging chironomids. In addition, a relative frequency distribution of size classes (1 mm) was determined for each habitat water-depth combination, based on adult chironomid body length (pronotum to penultimate abdominal segment).

Statistical Analyses

Seasonally summed numbers of emerging chironomids and their biomass were compared using a re-

Table 1. Repeated measures ANOVA table for numbers and biomass of emerging chironomids [\log_{10} -transformed data] from three habitats and two water depths over a four-year period in the experimental marshes.

Source of Variation	df	F	P
Numbers			
Depth	1,30	27.39	<0.0001
Habitat	2,30	11.34	0.0002
Depth \times Habitat	2,30	2.81	0.0758
Year	3,90	9.62	<0.0001
Depth \times Year	3,90	2.84	0.0423
Habitat \times Year	6,90	2.59	0.0233
Depth \times Habitat \times Year	6,90	2.01	0.0724
Biomass			
Depth	1,30	16.20	0.0004
Habitat	2,30	36.57	<0.0001
Depth \times Habitat	2,30	2.54	0.0957
Year	3,90	32.96	<0.001
Depth \times Year	3,90	1.34	0.2658
Habitat \times Year	6,90	8.42	<0.0001
Depth \times Habitat \times Year	6,90	3.73	0.0024

peated measures ANOVA with habitat, depth, and depth \times habitat as between-trap sources of variation. Year, year \times depth, year \times habitat, and year \times depth \times habitat were temporal or within-trap sources of variation. An autoregressive (order 1) error structure was used for modeling within-trap error dependence. Analyses were conducted using PROC MIXED of SAS (SAS Institute Inc. 1999). Year comparisons within habitat and depth, habitat comparisons within year and depth, and depth comparisons within habitat and year were all done using contrast statements. Data were \log_{10} -transformed prior to analysis to stabilize the variances.

RESULTS

The overall repeated measures ANOVA showed that numbers and biomass of emerging chironomids differed significantly between depths and among habitats and years (Table 1). The depth \times habitat interaction suggested a trend for both numbers and biomass of chironomids to respond differently to vegetation and depth of flooding. Numbers of chironomids emerging each year varied between depths, but biomass did not. Both annual numbers and biomass showed significant interactions between habitat and year, indicating that habitats had different chironomid outputs over the four years. The three-way depth \times habitat \times year interaction was significant for biomass but not for numbers, suggesting that chironomids responded differently to vegetation and water depth and that these differences also varied annually.

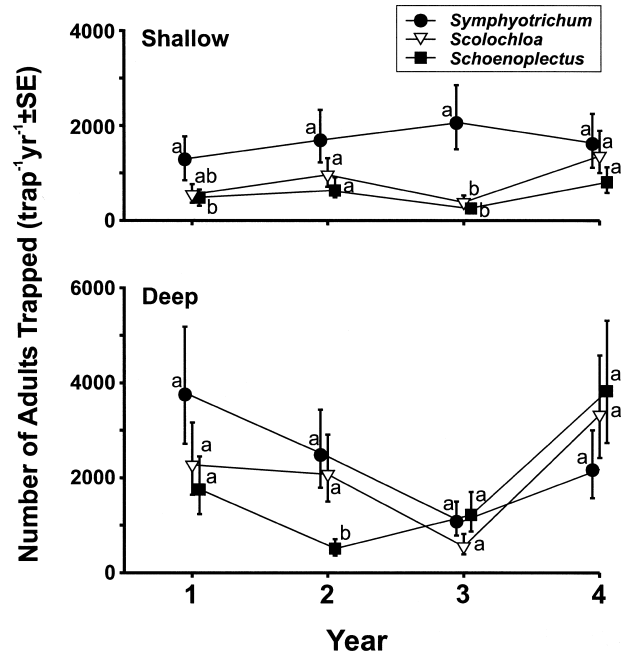


Figure 1. Back-transformed least squares mean (\pm SE) annual numbers of chironomids emerging over a four-year period from three habitats and two water depths in the experimental marshes. Comparisons among habitats within each water depth and year are indicated by letters, and means with the same letters are not significantly different ($P > 0.05$).

Habitat comparisons within depth and year showed that, in the first year after flooding, *Symphyotrichum*-shallow had a significantly greater emergence of chironomid numbers than the *Schoenoplectus* habitat, but *Scolochloa* did not differ from either (Figure 1). In the third year, *Symphyotrichum*-shallow had a greater emergence of chironomid numbers than both the *Scolochloa* and *Schoenoplectus* habitats, but in year four, all three habitats had similar emergence numbers. In the deep-water sites, no differences were found among the three habitats, except a lower emergence of chironomid numbers from the *Schoenoplectus* habitat in year two. For chironomid biomass, a greater number of differences among habitats was found (Figure 2). Biomass of chironomids emerging from *Symphyotrichum* was greater than from the other two habitats in years one, two, and three in the shallow depths, and years one and two in the deeper habitats. *Scolochloa* had a greater biomass of chironomids emerging than the *Schoenoplectus* habitat in the shallow depths in year three and the deep sites in year two. No differences among the three habitats were found in the fourth year of flooding.

In comparing deep and shallow sites within a vegetation type and year, significantly greater numbers of chironomids emerged from the deep sites of all three habitats in the first year (Figure 3). Differences were

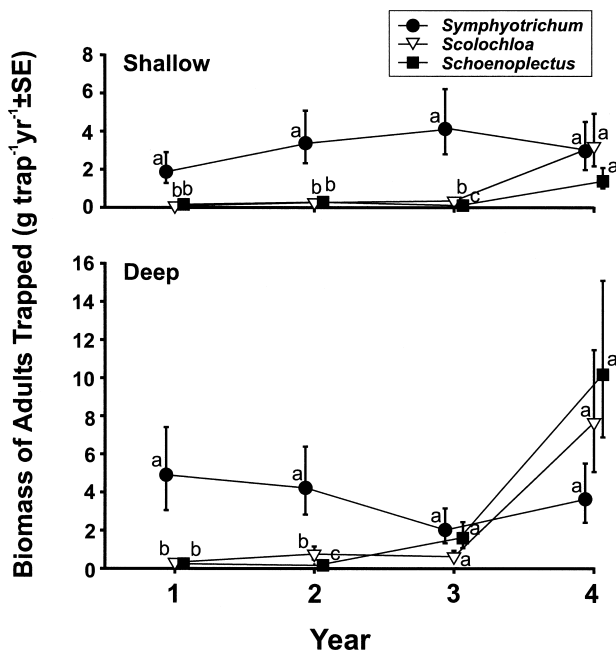


Figure 2. Back-transformed least squares mean (\pm SE) annual biomass of chironomids emerging over a four-year period from three habitats and two water depths in the experimental marshes. Comparisons among habitats within each water depth and year are indicated by letters, and means with the same letters are not significantly different ($P > 0.05$).

only significant in the *Scolochloa* habitat for biomass (Figure 4). These differences probably reflect the fact that deep sites were flooded earlier, and for a longer period, than shallow sites. In the second year, no differences were found between depths (Figures 3, 4). In both years three and four, greater numbers and biomass of chironomids emerged from the deep sites in *Schoenoplectus* compared to the shallow sites. A similar difference was also found for chironomid numbers in *Scolochloa* sites in year four.

When comparing emergence over time within habitat and depth, similar numbers of chironomids emerged in all years from *Symphyotrichum*-shallow sites (Figure 3). In *Scolochloa* and *Schoenoplectus*-shallow sites, numbers of chironomids emerging in year three were significantly lower than in both year two and year four. In the deep water sites for all three habitats, a pattern of large emergence was observed in the first year, followed by decreasing numbers during year two and/or year three and a subsequent increase in the fourth year (Figure 3). In terms of biomass, significant increases in emergence were observed in *Scolochloa*-shallow sites from first to second year and again from third to fourth year (Figure 4). Significant increases were observed in *Schoenoplectus*-shallow sites from the third to fourth year. These increases were also observed in the deep sites for both habitats

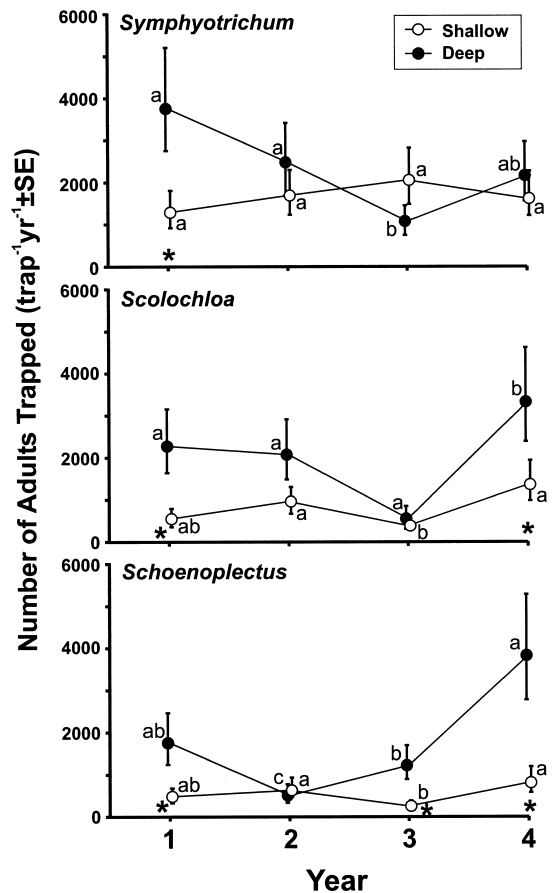


Figure 3. Back-transformed least squares mean (\pm SE) annual numbers of chironomids emerging over a four-year period from three habitats and two water depths in the experimental marshes. Asterisk (*) indicates a significant difference ($P < 0.05$) between depths within habitat and year. Comparisons among years within each water depth and habitat are indicated by letters, and means with the same letters are not significantly different ($P > 0.05$).

but started in year three in *Schoenoplectus*. Biomass of emerging chironomids did not differ over the four years in shallow or deep waters from *Symphyotrichum*.

There were conspicuous changes in size of emerging chironomids in *Scolochloa* and *Schoenoplectus* habitats during the four years (Figure 5), which reflected changes in species composition (Wrubleski 1991, 1999). In the first year of flooding, emergence from both depths was dominated by small individuals, particularly in the 1–2-mm size class (mostly *Corynoneura* cf. *scutellata* Winn.). Over the next three years, there was a shift to much larger individuals [8–10-mm size classes; predominantly *Chironomus dilutus* Shobanov, Kiknadze, and Butler [formerly *Chironomus tentans* Fab. (see Shobanov, Kiknadze, and Butler 1999)] and *Glyptotendipes barbipes* (Staeg.). This size transition was most apparent for the deep habitats, where the 9–10-mm size class dominated emergence

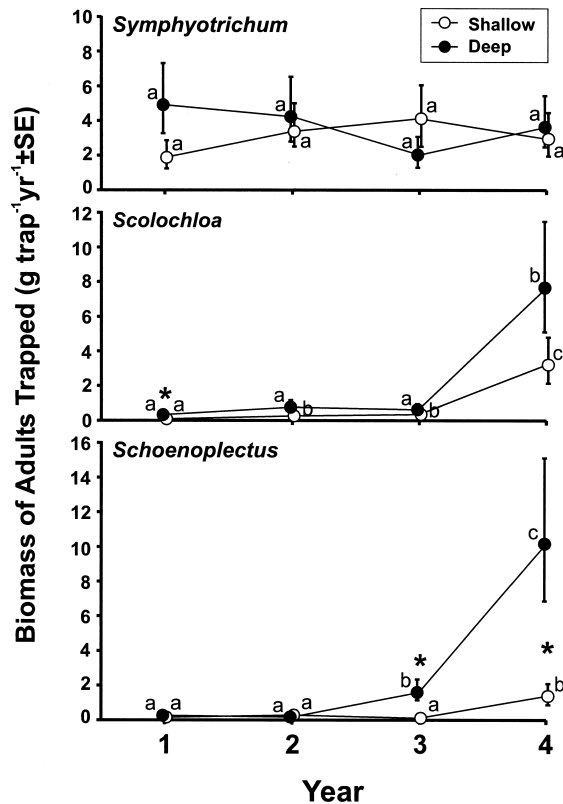


Figure 4. Back-transformed least squares mean (\pm SE) annual biomass of chironomids emerging over a four-year period from three habitats and two water depths in the experimental marshes. Asterisk (*) indicates a significant difference ($P < 0.05$) between depths within habitat and year. Comparisons among years within each water depth and habitat are indicated by letters, and means with the same letters are not significantly different ($P > 0.05$).

in years three and four. Shallow *Scolochloa* and *Schoenoplectus* habitats shifted to a more bimodal distribution of sizes in the later years, similar to the pattern observed in the *Symphyotrichum* habitat. In *Symphyotrichum*, the pattern present in all four years and both depths was a bimodal distribution of sizes that peaked at 2–5 mm (predominantly *Cricotopus*, *Tanytarsus*, and *Paratanytarsus* spp.) and 7–10 mm (predominantly *C. dilutus*, *Chironomus atrella* (Town.), and *G. barbipes*).

DISCUSSION

Chironomid Responses to Reflooding of Drawdown Marshes

Several studies have reported greater numbers of invertebrates in newly flooded marsh habitats than in nearby older wetlands (McKnight and Low 1969, Whitman 1974, Street and Titmus 1979, Walton et al. 1990, Beehler and Mulla 1993, Keiper et al. 2002).

During the first four years of flooding, the greatest number of chironomids recorded from the experimental marshes ($7,651 \text{ m}^{-2} \text{ yr}^{-1}$ from *Schoenoplectus*-deep sites in year four) was only about half the maximum previously recorded from the unmanaged Delta Marsh ($15,601 \text{ m}^{-2} \text{ yr}^{-1}$ from the pondweed habitat of Bone Pile Pond [BPP] [Wrubleski and Rosenberg 1990]). *Schoenoplectus*-deep sites, however, had comparable emergence numbers ($1,017\text{--}7,651 \text{ m}^{-2} \text{ yr}^{-1}$) to those found in the *Schoenoplectus* habitat of BPP ($4,024\text{--}6,193 \text{ m}^{-2} \text{ yr}^{-1}$). Numbers of chironomids emerging from *Scolochloa*-shallow sites ($766\text{--}2,715 \text{ m}^{-2} \text{ yr}^{-1}$) tended to be similar to those from a seasonally flooded *Scolochloa* habitat in the Delta Marsh ($2,500 \text{ m}^{-2} \text{ yr}^{-1}$ [Wrubleski 1987]), but numbers emerging from *Scolochloa*-deep sites, particularly in the fourth year ($6,649 \text{ m}^{-2} \text{ yr}^{-1}$), were greater.

Although numbers of chironomids emerging from the MERP marshes were either comparable or lower than those found in the unmanaged Delta Marsh, biomasses were greater. The largest biomass emerging from the experimental marshes was from the *Schoenoplectus*-deep sites in year four ($20.3 \text{ g m}^{-2} \text{ yr}^{-1}$), which was more than five times that found in the *Schoenoplectus* habitat of BPP ($2.9\text{--}3.9 \text{ g m}^{-2} \text{ yr}^{-1}$) and almost twice the largest biomass estimated from the pondweed habitat ($9.2\text{--}13.4 \text{ g m}^{-2} \text{ yr}^{-1}$), the most productive habitat in BPP (Wrubleski and Rosenberg 1990). Chironomid emergence from BPP was dominated by smaller size classes, explaining the lower biomass (Wrubleski 1991, 1999). The greater biomass from the experimental marshes was a result of large numbers of the larger size classes.

Whitman (1974) reported largest numbers of larval chironomids in wetland impoundments less than one year old. Danell and Sjöberg (1982) found largest numbers of chironomids emerging in year five of a newly flooded lake managed for waterfowl (emergence was only sampled during years 4–7). In the experimental marshes, peak production of chironomid adults varied among the habitats and water depths sampled, and over the four years. Numbers of chironomids emerging from the shallow water depths showed few changes over time other than a significant decrease during the third year in both emergent vegetation habitats. There was a general trend for large numbers emerging in the first year in the deep-water sites, with a decrease in numbers in the second and/or third years in all three habitats, and significant increases by the fourth year in *Scolochloa* and *Schoenoplectus* habitats. Biomass of chironomids emerging from both water depths showed little change over time in *Symphyotrichum*, whereas *Scolochloa* and *Schoenoplectus* habitats had significant increases in emergent biomass by the third or fourth years of flooding at both depths.

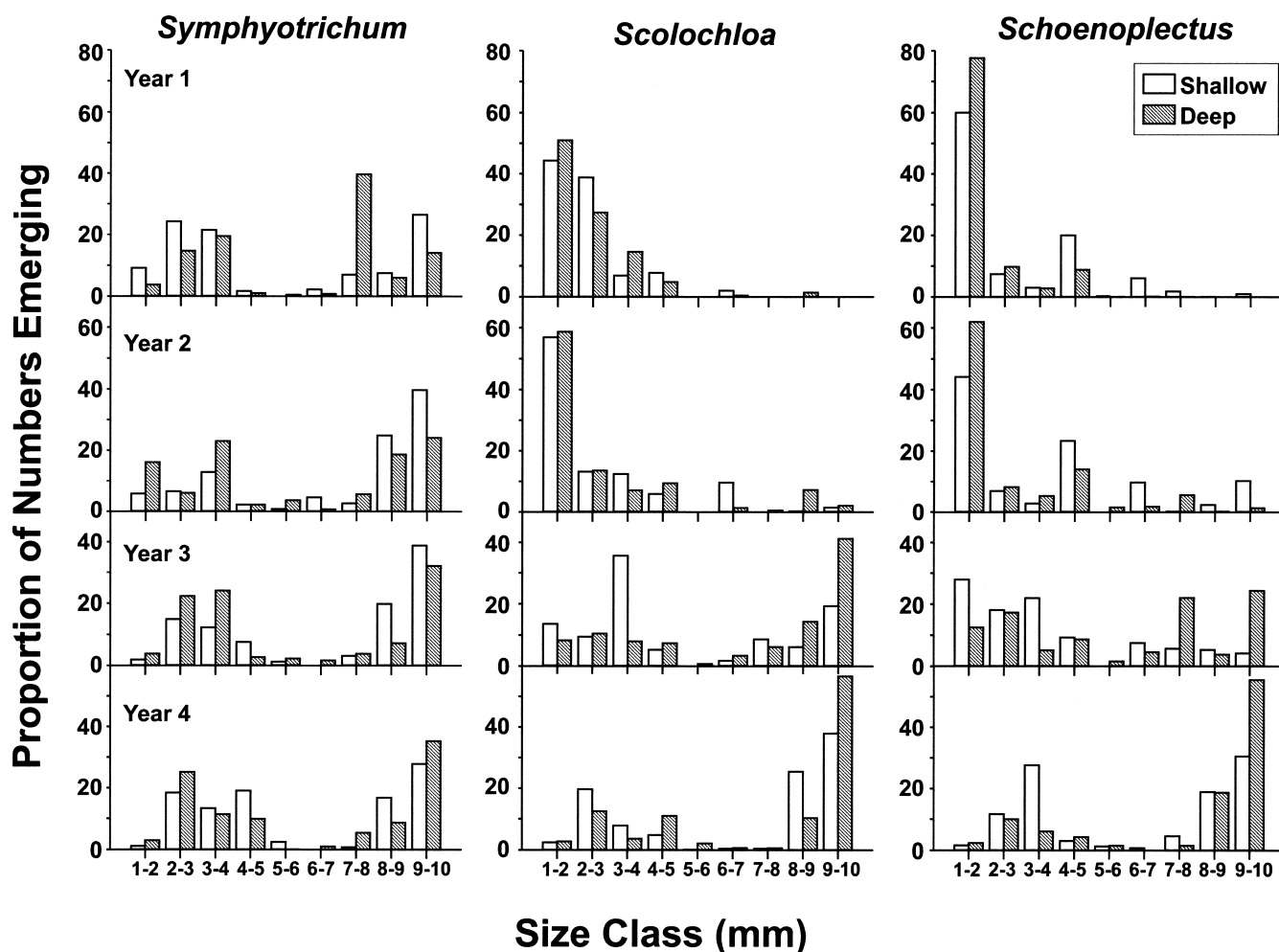


Figure 5. Proportion of annual chironomid emergence represented by each 1mm size class over a four-year period from three habitats and two water depths sampled in the experimental marshes.

Danell and Sjöberg (1982) noted a decrease in mean larval chironomid size from the third to seventh years of flooding. Results of the present study showed a different pattern. There was little change in size of adults emerging from the *Symphyotrichum* habitat, but in *Scolochloa* and *Schoenoplectus* habitats, there was a shift from small epiphytic to large benthic species, particularly in the deep sites, over the four years (Wrubleski 1991, 1999).

Aquatic invertebrate populations in wetland habitats do respond to changes in vegetation and water depth (e.g., Voigts 1976, Murkin and Kadlec 1986, Kenow and Rusch 1989, Murkin et al. 1991, Batzer and Resh 1992, Batzer et al. 1997, de Szalay and Resh 1997, Murkin and Ross 1999, 2000), and this was also the case for the chironomids in this study. Chironomid emergence differed between the *Symphyotrichum* and the two emergent macrophyte habitats sampled. *Symphyotrichum ciliatum* is a terrestrial annual characteristic of mudflats and could not survive flooding. Con-

sequently, a large amount of plant litter was added to the bottom in one large pulse, leaving only sparse standing emergent vegetation. Submersed vegetation (primarily *Stuckenia pectinatus* (L.) Boerner [sago pondweed] and *Utricularia macrorhiza* Le Conte [common bladderwort]) and mat-forming metaphytic algae (metaphyton) developed extensively in these open, sunlit areas (Murkin and Ross 1999, Wrubleski, *personal observations*). This structurally complex habitat, with abundant algal production, was colonized by a variety of chironomid species, including many small epiphytic taxa such as *Paratanytarsus* and *Cricotopus* species, but also larger benthic and mining species such as *C. dilutus*, *C. atrella*, and *G. barbipes* (Wrubleski 1991).

Scolochloa and *Schoenoplectus* persisted due to their initial tolerance of flooding (Squires and van der Valk 1992, van der Valk et al. 1994, van der Valk 2000), providing an abundance of vertical plant stems within the water column. These stems provided surface

area for *C. cf. scutellata*, the most abundant chironomid in these habitats during the first two years of flooding (Wrubleski 1991, 1999). Epiphyton on the submersed stems probably provided food resources for these small free-living grazers (Kesler 1981). Large benthic chironomids were notably absent from these habitats (Wrubleski 1991, 1999). Reasons for their absence are not known but may be related to poor habitat conditions on the bottom. For example, dense stands of emergent vegetation prevent mixing of the water column, leading to low oxygen conditions (Suthers and Gee 1986, Rose and Crumpton 1996, de Szalay and Cassidy 2001). Emergent macrophytes also shade the bottom (e.g., Rose and Crumpton 1996, Grimshaw et al. 1997), restricting algal growth that is an important food resource for many benthic chironomids (see Wrubleski 1999).

After several years of flooding, both *Scolochloa* and *Schoenoplectus* died back, particularly at the deeper flooding depths (van der Valk et al. 1994, van der Valk 2000). Consequently, there was a dramatic decrease in the smaller epiphytic chironomids and an increase in the same benthic and mining species observed in the *Symphyotrichum* habitat (Wrubleski 1991, 1999). Driver (1977) and Murkin and Kadlec (1986) also have reported increases by *C. dilutus* following the death of emergent macrophytes due to excessive flooding. Without information on larval distributions, it is unclear whether these benthic chironomids were responding to an increase in plant litter or some other change in the habitat brought about by the death of the these plants.

Management Implications

Although larval and adult chironomids are important food resources for waterfowl (e.g., Sugden 1973, Euliss and Grodhaus 1987, Murkin and Batt 1987, Batzer et al. 1993), the relative value of each species is largely unknown. Size is one parameter that is probably important (Nudds and Bowlby 1984). Batzer et al. (1993) demonstrated that larger larval chironomids are more likely to be consumed by waterfowl. The results of the present study show that areas dominated by mudflat annuals would be more productive of chironomids initially than areas dominated by emergent macrophytes. The *Symphyotrichum* habitat produced a variety of chironomids, with many in the larger size classes emerging in the first two years after flooding. *Scolochloa* and *Schoenoplectus* habitats produced very small chironomids during the first two years and, not until these plants began to die back in the third and fourth years of flooding, were high numbers of larger-sized chironomids produced.

The findings of the present study suggest that an

ample growth of a mixture of plant species should be encouraged during the drawdown phase of prairie marshes. Mudflat annuals make up a significant part of the plant community during drawdown (van der Valk and Davis 1976, 1978, Davis and van der Valk 1978, Welling et al. 1988a,b, van der Valk 2000) and provide an excellent habitat for chironomid production when northern prairie marshes are reflooded. Conversely, emergent macrophytes provide habitat for many small epiphytic chironomid species but apparently inhibit the development of a benthic community. Although dense stands of emergent vegetation may not be productive initially, their eventual death due to flooding will result in the production of larger benthic species. Thus, the differential responses of the various plant species following drawdown will ensure continued chironomid production over a longer term.

Chironomid larvae present in the deep-water habitats of the experimental marshes would be available to diving waterfowl but would probably be too deep for foraging by most dabbling duck species. These chironomids would be available during emergence periods (Swanson and Sargeant 1972, Swanson 1977, Sjöberg and Danell 1982, King and Wrubleski 1998) but also could be made available by partial drawdowns (Euliss and Grodhaus 1987, Batzer et al. 1993).

Whitman (1974) suggested that optimum conditions for invertebrate production in newly created wetlands occurred during the first 1.5 to 4 years and recommended drawdown between years 5 to 7 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 mudflat annuals and then from the drowned emergent macrophyte habitats. In these experimental marshes, it is anticipated that the high chironomid production observed would eventually decrease as the emergent macrophytes continued to dieback and decomposition proceeded. By the end of my study, submersed macrophytes were beginning to develop in these experimental marshes (Murkin and Ross 1999), and their effects on chironomid production are not known. Further study is needed in northern prairie marshes to determine how long the high levels of chironomid production observed in the present study will be sustained.

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