

COASTAL WETLAND INSECT COMMUNITIES ALONG A TROPHIC GRADIENT IN GREEN BAY, LAKE MICHIGAN

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Abstract: Insects of Great Lakes coastal wetlands have received little attention in spite of their importance in food webs and sensitivity to anthropogenic stressors. We characterized insect communities from four coastal wetlands that spanned the length of a trophic gradient in Green Bay during spring and summer of 1995. We sampled flying insects using sticky traps in dense emergent, sparse emergent, and open water-submergent vegetation zones within each wetland and estimated numerical abundance, biomass (mg dry weight) and taxonomic composition. We found that insect abundance and biomass were distributed differently among vegetation zones within wetlands along the gradient during both spring and summer. Insect abundance was highest at oligotrophic Portage Marsh during spring and lowest in wetlands toward the lower (southern), eutrophic end of the bay. Biomass did not differ consistently along the trophic gradient but increased with increasing emergent vegetation cover in 3 of 4 wetlands during both seasons. Ordination revealed distinct gradients in community structure on both regional (i.e., upper, middle, and lower Green Bay) and local (vegetation zones within wetlands) scales. Wetlands sorted in order of trophic status during both seasons, primarily due to abundant small Chironomidae, such as trophic-sensitive *Heterotrissocladius changi*, in middle and upper bay wetlands. Chironomidae also were a dominant component of open water-submergent assemblages in all wetlands. Lower bay wetlands were characterized by fewer but larger Chironomidae (e.g., *Chironomus* spp.), as well as Ceratopogonidae, Calliphoridae, and Ephydriidae, which were most abundant in stands of emergent vegetation. Our results suggest that eutrophy in the lower bay may contribute to relatively poor foraging conditions for insectivorous fish and young waterfowl during spring, and they demonstrate the utility of using insect communities to assess environmental degradation, such as excessive nutrient loading, in coastal wetlands of the Great Lakes.

Key Words: Chironomidae, eutrophication, food availability, Great Lakes, invertebrates, ordination, sticky trap

INTRODUCTION

Green Bay, Lake Michigan has some of the most extensive coastal wetland habitat remaining in the Great Lakes region of North America (Bosley 1978). These coastal wetlands provide critical food and habitat to breeding and migrating waterfowl (Bookhout et al. 1989), resident and transitory fishes (Jude and Pappas 1992), and other wildlife (e.g., Harris et al. 1983). However, Green Bay has been degraded by a variety of pollutants resulting from industrial and human de-

velopment. The most severe degradation has been within the Fox River watershed, which feeds the southern end of the bay with a high nutrient load (Bertrand et al. 1976, Harris et al. 1987). This has resulted in highly eutrophic conditions in the lower bay and contributed to a strong north-to-south trophic gradient throughout the bay (Sager and Richman 1991, Brazner and Beals 1997). Nutrient enrichment and associated turbidity has had profound effects on biota, including phytoplankton (Richman et al. 1984b, Auer et al. 1986,

Sager and Richman 1991), zooplankton (Richman et al. 1984a, Sager and Richman 1991), macrophytes (Harris et al. 1988, Harris et al. 1991, Brazner 1997), and fish (Brazner and Beals 1997). Effects on wetland insects or other macroinvertebrates only have been investigated indirectly (McLaughlin and Harris 1990).

Insect communities of Great Lakes coastal wetlands have received minimal attention from researchers (Krieger 1992), yet they are clearly important to fish and wildlife as food and may play a significant role in nutrient cycling and other ecosystem functions (e.g., Crow and MacDonald 1978, Murkin 1989). There are baseline data on abundance, biomass, and species composition of emerging insects from two coastal wetlands in lower Green Bay (McLaughlin and Harris 1990). These results suggested that turbidity-induced suppression of macrophyte diversity and cover resulted in reduced insect abundance and biomass compared to a nearby diked wetland. These findings may have larger-scale regional implications for fish and wildlife since there is lower turbidity and greater submersed macrophyte diversity and cover in meso-oligotrophic coastal wetlands in middle and upper Green Bay compared to hypereutrophic wetlands in the lower bay (Brazner and Beals 1997). Low insect production in wetlands could influence waterfowl use and brood survivorship (e.g., Hunter et al. 1984, Bélanger and Couture 1988, Pehrsson and Nyström 1988, Cox et al. 1998), as well as the distribution of insectivorous fish such as centrarchids (Brazner 1997).

Based on the limited knowledge of coastal wetland insect communities, their potentially important role in Great Lakes food webs, and their sensitivity to anthropogenic stresses, we set out to characterize insect assemblages from four coastal wetlands that spanned the length of Green Bay. Our objectives were to investigate insect community response to the trophic gradient in the bay and associated differences in macrophyte habitat structure, as well as assess implications for foraging fish and waterfowl. We expected that potentially less-complex macrophyte structure and degraded water quality in the more turbid lower bay would result in reduced insect abundance and biomass and, therefore, less suitable foraging conditions for fish and waterfowl.

METHODS

Study Area

Green Bay is a 193-km long, 20- to 30-km-wide embayment of northwestern Lake Michigan (Figure 1). It is relatively shallow, with few areas deeper than 40 m and nearly all of the western side less than 5 m deep within 1 km of shore. The 30 to 60 km² of coastal

wetlands in Green Bay are most concentrated along the west shore (Bosley 1978).

The four coastal wetlands we sampled were all located along the western shore. Peter's Marsh was the most southern wetland sampled. It is an approximately 0.5-km² embayment marsh, 9-km south of Little Tail Point (Figure 1). *Typha latifolia* L. was the dominant emergent plant, and *Potamogeton pectinatus* L. was the dominant submersed macrophyte species. Little Tail Point Wetland is also a shallow embayment marsh near the Brown and Oconto County lines, protected by a 3-km-long barrier beach on its east side, and approximately 3-km² in size. Dominant emergent plants were *T. latifolia*, *Scirpus validus* Vahl., and *Sparganium* spp. Dominant submergents were *Vallisneria americana* Michaux., *Najas* sp., and *P. pectinatus*. Seagull Bar Wetland is heavily protected by a 2-km² barrier beach. This lagoon-type wetland is located on the delta of the Menominee River 1.5-km south of the mouth of the river (Figure 1). *Typha latifolia* and *S. validus* were the dominant emergent plants, and *Myriophyllum* spp. and *P. pectinatus* were the dominant submersed species. The final wetland sampled was Portage Marsh, another heavily protected, barrier beach, lagoon-type wetland about 2 km² in size located 2 km south of Escanaba, Michigan. A 100-m-wide constriction at its opening isolates it from adjacent Green Bay proper more than any of the other wetlands we sampled. Dominant emergent macrophytes were *Typha* spp. and *S. validus*, and dominant submergent species were *P. richardsonii* (Benn.) Rydb., *Elodea canadensis* Michaux., *Ceratophyllum demersum* L., and *Myriophyllum* spp.

Insect Sampling

We sampled flying insects during spring (late-May) and summer (mid-July) of 1995, concomitant with peak dabbling duck brood rearing (Bookhout et al. 1989, Sedinger 1992) and juvenile fish abundance (Brazner 1997) in these coastal wetlands. Flying insects are directly available to waterfowl, especially dabbling ducklings, and comprise a large proportion of duckling diets since young dabblers are restricted to food at and above the air-water interface (Chura 1961, Collias and Collias 1963, Bengtson 1975, Pehrsson 1979). Although flying insects are not readily available to fish, their abundance and species composition reflect the immature, aquatic community (specifically emerging nymphs and pupae) most available to juvenile fishes. We collected flying insects using floating sticky traps (STs) as described by King and Wrubleski (1998). STs were made using gray plastic pipe, acetate transparency sheets, polystyrene, and Tangle-Trap Insect Trap Coating (Tanglefoot Compa-

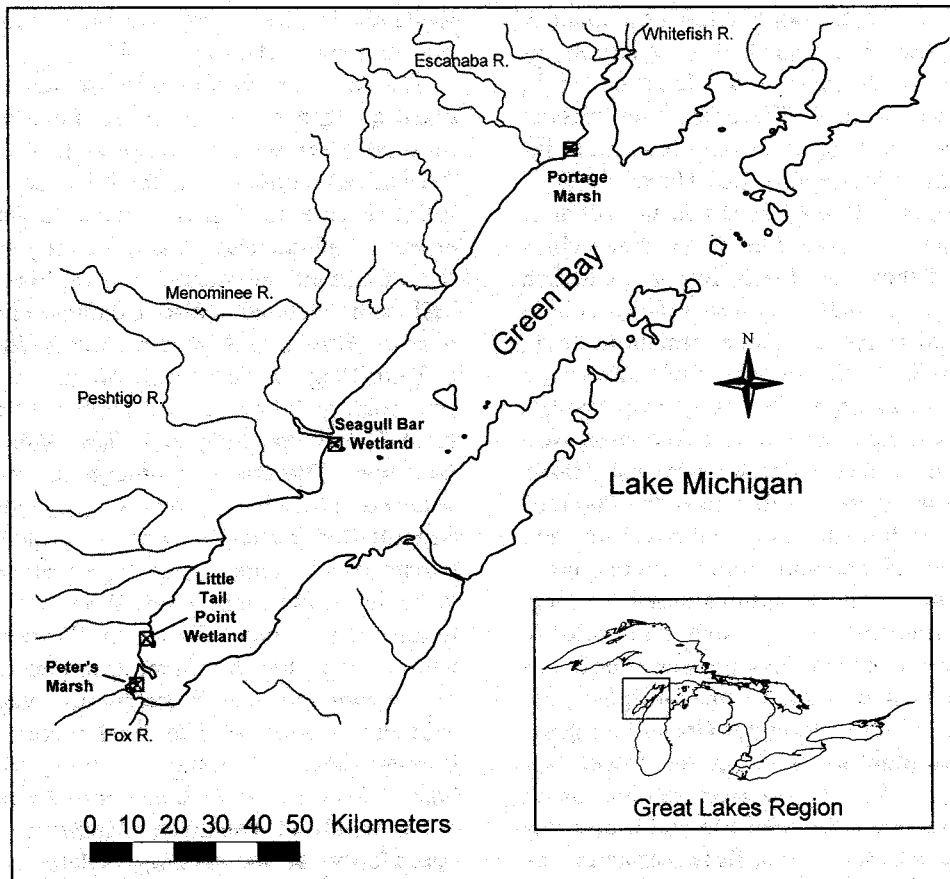


Figure 1. Map of Green Bay showing its relative position in the Great Lakes region and Lake Michigan, as well as locations of 4 coastal wetlands sampled during spring and summer 1995.

ny, Grand Rapids, MI, USA). Transparencies were fixed around the surface of pipe sections. Pipes were secured and supported vertically in the center of polystyrene blocks, which provided flotation. Tangle-Trap then was applied in a thin layer to the surface (18 cm × 24 cm) of the transparency sheets. STs sampled a 24-cm insect flight zone directly above the water surface. We used STs because they (1) capture emerging insects, as well as those feeding, mating, or ovipositing near the water surface, and thus integrate over larger areas and time intervals than other methods (e.g., aquatic or aerial sweep nets), (2) are inexpensive to build and cost-effective because they require no time-intensive sorting of immature aquatic insects from detritus or vegetation, often a limiting factor in studies of this kind, and (3) estimate insect availability to foraging waterfowl since insects are captured at and immediately above the air-water interface.

We placed five traps in each of two (spring) or three (summer) vegetation zones at each wetland. Density of emergent vegetation in coastal wetlands typically decreases with increasing depth and thus delineates relatively distinct zones within a wetland along a depth gradient from upland (0 cm) to open water-submer-

gent vegetation (> 50 cm). Emergent macrophyte cover was low at all sites during spring, so we defined only two zones, sparse emergent (SE; depth = 10 to 50 cm) and open water-submergent (OW; depth > 50 cm). In summer, emergent macrophyte cover was much greater and thus was split into dense emergent (DE; depth = 10 to 25 cm) and SE (depth = 25 to 50 cm) zones in addition to the OW zone. Summer SE was an edge/transition zone. Since we expected wetlands to differ in terms of vegetation structure in response to the trophic gradient, we standardized vegetation-zone comparisons among wetlands based on depth rather than specific percent coverage of vegetation. STs were spaced 20 m apart within each zone, parallel to shore, and secured by metal posts driven into the substrate. STs were positioned by sliding the trap over the post, float first. Posts fixed the horizontal position of STs but permitted them to move up and down with surface waves and seiches.

We deployed STs for one 72-h interval at each site during each season. Due to the distance between upper and lower bay sites (~150 km), we could not sample all wetlands simultaneously. Portage Marsh and Seagull Bar Wetland were sampled for 72 h (18–21 May,

12–15 July 1995), then traps were moved to Little Tail Point Wetland and Peter's Marsh for 72 h (22–25 May, 16–19 July 1995). At the end of each deployment, samples (transparency sheets) were removed from STs, stored in bags, and frozen. As a result of high winds and waves during storm events, 3 samples (1 from SE, 2 from OW) were lost at Little Tail Point Wetland in spring and 1 each at Portage Marsh (OW) and Seagull Bar Wetland (SE) in summer.

Sample Processing

We examined transparencies using a dissecting microscope. We subsampled transparencies for insect counts because of very large numbers of insects (some samples had >2,000 individuals). We used a stratified-random subsampling technique with a 2-cm × 2-cm grid. Sample dimensions were 18-cm wide × 24-cm high, so we selected randomly (using 10,000 random-digit table) two 2-cm × 2-cm squares along each of 12 horizontal rows (2/9 of the total transparency surface area was subsampled). Vertical stratification ensured a representative subsample since insects were often in greatest number near the base (water surface) of STs.

All insects were identified initially to family, with the exception of the Chironomidae, which were identified to subfamily (Orthocladiinae and Tanypodinae) or tribe (Chironomini and Tanytarsini of the subfamily Chironominae). Within these higher taxon groups, counts were recorded based on insect "morphospecies," a level of taxonomy that distinguished probable species from one another but did not attach specific names (Oliver and Beattie 1996). A few specimens of each morphospecies were removed with paint thinner (a solvent for the Tangle-Trap coating), preserved in ethanol, and used as voucher specimens for tallying. Many insect specimens were in poor condition due to strong winds and surface waves during deployment of STs. Therefore, we were only able to complete genus or species identifications of morphospecies that constituted greater than 10% of the total count or biomass at each wetland on each date.

Insect counts recorded from STs also were used to estimate biomass (mg drymass). We used length-mass regression equations developed by Sage (1982), Wrubleski and Rosenberg (1990), and Sample et al. (1993) to estimate individual dry-mass of insects because ST-caught insects had Tangle-Trap residue on them and were not usable for dry-mass estimates. Insect morphospecies were measured for total length (0.1-mm) using an ocular micrometer. Median lengths were used in the length-mass regression equations.

Environmental Sampling

Several environmental variables expected to reflect the trophic gradient in Green Bay based on previous studies (e.g., Brazner and Beals 1997) were measured concurrently with insect sampling. Water temperature, conductivity, and turbidity were measured daily ($n = 4$ per season) at mid-depth between the 0.5-m and 1-m depth contours with a Hydrolab DataSonde III multi-probe sensing unit (Hydrolab Corp., Austin, TX, USA). Water temperature was measured to assess whether wetlands were functioning under similar temperatures seasonally despite their 150-km latitudinal separation. Conductivity is often highly correlated to total dissolved solids and thus was expected to be higher in the lower, eutrophic end of the bay (Brazner and Beals 1997). Similarly, turbidity was expected to be higher in the lower bay due to high productivity and standing-stock biomass of phytoplankton and other suspended solids related to development (Richman et al. 1984b, Sager and Richman 1991, Millard and Sager 1994, Brazner and Beals 1997). The number of macrophyte species and the percentage of area covered by macrophytes were estimated visually in the DE, SE, and OW zones where insects were sampled once in each season of sampling.

Statistical Analysis

We inspected total insect count and biomass data for normality using normal-probability residual plots and tested variance homogeneity using Bartlett's test. Data from each sampling period were analyzed separately because of differences in vegetation cover (SE and OW in spring; DE, SE, and OW in summer). All data required a log transformation to normalize residuals and homogenize variances. After transformation, p values from Bartlett's tests ranged from 0.1164 to 0.8337, verifying normality of residuals (Sokal and Rohlf 1995). We assessed the effects of wetland and vegetation zone on transformed counts and biomass of insects using split-plot ANOVA, with wetland and vegetation zone tested against the wetland × vegetation zone interaction and wetland × vegetation zone tested against the residual (trap [wetland × vegetation zone]) (Sokal and Rohlf 1995). Tukey's HSD test was used to compare means for effects deemed significant from ANOVAs. Main effects and interactions were considered significant when $p \leq 0.05$.

We assessed gradients in insect community structure among wetlands and vegetation zones using non-metric multi-dimensional scaling (NMDS). NMDS is an ordination technique based on simple rank similarities among samples rather than an actual distance metric in the original ordination algorithm (Ludwig and

Reynolds 1988). Hence, NMDS is ideal for community data, which rarely, if ever, meet assumptions of multivariate normality or linearity required by many other ordination techniques (Clarke 1993). We used Bray-Curtis dissimilarity as a basis for sample ranks, a coefficient shown to be one of the most robust performers (Faith et al. 1987). Since only dominant morphospecies were identified to genus or species, we used abundance (relativized by each taxon maximum abundance to give equal weight among taxa; Faith and Norris 1989) of insect families for Bray-Curtis dissimilarities, with the exception of the Chironomidae, which were separated based on subfamily (Orthocla-diinae and Tanypodinae) or tribe (Chironomini and Tanytarsini of the subfamily Chironominae). We separated chironomids because of their dominant numerical presence in wetland insect communities and wide range of tolerances to environmental stressors, which often can be detected at the subfamily and tribe level (e.g., Armitage et al. 1995). Dissimilarity based on these taxon groups rather than species is likely a better indicator of functional differences among wetlands since one could expect geographical differences in species composition regardless of trophic or other gradients. We ran ordinations separately for each date to avoid confounding effects of seasonality on community structure. Starting with two axes, successive dimensions were added, if necessary, until decreases in stress (a metric of agreement between compositional dissimilarities and distance among samples in ordination space) were small (Faith and Norris 1989, Clarke 1993). Monte-Carlo permutation tests (100 runs) were run on both ordinations to assess the probability that sample scores in ordination space reflected an accurate display of compositional dissimilarity and, therefore, verify that additional dimensions were not needed (critical value $p \leq 0.05$). Correlations between taxa abundance and NMDS axes also were calculated for each ordination to assess which taxa were related to potential gradients among wetlands or vegetation zones.

RESULTS

Environmental Characterization

Water temperatures ranged from 14 to 18 °C during spring sampling and 24 to 28 °C during summer sampling, indicating that the four wetlands were functioning under similar temperatures seasonally despite their 150-km latitudinal separation (Figure 2a). Both conductivity (Figure 2b) and turbidity (Figure 2c) increased from northern to southern wetlands, reflecting the trophic gradient as well as the phytoplankton- and erosion-derived turbidity in the highly eutrophic south-

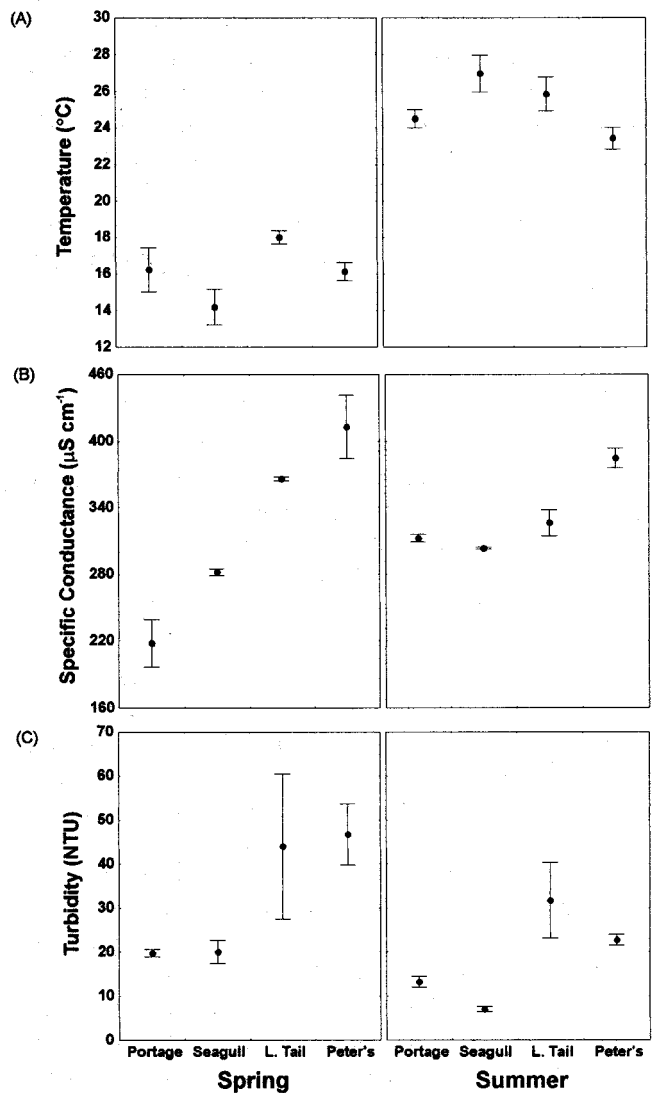


Figure 2. Mean (\pm SE, $n = 4$) (a) temperature (°C), (b) specific conductance ($\mu\text{S cm}^{-1}$), and (c) turbidity (NTU) from Green Bay coastal wetlands during spring and summer 1995.

ern part of the bay. North-to-south gradients were most striking in the spring for both parameters. Macrophyte coverage and species richness was variable among wetlands along the trophic gradient during both seasons (Table 1). Portage Marsh generally had the greatest macrophyte cover and the most diverse macrophyte community in both seasons and all vegetation zones, but coverage was sparse in spring at all sites and the dense emergent zone at Little Tail Point was more diverse than at any other wetland in summer.

Insect Abundance and Biomass

Our ANOVA models revealed that both insect abundance and biomass varied among and within wetlands

Table 1. Macrophyte species richness and % cover from Green Bay marshes within vegetation zones during spring and summer of 1995. Vegetation zone codes: DE = Dense Emergent, SE = Sparse Emergent, and OW = Open Water/submergent.

Marsh	Species richness					% cover				
	Spring		Summer			Spring		Summer		
	SE	OW	DE	SE	OW	SE	OW	DE	SE	OW
Portage	9	3	14	16	8	15	5	90	60	30
Seagull Bar	2	2	17	7	1	10	<1	50	15	1
Little Tail Point	7	1	19	10	7	5	<1	75	55	40
Peter's	4	0	7	2	1	15	0	50	15	5

during spring, resulting in significant wetland \times vegetation zone interactions (Table 2). Both vegetation zones at Portage Marsh had significantly higher insect counts than all others, with counts decreasing from the oligotrophic, upper bay wetlands to the eutrophic wetlands at the lower end of the bay (Figure 3a). However, most insects at Portage Marsh were small relative to other wetlands, resulting in similar levels of biomass (Figure 3b). Within wetlands, counts between zones were not different except at Seagull Bar Wetland, where significantly more insects were captured in the SE zone (Figure 3a). A similar trend was found at Portage Marsh, Seagull Bar Wetland, and Peter's Marsh for insect biomass, with relatively little captured in OW and high biomass in SE; however, biomass was not different between zones at Little Tail Point (Figure 3b). Differences in spring trends in count

and biomass distribution among wetlands and between vegetation zones were primarily a reflection of differences in community composition, with larger-bodied insects comprising a higher proportion of the community at lower and middle bay wetlands and within sparse emergent vegetation.

Summer counts and biomass also varied significantly among wetlands and vegetation zones (Table 2). All marshes had similar total insect counts, but distributions differed among vegetation zones within wetlands (Figure 4a). Counts were not different among vegetation zones at Portage or Seagull Bar but were at Little Tail Point and Peter's (Figure 4a). The latter two wetlands showed opposite trends. OW had significantly more insects than DE at Little Tail Point, but DE had significantly greater abundance than OW at Peter's. Peter's also had greater biomass in DE and SE

Table 2. Results from two-way split-plot ANOVA (wetland \times vegetation zone) on insect counts and biomass (log transformed data, no. trap⁻¹ 24-h⁻¹) from Green Bay coastal wetlands during spring and summer of 1995.

Source of Variation	NDF	DDF	MS	F	P
Insect Counts—Spring					
Wetland	3	3	1.3441	23.31	0.0110
Vegetation Zone	1	3	0.0437	0.76	0.4477
Wetland \times Veg. Zone	3	29	0.0576	3.88	0.0189
Trap (Wetland \times Veg. Zone)	29		0.0149		
Insect Biomass—Spring					
Wetland	3	3	0.0266	0.64	0.5980
Vegetation Zone	1	3	2.3358	4.79	0.1164
Wetland \times Veg. Zone	3	29	0.4875	11.67	0.0001
Trap (Wetland \times Veg. Zone)	29		0.0418		
Insect Counts—Summer					
Wetland	3	6	0.1327	1.08	0.4250
Vegetation Zone	2	6	0.0296	0.24	0.7922
Wetland \times Veg. Zone	6	46	0.1226	9.54	0.0001
Trap (Wetland \times Veg. Zone)	46		0.1285		
Insect Biomass—Summer					
Wetland	3	6	0.4757	3.51	0.0890
Vegetation Zone	2	6	0.1388	1.02	0.4145
Wetland \times Veg. Zone	6	46	0.1356	5.97	0.0001
Trap (Wetland \times Veg. Zone)	46		0.2272		

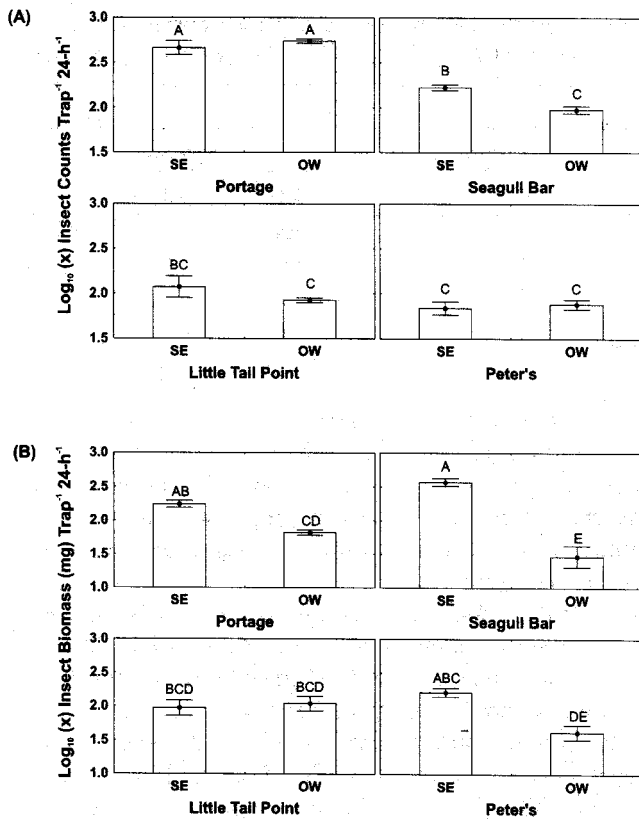


Figure 3. Mean (\pm SE, $n = 5$, log transformed data) insect (a) counts and (b) biomass from Green Bay coastal wetlands and vegetation zones during spring of 1995. Means with the same letter are not significantly different ($p > 0.05$).

than OW, as well as the highest overall biomass among all wetlands in the DE habitat (Figure 4b). Portage and Little Tail Point did not have differences between or within them for biomass, but Seagull Bar had greater biomass in DE than OW, with SE intermediate. Although not compared statistically, counts and biomass were generally higher in summer than in spring in wetlands at the two lower bay sites (Figures 3 and 4). Biomass was also somewhat higher in summer at Portage, but Seagull Bar had similar counts and biomass in both seasons (Figures 3 and 4).

Community Composition

We collected only 13 taxon groups during spring (Table 3), yet differences in community composition among wetlands were clear. NMDS ordination of wetlands and vegetation zones based on these insect taxa showed two distinct gradients among samples (Figure 5; two-dimension stress = 0.1783, Monte-Carlo permutation test $p \leq 0.01$). Wetlands sorted in order of trophic status along axis 1, with Little Tail Point and Peter's Marsh (lower bay, eutrophic) at one end, Seagull Bar (middle bay, mesotrophic) intermediate to

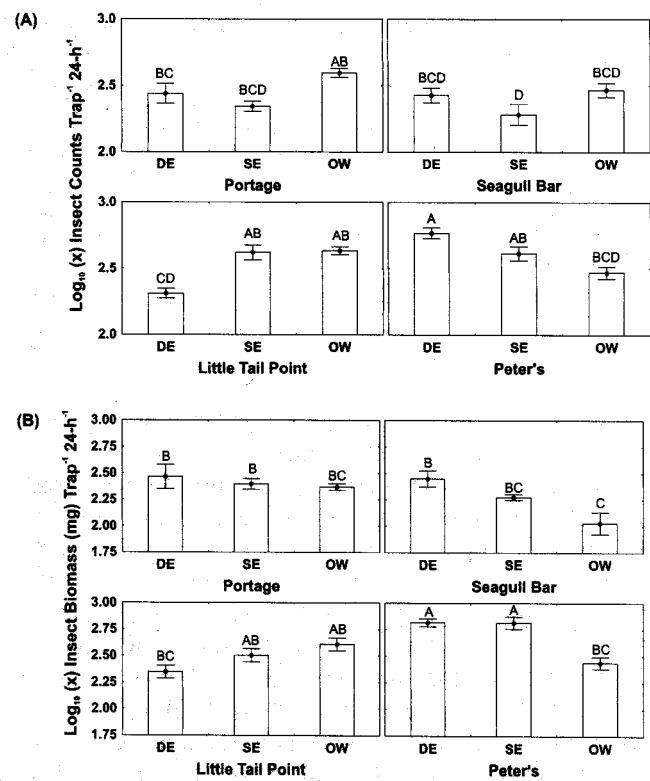


Figure 4. Mean (\pm SE, $n = 5$, log transformed data) insect (a) counts and (b) biomass from Green Bay coastal wetlands and vegetation zones during summer of 1995. Means with the same letter are not significantly different ($p > 0.05$).

lower and upper bay marshes, and Portage Marsh (upper bay, oligotrophic) clearly separated from all other marshes at the opposite end (Figure 5). Small Tanytarsini and Orthoclaadiinae (chironomids) were primary contributors to this wetland gradient (Tables 3 and 4). Portage had the highest abundance of these taxa relative to other wetlands, and within these groups, *Cladotanytarsus* sp., *Orthocladus* spp., and *Heterotrissocladius changi* Saether were dominant. *Heterotrissocladius changi*, an indicator of oligotrophic conditions, was almost exclusively found at Portage Marsh, in limited numbers at Seagull Bar, and absent from lower bay marshes. Conversely, lower bay marshes had higher numbers of generalist Chironomini, particularly *Chironomus* spp. (Tables 3 and 4). *Tanytarsus* spp. (Tanytarsini) and *Cricotopus* spp. (Orthoclaadiinae), variable but often disturbance-tolerant genera, were also more common at Little Tail Point and Peter's Marsh. Several other taxa were abundant but did not show consistent patterns in their distribution along the trophic gradient. These included scathophagids (mostly *Cordilura* sp.), sciomyzids (mostly *Sepedon fuscipennis* Loew), and hydroptilids (mostly *Hydroptila* spp.).

There were also consistent spring differences among

Table 3. Insect taxa collected from Green Bay coastal wetlands during spring and summer of 1995, including overall rank abundance and biomass (ranging from 1 [greatest] to 29 [smallest]—taxa with equal abundance or biomass given equal ranks), distribution among wetlands (shown in rank order of abundance, with wetland listed first having greatest abundance), seasonal distribution (in rank order), and distribution among vegetation zones (in rank order), shown by season. Wetland codes: PO = Portage Marsh, SB = Seagull Bar Wetland, LT = Little Tail Point Wetland, and PE = Peter's Marsh. Vegetation zone codes: DE = Dense Emergent, SE = Sparse Emergent, and OW = Open Water-submergent.

Taxonomic Group	Rank		Wetland	Season	Vegetation Zone	
	Abundance	Bio-mass			Spring	Summer
COLEOPTERA						
Chrysomelidae	27	20	PO	Sum	—	SE
Curculionidae	21	24	SB, LT	Sum	—	DE, SE
DIPTERA						
Calliphoridae	10	3	LT, PE, PO, SB	Sum, Spr	OW	DE, SE, OW
Ceratopogonidae	5	15	LT, PE, SB, PO	Sum, Spr	SE, OW	SE, DE, OW
Chironomidae						
Chironominae						
Chironomini	9	7	LT, PE, SB, PO	Spr, Sum	OW, SE	OW, SE, DE
Tanytarsini	1	8	PO, SB, PE, LT	Spr, Sum	OW, SE	OW, SE, DE
Orthoclaadiinae	3	14	PO, SB, PE, LT	Spr, Sum	SE, OW	OW, SE, DE
Tanypodinae	18	27	SB, LT	Sum	—	OW, SE, DE
Dolichopodidae	13	12	LT, SB, PE, PO	Sum	—	DE, SE, OW
Empididae	8	10	PO, SB, LT, PE	Sum, Spr	OW	OW, SE
Ephydriidae	2	2	PE, PO, SB, LT	Sum, Spr	SE	DE, SE, OW
Muscidae	27	25	PO	Sum	—	SE, DE
Otitidae	21	23	PE, LT	Sum	—	OW, DE
Scathophagidae	4	1	PE, PO, SB, LT	Sum, Spr	SE, OW	DE, SE, OW
Sciomyzidae	11	4	SB, PO, LT, PE	Spr, Sum	SE, OW	DE, SE, OW
Sphaeroceridae	16	22	LT	Sum	—	SE, DE
Syrphidae	23	16	LT, SB, PE	Sum	—	OW, SE
Tabanidae	17	11	PO, SB	Sum	—	SE, OW, DE
Tipulidae	19	18	LT, SB, PO, PE	Sum, Spr	SE	SE, OW, DE
EPHEMEROPTERA						
Caenidae	23	26	PE	Sum	—	OW, SE
HEMIPTERA						
Gerridae	15	21	SB, LT, PO, PE	Sum, Spr	SE	SE, DE, OW
HOMOPTERA						
Cicadellidae	12	9	SB, PO, LT, PE	Sum	—	SE, DE
HYMENOPTERA						
Apidae	29	28	SB	Sum	—	OW
Braconidae	23	29	PO	Sum	—	DE
Ichneumonidae	14	17	SB, LT, PO, PE	Sum, Spr	SE	DE, SE, OW
ODONATA						
Aeshnidae	23	6	LT, PE	Sum	—	OW, SE
Coenagrionidae	20	19	PE, PO, LT	Sum	—	OW
TRICHOPTERA						
Hydroptilidae	7	13	LT, SB, PO, PE	Spr, Sum	SE, OW	OW, SE
Leptoceridae	6	5	LT, PO, SB, PE	Sum	—	OW, SE, DE

vegetation zones within each wetland along axis 2 (Figure 5). This habitat gradient reflected two distinct insect assemblages within wetlands. OW areas were chiefly characterized by chironomids, with Tanytarsini

and Orthoclaadiinae at Portage and Seagull Bar, and Chironomini and Tanytarsini at Little Tail Point and Peter's (Tables 3 and 4). All of these taxa, particularly Orthoclaadiinae, also were collected in SE but were less

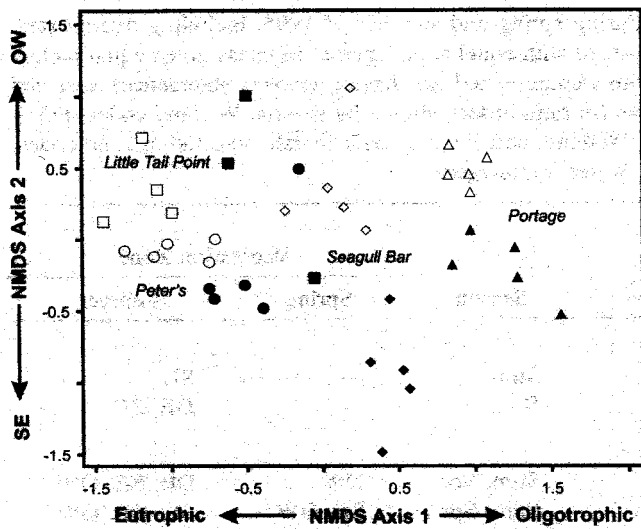


Figure 5. Non-metric multi-dimensional scaling ordination (Bray-Curtis dissimilarity) of insect abundance samples from wetlands and vegetation zones of Green Bay coastal wetlands during spring of 1995. Stress = 0.1783, Monte-Carlo permutation test $p \leq 0.01$. Portage = \blacktriangle , Seagull Bar = \blacklozenge , Little Tail Point = \blacksquare , and Peter's = \bullet . Filled symbols = SE, open symbols = OW.

common relative to Hydroptilidae, Scathophagidae, Sciomyzidae, and Ceratopogonidae (Tables 3 and 4).

During summer, we collected 29 taxon groups, over twice the number captured in spring. However, NMDS ordination based on these summer taxa showed remarkably similar trends to those of spring (Figure 6, two-dimension stress = 0.2062, Monte-Carlo permutation test $p \leq 0.01$). Again, axis 1 reflected the trophic gradient, with wetlands sorting in order of trophic status (Figure 6). However, wetlands became more similar with increased macrophyte cover, as indicated by the vegetation zone gradient along axis 2 (Figure 6). Ephydriidae (mostly *Notiphila olivacea* Cresson, *N. scalaris* Loew, and *N. solita* Walker) and Scathophagidae (mostly *Cordilura* sp.) were very abundant in DE and SE in all wetlands, which contributed to the increased similarity among them in the ordination (Tables 3 and 4). However, much greater abundance of Calliphoridae (almost exclusively *Lucilia illustris* Meigen) and Ceratopogonidae (mostly *Atrichopogon [Psilokempia]* sp.) at lower bay sites resulted in separation of DE and SE among wetlands along the gradient (Figure 6, Tables 3 and 4). Summer OW areas were the most clearly separated and ordered in terms of wetland trophic status (Figure 6). Although less abundant than during spring, Tanytarsini, Orthocladiinae, and Chironomini were an important component of OW insect assemblages. Trends for these taxa along the trophic gradient were almost identical to those of spring. They also became less abundant with increased macrophyte

Table 4. Insect taxon groups most closely correlated (r) with non-metric multidimensional scaling (NMDS) axes 1 and 2.

	NMDS Axis 1	NMDS Axis 2
Spring		
Orthocladiinae	0.808	
Tanytarsini	0.732	
Chironomini	-0.664	
Hydroptilidae	0.564	-0.674
Scathophagidae		-0.727
Sciomyzidae		-0.612
Gerridae		-0.454
Summer		
Orthocladiinae	0.628	0.557
Tabanidae	0.625	
Calliphoridae	-0.526	-0.472
Empididae	0.504	
Ceratopogonidae	-0.496	
Tipulidae	0.484	
Scathophagidae	-0.450	
Ephydriidae	-0.398	-0.467
Dolichopodidae	-0.346	-0.398
Tanytarsini		0.745
Chironomini		0.657
Sciomyzidae		-0.648
Ichneumonidae		-0.474
Hydroptilidae		0.416
Tanypodinae		0.410

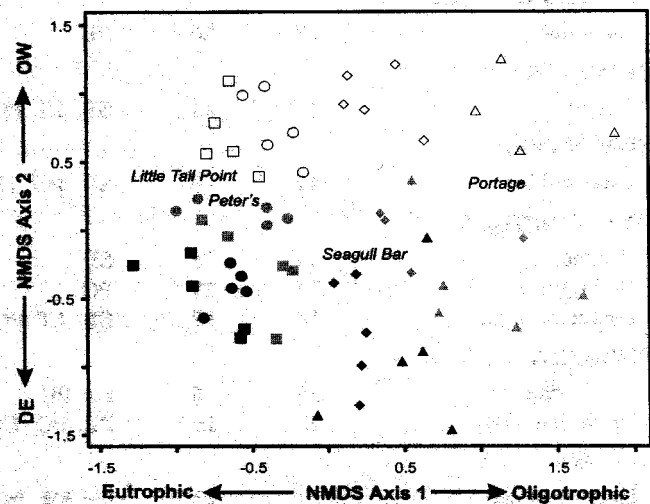


Figure 6. Non-metric multi-dimensional scaling ordination (Bray-Curtis dissimilarity) of insect abundance samples from wetlands and vegetation zones of Green Bay coastal wetlands during summer of 1995. Stress = 0.2062, Monte-Carlo permutation test $p \leq 0.01$. Portage = \blacktriangle , Seagull Bar = \blacklozenge , Little Tail Point = \blacksquare , and Peter's = \bullet . Black-filled symbols = DE, gray-filled symbols = SE, open symbols = OW.

cover (Tables 3 and 4). Empididae (cf. *Hemerodromia* sp.) and Leptoceridae (mostly *Oecetis* sp.) were the most notable taxa with wetland or vegetation zone affinities that were not collected during spring. Empididae were rare at Peter's Marsh and Little Tail Point but common at Seagull Bar and very abundant at Portage Marsh. They were collected almost exclusively in OW (Tables 3 and 4). Leptoceridae also preferred OW and decreased in abundance with increased macrophyte cover; however, they were not sensitive to wetland trophic status (Tables 3 and 4).

DISCUSSION

Small numbers of insects at lower bay wetlands during spring suggest that eutrophication or other anthropogenic stressors (e.g., contaminants) may be influencing insect communities of Green Bay coastal wetlands. Late-spring is peak time for waterfowl breeding and brood hatching in this region (Bookhout et al. 1989). For mallards and most other dabbling duck species, diets during the first 2 weeks of life consist almost entirely of aquatic invertebrates, particularly flying insects (Chura 1961, Collias and Collias 1963, Pehrsson 1979). Most mortality of ducklings also occurs during the first 2 weeks of life (Orthmeyer and Ball 1990, Rotella and Ratti 1992), highlighting the importance of early developmental phases in the life cycle of waterfowl (Sedinger 1992). Decreased availability of food is often identified as a source of duckling mortality (Hunter et al. 1984, Johnson et al. 1992), and duckling broods often avoid or leave wetlands having small numbers of invertebrates (Bélanger and Couture 1988, Cooper and Anderson 1996). Thus, depressed insect abundance in spring may indicate relatively poor foraging conditions for ducklings in the lower bay. Although we did find similar insect biomass among wetlands along the trophic gradient during spring, Cox et al. (1998) found that invertebrate abundance, not biomass, was the best predictor of mallard duckling growth and survival in an experimentally controlled setting. Ducklings may not selectively feed on large, infrequently encountered food items but forage on insects most numerous and available, such as abundant Chironomidae found at middle and upper bay wetlands.

Small numbers of insects during spring may have similar effects on the distribution of insectivorous fish among wetlands along the trophic gradient. Brazner (1997) and Brazner and Beals (1997) indicated that distinct regional differences (i.e., lower, middle, and upper bay) exist in fish assemblages among wetland and beach habitats in Green Bay. In particular, the distribution of many species classified as insectivores (Lyons 1992) was strongly skewed toward upper bay

sites (Brazner and Beals 1997). Although we did not find small numbers or biomass of insects at lower bay sites during summer, many of the abundant insects at these wetlands were semi-aquatic and not likely to be available to fish during emergence. For example, the dung fly, *Lucilia illustris*, was dominant at Peter's Marsh and Little Tail Point Wetland during summer, yet it emerges from wet soils and rotting organic matter inaccessible to fish (Shewell 1987). In contrast, Chironomidae are considered to be one of the most important sources of food for insectivorous fish (reviewed by Armitage 1995) because of their ubiquity and highly-available larvae and pupae. They were most abundant at Portage Marsh and Seagull Bar Wetland during both seasons. Although a complex interaction of factors have been shown to structure fish communities in Green Bay (Brazner and Beals 1997), our data suggest that availability of insect forage might also contribute.

Distribution of insect abundance and biomass among vegetations zones in our study was not consistent among wetlands. Although we expected lowest insect abundance and biomass in the open water-submergent vegetation habitat in lower bay wetlands, this only occurred for insect abundance during spring. Our result may reflect the similarity in macrophyte species richness and percent cover among wetlands, especially during summer. Turbidity in lower bay wetlands during summer was much lower than recorded in recent years (15–50 NTU during our study, mean value of 104 JTU [Jackson Turbidity Units ~ NTU] in 1990–91; Brazner and Beals 1997), which suggests that lower bay macrophyte communities and associated insects may have benefited from increased water clarity (Sager et al. 1998). It seems likely that this response is related to the recent invasion of zebra mussels (*Dreissena polymorpha* Pallas) in Green Bay (Skubinna et al. 1995), as increased zebra mussel densities and filtration rates in summer often result in reductions in turbidity (Brady et al. 1995). Future monitoring of macrophytes and other biota in coastal wetland habitats along the bay is needed to better understand the role of zebra mussels in the Green Bay ecosystem.

While insect abundance was highly variable among vegetation zones within wetlands, emergent vegetation zones supported more insect biomass than OW in 3 of 4 wetlands during both seasons. Somewhat contrary to the findings of McLaughlin and Harris (1990), who found significantly more insect biomass emerging from sparse emergent vegetation than other zones in two lower bay wetlands, we collected as much or more insect biomass from dense emergent vegetation than sparse emergent during summer. This could be due to highly abundant Calliphoridae (e.g., *Lucilia illustris*) and Scathophagidae (e.g., *Cordilura* sp.), both semi-

aquatic insect taxa that showed high affinities as adults for the DE zone. Neither of these taxa was found in any vegetation zone in emergence traps used by McLaughlin and Harris (1990), suggesting that much of this biomass may be coming from fringing wet soils or outside the wetlands. Nevertheless, dense emergent vegetation of these coastal wetlands appears to be favorable habitat for adult insects and thus may be beneficial for foraging wildlife.

Ordination revealed the importance of both regional (lower, middle, and upper bay) and local (vegetation zones within wetlands) processes in structuring insect communities of Green Bay coastal wetlands. High dissimilarity among wetlands was consistent with position along the trophic gradient during both seasons, suggesting that trophic status or some covariate play a role in community organization. Since we calculated dissimilarities using families and subfamilies/tribes (Chironomidae), we may have lost resolution relative to comparisons made using species (Clarke 1993). Collection of eutrophic-intolerant taxa such as *Heterotrissocladius changi* (Saether 1975) at middle and upper bay wetlands but not in the lower bay is further evidence that differences found among wetlands were related to cultural eutrophication. Although not well studied in coastal wetland habitats, eutrophication has been shown to alter macroinvertebrate communities in other wetlands, including wetlands in western Australia (Growth et al. 1992) and in the northern Everglades, USA (Rader and Richardson 1994). These findings are encouraging from a biological monitoring perspective, suggesting that insects and other macroinvertebrates may be useful in assessing environmental degradation such as excessive nutrient loading in coastal wetlands (Krieger 1992). Although our study was somewhat spatially and temporally limited, and additional macroinvertebrate data from other Great Lakes coastal wetlands will certainly help elucidate patterns, our data suggest that insect communities from lower Green Bay have responded to human influences and, as a result, may be influencing trophic structure differently than in meso-oligotrophic coastal wetlands of the middle and upper bay.

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