

The community dynamics of epiphytic midge larvae across the pelagic–littoral interface: do animals respond to changes in the abiotic environment?

Bradley J. Cardinale, Thomas M. Burton, and Valerie J. Brady

Abstract: In some littoral systems, abiotic heterogeneity results from the edge of vegetation towards the shore as macrophytes gradually impede mixing between pelagic and littoral water. During the summer of 1994, we investigated whether such abiotic heterogeneity influenced epiphytic midge larvae (Diptera:Chironomidae) inhabiting a stand of *Scirpus americanus* in Saginaw Bay, Lake Huron. After macrophytes became well established, gradients in six parameters of water quality (turbidity, alkalinity, pH, dissolved oxygen, conductivity, and chloride) formed horizontally from the macrophyte edge towards the shore. In outer portions of the stand where physico-chemical properties were influenced by the influx of pelagic surface waves, chironomid abundance increased to 1076 larvae · stem⁻¹. Diversity (*H'*) in these areas remained constant over the summer with grazing and filter-feeding taxa equally represented. Further into the macrophyte bed where water quality indicated highly reduced mixing, midge abundance never exceeded 27 individuals · stem⁻¹ and larval biomass was reduced 2–4 fold. Loss of filter-feeding taxa resulted in a dramatic decline in diversity in these areas after formation of the abiotic gradients. This study suggests that pelagic–littoral water exchange may result in environmental heterogeneity that directly or indirectly influences epiphytic invertebrate community structure and function.

Résumé : Dans certains systèmes littoraux, il se produit une hétérogénéité abiotique entre la bordure de la végétation et le rivage à mesure que le mélange des eaux pélagiques et des eaux littorales est entravé par la croissance des macrophytes. Durant l'été de 1994, les auteurs ont tenté de savoir si cette hétérogénéité abiotique avait une influence sur les larves épiphytes de moucheron (diptères : Chironomidae) qui s'abritent dans une colonie de *Scirpus americanus* de la baie Saginaw, dans le lac Huron. Une fois les macrophytes bien établis, des gradients horizontaux se sont formés pour six paramètres de la qualité de l'eau (turbidité, alcalinité, pH, oxygène dissous, conductivité et chlorure) depuis la bordure des macrophytes jusqu'au rivage. Du côté extérieur de la colonie, là où les propriétés physico-chimiques étaient modifiées par l'afflux des vagues de surface du secteur pélagique, l'abondance des chironomidés a augmenté pour atteindre 1 076 larves · tige⁻¹. Dans ces secteurs, la diversité (*H'*) est demeurée constante durant l'été, les espèces brouteuses et les espèces filtreuses étant également représentées. Plus loin dans l'herbier de macrophytes, où la qualité de l'eau indique que le brassage est extrêmement réduit, l'abondance des moucheron n'a jamais dépassé 27 individus · tige⁻¹, et la biomasse des larves a été réduite de 2 à 4 fois. La perte d'espèces filtreuses a entraîné une très grave diminution de la diversité à cet endroit après la formation de gradients abiotiques. Les résultats de l'étude semblent indiquer que l'échange entre les eaux littorales et les eaux pélagiques peut entraîner une hétérogénéité environnementale qui influence, directement ou non, la structure et les fonctions de la communauté d'invertébrés épiphytes.

[Traduit par la Rédaction]

Introduction

Many freshwater and marine studies have shown that aquatic macrophytes impede water flow and circulation (e.g., Fonseca et al. 1983; Madsen and Warnke 1983; Eckman 1987; Losee

and Wetzel 1988, 1993; Ackerman and Okubo 1993; Leonard and Luther 1995). In some macrophyte beds a reduction in flow occurs abruptly across the open water – macrophyte interface. For instance, Losee and Wetzel (1993) found that flows into beds of *Scirpus subterminalis* were reduced by 98% within the first 10–15 cm of vegetation. Similar results have been reported for patches of stream vegetation (Madsen and Warnke 1983) and for marine seagrass beds (Ackerman and Okubo 1993).

However, an abrupt reduction in water flow at the macrophyte edge is not always the case. Depending on plant density and initial flow speed, current may penetrate some distance into a stand before being dissipated (e.g., Eckman 1987; Leonard and Luther 1995). Various forms of environmental heterogeneity may result horizontally through the vegetation as circulation is gradually reduced due to resistance from plant stems. The physical and chemical properties of water often

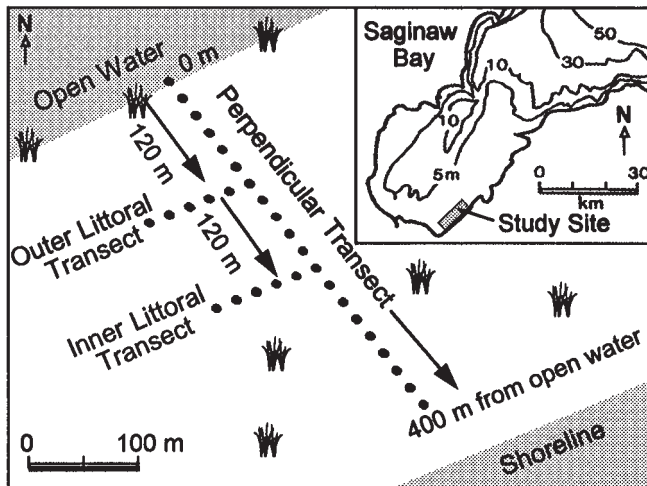
Received May 6, 1996. Accepted February 28, 1997.
J13459

B.J. Cardinale,¹ T.M. Burton, and V.J. Brady,² Department of Zoology, Michigan State University, East Lansing, MI 48824, U.S.A.

¹ Author to whom all correspondence should be addressed. Present address: Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A. e-mail: cardinal@zool.umd.edu

² Present address: Department of Biology, The College of New Jersey, Trenton, NJ 08650, U.S.A.

Fig. 1. Location of the study site and orientation of sampling transects in Saginaw Bay, Lake Huron. The inner littoral (IL) and outer littoral (OL) transects each had five fixed sampling stations 20 m apart. The perpendicular transect had 20 stations with the first located at the open water – littoral interface and the last located 400 m from open water.



change from the pelagic–littoral edge towards shore (Dvorak 1970; Howard-Williams and Lenton 1975; Klosowski 1992; Suzuki et al. 1995). The transport and deposition of suspended particulates may be inversely related to distance from open water (Fonseca and Fisher 1986; Leonard and Luther 1995). Even rates of photosynthesis and respiration may change as circulation is increasingly reduced into a macrophyte bed (Dvorak 1970; Fonseca and Kenworthy 1987).

Despite the likelihood of strong environmental gradients within macrophyte beds, few studies have examined the biological consequences of such heterogeneity. The goal of our research was to determine whether the abundance, biomass, and diversity of epifauna were related to changes in water quality that occurred horizontally through an emergent macrophyte stand in Saginaw Bay, Lake Huron. Here we focus on midge larvae (Diptera:Chironomidae), which were the numerically dominant invertebrate taxon in our study system. Trends for other epiphytic invertebrates have been presented elsewhere (Cardinale 1996).

Methods

Study site

The study site was located in a littoral complex which extends around the southeastern shore of Saginaw Bay, Lake Huron (Fig. 1). Vegetation in this area is unprotected from prevailing northwesterly winds that sweep across the shallow open water of the bay. Pelagic surface waves generally arrive perpendicular to the stand, and during our study were observed to penetrate 160–200 m into the vegetation. As a result, water chemistry changes from the macrophyte edge towards the shore (Suzuki et al. 1995).

Emergent vegetation extended 460 m from shore during this study and was dominated by three-square bulrush, *Scirpus americanus*. Macrophytes grew on substrates composed mostly of sand (85–97%) with lesser fractions of clay and silt (Suzuki et al. 1995). Smaller, isolated patches of *Scirpus acutus*, *Typha angustifolia*, and *Sagittaria sp.* occurred in the area but were not sampled during this study. Growth of the macrophytes was seasonal with regeneration from

rhizomes after winter ice-scour. Our project began in June 1994 on the first date emergent vegetation was present, and continued until the onset of senescence in September.

Water quality

Littoral water quality was characterized using physical and chemical parameters that have been shown to change horizontally through macrophyte beds: turbidity (Suzuki et al. 1995), dissolved oxygen (Dvorak 1970; Howard-Williams and Lenton 1975), alkalinity and pH (Dvorak 1970; Klosowski 1992). Conductivity and chloride were also measured because of their biologically conservative behaviors (Wetzel and Likens 1991; Gaspar 1987), and thus, utility in inferring physical processes responsible for water mixing (Bertin and Bourg 1994; Gaudet and Roy 1995).

On nine sampling dates, emergent macrophyte density and the six water quality parameters were measured at 40 m intervals along a transect that ran from open water perpendicular to the shoreline (Fig. 1). At each station on each date, a random distance (0–10 m) and direction (0–360°) was selected for sampling. The number of *S. americanus* stems in a 0.25 m² plot was counted. A BOD bottle was carefully filled at the water surface and fixed for analysis of dissolved oxygen. A second water sample was collected in an opaque plastic bottle at one-half the depth of the water column. Samples were placed on ice and transported to the laboratory where total alkalinity was measured by titration (APHA 1985), dissolved oxygen was determined by the modified Winkler method (APHA 1985), pH was measured with an Altec monitor II pH meter, conductivity was measured with a YSI model 31 conductivity bridge with corrections for in situ temperature (Wetzel and Likens 1991), and turbidity was determined using a HACH model 2100A turbidimeter. All measurements were made within 4 h of sample collection with the exception of pH, which was determined within one-half hour. Subsamples of water were filtered through 0.45 µm millipore filters and frozen. Filtrates were later analyzed for chloride using an Orion model 407A Ionanalyzer.

For each date, the six water quality parameters were summarized into a single variable using principal components analysis (PCA, Systat 1992) on the correlation data matrix. Here we present only the first principal component (hereafter referred to as PC1), which represented the major axis of covariation in the six measures (Phillipi 1993). To determine whether water quality varied randomly or was spatially dependent throughout the stand, we calculated spatial autocorrelations of the PC1 factor scores with a lag of 40 m (the distance between adjacent sampling stations) for each date. If autocorrelations were non-significant, indicating a random distribution, we assumed that no gradient in water quality was present on that date. For dates with a significant autocorrelation, PC1 scores were plotted against distance from open water, as well as against the cumulative stem density of *S. americanus* from the pelagic–littoral edge. In this system, cumulative stem density was probably a reasonable measure of resistance to pelagic influx because (a) the emergent stand was almost monotypic with no other notable barriers to impart drag on surface waves and (b) *S. americanus* is morphologically simple with no leaves or protrusions.

Epiphytic Chironomidae

To compare temporal trends in chironomids from contrasting abiotic environments, two fixed transects were established at different distances from open water (Fig. 1). The outer littoral (OL) transect was placed 120 m into the stand while the inner littoral (IL) transect was placed at 240 m. Each transect had five fixed stations located 20 m apart and running parallel to the shoreline. On each date, *S. americanus* density and water temperature were determined at a randomly selected distance (0–10 m) and direction (0–360°) around each station. In addition, two stems of *S. americanus* were enclosed in a 2.54 cm diameter PVC tube to prevent the escape of invertebrates. Stems were clipped at the water surface and the sediment–water interface so that only the submerged portions were collected. The tube

Table 1. Summary of the gradient in littoral water quality on each date. PCA was used to group six separate measurements. Loadings to the first principal component (PC1) are shown below along with the total variation in water quality explained by PC1.

	June 2	June 9	June 14	June 22	June 29	July 6	July 13	July 27	Sept. 10
Variance explained by PC1 (%)	73	57	82	67	74	64	68	70	63
Variable loadings = correlations to PC1									
Turbidity	0.97	0.19	0.90	0.81	0.94	0.58	0.98	0.89	0.84
Dissolved oxygen	-0.91	0.80	0.92	0.10	0.97	0.97	0.37	0.77	0.71
pH	-0.92	0.87	0.86	0.74	0.95	0.97	0.87	0.96	0.93
Alkalinity	-0.18	-0.92	-0.98	-0.98	-0.91	-0.50	-0.82	-0.98	-0.73
Conductivity	-0.92	-0.94	-0.83	-0.97	0.56	0.76	0.99	-0.78	-0.96
Chloride	-0.93	-0.53	-0.94	-0.97	-0.77	0.91	0.77	-0.60	-0.53

was capped at both ends, enclosed water was drained through 250 µm nitex mesh, and then both stems and invertebrates were rinsed into a composite sample. A third stem was collected for analysis of chlorophyll *a*.

Stems were placed in plastic bags and transported to the laboratory on ice. Periphyton was removed by hand and suspended in filtered water collected at that same station. Subsamples were filtered onto 0.45 µm millipore filters, which were frozen and placed in buffered 90% acetone to extract pigments. Chlorophyll *a* was determined fluorometrically with corrections for phaeophytin (APHA 1985). Invertebrates were removed from the other two stems by hand, rinsed through a 250 µm sieve, and preserved in 95% ethanol with rose bengal dye. All stems were dried, pressed, and measured for colonizable surface area using a Li-Cor LI-3100 area meter.

On all dates, chironomid larvae were enumerated and identified to subfamily or tribe. At monthly intervals, ~50 larvae per transect were identified to genus or species using keys from Simpson and Bode (1980), Wiederholm (1983), and Merritt and Cummins (1984). Identifications of representative taxa were verified by an expert. Shannon–Wiener diversity (H') was calculated for each transect and Horn's index of community similarity was used to compare species composition (Brower et al. 1990).

To estimate biomass, 20 larvae were randomly selected from each sample on each date and individual size was determined using the size–biovolume relationships of Smit et al. (1993). Mean larval size was multiplied by abundance to obtain total biomass per stem. Repeated measures analysis of variance (ANOVA) was used to test for differences in chironomid abundance and biomass between the IL and OL transects. We also tested for differences in water temperature, colonizable stem surface area, and algal biomass because these factors may influence invertebrate standing stock (Lalonde and Downing 1992). Data for each of the tests were $\log_{10}(x + 1)$ transformed to meet assumptions of normality and homogeneity of variance.

On two dates (June 14 and July 27), we performed a detailed analysis of the spatial distribution of Chironomidae from open water towards shore. Dates were specifically chosen to allow a comparison of distributions during low macrophyte density (June 14) with those at maximum density (July 27). On each date, three stems of *S. americanus* were collected every 20 m along the perpendicular transect (Fig. 1). Larval chironomid abundance and biomass were analyzed from two of these stems as described above, algal biomass was estimated from the third, and stem surface area was measured for all samples. Stem density and water temperature were also determined at each location.

Results

Temporal–spatial changes in water quality

PC1 was a good summary of the six water quality parameters explaining up to 82% of the total variation in the measures (Table 1). During the first two weeks of June, factor scores

from PC1 were not autocorrelated between sampling stations, indicating that water quality varied at random from open water towards shore (Fig. 2). During this time, *S. americanus* was just starting to emerge above the water surface and density averaged only 10 stems · m⁻². The interval between June 9 and June 14 had the largest proportional increase in macrophyte density during the study as the number of stems rose to 84 · m⁻². June 14 was also the first date for which PC1 factor scores were significantly autocorrelated between stations (0.71, $p < 0.05$). The distribution of the scores indicated a gradient in water quality extending from the pelagic–littoral edge towards the shore (Fig. 2). A similar gradient was present on all of the subsequent sampling dates (Fig. 2), with the distribution of PC1 strongly correlated with the cumulative stem density of *S. americanus* (Pearson $\rho = -0.84$, Fig. 3).

After June 14, a considerable amount of abiotic heterogeneity developed throughout the littoral zone. Turbidity was generally reduced by 50% or more at stations beyond 160 m from open water (Fig. 4). Dissolved oxygen decreased by 45–55% from the macrophyte edge towards shore. pH averaged 8.58 at the pelagic–littoral interface and 7.84 at stations farthest into the stand. Bicarbonate alkalinity increased by 45 mg CaCO₃ · L⁻¹ through the stand. Conductivity and chloride were similarly distributed as gradients and generally increased from open water towards shore (Fig. 4). For an unknown reason, the distribution of these two measures was reversed on July 6 and 13 when each variable decreased from open water towards shore (Fig. 4).

Temporal changes in Chironomidae

The temporal trends in chironomid abundance differed significantly between the IL and OL transects (transect · date, $p < 0.01$) with *S. americanus* stems from the OL transect supporting a greater number of larvae (transect, $p < 0.01$; Fig. 5). Abundance was initially comparable between the two areas of the littoral zone but began to diverge after June 14. At OL stations the abundance of larvae increased to a maximum of 134 · stem⁻¹ on July 27 (Fig. 5). Abundance at IL stations remained low over the entire summer reaching a maximum of only 27 · stem⁻¹ on July 27.

The size of individual larvae did not differ between the two transects for all dates combined (transect, $p = 0.56$). However, due to the large difference in abundance, total biomass per stem was significantly higher at OL stations (transect, $p < 0.01$; Fig. 5). Values were comparable through June 14, after which biomass at OL stations increased to a maximum of 31 mg · stem⁻¹ (Fig. 5). Biomass at IL stations remained comparatively low with a maximum of only 10 mg · stem⁻¹.

Fig. 2. Temporal and spatial changes in littoral water quality. PC1 factor scores represent the first principal component of six different measures of water quality. Scores indicate similarity or dissimilarity in the physical and chemical properties between stations with average conditions centered at 0. Spatial autocorrelation of the factor scores, shown next to each date, were significant ($p < 0.05$) unless indicated by “ns” (nonsignificant). Cumulative stem density was calculated as the total number of *S. americanus* stems from the littoral edge, thus providing a measure of resistance to pelagic influx. Note that stem densities were not measured on July 13.

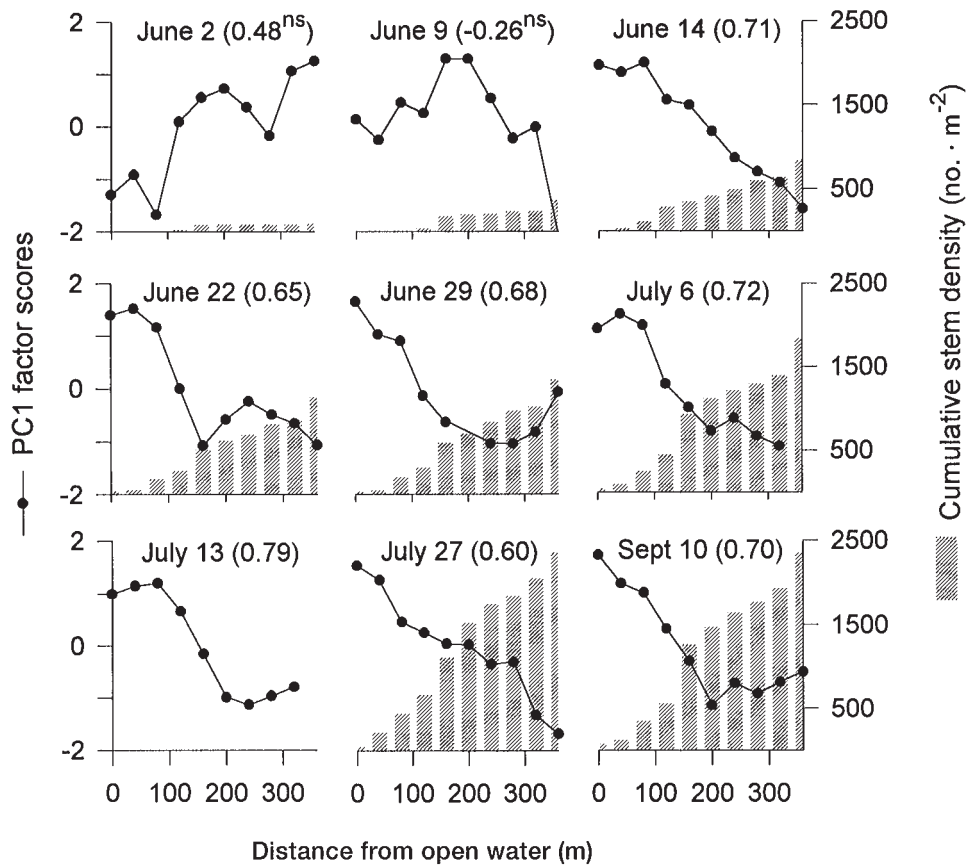
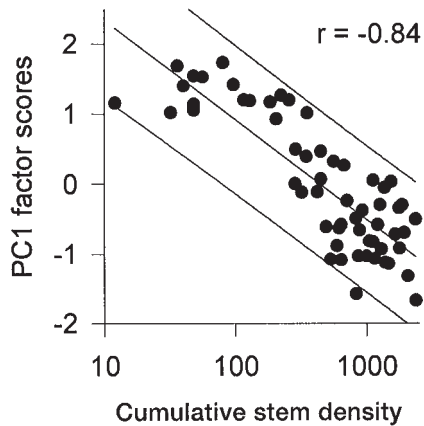


Fig. 3. Relationship between PC1 factor scores and the cumulative stem density of *S. americanus*. The inner line shows the best linear fit, while outer lines show the 95% prediction interval.

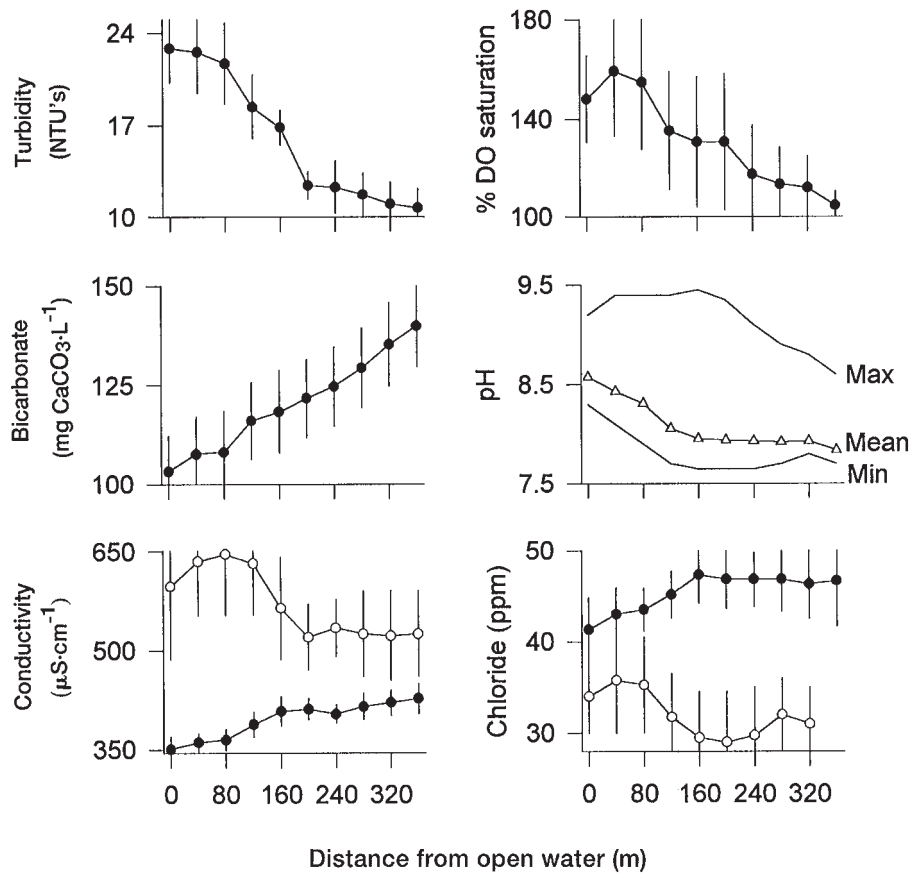


The taxonomic diversity of Chironomidae also differed between the two areas of the littoral zone. In early June, stems from both transects supported a diverse community ($H' = 0.84\text{--}0.94$) with Horn’s index indicating 84% overlap in the taxonomic composition (Table 2). The relative abundances of

Orthocladiinae/Chironomini and Tanytarsini were approximately equal in both areas of the littoral zone (Fig. 5). Over the summer, richness at IL stations declined from 12 taxa to 5, and Shannon–Wiener diversity decreased to 0.22 (Table 2). Taxonomic losses were disproportionately high for the tribe Tanytarsini, which dropped from 33% of relative abundance at IL stations on June 2 to only 7% by June 14 (Fig. 5). In contrast, diversity at OL stations remained relatively constant over the summer (Table 2) with Tanytarsini averaging 40% of total abundance (Fig. 5). By September 10, Horn’s index indicated only 7% overlap in the taxonomic composition between the IL and OL transects. On this final sampling date *Rheotanytarsus* dominated the OL community but was not found at IL stations (Table 2). In the same manner, *Corynoneura* dominated the IL community but was not found at OL stations.

Epifaunal differences between transects could not be attributed to water temperature or surface area available for colonization. Water temperature was usually homogeneous throughout the stand and did not differ between transects (transect, $p = 0.88$). Submerged stem surface area also did not differ (transect, $p = 0.71$). There was, however, a highly significant difference in algal biomass on the stems of *S. americanus* from the two areas of the littoral zone (transect, $p < 0.01$). On average, each stem collected from the OL stations had 5.4 times more chlorophyll *a* than those from the IL stations (Fig. 5).

Fig. 4. Spatial gradients in littoral water quality. Data for turbidity, % DO saturation, and bicarbonate are the mean of seven sampling dates ± 1 SE. For pH, both the range and the mean are shown. The distribution of conductivity and chloride changed on July 6 and 13; dates are plotted separately (open circles, July 6 and 13; solid circles, June 14–22 and July 27 – September 10 for conductivity and June 14–29 for chloride).



Spatial distribution of Chironomidae

On June 14, we found no evidence of any spatial trends in the abundance, biomass, or taxonomic composition of Chironomidae throughout the macrophyte stand. This was not the case on July 27 when the total number of larvae declined from 1076 individuals \cdot stem $^{-1}$ at the pelagic-littoral edge to an average of 18 individuals \cdot stem $^{-1}$ at distances beyond 160 m from open water (Fig. 6). Individual larvae in the outer 160 m were 2–4 times larger than those collected at stations deeper into the stand (Fig. 6). This trend was only seen in the Orthocladiinae/Chironomini because Tanytarsini were rarely found on stems beyond 160 m from open water (Fig. 6).

The abundance and biomass of chironomid larvae on July 27 was not correlated with water temperature (Pearson $\rho < 0.52$ for each) or colonizable stem surface area (Pearson $\rho < 0.17$ for each). However, both abundance and biomass were strongly correlated with the factor scores of PC1 (Pearson $\rho = 0.73$ and 0.75 , respectively) and epiphytic algal biomass (Pearson $\rho = 0.78$ and 0.82 , respectively), which decreased from 553 $\mu\text{g} \cdot \text{stem}^{-1}$ at the outer edge of the macrophyte bed to 17 $\mu\text{g} \cdot \text{stem}^{-1}$ at stations in the inner part of the stand (Fig. 6).

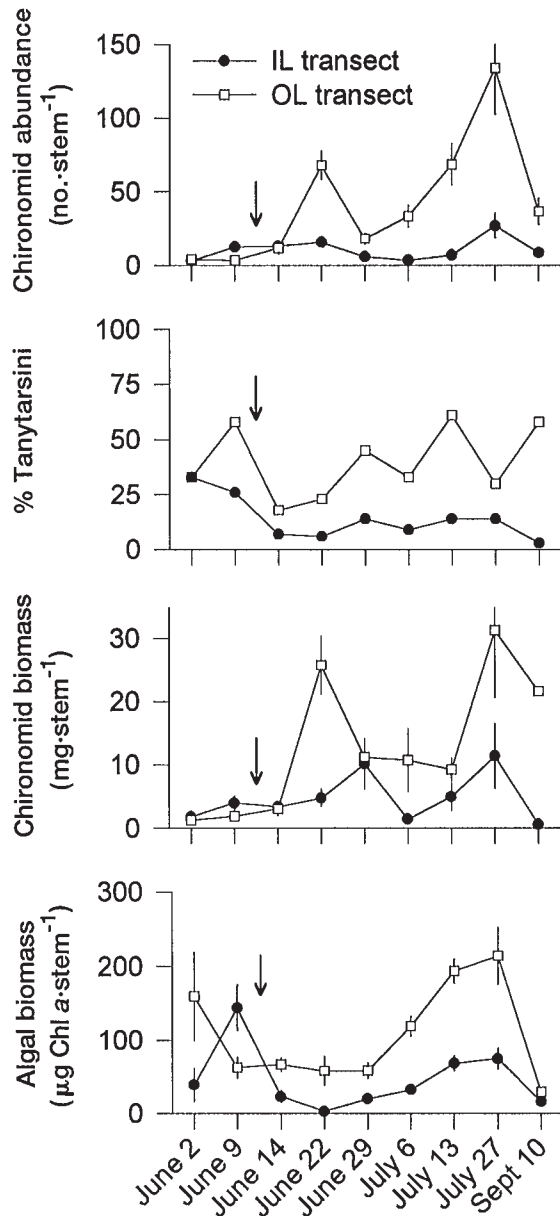
Discussion

Wind or tides can “push” pelagic water a considerable distance

into a macrophyte bed. When this occurs, a variety of environmental gradients may result as circulation is gradually reduced into the vegetation (Dvorak 1970; Howard-Williams and Lenton 1975; Leonard and Luther 1995; Suzuki et al. 1995). Our study has provided temporal and spatial evidence that such gradients influence the abundance, biomass, and diversity of epifauna. In early June, water quality varied at random throughout the littoral zone probably because the density of *S. americanus* was too low to impede circulation. During this time, there were no detectable differences in the chironomid community at different distances from open water: abundance and biomass were low but approximately equal along the inner and outer littoral transects; diversity and species composition were nearly identical; and there was no evidence of any spatial trends throughout the macrophyte bed.

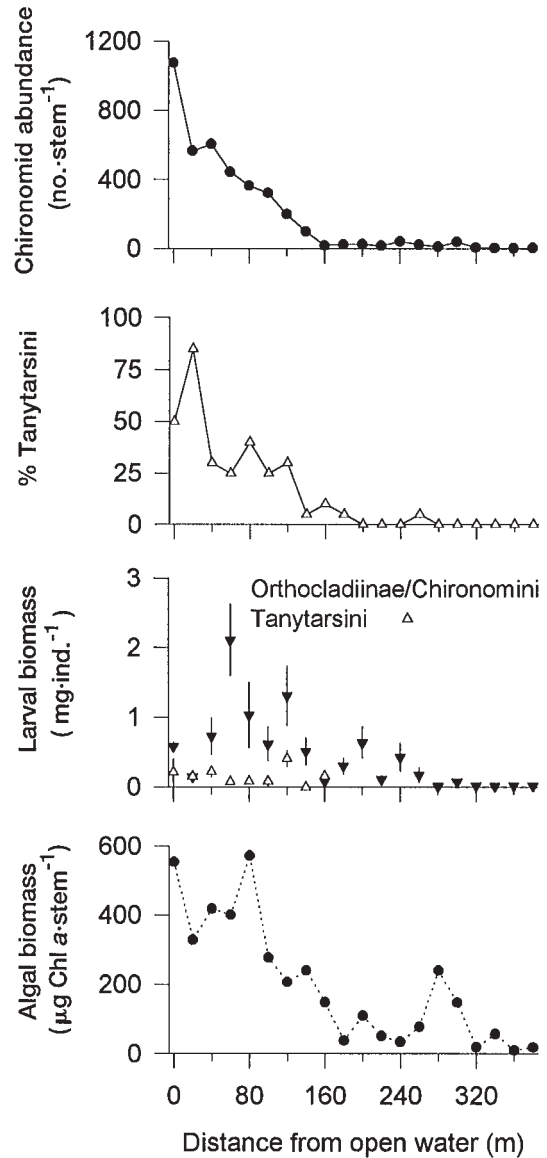
Following a large increase in macrophyte density, gradients in water quality formed from the edge of vegetation towards the shore. These gradients were spatially related to the cumulative density of *S. americanus*, suggesting that they resulted as stems imparted drag on incoming surface waves and gradually reduced circulation. This possibility is further supported by the distributions of conductivity and chloride, two variables that have been widely used as tracers of mixing between water masses because of their conservative behaviors (e.g., Bertin and Bourg 1994; Gaudet and Roy 1995). Both conductivity and chloride strongly correlated with PC1 on the majority of

Fig. 5. The temporal response of Chironomidae and periphyton collected from the IL and OL transects. Data for chironomid abundance, chironomid biomass, and algal biomass are the mean of five replicate samples \pm 1 SE. Each variable was significantly different between the two transects over time (date \cdot transect, $p < 0.01$) and significantly higher at the OL transect (transect, $p < 0.01$). % Tanytarsini was calculated as the proportion of all larvae collected from each transect on each date. Arrows show the time when horizontal gradients in water quality formed throughout the macrophyte stand.



sampling dates (loadings > 0.70 , see Table 1), and their distributions were strikingly similar to the other non-conservative measures. Thus PCI is most parsimoniously interpreted as a "pelagic-littoral mixing gradient." This interpretation is consistent with others who have found circulation to be inversely proportional to stem density and distance from the littoral edge (Fonseca and Fisher 1986; Eckman 1987; Leonard and Luther 1995).

Fig. 6. The spatial distribution of Chironomidae and periphyton relative to distance from open water on July 27, 1994. Larval biomass is the mean of 20 larvae \pm 1 SE.



Soon after the abiotic gradients formed we began to note differences in the abundance, biomass, and diversity of Chironomidae at different distances from open water. At stations along the OL transect where water quality indicated partial mixing, larval abundance and biomass increased significantly over the summer. This area sustained a high diversity of Chironomidae with approximately equal abundance of the two major taxa. At sampling stations closer to the shore where deviations in water quality suggested highly reduced circulation, the abundance and biomass of larval chironomids never increased over the summer. Diversity in these areas declined dramatically after formation of the gradients, mostly due to a complete loss of Tanytarsini.

The spatial distribution of Chironomidae along the perpendicular transect confirmed the results from temporal comparisons between the IL and OL transects. On July 27, after abiotic heterogeneity had been established in the littoral zone for some

Table 2. Relative abundance (% composition), taxon richness, diversity, and similarity of epiphytic chironomids between the IL and OL transects on four dates in 1994.

Taxon	June 2–9		June 29		July 27		Sept. 10	
	IL	OL	IL	OL	IL	OL	IL	OL
Chironomini								
<i>Chironomus</i> sp.	2							
<i>Endochironomus nigricans</i>	20	10	41	22	67	28	2	13
<i>Endochironomus subtendens</i>						11		2
<i>Glyptotendipes</i> species group A	2		2	6		30		30
<i>Glyptotendipes</i> species group B	5	2	2	4				7
<i>Glyptotendipes</i> species group C		2						2
<i>Parachironomus arcuatus</i> group	12	20	14	12	2	2	2	2
<i>Pseudochironomus</i> sp.					19			
Orthoclaadiinae								
<i>Corynoneura</i> sp.	2						88	
<i>Cricotopus sylvestris</i>	17	10	27	22		2		
<i>Nanocladius bicolor</i>						2	2	
<i>Parakiefferiella</i> sp.							5	
<i>Psectrocladius psilopterus</i>	2	2						
Tanypodinae								
<i>Larsia</i> sp.			2					
<i>Paramerina</i> sp.								2
<i>Thienemannimyia</i> group		2						
Tanytarsini								
<i>Paratanytarsus</i> sp.	5		2		2			
<i>Rheotanytarsus</i> sp. 1	20	36	8	20	4	13		33
<i>Rheotanytarsus</i> sp. 2	2	6	2	14		6		9
<i>Tanytarsus</i> sp. 1	10	6			4	6		
<i>Tanytarsus</i> sp. 2		2			2	2		
Taxon richness	12	11	9	7	7	10	5	9
Shannon–Wiener diversity	0.94	0.84	0.69	0.79	0.47	0.80	0.22	0.74
Horn's index of similarity	0.84		0.89		0.57		0.07	

time, chironomid abundance declined by almost two orders of magnitude from the macrophyte edge towards shore. The size of individual larvae was highly reduced at stations beyond the extent of mixing (~160 m from open water), and taxonomic composition changed with Tanytarsini declining from 50% of relative abundance at the macrophyte edge to 0% at most stations beyond 160 m.

All of the above changes in the chironomid community strongly correlated with the abiotic gradients. Despite this, we think it is unlikely that the physical and chemical parameters directly influenced larval distributions. pH rarely affects osmoregulation except below values of 5.5 (Pinder 1986; Johnson et al. 1993). During this study, pH ranged from 7.7 to 9.45. Diel extremes may have been lower but the relatively alkaline water would have prevented any dramatic changes. Water throughout the stand was typically supersaturated with dissolved oxygen and there was never any evidence that waters became anoxic. Furthermore, larval distributions were contrary to that expected if turbidity were interfering with respiration or feeding.

Rather than a direct effect of water quality, chironomids in the unmixed portions of the macrophyte bed may have been limited by biofilm production. Larval abundance and biomass temporally corresponded to periphyton accrual and were spatially correlated with changes in algal biomass. Both measures of the periphyton were inversely related to distance from the

littoral edge, similar to that shown by Suzuki et al. (1995) in a nearby site. Because most Orthoclaadiinae and Chironomini that we identified have been functionally classified as collector–gatherers that graze from the epiphyte–detrital complex (Merritt and Cummins 1984; Berg 1995), large changes in the primary food resource should influence epifaunal distributions. Indeed, others have found periphyton to be a primary determinant of chironomid standing stock (Mason and Bryant 1975; Dudley 1988).

We did not consider the possibility of differential predation throughout the stand, even though predators can have strong influences on littoral invertebrate assemblages (e.g., Keast 1985; Mittlebach 1988). However, it seems unlikely that predation was a major factor in this site. The number of invertebrate predators on stems of *S. americanus* was extremely low during this study (Cardinale 1996). In addition, the most abundant predators, juvenile fish, were 7–10 times more abundant in the outer 160 m of the macrophyte bed where the highest standing stocks of chironomid larvae occurred (Burton and Prince 1994).

While a gradient in periphyton might explain the distributions of Orthoclaadiinae and Chironomini, it cannot account for the distribution of Tanytarsini in this site as all of the taxa we identified are classified as collector–filterers (Merritt and Cummins 1984; Berg 1995). The most abundant of these, *Rheotanytarsus*, is an obligate filter-feeder that constructs a

catchnet around the lumen of its tube retreat (Oliver 1971). Because of this feeding habit, Cranston (1995) reported that this taxa only inhabits flowing waters. Presumably, the outer 160 m of this littoral zone had enough circulation to support a substantial *Rheotanytarsus* population as well as other filter-feeding Tanytarsini. Brady et al. (1995) found that the dominant benthic filter-feeders in this system (zebra mussels, *Dreissena polymorpha*) were also limited to the outer portions of the macrophyte bed. These distributions parallel those of bivalves in seagrass beds which result from limits to planktonic dispersal and reduced survival caused by the settlement of suspended particulate food (Peterson 1986; Eckman 1987). The absence of filter-feeders beyond 160 m from open water may illustrate the potential for a pelagic–littoral mixing gradient to alter community structure and biological function throughout a macrophyte bed.

Acknowledgments

Funding for this project was provided by the Michigan Department of Natural Resources and MSU's Ecology and Evolutionary Biology Program. We thank Ted Batterson, Elizabeth Capaldi, Richard Merritt, Margaret Palmer, Harold Prince, and two anonymous reviewers for their insightful comments on earlier versions of this manuscript. We also thank Martin Berg for verifying the identifications of the larval Chironomidae.

References

- Ackerman, J.D., and Okubo, A. 1993. Reduced mixing in a marine macrophyte canopy. *Funct. Ecol.* 7:305–309.
- American Public Health Association. 1985. Standard methods for the examination of water and wastewater. 16th ed. American Public Health Association, Washington.
- Berg, M.B. 1995. Larval food and feeding behaviour. *In* The Chironomidae: the biology and ecology of non-biting midges. *Edited by* P. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman and Hall, London, U.K. pp. 136–167.
- Bertin, C., and Bourg, A.C.M. 1994. Radon-222 and chloride as natural tracers of the infiltration of river water into an alluvial aquifer in which there is significant river/groundwater mixing. *Environ. Sci. Technol.* 28(5): 794–798.
- Brady, V.J., Cardinale, B.J., and Burton, T.M. 1995. Zebra mussels in a coastal marsh: the seasonal and spatial limits of colonization. *J. Great Lakes Res.* 21(4): 587–593.
- Brower, J.E., Zar, J.H., and Von Ende, C.N. 1990. Field and laboratory methods for general ecology. Wm. C. Brown Publishers, Dubuque, Iowa.
- Burton, T.M., and Prince, H.H. 1994. Wetland restoration in the coastal zone of Saginaw Bay. Annual Report to the Michigan Department of Natural Resources, Lansing, Mich.
- Cardinale, B.J. 1996. The effects of a pelagic–littoral mixing gradient on an epiphytic invertebrate community. M.S. thesis, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Mich.
- Cranston, P.S. 1995. Biogeography. *In* The Chironomidae: the biology and ecology of the non-biting midges. *Edited by* P. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman and Hall, London, U.K. pp. 62–82.
- Dudley, T.L. 1988. The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. *Verh. Int. Ver. Limnol.* 23: 1153–1158.
- Dvorak, J. 1970. Horizontal zonation of macrovegetation, water properties and macrofauna in a littoral stand of *Glyceria aquatica* (L.) Wahlb. in a pond in South Bohemia. *Hydrobiologia*, 35: 17–30.
- Eckman, J.E. 1987. The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J. Exp. Mar. Biol. Ecol.* 106: 165–191.
- Fonseca, M.S., and Fisher, J.S. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Mar. Ecol. Prog. Ser.* 29: 15–22.
- Fonseca, M.S., and Kenworthy, W.J. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquat. Bot.* 27: 59–78.
- Fonseca, M.S., Zieman, J.C., Thayer, G.W., and Fisher, J.S. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine. Coastal Shelf Sci.* 17: 367–380.
- Gaspar, E. 1987. Modern trends in tracer hydrology. CRC, Boca Raton.
- Gaudet, J.M., and Roy, A.G. 1995. Effect of bed morphology on flow mixing length at river confluences. *Nature (London)*, 373: 138–139.
- Howard-Williams, C., and Lenton, G.M. 1975. The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. *Freshwater Biol.* 5: 445–459.
- Johnson, R.K., Wiederholm, T., and Rosenberg, D.M. 1993. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. *In* Freshwater biomonitoring and benthic macroinvertebrates. *Edited by* D.M. Rosenberg and V.H. Resh. Chapman and Hall, N.Y. pp. 52–56, 88–90, 289–293.
- Keast, A. 1985. Planktivory in a littoral-dwelling lake fish association: prey selection and seasonality. *Can. J. Fish. Aquat. Sci.* 42: 1114–1126.
- Klosowski, S. 1992. Temporal and spatial variation of habitat conditions in the zonation of littoral plant communities. *Aquat. Bot.* 43: 199–208.
- Lalonde, S., and Downing, J.A. 1992. Phytofauna of eleven macrophyte beds of differing trophic status, depth, and composition. *Can. J. Fish. Aquat. Sci.* 49: 992–1000.
- Leonard, L.A., and Luther, M.E. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnol. Oceanogr.* 40(8): 1474–1484.
- Losee, R.F., and Wetzel, R.G. 1988. Water movement with submersed littoral vegetation. *Verh. Int. Ver. Limnol.* 23: 62–66.
- Losee, R.F., and Wetzel, R.G. 1993. Littoral flow rates within and around submersed macrophyte communities. *Freshwater Biol.* 29: 7–17.
- Madsen, T.V., and Warncke, E. 1983. Velocities of currents around and within submersed aquatic vegetation. *Arch. Hydrobiol.* 97(3): 389–394.
- Mason, C.F., and R.J. Bryant. 1975. Periphyton production and grazing by chironomids in Alderfen Broad, Norfolk. *Freshwater Biol.* 5: 271–277.
- Merritt, R.W., and K.W. Cummins. 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Mittelbach, G.G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology*, 69(3): 614–623.
- Oliver, D.R. 1971. Life history of the Chironomidae. *Annu. Rev. Entomol.* 15: 211–230.
- Peterson, C.H. 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: is pattern fixed during settlement season or altered by subsequent differential survival? *Limnol. Oceanogr.* 31: 200–205.
- Phillips, T.E. 1993. Multiple regression: herbivory. *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Chapman and Hall, London, U.K. pp. 182–210.
- Pinder, L.C.V. 1986. Biology of freshwater Chironomidae. *Annu. Rev. Entomol.* 31: 1–23.

- Simpson, K.W., and Bode, R.W. 1980. Common larvae of Chironomidae (Diptera) from New York state streams and rivers. Bulletin No. 439. New York State Education Department, Albany.
- Smit, H., Dudok Van Heel, E., and Wiersma, S. 1993. Biovolume as a tool in biomass determination of Oligochaeta and Chironomidae. *Freshwater Biol.* **29**: 37–46.
- Suzuki, N., Endoh, S., Kawashima, M., Itakura, Y., McNabb, C.D., D'Itri, F.M., and Batterson, T.R. 1995. Discontinuity bar in a wetland of Lake Huron's Saginaw Bay. *J. Freshwater Ecol.* **10**(2): 111–123.
- Systat, Inc. 1992. SYSTAT for Windows: statistics, version 5, Evanston, Ill.
- Wetzel, R.G., and Likens, G.E. 1991. *Limnological analyses*. 2nd ed. Springer-Verlag Inc., New York.
- Wiederholm, T. 1983. Chironomidae of the Holarctic region. Part 1: Larvae. Supplement No.19. *Entomologica Scandinavica*, Motala.