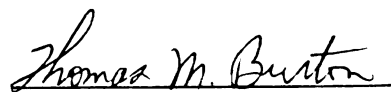




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Bradley J. Cardinale

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**THE EFFECT OF A PELAGIC-LITTORAL MIXING GRADIENT ON
AN EPIPHYTIC INVERTEBRATE COMMUNITY**

By

Bradley J. Cardinale

A THESIS

**Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of**

MASTER OF SCIENCE

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ABSTRACT

THE EFFECT OF A PELAGIC-LITTORAL MIXING GRADIENT ON AN EPIPHYTIC INVERTEBRATE COMMUNITY

By

Bradley J. Cardinale

Some studies have suggested that the littoral edge forms a barrier at which ambient circulation is abruptly reduced. Others have found that pelagic flows can extend a considerable distance into a stand, and that such conditions may have a substantial influence on littoral biota. During the summer of 1994, I investigated this possibility for a littoral zone in Saginaw Bay, Lake Huron. At this site, the predominant environmental gradient was one of water quality which changed from the littoral edge into the stand as macrophytes gradually impeded pelagic flows. The composition of the epiphytic invertebrate community changed along this gradient apparently in response to declining algal biomass. In areas that were un-mixed with open water, levels of chlorophyll a were only 5-21 $\mu\text{g stem}^{-1}$ and invertebrate abundance never increased above 54 individuals stem^{-1} of *Scirpus americanus*. Yet, stems taken from stations receiving some circulation with open water supported 375 μg chlorophyll a and 1175 invertebrates per stem. In areas of stagnant water, Shannon-Wiener diversity dropped from 0.94 before formation of the gradient to 0.22 by the end of the sampling period. This was mostly due to a loss of filter-feeders. Diversity closer to the littoral edge remained constant with both grazing and filtering taxa well represented. Others have described similar distributions in water quality, and there is evidence this mixing gradient has implications at higher trophic levels. Thus, the results presented here may be widely applicable.

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INTRODUCTION

One of the most obvious changes that occurs across the pelagic-littoral transition is the reduction in water circulation caused by the presence of macrophytes (Carpenter and Lodge 1986). In some littoral zones this change can be rather abrupt. Madsen and Warnke (1983) found that beds of *Callitriche stagnicalis* dissipated stream currents by as much as 92% in the first 5 cm of vegetation. Losee and Wetzel (1993) found similar results for two lake littoral zones in Michigan. However, in other systems the reduction of circulation across the pelagic-littoral transition is much more gradual. This is particularly true of stands exposed to wind fetches that can “push” pelagic water a significant distance into the vegetation (for examples see Carter 1955, Suzuki *et al.* 1995).

Under the latter conditions the environment within a macrophyte bed can become quite heterogeneous. Dissolved oxygen and turbidity are often highest at the pelagic-littoral interface where waters are well-mixed, but measures gradually decrease into a stand as flow is increasingly reduced (Dvorak 1970, Suzuki *et al.* 1995). Horizontal gradients in alkalinity, pH, and conductivity may also result (Klosowski 1992, Suzuki *et al.* 1995). Because these abiotic variables often influence species composition (for examples see Johnson *et al.* 1987, Winget and Mangum 1991, Grown *et al.* 1992), the extent of pelagic flow into a littoral stand might be expected to have some control over the distribution of biota. A few studies have suggested this may be true. Using spatial changes in water quality, Dvorak (1970) was able to differentiate between the portion of a *Glyceria aquatica* bed that was mixed with open water, and the portion that was isolated from mixing. Limited data on the distributions of phytoplankton and invertebrates led

Dvorak to conclude that “the part of the stand influenced by open water had more favorable living conditions as compared with the isolated part, which was inhabited by different species of animals.”

More recently, Suzuki *et al.* (1995) noted a spatial correlation between algal biomass and a chemical “discontinuity” that formed as pelagic flows were reduced into a large stand of emergent macrophytes. Planktonic and epiphytic chlorophyll *a* were very low in the inner 250 m of vegetation which was isolated from circulation. Estimates increased 5-8 fold in the outer 200 m of the stand where water was well mixed by pelagic influx. Although this study implied a strong relationship between the extent of pelagic-littoral circulation and the distribution of littoral algae, the implications for higher trophic levels have yet to be explored.

My research was designed to examine the influence of pelagic-littoral mixing on an epiphytic invertebrate community. I took advantage of a natural circulation gradient that exists in a littoral site in Saginaw Bay, Lake Huron. Emergent macrophytes in this area were unprotected from high wind-fetch coming from the shallow open waters of the bay. Surface waves tended to penetrate a significant distance into the stand, but were gradually reduced as they encountered more and more vegetation.

The effects of this circulation gradient on epiphytic invertebrates were determined in two ways. First, temporal changes in the invertebrate community were compared between two areas of the littoral zone that experienced differential mixing with open water. Second, in much more detail than previous studies, I examined the spatial distribution of epiphytic biota from the open water/littoral boundary towards shore. The

objectives of this research were to (1) determine if epiphytic invertebrate abundance, biomass, and community composition change as macrophytes gradually reduce circulation, and (2) identify mechanisms by which a mixing gradient might regulate the spatial distribution of littoral epifauna.

STUDY SITE

The study site was part of a littoral complex that extended around the southeastern shore of Saginaw Bay, Lake Huron (Figure 1). Littoral zones in this area were exposed to pelagic surface waves that often result from the prevailing westerly winds (Batterson *et al.* 1991). Vegetation extended approximately 480 m from shore and was dominated by the emergent three-square bulrush, *Scirpus americanus*. Smaller, isolated patches of *Scirpus acutus*, *Typha angustifolia*, and *Sagittaria* also occurred in the area, but none of these were sampled during this study. Submergent vegetation was previously described by Batterson *et al.* (1991).

Growth of the macrophytes was seasonal. During the earliest period of sampling, the vegetation was just beginning to grow from rhizomes that had survived ice-scour from the previous winter. By the end of the sampling period the bulrush had begun to senesce. The gradient from the open water/littoral interface towards shore was very shallow. Water depth ranged from a maximum of 88 cm at the outer edge of the stand to 45 cm at the most shoreward station. Water temperature within the littoral zone was almost always

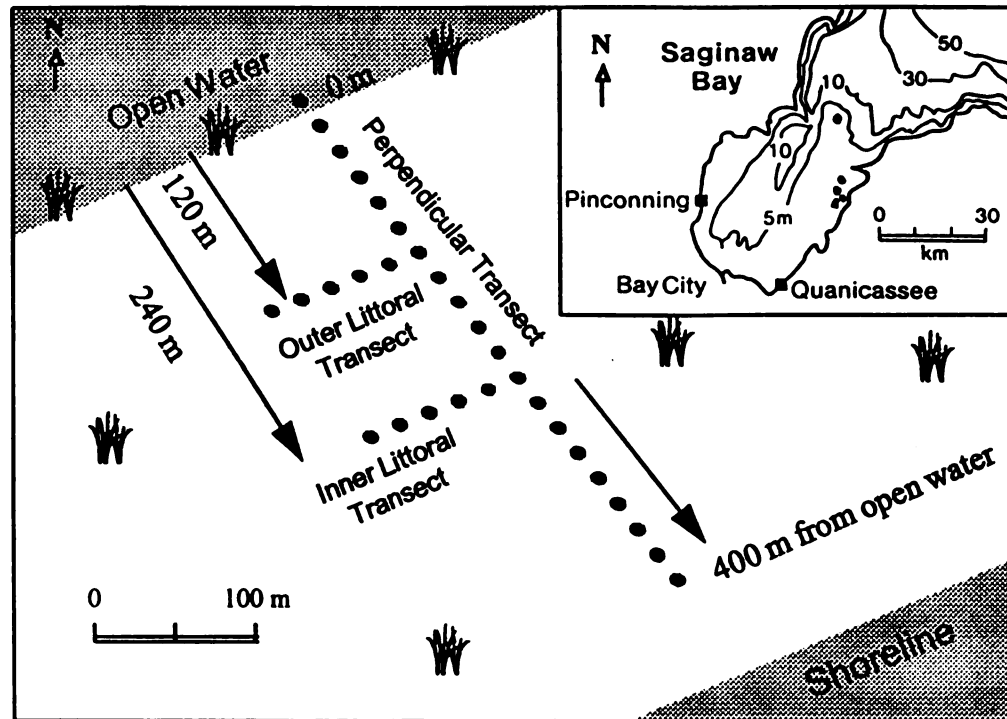


Figure 1. Location of the study site and orientation of sampling transects in Saginaw Bay, Lake Huron. The study site was located just outside the town of Quanicassee, MI (see inset). The inner littoral (IL) and outer littoral (OL) transects each had five fixed sampling stations 20 m apart. The perpendicular transect had 20 sampling stations with the first located at the open water / littoral interface, and the last located 400 m from open water.

homogeneous during this study. When differences did occur they never exceeded 2°C. The substrates were composed of mostly sand (85-97%) with lesser fractions of silt and clay also present (Suzuki *et al.* 1995).

MATERIALS & METHODS

Water Quality

On nine dates during the summer of 1994, water quality and vegetation density were determined at fixed 40 m intervals along a transect that ran from open water perpendicular towards shore (Figure 1). The density of *Scirpus americanus* was determined by counting the number of emergent stems in a 0.25 m² plot that was placed at a random distance (0-10 m) and direction (0-360°) from each station. Water samples were collected from this same area in opaque plastic bottles at one-half the depth of the water column. Samples for dissolved oxygen were taken from the water surface and fixed in BOD bottles. All samples were placed on ice and transported to the laboratory where the following analyses were performed within 4 hours: total alkalinity by titration (APHA 1985), dissolved oxygen - the modified Winkler method (APHA 1985), pH - determined within one-half hour of sample collection using a Altec monitor II meter, conductivity - YSI model 31 conductivity bridge, and turbidity - HACH model 2100A turbidimeter. Subsamples were filtered, frozen, and later sent to Michigan State University's Soils Testing Laboratory for analysis of dissolved electrolytes (Na⁺, K⁺, Mg²⁺, Ca²⁺). Chloride was measured separately using an Orion model 407A Ionanalyzer.

For each date, the ten measurements of water quality were combined into a single principal component using their correlation matrix (PCA, Systat v. 5 1992). First-order autocorrelations (i.e. lag = 40 m intervals) of the factor scores from PC1 were used to determine the spatial dependency of water quality throughout the stand. If autocorrelations were non-significant (i.e. PC1 factor scores varied at random along the

perpendicular transect) then I interpreted this to mean that the littoral zone was well-mixed on these dates. Alternatively, if spatial autocorrelation was significant I determined the relationship between littoral water quality and pelagic influx by regressing PC1 factor scores against the cumulative density of *Scirpus americanus* stems from the pelagic-littoral edge. Since the perpendicular transect was located in a monotypic stand of the bulrush it was assumed that cumulative stem density approximated the total drag on pelagic surface waves.

Temporal Response of Invertebrates

Two fixed transects were established in the littoral zone at different distances from open water. The outer littoral (OL) transect was placed 120 m from open water while the inner littoral transect was established at 240 m into the stand (Figure 1). Each transect had five fixed sampling stations (20 m apart) that ran parallel to the shoreline. This design was used to ensure that the two transects would experience differential mixing with open water after macrophytes became well established, but at the same time minimize the variation of other factors such as vegetation density, water depth, temperature, etc.

On nine dates, *Scirpus americanus* density, water depth, and water temperature were determined at an area randomly selected in distance (0-10 m) and direction (0 - 360°) around each of the inner and outer littoral sampling stations. In addition, three stems of *S. americanus* were collected at each station. Two were enclosed in a 2.54 cm diameter PVC tube to prevent the escape of invertebrates. Stems were clipped at the sediment and water interfaces and the tube capped at both ends. The water column was

drained through 250 μm nitex mesh and both stems and any loose invertebrates were rinsed into a composite sample. The third stem, for analysis of epiphyton, was clipped at the sediment and water interfaces and the submerged portion collected by hand. All samples were placed in plastic bags and transported to the laboratory in the dark and on ice.

In the laboratory, attached algae were rubbed from the stems by hand and then suspended in a portion of filtered water collected at that same station. Subsamples were filtered through 0.45 μm millipore filters, which were then frozen and placed in buffered 90% acetone to extract pigments. Chlorophyll a was determined fluorometrically and the appropriate corrections were made for phaeophytin (APHA 1985). Invertebrates were rubbed from the other two stems by hand, rinsed through a 250 μm sieve, and preserved in 95% ethanol with rose bengal dye added to facilitate processing. All of the stems were dried, pressed, and measured for submerged surface area using a Li-Cor LI-3100 area meter.

Invertebrates were enumerated and identified to an operational taxonomic unit under 10x magnification. Each taxon was classified as a collector-gatherer, collector-filterer, omnivore, or predator based on the most common feeding strategy reported in Merritt and Cummins (1984) or Thorpe and Covich (1991). The collector-gatherer classification was intended to include all invertebrates feeding on the biofilm. Thus, obligate scrapers were also included in this category.

Biomass, species diversity, and trophic structure were examined at a finer taxonomic resolution for the most abundant group of invertebrates - the Chironomidae.

Twenty larvae were randomly selected from each sample on each date, and the body size/biovolume relationships of Smit *et al.* (1993) were used to estimate mean individual biomass. To estimate diversity, approximately 50 larvae per transect were randomly selected from samples taken at near monthly intervals (June 2-9, June 29, July 27, and Sept. 10). Larvae were identified to genus and species when possible using keys in Simpson and Bode (1980), Wiederholm (1983), and Merritt and Cummins (1984).

Species of Chironomidae were then categorized into functional feeding groups according to the most common strategy reported in Berg (1995) and Merritt and Cummins (1984). I attempted to verify these classifications by performing gut analyses on 50 larvae that were selectively chosen to represent the six most abundant species from both transects. Entire guts were removed and the contents dissected from the peritrophic membrane. Samples were placed in 2 mL distilled water and vortexed for 30 seconds. A small subsample was then placed on a hemacytometer and the first 100 particles were categorized as large ($>130\ \mu\text{m}$), medium ($61 - 130\ \mu\text{m}$), or small detritus ($10 - 60\ \mu\text{m}$), filamentous green algae, green algae, diatoms, blue-green algae, or animal matter.

The data from the inner and outer littoral transects were analyzed in a variety of ways. First, repeated measures analysis of variance (ANOVA) was used to test for differences in invertebrate abundance, chironomid biomass, algal biomass, stem density, submerged stem surface area, water temperature, and water depth. Data were $\log_{10}$ or $\log_{10}(x + 1)$ transformed when appropriate. Repeated measures ANOVA was used because samples collected from the same station over time are not necessarily independent

since micro-habitat variability can influence population characteristics (Maceina *et al.* 1994).

The community structure of invertebrates was qualitatively examined for both the entire epiphytic community and at a finer resolution for the species of Chironomidae. The relative abundance of each functional feeding group was compared for the inner and outer littoral transects over time. In addition, Shannon-Wiener diversity (Brower *et al.* 1990) of the Chironomidae was calculated for the monthly intervals and Horn's index of community similarity (Brower *et al.* 1990) was used to compare composition between the two areas of the littoral zone.

Spatial Distribution of Invertebrates

On two dates I performed a detailed analysis of the spatial distribution of the biotic and abiotic variables. June 14 and July 27 were specifically chosen to allow a comparison of distributions early in macrophyte growth to those well after macrophytes were established. Three stems of *Scirpus americanus* were collected every 20 m ($n = 20$) along the perpendicular transect (Figure 1). These stems were analyzed for invertebrate abundance and community composition, chironomid biomass, algal biomass, and submerged stem surface area as previously described. In addition, stem density, water temperature, water depth, and the ten measures of water quality were determined at each location.

Data from July 27 were further used to test the relative influence of algal biomass and water quality on invertebrate distributions. The 10 measurements of water quality

were combined into a single principal component using the correlation matrix of PCA (Systat v.5 1992). A principal component was also generated for algal biomass so that the scales would be comparable. Factor scores for algal biomass were regressed against the $\log_{10}$ of invertebrate abundance and then separately against the $\log_{10}$ of chironomid biomass. These regressions were then repeated with the factors scores from PC1 of water quality included as a second independent variable. This allowed determination of the amount of variation in invertebrate standing stock which could be explained by algal biomass alone, and how much additional variance could be explained by the predominant gradient in water quality. Data from each regression passed tests for normality, independence of residuals, and homoscedasticity.

RESULTS

Water Quality

The first principal component generally explained a large proportion of the spatial variation in the measures of water quality. The minimum variation explained was 55% on July 27, but values more commonly approached or exceeded 70% (Table 1). Thus, PC1 appeared to be a good summary of the 10 separate, but highly collinear measurements. During the first two weeks of June, *Scirpus americanus* had just begun to emerge above the water surface. Stem density was very low throughout the stand at this time so there was little resistance to wind induced mixing (Figure 2). There was no autocorrelation of PC1 factor scores on June 2 or June 9 suggesting that the entire littoral zone was well mixed on these first two dates.

Between June 9 and June 14 stem density increased to an average of 84 m⁻². This period represented the largest proportional increase in stem density for the entire sampling period, and therefore the largest proportional increase in resistance to pelagic influx. June 14 was also the first date that water quality was distributed as a gradient throughout the stand (Figure 2). PC1 factor scores decreased from open water towards shore with significant autocorrelation between stations (0.67, $p < 0.05$). A similar gradient was present on each ensuing date (Figure 2), and a minimum of 6 of the variables were highly correlated, either positively or negatively (loadings $> |0.70|$), to the distribution of factor scores (Table 1). Seventy-percent of the spatial variation in PC1 was explained by the cumulative stem density from open water (Figure 3). Therefore, a strong relationship

Table 1. Summary of the gradient in littoral water quality on each date. Principal components analysis was used to group 10 separate measurements. Loadings to the first principal component (PC1) are shown below. Autocorrelation of factor scores was used to determine spatial dependency of water quality between stations. All correlations are significant ($p < 0.05$) unless otherwise indicated (ns).

	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
% Variance explained by PC1	67	59	73	74	56	69	64	55	72
Autocorrelation of factor scores	0.35 ^{ns}	-0.02 ^{ns}	0.67	0.63	0.67	0.72	0.77	0.68	0.74
Variable Loadings									
Turbidity	-0.92	0.20	0.90	0.77	0.91	0.50	0.95	0.88	0.86
Dissolved oxygen	0.76	0.65	0.86	0.12	0.94	0.98	0.51	0.72	0.66
pH	0.86	0.73	0.80	0.77	0.91	0.94	0.91	0.97	0.92
Conductivity	0.95	-0.96	-0.95	-0.95	0.63	0.87	0.99	-0.51	-0.96
Na ⁺	0.95	-0.89	-0.73	-0.98	-0.93	-0.69	-0.24	0.81	0.74
Cl ⁻	0.93	-0.73	-0.96	-0.97	-0.83	0.93	0.65	0.65	-0.52
K ⁺	0.92	-0.88	-0.62	-0.92	0.13	0.92	0.95	0.86	-0.90
Mg ²⁺	0.81	-0.76	-0.94	-0.98	-0.20	0.98	0.99	0.18	-0.96
Ca ²⁺	0.53	-0.75	-0.75	-0.78	0.58	0.84	0.65	0.43	-0.91
HCO ₃ ⁻	0.32	-0.86	-0.95	-0.97	-0.86	-0.42	0.78	-0.98	-0.93

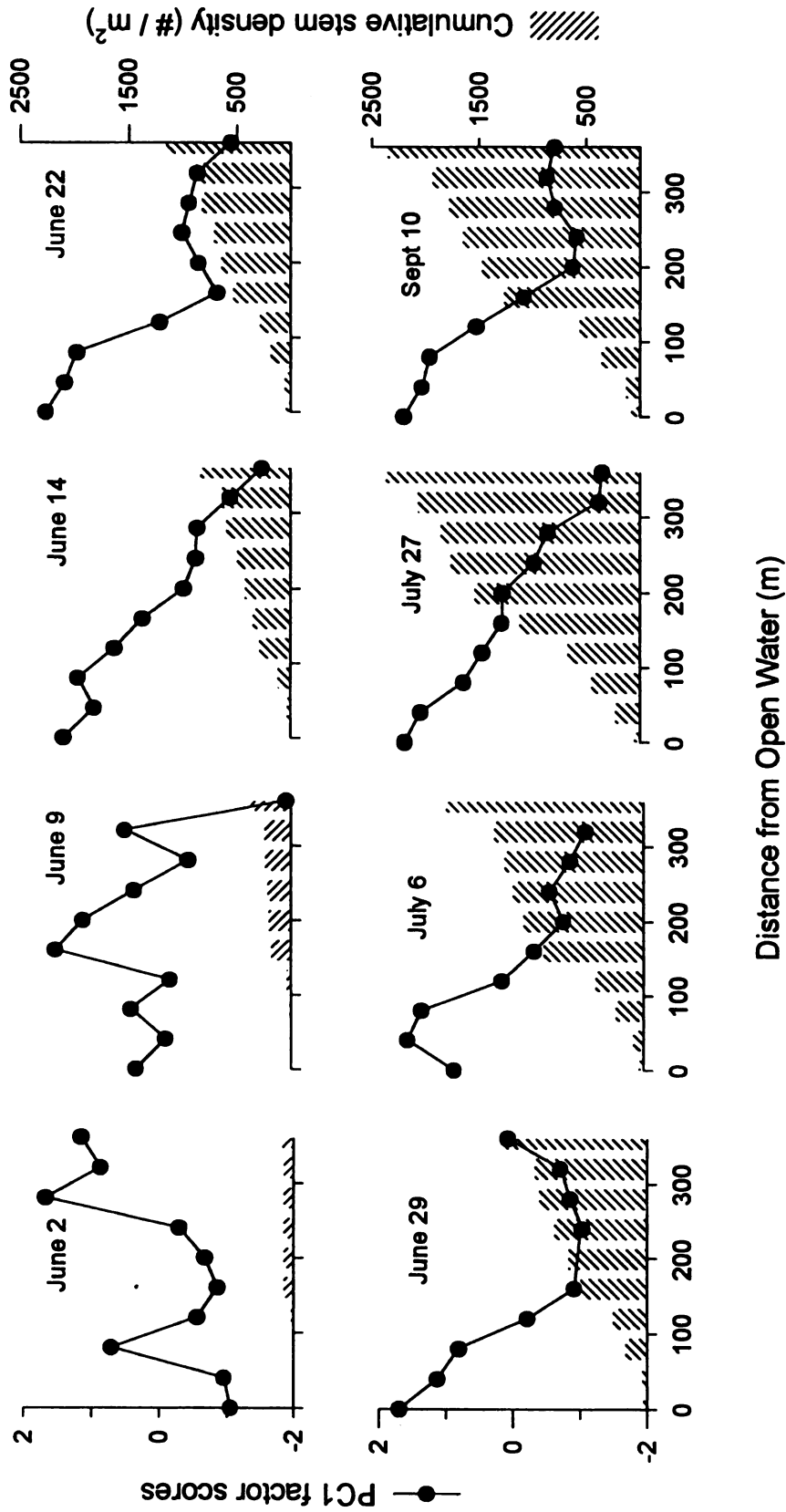


Figure 2. Temporal and spatial changes in littoral water quality. PC1 factor scores are from the first principal component of 10 independent measurements of water quality (see Table 1). Scores show similarity or dissimilarity in physico-chemical properties between stations with average conditions centered at zero (0). Cumulative stem density was calculated as the total number of *Scirpus americanus* stems from the littoral edge, thus providing a measure of vegetative resistance to pelagic-littoral water exchange. Data from July 13, 1994 are not shown because stem densities were not measured on this date.

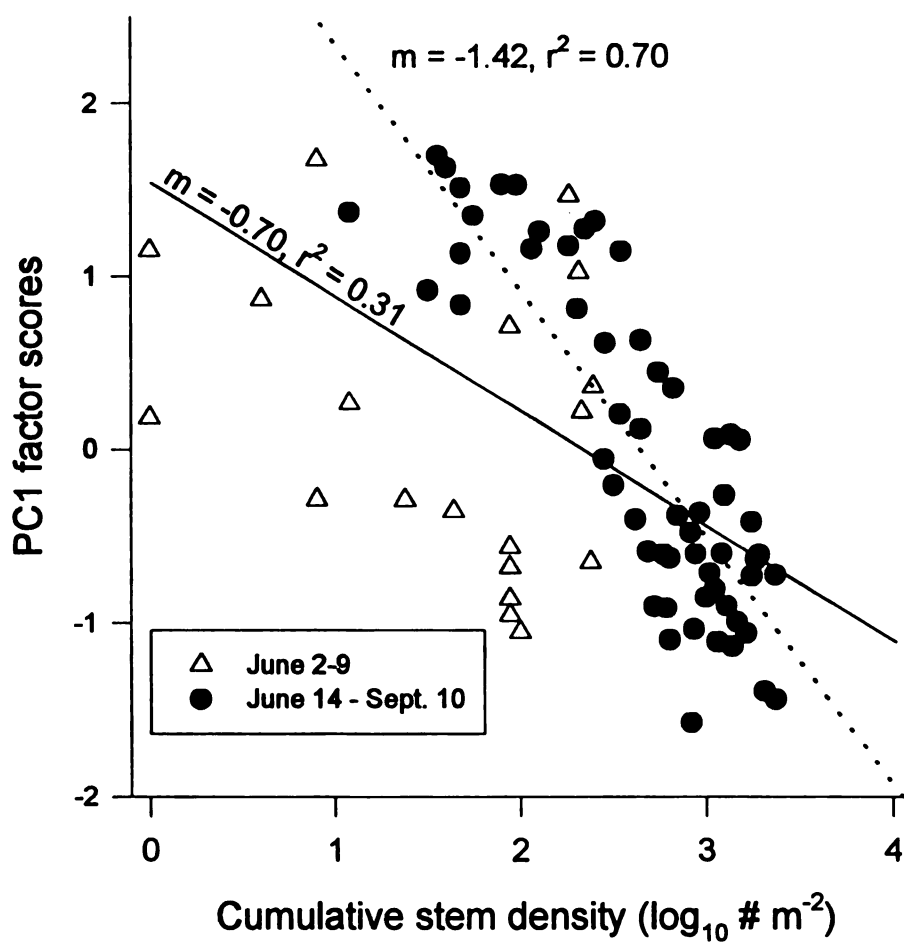


Figure 3. Relationship between PC1 factor scores and cumulative stem density. When data from June 2 and 9 are included, vegetative resistance to pelagic influx explains 31% of the spatial variation in water quality (solid line). When these dates are excluded from the regression, 70% of the variation in littoral water quality can be explained by cumulative stem density (dotted line).

existed between littoral water quality and vegetative resistance to the influx of surface waves.

After the macrophytes were well established, a significant amount of abiotic heterogeneity developed within the stand. Turbidity averaged 23 NTU's in the outer 80 m, but values were 50% lower at more shoreward stations (Figure 4). Average pH decreased from 8.67 at the pelagic-littoral boundary to 7.91 at stations closest to shore. Bicarbonate alkalinity was lowest in the outer 80 m of the stand ($104 \text{ mg CaCO}_3 \text{ L}^{-1}$). Values increased to $140 \text{ mg CaCO}_3 \text{ L}^{-1}$ at shoreward stations. Oxygen was usually super-saturated but averages were 45-50% higher at the littoral edge. Conductivity and the dissolved ions were typically distributed as gradients although there was some temporally variability. Between June 14 and June 22 measures increased from open water towards shore (Figure 4). Gradients were established in the opposite direction on July 6 and 13. This was primarily the result of increased ion concentrations in offshore water since values for the inner 160 m of vegetation remained constant. By September, conductivity and all ions except chloride again decreased from open water into the macrophyte bed. Chloride appeared to vary at random along the transect on this date.

Temporal Response of Invertebrates

Water depth at the outer littoral stations averaged 5 cm greater than depth at inner littoral stations. However, this did not influence the total surface area available for epifauna colonization since there was no significant difference in submerged stem surface area ($p > 0.70$) or stem density ($p > 0.78$) between the two transects. Furthermore, there

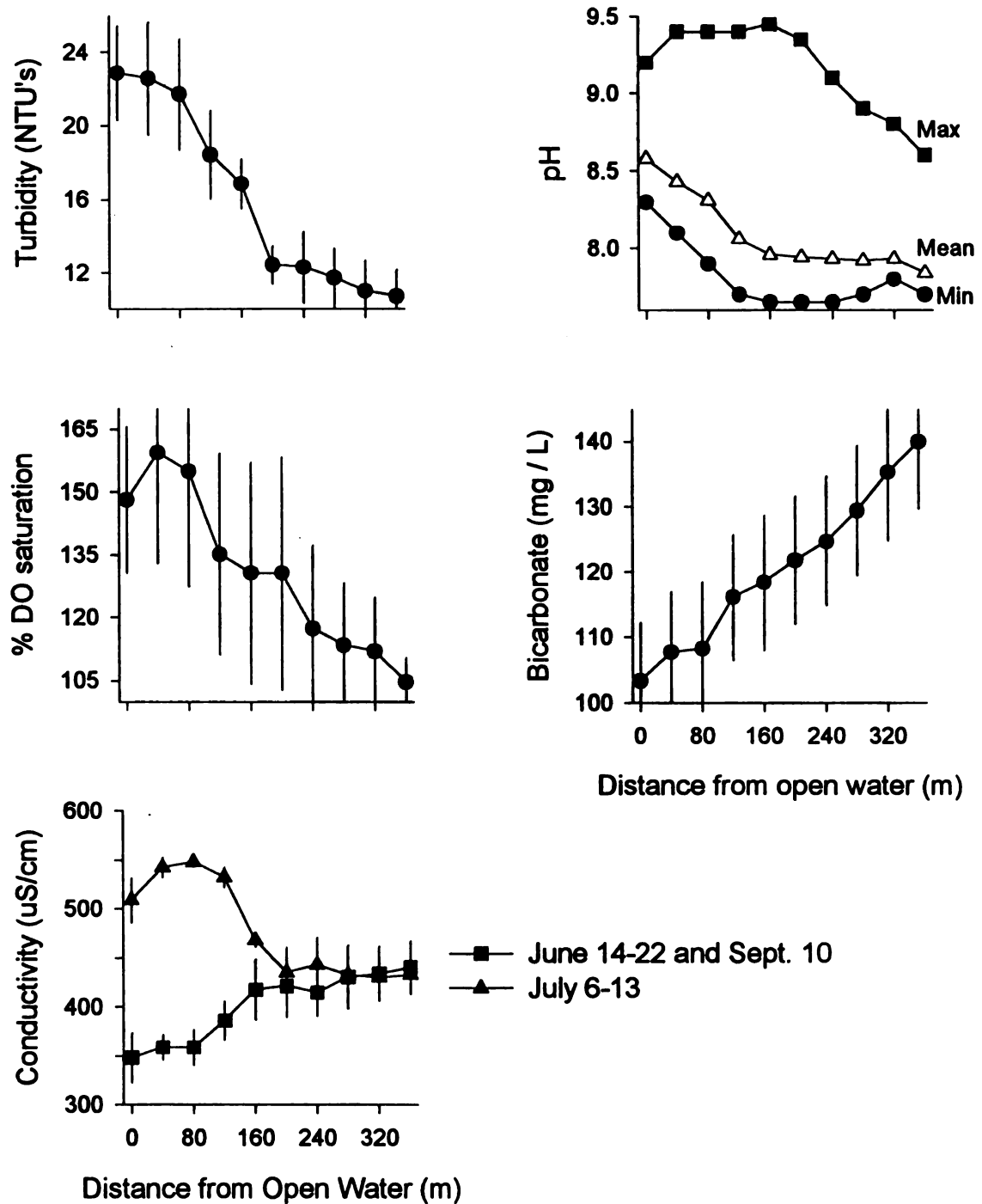


Figure 4. Spatial gradients in littoral water quality. Data are the mean of seven sampling dates (June 14 - Sept. 10, 1994) plus or minus one standard error. The range of pH is shown as well as the mean. The distribution of conductivity changed between July 6 and 13, thus, these dates have been plotted separately.

was no correlation between colonizable stem surface area and algal biomass ($\rho = -0.07$, $p = 0.514$), or stem surface area and invertebrate abundance ($\rho = 0.08$, $p = 0.448$). Thus, I chose to report and test all data on a per stem basis.

Stems collected from outer littoral stations had significantly higher invertebrate abundance ($p < 0.01$) for the combined data of the summer (Figure 5). During the first three weeks of June, the number of invertebrates per stem was comparable between the two transects. A significant difference did occur on June 9, but the overall magnitude was small since abundance was low at the time. Between June 9 and June 22, algal biomass at inner littoral (IL) stations dropped from an average $144 \mu\text{g stem}^{-1}$ to less than $3 \mu\text{g}$ (Figure 5). Invertebrate abundance in the two areas began to diverge at that time. Populations from the IL stations did not increase over the summer reaching a maximum of only 54 invertebrates stem^{-1} on July 27. Abundance in this area was moderately correlated with algal biomass ($\rho = 0.50$).

In contrast, invertebrate populations from the outer littoral stations increased substantially (Figure 5), with abundance more strongly correlated to the changes in algal biomass ($\rho = 0.63$). By July 27 each stem of *Scirpus americanus* taken from OL stations had $140 \mu\text{g}$ more chlorophyll a and 188 more invertebrates than those taken along the inner littoral transect. Using stem densities from this date, these numbers translated to areal differences of more than 24,000 epiphytic invertebrates m^{-2} . These large differences could not be attributed to water temperature which never differed by more than 1°C , and was not significantly different ($p > 0.88$) for the summer averages.

Chironomid biomass was also significantly higher ($p < 0.01$) at the outer littoral

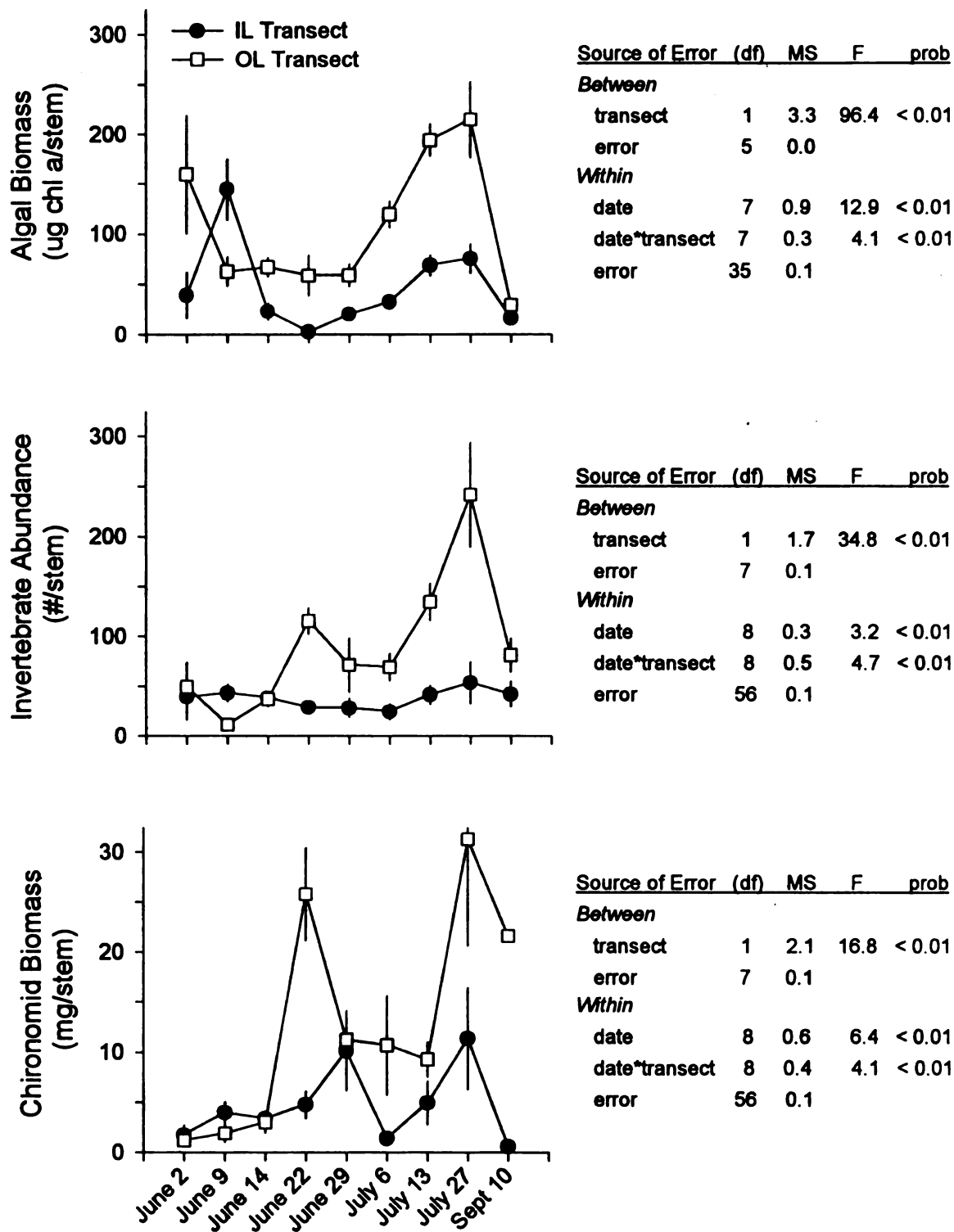


Figure 5. A comparison of the temporal response of epifauna collected from the inner littoral (IL) and outer littoral (OL) transects. Plotted data represent the mean of $n = 5$ samples plus or minus one standard error. Statistical analyses were performed using repeated measures ANOVA on the $\log_{10}$ transformed data.

stations (Figure 5). This appeared to be due to overall higher abundance since individual larval weights did not differ between transects for all dates combined ($p = 0.56$). Total biomass was comparable for the two areas through June 14, after which values increased from 3 to 26 mg stem⁻¹ at the outer littoral stations (Figure 5). With the exception of June 29, estimates remained higher at outer littoral stations for the duration of the summer.

Thirteen taxa of insects and 12 taxa of non-insectan invertebrates were used to make comparisons of community composition (Table 2). The majority of taxa were found infrequently, and abundance was highly skewed towards only two families. Midge larvae (Diptera:Chironomidae) were the most abundant, comprising 55% of all invertebrates collected. Segmented worms from the family Naididae (Class Oligochaeta) comprised an additional 37%.

Invertebrate community composition began to diverge between the two areas of the littoral zone on June 22. Both collector-gatherers and collector-filterers began to increase at outer littoral stations resulting in a substantial difference between the two transects (Figure 6). The difference in collector-filterers was largely due to an increase in the proportions of Tanytarsini at OL stations coupled with a simultaneous decrease in the proportions at IL stations (Figure 7). By September, Tanytarsini were not found on inner littoral stems even though substantial numbers were collected from the outer littoral stations. After their July spawning period, the other filtering taxa, zebra mussels (*Dreissena polymorpha*), were commonly found on stems at outer littoral stations, yet seldom occurred along the inner littoral transect.

Table 2. The operational taxonomic units used for this study and their generalized functional feeding groups (FFG). CG = collector-gatherer, CF = collector-filterer, P = predator, and O = omnivore. Assignments were based on the most common strategy reported by Merritt and Cummins (1984) or Thorpe and Covich (1991). 1 = abundant, 2 = common, 3 = uncommon.

Operational Taxonomic Unit	FFG	Operational Taxonomic Unit	FFG
INSECTS		NON-INSECTS	
Coleoptera		Amphipoda	
Dytiscidae	P ³	<i>Gammarus sp.</i>	O ²
<i>Gyrinus sp.</i>	P ³	<i>Hyallela azteca</i>	O ²
Scirtidae	CG ³		
		Bivalvia	
Diptera		<i>Dreissena polymorpha</i>	CF ²
Chironomidae*			
Orthocladiinae/Chironomini	CG ¹	Gastropoda	
Tanytarsini	CF ¹	<i>Ferrissia parallela</i>	CG ²
Tanypodinae	P ³	<i>Physa sp.</i>	CG ³
Ceratopogonidae	P ²	<i>Gyraulus parvus</i>	CG ³
Ephemeroptera		Hirudinea	P ³
<i>Caenis sp.</i>	CG ²		
		Hydracarina	P ²
Odonata			
<i>Enallagma sp.</i>	P ³	Hydrozoa	
<i>Ishmura verticalis</i>	P ³	<i>Hydra sp.</i>	P ²
Trichoptera		Nematoda	O ²
<i>Agraylea sp.</i>	CG ³		
<i>Hydroptila sp.</i>	CG ²	Oligochaeta	
<i>Nectopsyche sp.</i>	CG ²	Naididae	CG ¹
		Turbellaria	
		<i>Dugesia sp.</i>	O ³

*Species lists for the Chironomidae are provided in Table 3.

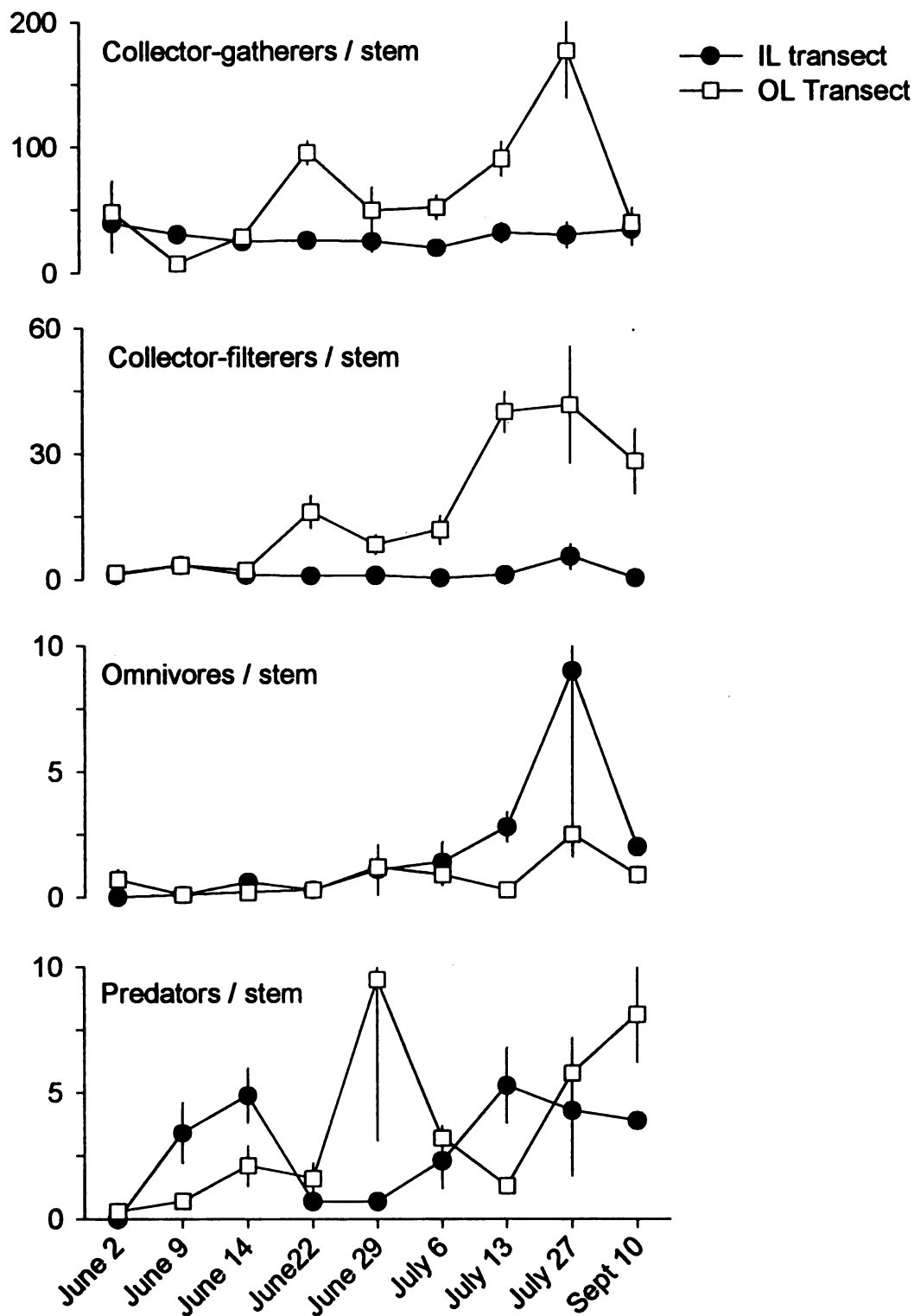


Figure 6. The temporal response of each functional feeding group of epiphytic invertebrates from the inner (IL) and outer littoral (OL) transects. Plotted data are the mean of $n = 5$ samples plus or minus one standard error.

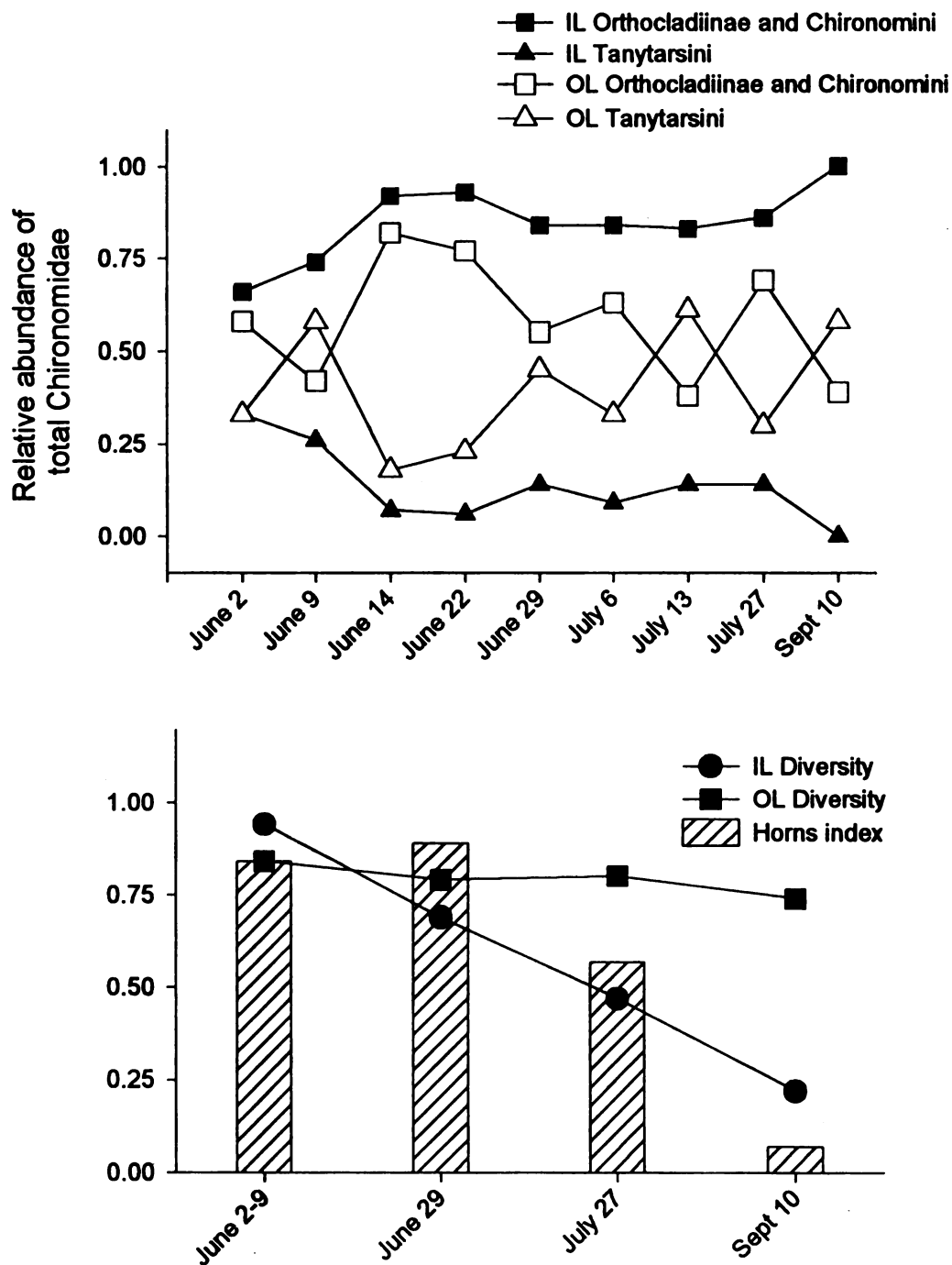


Figure 7. A temporal comparison of the Chironomidae collected from the inner littoral (IL) and outer littoral (OL) transects. (Top) The relative abundance of the two primary functional groups: Tanytarsini tend to be filterers, Orthoclaadiinae/Chironomini are most often classified as collector-gatherers. (Bottom) Shannon-Wiener diversity of the Chironomidae with Horn's index of community similarity as a comparison between transects.

The abundance of omnivorous invertebrates began to diverge on July 13 (Figure 6) when Nematoda and the amphipod, *Hyallela azteca*, became 5 times more abundant at inner littoral stations. Common predators included Ceratopogonidae larvae, water mites (Hydracarina), and *Hydra* sp. Although there was no definitive temporal trend of the predacious feeding group (Figure 6), predator abundance averaged 2 times higher at inner littoral stations for the combined data of the summer.

Twenty-one species groups of Chironomidae were identified during this study (Table 3). In early June, both areas of the littoral zone had a highly diverse community with Horn's index indicating 89% overlap in the species composition (Figure 7). *Endochironomus nigricans* and *Cricotopus sylvestris* were the dominant collector-gatherers and represented 20-37% of chironomid abundance in both areas (Table 3). The collector-filterers *Parachironomus arcuatus*, *Rheotanytarsus* spp., and *Tanytarsus* spp. were also common to both transects and ranged between 44 and 70% of relative abundance.

Over the four months of the study, Shannon-Wiener diversity of Chironomidae from inner littoral stations declined from 0.94 to 0.22 (Figure 7). Taxa richness dropped from an original 12 species to 5 by the end of the summer (Table 3). The IL community became increasingly dominated by collector-gatherers, notably *E. nigricans* and *Corynoneura* sp. (Table 3). In contrast, diversity at outer littoral stations remained constant over the summer (Figure 7) with abundances evenly distributed between collector-gatherers and collector-filterers (Table 3). By September 10, Horn's index indicated only 7% similarity between Chironomidae from the two areas. On this date,

Table 3. Chironomidae identified from the inner littoral (IL) and outer littoral (OL) transects during the summer of 1994. Each species has been categorized as a collector-gatherer (CG), collector - filterer (CF), collector - gatherer or filterer (CG/F), or predator (P). Assignments were based on information contained in (1) Merritt and Cummins (1984), (2) Berg (1995), (3) gut contents analyzed during this study, (4) inferred from gut contents of a member of the same genus. The relative abundance of each species is provided for 4 dates.

Taxa	2-9 June				29-Jun		27-Jul		10-Sep	
	FFG	SOURCE	IL	OL	IL	OL	IL	OL	IL	OL
Chironomini										
<i>Chironomus</i> sp.	CG	1, 2	2							
<i>Endochironomus nigricans</i>	CG	1, 2, 3	20	10	41	22	67	28	2	13
<i>Endochironomus subtidens</i>	CG	4						11		2
<i>Glyptotendipes</i> species group A	CG/F	1, 3	2		2	6		30		30
<i>Glyptotendipes</i> species group B	CG/F	1, 3, 4	5	2	2	4				7
<i>Glyptotendipes</i> species group C	CG/F	1, 3, 4		2						2
<i>Parachironomus arcuatus</i> group	CF	1, 2	12	20	14	12	2	2	2	2
<i>Pseudochironomus</i> sp.	CG	1					19			
Tanytarsini										
<i>Paratanytarsus</i> sp.	Unk		5		2		2			
<i>Rheotanytarsus</i> sp. 1	CF	1, 2, 3	20	36	8	20	4	13		33
<i>Rheotanytarsus</i> sp. 2	CF	1, 2, 4	2	6	2	14		6		9
<i>Tanytarsus</i> sp. 1	CF	1	10	6			4	6		
<i>Tanytarsus</i> sp. 2	CF	1		2			2	2		
Orthocladiinae										
<i>Corynoneura</i> sp.	CG	1, 2, 3	2						88	
<i>Cricotopus sylvestris</i>	CG	1, 2, 3	17	10	27	22		2		
<i>Nanocladius bicolor</i>	CG	1						2		
<i>Parakiefferiella</i> sp.	CG	1							5	
<i>Psectrocladius psilopterus</i>	CG	1	2	2						
Tanypodinae										
<i>Larsia</i> sp.	P	1			2					
<i>Paramerina</i> sp.	P	1, 2								2
<i>Thienemannimyia</i> group	P	1, 2		2						
Total Identified			41	50	49	50	48	54	43	54

Rheotanytarsus dominated the outer littoral samples but was not found at inner littoral stations (Table 3). In the same manner, *Corynoneura* dominated the inner littoral samples but was not found at outer littoral stations.

There were no significant differences in the diets of conspecifics collected from the two transects (Table 4). Small detritus (10-60 μm) was the most common particle found in larval chironomid guts, and represented no less than 51% in any species. Filamentous green algae were the second most common food item, representing 7 to 18% of diets. Diatoms were only common in *Endochironomus nigricans* and *Pseudochironomus* larvae. Even though means were not significantly different, percentages were 2x higher for larvae at inner littoral stations. *Rheotanytarsus* was the only taxa found to contain substantial proportions of blue-green algae (18-45%) with 27% more found in the guts of larvae from the OL transect. The contribution of green algae to diets was minimal for all species, and similarly, animal matter never represented more than 1% of the particle types.

Spatial Distribution of Invertebrates

On June 14, there was no evident spatial distribution of epifauna throughout the macrophyte stand. Invertebrate abundance ranged from 25 stem⁻¹ to a maximum of only 67 stem⁻¹, and numbers appeared to vary at random along the perpendicular transect. Ninety percent of the invertebrate community were collector-gatherers. Collector-filterers were uncommon representing no more than 3% of totals at any station. Predators comprised 1 to 15% of relative abundance and consisted mostly of water mites and

Table 4. Particle types found in the guts of larval chironomids. The first value in each cell is the mean percent of the total contents. The mean is followed by the values of a 90% confidence interval. FGA = filamentous green algae and BG = blue-green algae.

Species	Date	Transect	n	Detritus (10-50um) (61-130um)	FGA (>130um)	Green	Diatoms	BG	Animal Matter
<i>*Corynoneura sp.</i>	10-Sep	IL	5	91, 82-100	5, 0-13	2, 0-6	2, 0-5	<1	
<i>Cricotopus sylvestris</i>	22-Jun	IL	5	67, 60-74	4, 0-12	<1	1, 0-3	7, 0-17	
<i>Cricotopus sylvestris</i>	22-Jun	OL	5	68, 54-82	4, 0-11	<1	2, 0-6	4, 0-10	
<i>Endochironomus nigricans</i>	27-Jul	IL	7	53, 25-81	10, 2-18	<1	16, 0-45	<1	<1
<i>Endochironomus nigricans</i>	27-Jul	OL	10	71, 60-82	5, 1-9	<1	6, 1-11	3, 0-8	<1
<i>*Glyptotendipes sp. gr. A</i>	10-Sep	OL	5	75, 67-83	3, 2-4	10, 7-13	1, 0-2	8, 1-15	<1
<i>*Pseudochironomus sp.</i>	27-Jul	IL	3	63, 61-65	15, 7-23	<1	8, 3-13		<1
<i>Rheotanytarsus sp.</i>	14-Jun	IL	5	68, 58-78	3, 0-8	7, 0-20	2, 0-4	18, 0-37	
<i>Rheotanytarsus sp.</i>	14-Jun	OL	5	48, 32-64	3, 0-8	4, 0-9	<1	45, 26-64	

*A comparison of conspecifics was not possible because the taxon was only found at one of the two transects.

Hydra sp. Low numbers of omnivorous amphipods occurred at isolated stations.

Estimates of epiphytic algal biomass ranged from 5 to 21 μg chlorophyll a stem^{-1} , with values also appearing to vary at random along the perpendicular transect.

On July 27 there was a definitive spatial distribution of the epifauna. Periphyton declined from 553 $\mu\text{g chl a stem}^{-1}$ at the pelagic-littoral boundary to only 17 $\mu\text{g stem}^{-1}$ at stations farthest from open water (Figure 8A). The total abundance of invertebrates declined from 1172 stem^{-1} to less than 35 stem^{-1} at distances beyond 160 m of open water. Individual chironomid larvae were 2-4 times larger in the outer 160 m of the stand (Figure 8B). This was particularly evident for the Orthocladiinae/Chironomini, but Tanytarsini tended to reduce the overall trend due to their smaller size and because they were only found in the outer 160 m.

There was also a distinct spatial trend in the community composition of invertebrates. Collector-filterers represented 46% of relative abundance at the open water/littoral interface, but declined to less than 1% at distances beyond 160 m from open water (Figure 8C). These decreases were coupled by increasing proportions of omnivorous and predacious invertebrates. Nematodes and amphipods were not found until 140 m from open water, after which they comprised 5-17% of community abundance. Ceratopogonid larvae, one of the dominant predators, were not found in the outer 100 m but increased substantially beyond 140 m.

The spatial distribution of biota on July 27 was not correlated to colonizable surface area or water temperature. Water depth gradually decreased towards shore (Figure 8D), but this did not result in any notable trend in the amount of stem surface area

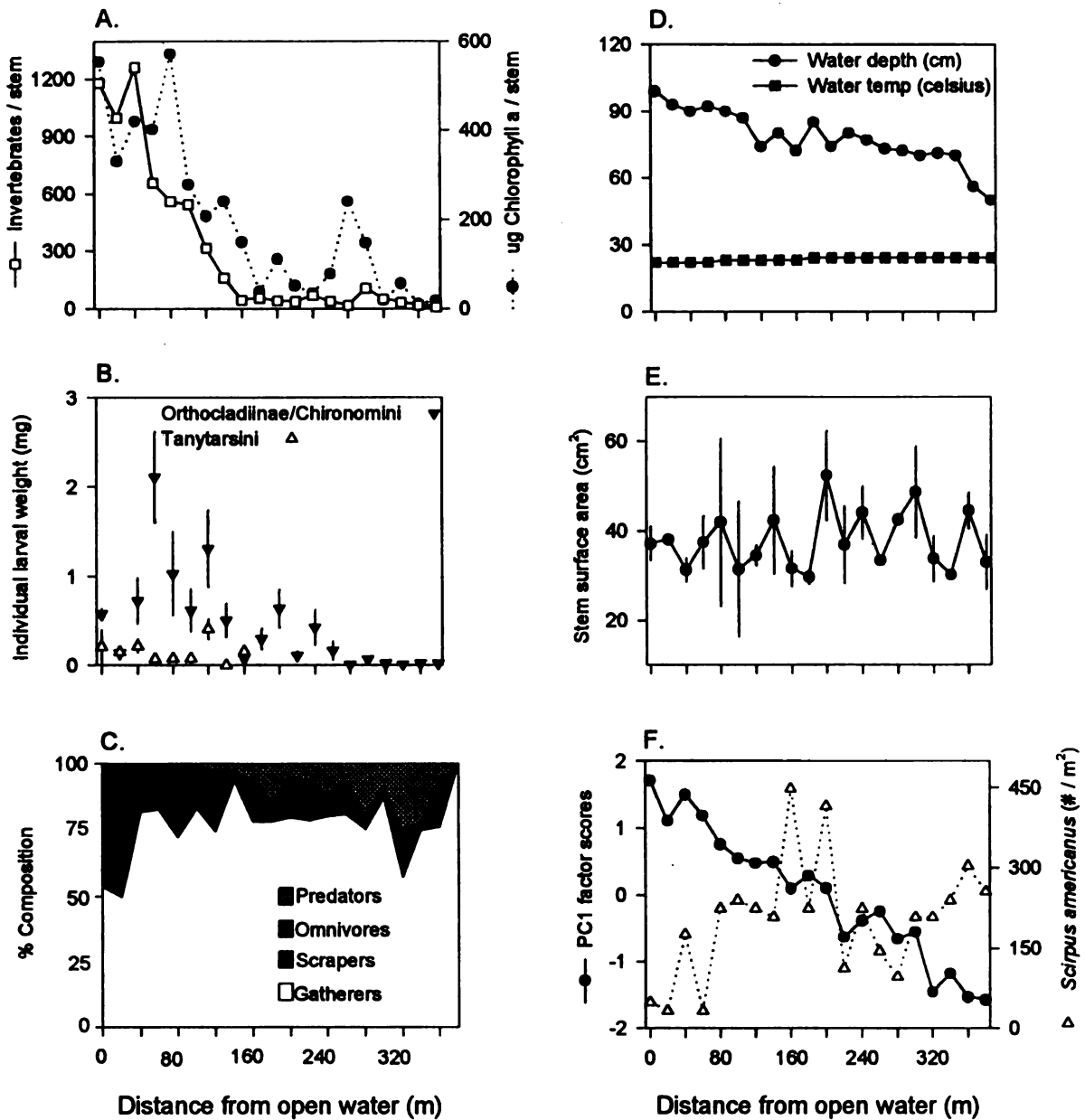


Figure 8. The spatial distribution of biotic and abiotic variables throughout the littoral zone on July 27, 1994. A) Epiphytic invertebrate abundance and algal biomass. B) Mean larval weight of the two dominant functional groups of Chironomidae ($n = 20$, plus or minus one standard error). C) % composition (relative abundance) of the four functional feeding groups. D) Water depth and temperature. E) Mean submerged stem surface area ($n = 3$, plus or minus one standard error). F) PC1 factor scores from the gradient in water quality and *Scirpus americanus* stem density.

available for epifaunal colonization (Figure 8E). Although *Scirpus americanus* density was variable there were no trends related to the steep decrease in biota between 0 and 160 m from open water (Figure 8F). The range in water temperature was 22-24°C with higher temperatures at the most shoreward stations (Figure 8D).

The spatial distribution of algae on July 27 was strongly correlated to the factor scores from the first principal component of water quality ($\rho = 0.84$, $p < 0.01$, see Figure 8A and F). Most of the spatial variation in invertebrates was explained by algal biomass alone. Factor scores from the principal component of algal biomass accounted for 70% of the total variation in invertebrate abundance, and 66% of variation in chironomid biomass (Table 5). Both regressions were highly significant ($p < 0.01$) and had moderate to strong effects on the dependent variables. Although the effect of the water quality gradient on invertebrates was also significant ($p < 0.01$, Table 5), adding PC1 factor scores to the model only increased the total variation explained by 13% for invertebrate abundance and 18% for chironomid biomass.

Table 5. The relative influence of algal biomass and water quality on the distribution of epiphytic invertebrates on July 27, 1994. The dependent variables of invertebrate abundance and chironomid biomass were first regressed against algal biomass to determine the proportion of variation explained by this factor alone. A multiple regression was then performed with both algal biomass and the factor scores from PC1 (the dominant environmental gradient) as independent variables. The difference in values of r^2 represent the increase in variation explained by adding water quality to the model. Data from each regression passed tests of normality, homoscedasticity, and independence of residuals.

Dependent Variable / PC	Slope	r^2	P
Invertebrate Abundance (log #/stem)			
Algal Biomass alone	0.579	0.703	< 0.001
With PC1	0.448	0.834	< 0.001
Chironomid Biomass (log mg/stem)			
Algal Biomass alone	0.827	0.661	< 0.001
With PC1	0.779	0.845	< 0.001

DISCUSSION

Pelagic-littoral mixing gradients

During early June, *Scirpus americanus* was just beginning to emerge above the water surface. The littoral zone appeared well mixed on these dates with factor scores of PC1 distributed at random (Table 1). After sufficient growth of emergent vegetation, abiotic gradients began to form from open water into the stand (Figure 2). Turbidity, pH, and dissolved oxygen were highest at the littoral boundary, but decreased substantially towards shore (Figure 4). Conversely, bicarbonate alkalinity tended to increase. Conductivity and the various dissolved ions were usually distributed as gradients either increasing or decreasing with distance from open water.

The simplest explanation for these distributions is that macrophytes gradually impeded ambient flows from open water. Thus, PC1 is best interpreted as a pelagic-littoral mixing gradient. This interpretation explains the strong relationship between PC1 factor scores and cumulative stem densities from the littoral edge (Figure 3). It is also consistent with field observations that surface waves notably penetrated 160 m into the vegetation. Yet, littoral waters were calm and clear shoreward of 160 m.

I performed limited sampling in 1995 and found similar distributions of water quality for three other sites in Saginaw Bay (Table A-2, Figure A-1). Suzuki *et al.* (1995) have documented these distributions at a fourth site, describing a horizontal chemocline that was established as macrophytes inhibited pelagic water flow. Although the distributions in water chemistry are consistent between our studies, our interpretations differ. Those authors concluded that the chemocline resulted in two separate littoral water

masses much like horizontal stratification. However, data from the present study are better explained as a mixing gradient. There were several dates on which PC1 factor scores decreased into the vegetation but showed no clear demarcation of a chemocline (see July 27, Figure 2). Furthermore, temperatures were usually homogeneous and any density differences caused by the concentrations of dissolved ions were minimal (see discussion by Suzuki *et al.* 1995). Thus, a pelagic-littoral mixing gradient is a more plausible explanation than horizontal stratification.

Others studies suggest that pelagic-littoral mixing gradients occur in a variety of littoral types. In a dense stand of *Glyceria aquatic* in a pond in South Bohemia, Dvorak (1970) noted distinct increases in dissolved oxygen and pH from the vegetation towards open water. He attributed these increases to mixing of pelagic and littoral water on windy days. Similar results have been found in a *Typha* swamp surrounding Lake Chilwas, Malawi (Howard-Williams and Lenton 1975), a dystrophic Carolina bay wetland (Schalles and Shure 1989), and a Polish lake (Klosowski 1992). Gradients caused by wind-induced mixing may also be important features of northern prairie wetlands (see Murkin *et al.* 1991).

Effects on Invertebrates

The results of this study show that the pelagic-littoral mixing gradient had a profound influence on the distributions of epiphytic organisms. Before a gradient was formed there were no detectable differences in the invertebrate community throughout the littoral zone. Abundances were low but approximately equal along the inner and outer

littoral transects (Figure 5). Spatial sampling early in the summer did not reveal any distinct distributions from open water towards shore, and there was no evidence that functional groups or species composition of the Chironomidae differed throughout the stand (Figures 6 & 7, Table 3).

By June 22 notable changes had taken place. Biota throughout the littoral zone had begun to encounter contrasting abiotic environments as macrophytes became dense enough to inhibit water flow (Figure 2). The outer 160 m of emergent vegetation experienced some mixing with open water, but beyond this point conditions became indicative of stagnancy (Figures 2 & 4). Invertebrate populations in the latter areas appeared “stunted” reaching a maximum of only 54 individuals stem⁻¹ (Figures 5). Diversity of the Chironomidae declined substantially in un-mixed waters due, at least in part, to declines in the abundance of filter-feeding taxa after formation of the gradient.

In contrast, invertebrate abundance and biomass increased significantly over the summer at stations where littoral waters were circulated (Figures 5). In these areas there was an equal number of collector-filterers and collector-gatherers, as well as a high diversity of Chironomidae. Sampling on July 27 revealed spatial trends that paralleled the pelagic-littoral mixing gradient (Figure 8). Abundance decreased from open water towards shore with more than an order of magnitude difference in the areal density of invertebrates throughout the stand. Collector-filterers declined from the open water/littoral boundary into the vegetation while the abundance of omnivores and predators increased. The average size of larval Chironomidae was highly reduced in

stagnant water (Figure 8) suggesting the possibility of lower growth rates, and/or differential developmental and emergence times.

Possible Mechanisms

Abiotic variables such as pH (Havas and Hutchinson 1982), dissolved oxygen (Murkin *et al.* 1991), conductivity (Peterson and Ross 1991), and alkalinity (Winget and Mangum 1991) are often major environmental determinants of invertebrate distributions. It appeared that these factors had little, if any, direct influence on the epiphytic invertebrate distributions observed during this study. All of the water quality variables combined explained only 13% of the spatial variation in invertebrate abundance and 18% of the variation in chironomid biomass. This was probably because these factors were within reported tolerance ranges of the dominant organisms. Osmoregulation of the various dissolved ions is rarely a problem for invertebrates when pH is above 5.5 (Pinder 1986, Johnson *et al.* 1993). The range during this study was 7.7 to 9.45. Although diel values would have been lower, the highly buffered waters would have prevented any dramatic changes. Dissolved oxygen was usually supersaturated throughout the stand. This was likely a function of the time at which measurements were taken (10:00 am - 1:00 pm), but there was no evidence that waters ever became anoxic.

Food quality and quantity can also be principal factors influencing aquatic invertebrate distributions (Andersen and Cummins 1979). Gresens and Lowe (1994) experimentally determined that chironomids will select patches of greatest periphyton quality when given the choice. Whether this applies under natural conditions is difficult to

assess since Chironomidae can feed either selectively (Botts and Cowell 1992) or indiscriminately in proportion to the food available in their immediate environment (Rasmussen 1983, Berg 1995). While there was no significant difference in the diets of larvae collected from the IL and OL transects, it should be noted that the nutritional value of the biofilm was not directly assessed by this study and the bacterial component was ignored. However, I speculate that any effects of food quality were minimal because the majority of variation was explained by algal biomass alone. Invertebrate abundance and chironomid biomass were temporally correlated to the amount of chlorophyll a on the *Scirpus* stems, and algal biomass accounted for 70% of the spatial variation in invertebrates during their peak abundance.

The invertebrate dependence on algae was further supported by gut analyses of the Chironomidae which suggested that most larvae were feeding on the biofilm. This is consistent with other reports that have classified these species (with exception of the Tanytarsini) as collector-gatherers that graze from the epiphyte-detrital complex (Berg 1995). Thus, it is likely that invertebrates in the stagnant water areas of this littoral zone were limited by the production of the biofilm. Many other studies have also concluded that epiphyte biomass is the primary determinant of grazer abundance (Mason and Bryant 1975, Cattaneo 1983, Dudley 1988, Hart and Robinson 1990, Campeau *et al.* 1994).

Suzuki *et al.* (1995) have previously documented these same spatial distributions in algal biomass. The authors proposed several possible hypotheses to explain this distribution including nutrient, carbon, or light limitation, or photo-inhibition. These hypotheses now seem unlikely. The rapid decline in algal biomass following the gradient

formation was not characteristic of nutrient limitation. It is unlikely that algae could have depleted nutrients so quickly from waters that are well known to be eutrophic in the area of Quanicassee (Smith *et al.* 1977, Stoermer and Theriot 1985). Carbon limitation cannot explain the distributions because high alkalinity coupled with relatively low pH resulted in the highest availability of inorganic carbon at stations with reduced mixing. Shading by macrophytes does not correspond to the declines in biomass between 80 and 160 m into the stand because there were no notable trends in macrophyte density or surface area throughout the littoral zone. Finally, if photo-inhibition was occurring one would expect a higher proportion of degraded algae in the biofilm. Yet, there was no difference in the ratios of chlorophyll a to phaeophytin at the IL and OL transects, or along the perpendicular transect.

As an alternative explanation, I hypothesize that biofilm production was limited by boundary layer diffusion. It is well known that the exchange of gases and solutes in aquatic plants is a function of current velocity (Leyton 1975, Madsen and Sondergaard 1983). Westlake (1967) found that photosynthetic rates of submergent plants were reduced as much as six fold when flows were diminished. Whitford and Schumacher (1961) showed that ^{32}P uptake by the freshwater algae *Oedogonium kurzii* decreased 10 fold in stagnant water. These changes in metabolism are usually attributed to increases in the size of the boundary layer surrounding a plant surface at low flow rates (Smith and Walker 1980, Madsen and Warnke 1983).

Losee and Wetzel (1993) estimated the size of the boundary layer for littoral vegetation at various distances from open water. They concluded that even small changes

in flow rate as one moves away from the littoral edge result in large increases in the zone of depletion. Thus, a circulation gradient such as the one represented by PC1 could directly regulate epiphytic algal biomass by gradually increasing the size of the boundary layer. This hypothesis is consistent with the strong correlation between algal biomass and the pelagic-littoral mixing gradient on July 27.

Further Implications

The boundary layer hypothesis further implies a trade-off for invertebrates which is seldom considered in littoral studies. Some authors have concluded that disturbance in the wave zone reduces epifaunal biomass and diversity (Bownik 1970, Lalonde and Downing 1992). Yet, given the positive relationship between flow rates and primary production, grazer production would almost certainly be a hyperbolic function of wave exposure. Where flows are highly reduced, primary production could become limiting to consumers. But photosynthesis and grazer biomass would be stimulated to some optima of wave exposure, beyond which epifauna would decrease due to disturbance. Thus, there may be some distance from a source of mixing where flow rates are optimal for both primary and secondary production. Such a relationship would not be limited to pelagic-littoral exchanges, but would also apply to areas of open water within a stand subject to wind fetch.

While much of this study was focused on the algal/grazer interaction, it is apparent that filter-feeding invertebrates experienced similar consequences of the pelagic-littoral mixing gradient. One of the most common taxa found in this site, *Rheotanytarsus*, is an

obligate filter-feeder which constructs a catchnet around the lumen of its tube retreat (Oliver 1971, Simpson and Bode 1980). This feeding habit is so widely accepted that Cranston (1995) reported *Rheotanytarsus* to only inhabit flowing waters. The outer 160 m of this littoral zone had enough circulation to support a substantial population of this genus. The decline of this taxa, and other Tanytarsini, from open water into the stand probably resulted as currents became inadequate to support their feeding habit.

Even filterers capable of creating their own currents, such as the zebra mussel (Reeders *et al.* 1993), were excluded from the inner half of emergent vegetation. Brady *et al.* (1995) provided some insight into the factors regulating zebra mussel distributions in this area, and their conclusions probably apply to other taxa as well. These authors noted that the dispersal of planktonic veligers was limited by the extent of water flow within the vegetation. After a spawning event the young “stacked up” in the middle of the littoral zone where flows were dissipated. Yet, larvae in this area had the lowest survivorship, possibly because phytoplankton abundance was highly reduced. Thus, one of the implications for planktonic organisms in this system is that flows may “push” them into the middle of the stand where their resources are quite scarce.

When the distribution of omnivorous invertebrates documented in this study is considered collectively with the spatial changes in water quality, the data may suggest a changing resource base throughout the stand. The well mixed portions appeared to be autotrophic with high standing stocks of algae, relatively high pH, and low alkalinity. Deeper into the vegetation where water was stagnant, higher proportions of amphipods and nematodes suggest increased importance of the detrital food web. This possibility is

consistent with low algal biomass, low pH, and high alkalinity which might indicate heterotrophic conditions in this area. While the data is still too limited to make any decisive conclusions, it seems plausible that the extent of water circulation into the littoral zone have a profound influence on P:R ratios throughout the system.

While predators are usually correlated to the availability of their prey (Dvorak and Best 1982, Schalles and Shure 1989, Murkin *et al.* 1991), the opposite trend was apparent at this site. These distributions may be explained, at least in part, by disturbance in the wave zone. Unlike Chironomidae which affix to the stems in tube retreats, the most abundant predators (Ceratopogonidae and Hydracarina) have rather inadequate means of attachment (Pennak 1978, Thorpe and Covich 1991). Thus, scour may have been a factor influencing predator distributions.

Invertebrates can represent a substantial part of the diets of both fish and waterfowl (Mackey 1979, Keast 1985, Murkin and Kadlec 1986, Armitage 1995). Thus, one might expect the gradient in resources documented here to influence the distribution of these higher trophic levels. Preliminary results from a concurrent investigation suggest this is true for the fish. Burton and Prince (1994) have reported fish catches 10 times higher in the outer 160 m of this site, in the same area where invertebrate abundance was highest. Interestingly however, a disproportionate number of sunfish (*Lepomis spp.*) were recorded from nets placed deeper into littoral stand. The calm waters in this area have highly reduced turbidity and may be particularly important for visually feeding centrarchids. Juveniles might also use this area for predator avoidance since cover of submergent macrophytes increases towards shore (Batterson *et al.* 1991, Suzuki *et al.*

1995). Werner *et al.* (1977) have shown the latter to be an important factor influencing habitat selection by sunfish. The implications are that a pelagic-littoral mixing gradient may partition fish habitat based on resource abundance, turbidity, and complexity of the vegetation.

SUMMARY & CONCLUSIONS

Some studies in both the freshwater and marine literature have shown pelagic flows to be abruptly reduced at the open water-littoral interface. These studies would lead one to believe that the littoral habitat is physically and chemically distinct from the open water system. However, this study does not support this generality. A very large portion of the littoral habitat and its biota were influenced by pelagic waters. The abundance, biomass, and diversity of the epiphytic invertebrate community all declined into the stand as macrophytes gradually impeded mixing. Most of these changes were explained by the decrease in algal biomass that accompanied inhibited flows. I hypothesize that epiphytic production was limited by boundary layer diffusion, but this still needs to be tested.

These results are not necessarily surprising since there are few factors that have more influence on aquatic organisms than circulation. Yet, it seems that many littoral studies have failed to consider this possibility. Perhaps this results from attempts to generalize the littoral zone as a homogeneous unit, thus making it much easier to predict its interactions with the lake ecosystem as a whole. However, this study demonstrates that such generalizations could be very misleading. I suggest that interactions in many littoral zones might be better understood by conceptualizing the stand as a transition with a gradually decreasing influence of open waters on the biotic and abiotic components. This would be particularly important in systems that (1) experience significant wind fetch or are exposed to waves, and/or (2) have relatively thin or patchy vegetation. These conditions probably apply to a great many littoral zones, and indeed, there is ample evidence to suggest pelagic-littoral mixing gradients are wide-spread.

APPENDIX

Table A-1. Summary of the physical data collected during temporal sampling. DFOW = distance from open water. *Samples were either lost or not collected.

Temperature (Celsius)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	15.0	20.0	26.0	24.0	21.0	25.0	39.0	22.0	20.0
40	15.0	20.0	26.0	24.0	21.0	25.0	39.5	22.0	19.0
80	15.0	20.0	27.0	24.0	21.0	25.5	40.0	23.0	19.0
120	16.0	20.0	26.0	24.0	21.0	26.0	40.0	23.0	19.0
160	16.0	20.0	26.0	24.0	21.0	26.0	41.0	23.0	19.0
200	16.0	20.0	26.0	24.0	21.0	26.0	41.0	24.0	20.0
240	17.0	19.0	25.0	24.0	21.0	27.0	41.0	24.0	20.0
280	17.0	19.0	25.0	24.0	21.0	26.0	42.0	24.0	20.0
320	17.0	18.5	24.0	24.0	21.0	26.0	42.0	24.0	20.0
360	18.0	18.5	24.0	24.0	21.0	26.0	42.0	24.0	21.0

Depth (cm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	88	88	74	81	84	90	*	99	92
40	88	77	70	79	74	83	*	90	84
80	72	70	60	66	63	72	*	90	74
120	73	63	49	65	61	70	*	74	74
160	76	63	56	67	64	72	*	72	71
200	72	61	53	66	62	71	*	74	70
240	65	62	57	65	65	74	*	77	64
280	63	55	56	60	59	64	*	72	63
320	60	52	54	53	57	70	*	71	63
360	45	45	38	34	41	54	*	56	46

Scirpus americanus (# stems/m²)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	0	0	12	40	36	48	*	48	80
40	4	8	20	16	12	48	*	176	48
80	4	4	84	128	156	160	*	224	224
120	16	32	172	100	116	192	*	224	208
160	64	140	60	248	296	480	*	448	704
200	0	24	72	108	112	192	*	416	208
240	0	8	72	68	136	96	*	224	176
280	0	24	104	120	136	80	*	96	128
320	0	8	44	56	48	96	*	208	160
360	12	128	196	268	320	448	*	304	416

Table A-1 (cont'd)

Turbidity (NTU's)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	32	24	23	19	16	20	35	18	29
40	31	20	19	25	15	16	39	20	24
80	31	27	21	28	13	15	36	17	22
120	25	26	14	22	11	12	27	18	25
160	20	28	17	16	12	13	19	19	22
200	20	33	11	17	9	11	13	15	11
240	23	24	7	20	10	15	14	15	5
280	24	29	9	16	10	15	13	15	4
320	17	31	8	15	10	14	15	12	3
360	17	28	10	13	11	12	15	11	3

Conductivity (uS/cm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	430	353	297	379	425	486	532	394	369
40	425	363	333	369	450	553	532	410	375
80	389	353	323	379	435	553	543	410	375
120	461	379	348	415	399	543	522	430	396
160	481	328	358	461	404	476	461	420	434
200	481	328	363	430	420	461	410	410	472
240	466	369	369	425	410	471	415	404	451
280	410	394	369	445	425	451	415	404	478
320	471	369	379	456	420	445	415	425	467
360	471	440	389	481	430	451	415	425	451

pH

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	8.40	9.10	9.20	8.30	8.50	8.50	8.70	8.70	8.60
40	8.50	9.15	9.40	8.10	8.30	8.45	8.60	8.60	8.40
80	8.20	9.30	9.40	7.90	8.40	8.35	8.50	8.40	8.25
120	8.70	9.35	9.40	7.70	8.10	8.10	8.45	8.30	7.80
160	8.70	9.35	9.45	7.70	7.85	8.00	8.40	8.20	7.65
200	8.80	9.30	9.35	7.70	7.80	8.00	8.30	8.20	7.65
240	8.90	9.30	9.10	7.80	7.80	7.90	8.20	8.10	7.65
280	8.80	9.20	8.90	7.90	7.70	7.80	8.10	8.10	7.75
320	8.80	9.10	8.80	7.90	7.80	7.80	8.00	8.00	7.80
360	9.00	8.90	8.60	7.85	7.80	7.70	7.70	7.95	7.75

Table A-1 (cont'd)

Bicarbonate Alkalinity (HCO_3^- as $\text{mg CaCO}_3/\text{L}$)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	120.04	58.45	59.36	99.04	105.70	98.90	137.28	107.68	115.48
40	106.67	72.65	61.28	91.85	116.71	116.77	138.61	113.55	115.16
80	89.59	64.00	54.80	98.23	111.25	115.46	143.57	116.13	117.94
120	108.63	66.82	63.70	113.44	114.58	119.52	145.99	127.51	128.21
160	109.59	58.56	61.34	137.33	122.15	106.94	133.72	126.04	141.38
200	109.21	55.58	70.12	127.37	130.20	115.86	121.62	130.97	156.32
240	99.20	69.05	79.91	124.23	129.20	115.10	118.16	140.28	116.28
280	84.66	82.86	83.38	130.98	132.35	123.24	122.49	141.27	172.06
320	112.98	83.49	84.66	135.95	131.19	126.22	137.66	158.46	172.94
360	101.92	113.15	96.20	142.02	120.26	124.39	151.26	165.57	173.06

Dissolved Oxygen (% saturation)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	74.19	170.65	183.79	102.03	150.40	192.32	204.03	111.74	92.57
40	74.19	171.76	233.23	89.88	140.14	233.27	228.19	107.08	84.07
80	74.19	196.30	217.54	74.09	146.98	232.01	235.76	96.31	81.89
120	75.79	216.38	182.53	65.59	125.33	173.65	234.05	97.50	67.69
160	75.79	227.53	191.40	58.30	97.99	150.84	249.57	96.31	69.88
200	76.81	234.22	181.26	61.95	*	128.02	237.35	108.10	66.92
240	76.38	223.82	162.55	70.45	90.01	117.83	212.92	99.60	68.04
280	77.42	221.64	145.17	99.60	82.03	103.94	187.20	102.03	73.61
320	78.47	187.96	122.68	105.67	90.01	110.28	181.85	94.74	78.07
360	79.09	150.15	121.46	109.32	110.52	111.54	*	91.10	84.31

Orthophosphate (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	0.04	0.04	0.04	0.05	0.03	0.00	0.05	0.02	0.03
40	0.04	0.01	0.04	0.03	0.04	0.03	0.03	0.02	0.02
80	0.05	0.03	0.03	0.03	0.04	0.02	0.03	0.02	0.02
120	0.04	0.04	0.04	0.03	0.03	0.02	0.02	0.03	0.03
160	0.03	0.04	0.04	0.04	0.03	0.00	0.02	0.03	0.03
200	0.00	0.04	0.03	0.05	0.03	0.03	0.03	0.02	0.03
240	0.00	0.04	0.04	0.04	0.04	0.03	0.02	0.02	0.01
280	0.03	0.04	0.04	0.04	0.04	0.02	0.02	0.02	0.03
320	0.02	0.04	0.04	0.04	0.03	0.02	0.00	0.03	0.03
360	0.02	0.04	0.04	0.03	0.00	*	0.02	0.02	0.03

Table A-1 (cont'd)

Potassium (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	2.6	2.6	2.6	3.2	3.2	4.7	4.7	4.2	2.6
40	2.6	2.6	2.6	3.7	3.7	4.7	4.7	4.2	2.6
80	2.6	2.6	2.6	3.7	3.2	4.7	5.3	4.2	2.6
120	3.2	2.6	2.6	4.2	3.2	4.2	4.7	4.2	3.2
160	3.2	2.1	3.2	4.2	3.2	4.2	4.2	4.2	3.7
200	3.2	2.6	3.2	4.2	3.2	4.2	4.2	4.2	3.7
240	3.2	2.6	2.6	4.2	3.2	4.2	3.7	3.7	3.7
280	2.6	2.6	2.6	4.2	3.2	4.2	3.7	2.6	3.2
320	3.2	2.6	3.2	4.2	3.7	4.2	3.7	2.1	3.2
360	3.7	3.2	3.2	4.2	3.7	*	4.2	2.1	3.7

Calcium (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	45.5	31.8	35.0	45.0	47.6	42.9	57.1	38.1	47.6
40	40.9	31.8	30.0	45.0	47.6	57.1	47.6	38.1	47.6
80	27.3	27.3	25.0	40.0	47.6	52.4	47.6	33.3	47.6
120	40.9	36.4	25.0	45.0	42.9	42.9	57.1	23.8	47.6
160	40.9	27.3	30.0	50.0	33.3	38.1	52.4	23.8	52.4
200	45.5	22.7	45.0	50.0	42.9	33.3	47.6	28.6	57.1
240	40.9	27.3	45.5	50.0	42.9	42.9	47.6	23.8	57.1
280	27.3	31.8	40.9	50.0	47.6	42.9	42.9	23.8	52.4
320	40.9	22.7	36.4	50.0	38.1	38.1	42.9	23.8	52.4
360	40.9	36.4	45.5	60.0	38.1	*	42.9	38.1	57.1

Magnesium (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	18.5	18.5	16.4	18.5	17.9	22.6	22.1	18.9	17.4
40	19.0	19.5	18.5	19.0	18.5	25.6	22.6	18.4	16.8
80	19.5	19.5	18.5	20.0	18.5	25.1	23.6	20.0	17.4
120	22.1	20.5	19.0	21.5	17.9	22.6	22.1	20.5	19.5
160	22.6	16.4	20.0	22.6	18.5	21.0	20.0	21.1	21.1
200	23.1	20.0	20.5	22.6	18.5	19.5	19.0	19.5	23.2
240	22.6	21.0	21.0	22.1	18.5	20.0	18.5	18.9	23.7
280	20.5	22.1	20.0	22.1	18.5	19.0	18.5	18.9	22.6
320	22.1	19.5	21.5	22.6	17.9	18.5	17.9	18.9	21.6
360	20.5	22.1	22.1	22.6	17.9	*	18.5	18.4	20.5

Table A-1 (cont'd)

Sodium (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	16.1	16.6	15.6	17.5	12.0	9.9	9.6	10.4	12.4
40	17.0	17.6	17.9	18.4	12.5	9.6	9.1	10.3	12.3
80	15.6	17.2	17.7	18.3	13.5	9.5	8.8	10.1	12.4
120	18.3	18.2	17.8	19.8	14.8	9.5	8.7	10.0	12.0
160	18.7	16.0	18.1	20.4	15.2	9.6	8.4	9.8	12.0
200	18.7	15.9	18.5	20.3	15.2	9.8	8.7	9.8	11.8
240	18.9	16.7	18.0	20.2	15.3	10.1	8.8	9.8	11.4
280	15.7	18.0	17.8	20.0	14.8	10.5	9.6	9.7	10.9
320	18.7	15.6	18.8	19.9	14.4	10.6	9.8	9.8	10.5
360	18.7	19.2	18.7	20.6	13.0	*	9.0	9.9	10.4

Chloride (ppm)

DFOW	2-Jun	9-Jun	14-Jun	22-Jun	29-Jun	6-Jul	13-Jul	27-Jul	10-Sep
0	38.5	44.2	47.0	42.0	35.0	38.0	30.0	29.5	30.5
40	43.0	46.5	48.0	43.0	38.0	41.5	30.0	31.0	32.0
80	40.0	47.0	47.0	44.5	39.0	40.5	30.0	31.5	31.5
120	44.5	50.0	47.5	48.0	40.0	36.5	27.0	34.0	31.0
160	46.5	43.0	50.5	50.5	41.0	34.5	24.5	29.5	33.5
200	46.0	44.5	51.0	49.0	40.5	34.5	23.5	28.5	36.0
240	44.5	46.0	51.0	48.5	41.0	35.0	24.5	28.0	34.5
280	42.5	50.5	52.0	48.5	40.0	36.0	28.0	28.0	32.0
320	47.5	43.0	51.5	48.5	39.0	35.0	27.0	27.5	31.0
360	46.2	49.0	54.0	49.0	37.0	*	22.0	27.0	30.5

Table A-2. A summary of the physical characteristics for three sampling sites in Saginaw Bay, Lake Huron. Samples were collected on August 25 and 26, 1995. See Figure A-1 for distributions of water quality.

Site 1: Finn Rd. Nearest town: Essexville
 Date: 8/25/95 Time: 7:15 pm
 Description: Dense *Scirpus americanus*, total littoral width = 120 m.

DFOW	pH	Temp (Celsius)	DO (% saturation)	Bicarbonate Alk (mg CaCO ₃ L ⁻¹)	Conductivity (uS cm ⁻¹)	Turbidity (NTU's)	Invertebrates (# stem ⁻¹)
0	8.60	19.0	162	97	481	25	105
15	8.60	18.0	139	111	502	22	7
30	8.50	18.5	149	114	532	22	11
45	8.60	22.0	133	108	522	27	12
60	8.20	19.0	140	117	543	16	9
75	8.20	22.5	84	114	532	16	6
90	7.90	20.5	106	113	543	14	4
105	8.10	23.0	93	117	532	14	0

Site 2: Coggins Rd. Nearest town: Pinconning
 Date: 8/26/95 Time: 12:15 pm
 Description: A heterogeneous stand of *Scirpus americanus* with many large patches of open water.

DFOW**	pH	Temp (Celsius)	DO (% saturation)	Alk (mg CaCO ₃ L ⁻¹)	Conductivity (uS cm ⁻¹)	Turbidity (NTU's)	Stems (# m ⁻²)
0	9.1	18	123	64	307	24	80
10	9	20	118	62	317	27	144
20	8.8	19	116	74	307	28	432
30	8.6	20	120	76	317	41	256
40	8.8	20	123	69	297	24	272
50	8.9	21.5	101	67	307	19	544
40	8.7	20.5	97	68	307	16	416
30	8.9	18	83	63	317	12	576
20	8.9	18	129	64	338	17	224
10	8.9	19	140	67	348	14	80

**See Figure A-1

Site 3: Tonkey Rd. Nearest town: Au Gress
 Date: 8/26/95 Time: 6:25 pm
 Description: Moderately dense *Scirpus americanus*

DFOW	pH	Temp (Celsius)	DO (% saturation)	Alk (mg CaCO ₃ L ⁻¹)	Conductivity (uS cm ⁻¹)	Turbidity (NTU's)	Stems (# m ⁻²)
0	8	22.5	127	88	358	21	*
40	8	19	118	86	379	18	256
80	8.3	18.5	132	100	358	13	352
120	8.1	19	114	109	379	11	432
160	8	19.5	93	119	410	10	496
200	7.5	18	109	125	420	10	288
240	8	18	86	124	430	10	256
280	8	19	76	123	399	11	304
320	8	19.5	99	124	410	11	400
360	7.9	19	94	116	440	9	224

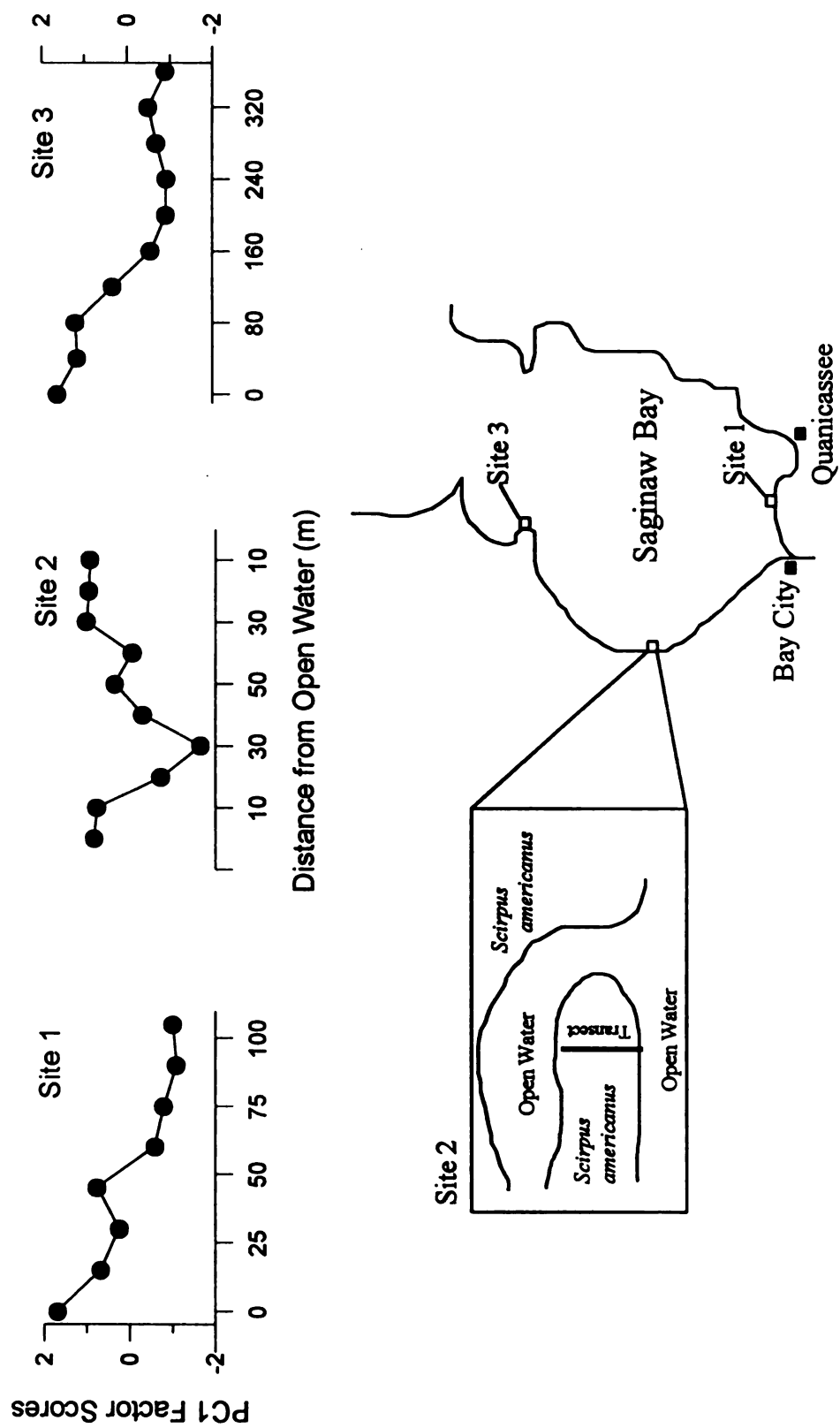


Figure A-1. Distribution of water quality for three sites in Saginaw Bay, Lake Huron. PC1 represents the factor scores for the first principal component of pH, % dissolved oxygen saturation, bicarbonate alkalinity, conductivity, and turbidity. Site 2 had several large patches of open water within the stand (see insert). This may explain why the gradient appeared to drop from both edges of open water towards the middle of the transect. See Table A-2 for more detail about the sites.

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LITERATURE CITED

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