

HYDROMORPHIC DETERMINANTS OF AQUATIC HABITAT VARIABILITY IN LAKE SUPERIOR COASTAL WETLANDS

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Abstract: Despite the recognized importance of wetlands as habitat for fishes and the growing need to assess and manage human impacts on that habitat, there is little information on patterns and variability of habitat within Great Lakes coastal wetlands. Our goal was to describe wetland aquatic habitat patterns and the natural factors that organize them as a step towards developing habitat assessment schemes and identifying experimental design elements for future synoptic surveys. We analyzed data on aquatic vegetation structure, water chemistry, and water movement (inferred from gypsum plug dissolution) in relation to hydrology and morphology in inundated segments of ten relatively un-impacted coastal marshes of western Lake Superior. Spatial differences in aquatic habitat within wetlands were as large or larger than differences among wetlands, and habitat patterns were strongly associated with morphology and hydrology. Back-bay segments tended to have greater vegetation cover and structural complexity and lower levels of water movement, and they were prone to high water temperatures and low dissolved oxygen levels in wetlands having little seiche activity. Increasing seiche inputs tended to homogenize habitat elements among wetland segments, while increasing tributary inputs tended to increase spatial variability. Patterns in emergent vegetation differed from patterns in submerged/floating vegetation, and different assessment metrics may be needed for different plant zones. Segment-scale sampling schemes like those used in this study have the potential to elucidate habitat patterns within inundated portions of wetlands with a reasonable level of effort. Human impacts on coastal wetland fish habitat must be interpreted in the context of natural spatial heterogeneity as structured by wetland morphology and magnitude of seiche and tributary inputs.

Key Words: coastal wetlands, hydrology, morphology, seiche, habitat variability

INTRODUCTION

The importance of Great Lakes coastal wetlands as habitat for fishes is widely recognized (e.g., Jude and Pappas 1992, Whillians 1992, Wilcox 1995, Brazner et al. 2000), as is the threat of continued loss and degradation of that habitat. The value of coastal wetlands to fish accrues from a variety of factors including favorable physio-chemical environment (e.g., warmer water, reduced wave energy; Suzuki et al. 1995, Cardinale et al. 1998) and an abundance of structurally complex aquatic plants that provide food, shelter, and spawning habitat (e.g., Voigts 1976, Engle 1985, Chubb and Liston 1986, Brown et al. 1988, Stephenson 1990, Höök 2001). Anthropogenic activities can degrade the quality of wetland habitat (Harris et al. 1988, Whillians 1992, Brazner 1997, Crosbie and Chow-Fraser 1999, Loughheed et al. 2001) via both direct and indirect pathways. For example, dredging, shoreline armoring, and motor boat activity destroy aquatic vegetation directly, while land-use practices that increase nutrient and sediment loading indirectly

degrade submerged vegetation via increased turbidity and planktonic production.

An understanding of what organizes patterns of aquatic habitat within and among wetlands is needed to develop appropriate sampling strategies, produce wetland assessment and valuation schemes that properly reflect their habitat mosaics, and separate degraded from natural conditions (Lewis et al. 1996, Minns et al. 1996, Bauer and Ralph 1999, Siemenstad et al. 2000). For example, it is difficult to diagnose apparent destruction of submerged vegetation unless we understand patterns due simply to tributary and wave scouring. Unfortunately, information on the relative amount, variability, and spatial arrangement of aquatic habitat elements (substrate, bathymetry, shoreline morphology, vegetation, etc.) is quite limited, despite many studies describing the habitat associations and needs of wetland and littoral fishes (e.g., Keast et al. 1978, Casselman and Lewis 1996, Lane et al. 1996, Castellanos and Rozas 2001, Tanner and Brazner 2004) and a general recognition that more diverse and structurally

complex littoral habitats harbor more abundant and diverse fish assemblages (e.g., Eadie and Keast 1984, Benson and Magnuson 1992, Hinch and Collins 1993, Peterson and Turner 1994, Brazner and Beals 1997, Weaver et al. 1997, Höök et al. 2001, Rozas and Minello 2001, Bologna and Heck 2002).

Factors that organize differences among broad categories of Great Lakes coastal wetlands (e.g., forested swamps vs. herbaceous marshes, lacustrine vs. river-mouth) are understood to include geomorphology, hydrologic setting, and water-level fluctuations (e.g., Geis 1985, Keddy and Reznicek 1985, Smith et al. 1991, Bedford 1992, Minc 1997, Keough et al. 1999). However, there is little literature quantifying patterns on finer spatial scales within wetlands and among wetlands of the same type. The goals of our study were to examine coastal wetland aquatic habitat patterns and the factors that organize them on such spatial scales as a step towards developing habitat assessment and classification schemes and identifying experimental design elements for future synoptic surveys. We focus on the inundated, herbaceous vegetation portions of the wetlands that provide habitat for Great Lakes fishes. Specifically, we describe within- and among-wetland patterns and variability in water depth, water movement and chemistry, and aquatic plant structure, and examine their relationship to wetland water inputs and morphology.

METHODS

The ten study wetlands (Amnicon, Middle, Little Fish, East Bibon, West Bibon, Bark, Lost, Sioux, East Fish, and West Fish, in west-to-east order) are located along an approximately 150-km stretch of the Wisconsin, USA, shoreline of Lake Superior (Figure 1) that falls within the Lake Superior Clay Plain ecological unit (Albert 1995) of the Northern Lakes and Forests ecoregion (Omernick and Gallant 1988). Land-cover around these wetlands is primarily forest and low-intensity agriculture, with relatively little residential and urban development. Although these wetlands are not pristine and their morphology and hydrology has been altered in the past, their shorelines are natural vegetation except for some road crossings and cottages, and current human impacts on aquatic habitat and water quality are relatively minor. The wetlands include areas of peatland, floating bog, shrub vegetation, and wet meadow, but our study focuses on the herbaceous, inundated areas which are accessible to fish and have a direct surface connection to Lake Superior.

Segment and Wetland Morphology and Water Inputs

Habitat data were collected within sub-divisions of the inundated portions of the wetlands referred to as

segments. Segments were divided (by inspection at the time of the plant survey) at obvious morphological boundaries (e.g., junctions of wetland arms) and transitions in aquatic plant cover or dominant taxa, so each represented a relatively homogeneous area. This resulted in anywhere from 6 to 20 segments per wetland, depending on size and complexity (Figure 1). The entire inundated area of each wetland was represented, with the exception of Bark, where only riverine portions of the wetland were included in habitat analyses (the large lagoon at the upstream end was excluded because it is surrounded by peatland and the water is too deep to support emergents).

Each segment was classified by type (back-bay, channel, lake-like) and position relative to the stream flow path through the wetland (variables defined in Table 1). Morphology descriptors, including wetland inundated area, ratio of watershed to wetland area, wetland shape factor, and percent area in various segment types, were obtained using geographic information systems analyses (Table 1). Characterization of wetland water inputs focused on identifying typical conditions (tributary baseflow, watershed area as a predictor of baseflow—Hughes and Omernick 1983, typical seiche amplitude and flow; Table 1). The lagoon surface area was included in computing the seiche volume flowing into Bark wetland (seiche flow depends on area inundated as well as amplitude of seiche). To compute segment water inputs, all segments were assumed to be subject to the seiche, while only segments on the stream flow path were assumed subject to the tributary flow.

Physical Habitat

Maximum segment water depth was obtained by aggregating data from an earlier bathymetric survey (in 7 of the 10 wetlands, Trebitz et al. 2002) to the segment scale (Table 1). Dissolved oxygen, water temperature, and water-movement information was collected in August of 2000 from a subset of segments in each wetland thought to have contrasting water inputs and morphology (e.g., back-bays versus channels; Figure 1). Oxygen concentration and percent saturation were highly correlated ($r^2=0.92$), indicating that spatial patterns were not driven by water temperature, so we present concentration units only. Out of the 130 total segments across the wetlands, there are water chemistry and movement data for 61 and depth data for 77.

Water movement within segments was inferred from the rate of dissolution of gypsum plugs (Thompson and Glenn 1994). Pairs of pre-weighed gypsum plugs (plaster of paris molded in small plastic drinking cups) were suspended under water, retrieved after ~24 hrs,

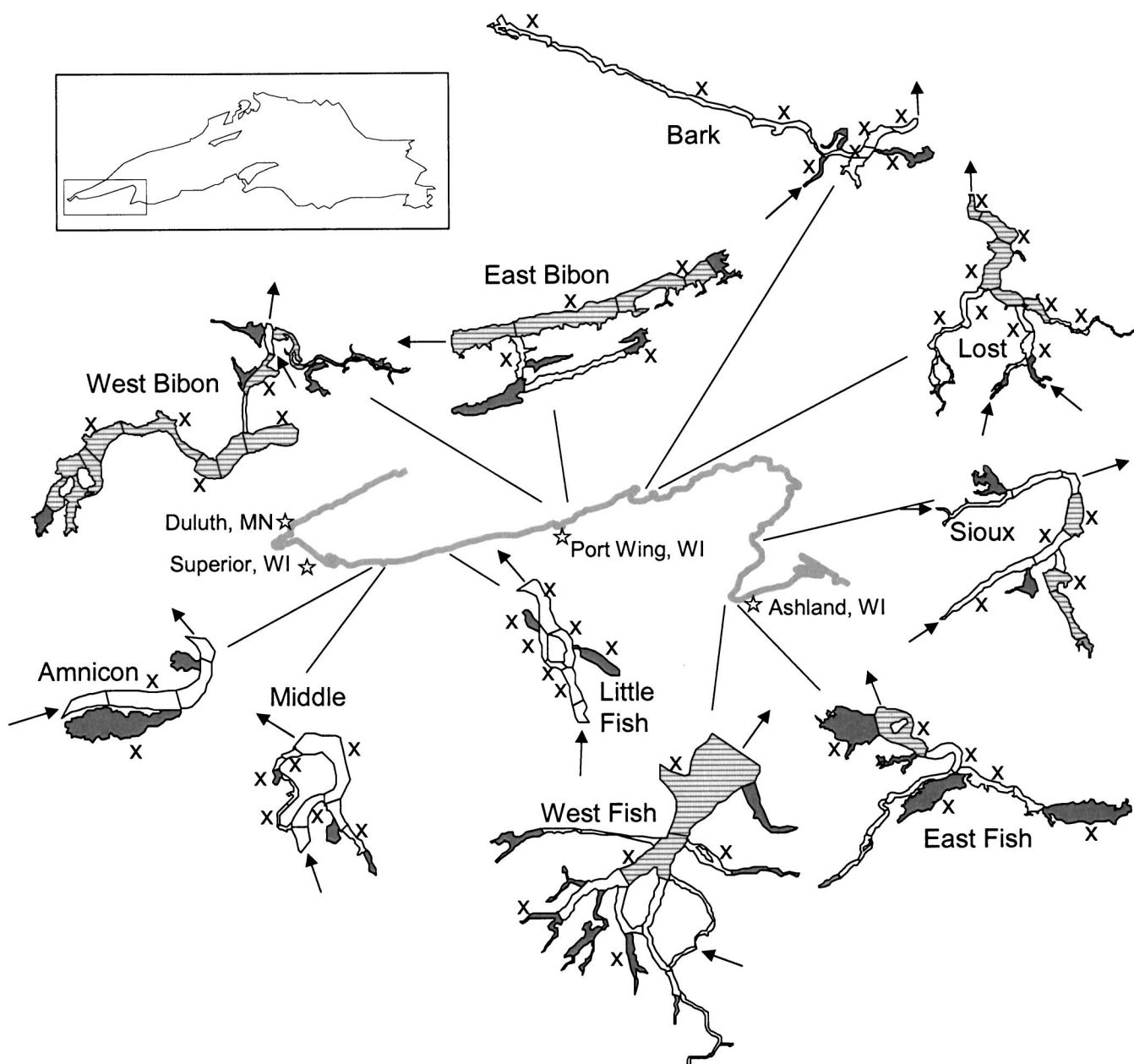


Figure 1. Outlines of the inundated portions of the wetlands showing segment divisions used for habitat assessments. Arrows show tributary entry and exit points; segments between these are on the tributary flow path. Channels are unshaded, lake-like segments are crosshatched, and back-bays are dark grey. Segments in which gypsum plugs were deployed and temperature and dissolved oxygen measured are denoted with an "X." Heavy line shows wetland positions along the shoreline of western Lake Superior. Wetland areas are not to scale.

and oven-dried and re-weighed to determine average dissolution rate (gm/hr) of the replicates per unit time in the water. Plugs were held in position ~30 cm above the wetland bottom by a wire running through their middle attached to a weight below and a sub-surface (to minimize wind effects) fishing bobber above. Prior to deployment, gypsum plugs averaged 31 gm, sufficient that the weight lost in 24 hrs did not exceed the 30% threshold for linearity (Jokiel and

Morrissey 1993). Dissolved oxygen and water temperature were measured adjacent to the plugs on the morning of their deployment or retrieval. Diurnal time series obtained from Lost wetland indicated that temperature and dissolved oxygen remained near their daily low from roughly 3:00 to 9:00 AM, so our 7:00 to 10:00 AM measurements approximate the diurnal minima.

Water temperature (T) and movement together de-

Table 1. Description of habitat and hydromorphic variables analyzed.

Name	Description and Units	Method Summary
Wetland Hydrology and Morphology		
ShedArea	Watershed area (ha)	Digitized from 1:24000 digital topographic maps
WetArea	Wetland inundated area (ha)	Digitized from 1 m resolution orthophotographs
AreaRatio	Ratio of watershed to wetland area	= ShedArea/WetArea
ShapeFac	Wetland shape factor	Ratio of wetland perimeter to circle of same area
%Off, %Bay, %Channel, %Lakelike	% area in segments that are off the flow path, back-bays, channels, or lake-like	Ratio of surface area of segments of the relevant type to all segments
TribFlow	Tributary base flow (m ³ /s)	Median of 3 smallest measured discharges (out of 5 to 16 per wetland over 1998 to 2000 growing seasons); base flow for E. Bibon and E. Fish assumed zero (intermittent streams)
SechAmp	Typical seiche amplitude (m)	Hourly time series from mid-wetland water level recorders; summarized as Jun.-Aug. 2000 avg. daily range in water level
SechFlow	Typical seiche flow (m ³ /s)	Seiche volume (SechAmp X WetArea) scaled to half the 8 hr seiche period (Trebitz et al. 2002)
CombFlow	Seiche and tributary flow combined (m ³ /s)	= TribFlow + SechFlow
Segment Hydrology and Morphology		
FlowPath	Position relative to stream flow path (on, off)	Photograph inspection of path tributary takes through wetland to lake at base flow, all segments "off" flow path if no perennial tributary
SegType	Segment type (channel, back-bay, lake-like)	Photograph inspection: channel - narrow, smooth shoreline; back-bay - small sheltered indentations or cul-de-sac ends of wetland arm; lake-like - broad open area
SegFlow	Seiche and tributary flow affecting segment (m ³ /s)	= wetland TribFlow + SechFlow for segments <i>on</i> FlowPath; = SechFlow alone for segments <i>off</i> Flow path
Segment-Scale Habitat Variables		
WaterAgit	Inferred water movement (cm/s)	Computed from rate of dissolution of gypsum plugs; see text for details
DO, T	Dissolved oxygen (mg/L), water temperature (°C)	YSI® multiprobe, avg. of morning readings 25 and 75 cm below surface
ZMax	Maximum water depth (cm)	Deepest measurement (out of 1 to 3 transects per segment, 3 to 6 measurements per transect)
SCov, FCov	Submerged cover, floating cover (0-4 point scale)	Ratio of plants to open water: 0 = no plants, 1 = a plant here and there, 2 = plant patches separated by at least 4X as much open water, 3 = distance between patches 1-4 X patch width, 4 = distance between patches less than their width.
ECCov, EFCov	Emergent cover (0-4 scale) in center or along fringe of segments	Appearance of stands from water level: 0 = no plants; 1 = a stem here and there, 2 = many stems but separated by open water, 3 = stems cross but water still visible, 4 = dense stems, water barely visible.
SFCplx	Submerged & floating complexity	= SFForms/6 * (Scov+FCov)/8 (see text)
EFCplx	Emergent complexity	= (EFCov+ECCov)/8 * Eforms/3 (see text)
FringeWid	Emergent fringe width	To nearest 0.5 m, or listed as "all across" when ECCov > 0 and EFCov = ECCov

termine the dissolution rate of gypsum according to the equation: *dissolution rate* = ($c_1 + c_2 T$) + ($c_3 + c_4 T$) · *water movement*, where c_1 and c_3 are the free (still-water) and forced (flowing-water) convection at 0°C (the intercept) and c_2 and c_4 represent the effect

of temperature (the slope; Petticrew and Kalff 1991). We conducted experiments in circular tanks at three flow rates (0.0, 3.6, and 12.0 cm/sec, attained by moving plugs through the water on a rotating arm) and three water temperatures (6, 16, and 23°C) to param-

eterize this equation for our particular gypsum plug dimensions (values for c_1 through c_4 were 0.0439, 0.01132, 0.00458, and 0.000612). The above equation was then rearranged to predict water movement given wetland dissolution rates and temperatures as: *water movement* = (*dissolution rate* - $c_1 + c_2T$) / ($c_3 + c_4T$). As a reminder that plug dissolution in the field is influenced by seiche and wind and wave turbulence, as well as the linear flow to which the above equation is calibrated (Porter *et al.* 2000), we refer to plug-derived wetland water movement as “water agitation.” We lack temperature from gypsum plug locations in Little Fish wetland due to equipment malfunction, so we used the value recorded by a mid-wetland temperature logger to compute water agitation.

Plant Structure

We surveyed cover and composition of aquatic plants at the segment scale across the entire inundated area of the wetlands rather than conducting labor-intensive and typically spatially limited plot or transect measurements (Fenessey *et al.* 2001, Richardson and Vymazal 2001). The plant survey took < 1 day per wetland and was conducted in July, 2000. Emergent, floating, and submerged plant zones were each assigned a segment-wide cover index ranging from 0 (no plants) to 4 (Table 1). Indices of 1 to 4 correspond to approximately <5%; 5–20%, 20–50%, and >50% cover, based on numeric estimates made in a subset of segments. Cover was assessed separately for emergents fringing the bank and for emergents growing in the segment center, although species were tallied across the fringe and center combined. The typical width of the emergent fringe was also noted (Table 1). All taxa observed while slowly traversing segments by boat were recorded (a rake was used to retrieve plants when the bottom could not be seen), and we noted the dominant taxa when the cover index exceeded 1. Taxonomy was to species level for submerged/floating plants and to species or genus level for emergents. We excluded from analyses taxa that were found “emerging” during our survey but do not typically grow standing in water.

Submerged and floating plants were classified into one of six growth forms based on their underwater structure (habitat for fish), while emergents were classified into one of three growth forms (Table 2). We then constructed submerged/floating and emergent vegetation complexity indices as the product of the ratio of actual to maximum number of growth forms and ratio of actual to maximum cover index (Table 1, after Brazner and Beals 1997). The combined floating and submerged complexity index effectively summarized submerged and floating vegetation parameters;

its correlation with floating cover, submerged cover, and number of submerged and floating growth forms each exceeded 0.7, and it combined somewhat skewed ordinal variables into an approximately normally distributed continuous variable. The emergent complexity index, which combined emergent cover measured in the fringe and center, was not as effective as a summary variable (correlation with emergent fringe cover was weak) because fringe cover was high almost everywhere. Both plant complexity indices and cover values were retained for analyses of habitat patterns.

Analyses at the Segment Scale

Relationships among habitat variables were identified with Pearson correlations using pair-wise deletion of missing values. Analysis of covariance (ANCOVA) was used to relate habitat variables to segment type (back-bay, channel, or lake-like), segment position relative to the tributary flow path (on or off) and typical segment water inputs. Graphical analyses were used to interpret significant ANCOVA relationships ($p < 0.01$). We did not consider models with interaction terms because flow path and segment water inputs interact inherently (flow path determines whether the tributary contributes to segment flow) and because there were insufficient cases in some flow path X segment type combinations. Variable distributions were inspected for normality prior to analyses. Transformations that squared temperature and took the square root of maximum water depth and water agitation corrected mild departures from normality but only trivially altered correlation or ANCOVA structure, so we present untransformed data only. Segments where emergents extended “all across” prevented treating fringe width as a continuous variable, so we used case frequency summaries and graphical analyses to determine the relationship with other vegetation variables and to segment descriptors. We also examined whether patterns in plant growth forms (Table 2) reproduce patterns in aggregated plant cover and complexity. Growth-form data are ordinal, taking values of absent (0), present (1), or dominant (2) in each segment, so we used Spearman rank correlations to look for associations and logistic regression combined with graphical analysis to relate growth forms to flow path, segment flow, and segment type.

Analyses at the Wetland Scale

Relationships among habitat variables (summarized by their wetland median and range) and wetland water input and morphology variables were evaluated by pair-wise correlation and principal components (PC) analysis. Habitat variables were standardized prior to

Table 2. Growth forms into which aquatic plants were classified. All growth forms were found somewhere in each wetland. Nomenclature follows Itis (Integrated Taxonomic Information System: www.itis.usda.gov).

Form	Description	Taxa Included
Submerged and Floating Forms		
Dissected	Finely dissected leaves, grow to and along surface	<i>Ceratophyllum demersum</i> L., <i>Megalodonta beckii</i> (Torr. ex Spreng.), <i>Myriophyllum</i> spp., <i>Hippuris vulgaris</i> , L. <i>Ranunculus aquatilis</i> L., <i>Utricularia macrorhiza</i> LeCont
Ground-cover	Small leaves, low-growing, can form mats on bottom	<i>Callitriche palustris</i> L., <i>Elodea canadensis</i> Michx., <i>Lemna trisulca</i> L., <i>Najas flexilis</i> (Willd.) Rostkov and Schmidt, <i>Utricularia intermedia</i> Hayne
Broad-leaf pondweed	Relatively large submerged leaves, grow to surface, floating leaves often present	<i>Potamogeton amplifolius</i> Tuckerman, <i>P. epihydrus</i> Raf., <i>P. natans</i> L., <i>P. richardsonii</i> (Benh) Rydb.
Small-leaf pondweed	Submerged leaves relatively small/narrow, grow to/along surface, floating leaves not often present	<i>Potamogeton diversifolius</i> Raf., <i>P. foliosus</i> Raf., <i>P. obtusifolius</i> Mert. & Koch, <i>P. pusillus</i> L., <i>P. spirillus</i> Tuckerman, <i>P. zosteriformis</i> Fern., <i>Stuckenia pectinatus</i> (L.) Boerner
Floating disc	Broad floating leaves, stems bare below surface	<i>Brasenia schreberi</i> J. F. Gmel., <i>Nuphar lutea</i> L.
Ribbon	Long narrow leaves, grow to/float along surface	<i>Sparganium fluctuans</i> (Morong.) B. L. Robins
Emergent Forms		
Slender stem	Dense but pliable stems, fish can swim or push through	<i>Carex</i> spp., <i>Cyperus</i> spp., <i>Dulichium arundinaceum</i> (L.) Britt, <i>Eleocharis</i> spp., <i>Equisetum</i> spp., <i>Glyceria</i> spp., <i>Juncus</i> spp., <i>Phalaris arundinacea</i> L., <i>Scirpus cyperinus</i> Knuth
Stout stem	Stiff, closely-spaced stems, can form fish barrier	<i>Iris versicolor</i> L., <i>Phragmites australis</i> (Cav.) Trin ex Steud, <i>Schoenoplectus tabernaemontani</i> (K. C. Gmel.) Palla, <i>Sparganium</i> spp., <i>Typha</i> spp.
Broad leaf	Broad emergent leaves, widely spaced fleshy stems	<i>Pontederia cordata</i> L., <i>Sagittaria</i> spp.

ordination to prevent those with larger absolute values from dominating the solution. To enable plotting positions for all wetlands in PC space, missing values for maximum depth (Amnicon, East Bibon, West Bibon) and for temperature and dissolved oxygen (Little Fish) were replaced by the median and range averaged across the other wetlands, after verifying that this produced results very similar to a PC analysis with missing cases deleted. Hydromorphic wetland descriptors were overlaid on the habitat ordination by computing their correlation with their PC axes.

RESULTS

Segment-Scale Patterns in Aquatic Habitat

The correlation structure among habitat variables at the segment scale suggested three groupings, which were confirmed by analyses of covariance. Water movement and quality constituted one group of inter-correlated habitat variables. The magnitude of water inputs seemed to organize segment-scale patterns in this variable group, as water agitation and dissolved oxygen increased with segment seiche and tributary

inputs, while water temperature decreased (Table 3). Segment water agitation in particular was strongly related to segment seiche and tributary inputs (Figure 2). A plot comparing temperature and dissolved oxygen to water agitation suggests a threshold for water quality conditions potentially of concern to fish (low dissolved oxygen, high temperature) below water agitation levels of 5 (Figure 3). Information over the growing season available from one wetland having low tributary and seiche flow confirmed that dissolved oxygen levels were consistently lowest in areas far from both lake and tributary inflows (Figure 4). Tributaries were generally colder than lake or wetland water, explaining the lower temperature values in on-flow path segments (Table 3). Water agitation, temperature, and dissolved oxygen patterns did not differ among segment types even though plant patterns did (Table 3), suggesting that vegetation influences on these parameters were minimal.

Descriptors of submerged and floating vegetation constituted a second group of habitat variables that were related to both segment water inputs and morphology. Submerged/floating cover and structural

Table 3. ANCOVA results relating habitat variables to segment type (Back-bay, Channel, or Lake-like), position along the tributary flow path, and typical seiche and tributary inputs to the segment (inc. and dec. indicate whether the level of the habitat variable increases or decreases with increasing segment flow). SegType comparisons have 2 degrees of freedom and FlowPath and SegFlow comparisons have 1 degree of freedom. Only model terms having $p \leq 0.01$ are reported. The ANCOVA model for emergent fringe cover was not significant.

		Significant terms (F-ratio, p-value, nature of relationship)		
Habitat variable	Model r ²	SegType (B, C, L)	FlowPath (on, off)	SegFlow (m ³ /s)
Group 1 - Response to Hydrology Only				
WaterAgit	0.73			F = 127, p = 0.000, inc.
DO	0.29			F = 13.1, p = 0.001, inc.
T	0.25		F = 7.3, p = 0.01 off > on	F = 7.8, p = 0.008, dec.
Group 2 - Response to Morphology and Hydrology				
SFCplx	0.48	F = 25.8, p = 0.000 C < L & B	F = 12.9, p = 0.000, off > on	F = 29.1, p = 0.000, dec.
FCov	0.32	F = 15.8, p = 0.000 C < L & B		
SCov	0.47	F = 16.8, p = 0.000 C < L < B	F = 33.1, p = 0.000 off > on	F = 19.3, p = 0.000, dec.
Group 3 - Response to Morphology Only				
ZMax	0.19	F = 7.7, p = 0.001 L > C > B		
ECCov	0.41	F = 29.1, p = 0.000 L & C < B		
ECplx	0.19	F = 13.1, p = 0.000 L < C < B		

complexity generally decreased with increasing segment flow and were greater in segments off the tributary flow path (Table 3). The joint significance of flow path and segment flow indicates that seiche and tributary flows combined (on flow-path) had different effects than the same flow due to seiche alone (off flow-path). Submerged/floating cover and complexity were generally lower in channels than back-bay or

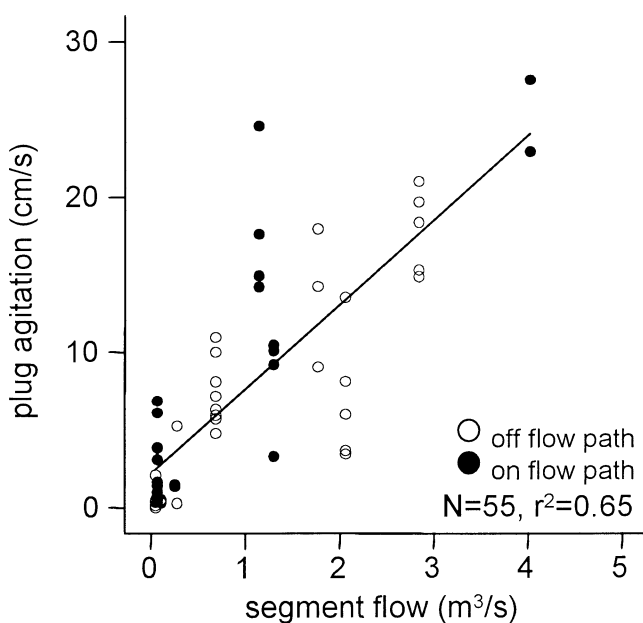


Figure 2. Relationship between water agitation in wetland segments and typical segment water inputs (seiche plus tributary for segments on the flow path, seiche alone for segments off the flow path).

lake-like segments regardless of base flow inputs, perhaps due to flood scouring (Table 3).

A third group of habitat variables included water depth and some emergent vegetation descriptors (complexity, center cover, fringe width) but notably *not* fringe cover. Size of tributary and seiche inputs did not organize patterns in this group, but segment type did. Emergent complexity and center cover were greater and maximum water depth lower in back-bays than channel or lake-like segments (Table 3), and of the cases where the emergent fringe extended “all across,” 86% were in back-bays, none were in lake-like segments, and 90% were off the flow path. The lack of relationship of maximum depth to flow suggests that base flow does not equate with flood scouring; in fact, the two wetlands with the largest base flow were also the shallowest (Table 4). Emergent fringe cover was uncorrelated with other habitat descriptors and poorly predicted by the ANCOVA (Table 3).

Patterns in cover and structural complexity of emergent vegetation seemed unrelated to patterns in floating/submerged vegetation cover and complexity, as there was a notable absence of correlations among them, and they fell into separate ANCOVA response groups. Relationships among plant growth forms confirmed this, as none of the pair-wise Spearman rank correlation coefficients between emergent and submerged/floating forms exceeded 0.25, while most correlations among submerged/floating forms or among emergent forms were in the 0.25 to the 0.45 range. Response patterns of submerged/floating growth forms were generally concordant with those for overall sub-

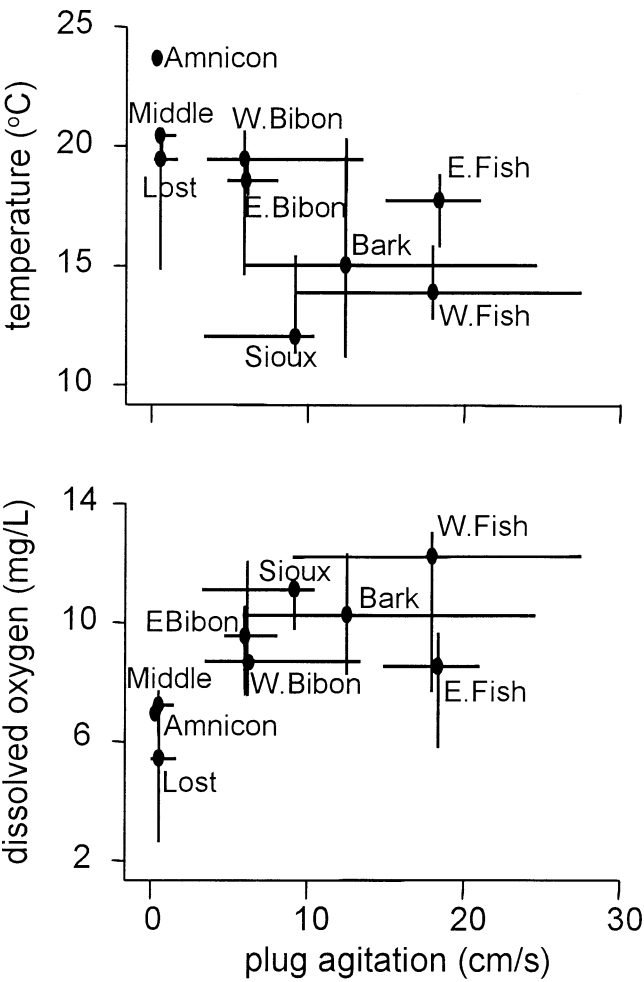


Figure 3. Relationship between gypsum-plug inferred water agitation and water temperature and dissolved oxygen. Circles show the median for each wetland while bars indicate the range in the x- and y- variable.

merged/floating cover and complexity. Likelihood of presence and dominance of submerged/floating forms was generally reduced in channels, on the flow path, and with increasing segment flow (Table 5), although

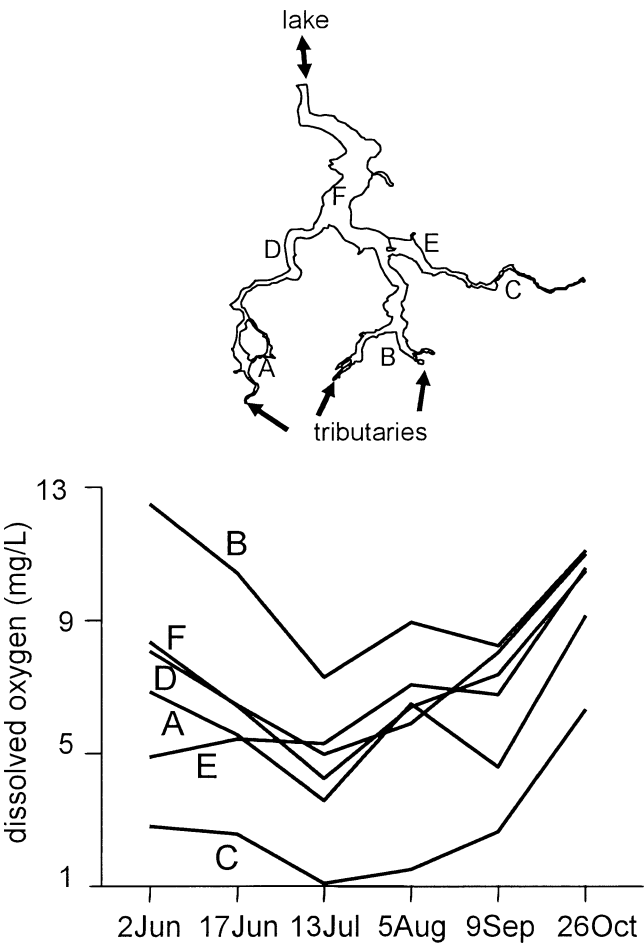


Figure 4. Comparison of morning dissolved oxygen concentrations across time and location in Lost wetland. Arrows show stream inputs and exchange with lake. Dissolved oxygen levels are lowest in sheltered locations far from the lake and the tributary flow path.

ribbon forms were more prevalent in channels. Large-leaf pondweeds seemed an exception to this pattern, as logistic regression models for them were not significant and their correlation with other submerged/

Table 4. Summary of wetland hydrology and morphology. Morphology statistics for Bark exclude its large lagoon.

	Avg. Depth (m)	Area (ha)	Shape Factor	Tributary Flow (m ³ /s)	Seiche Amplitude (m)	Seiche Flow (m ³ /s)	Combined Flow (m ³ /s)	% Off Flow Path
Amnicon	—	4.7	2.9	0.45	0.08	0.28	0.73	48
Bark	0.78	3.1	7.7	0.46	0.03	0.69	1.15	76
E. Bibon	—	7.3	5.8	0	0.14	0.69	0.69	100
E. Fish	0.80	18.0	5.8	0	0.23	2.84	2.84	100
Little Fish	0.89	0.8	3.3	0.02	0.09	0.05	0.07	24
Lost	0.89	6.3	7.0	0.08	0.06	0.24	0.32	31
Middle	0.84	1.5	3.8	0.16	0.09	0.09	0.25	39
Sioux	0.68	3.8	5.7	1.02	0.10	0.27	1.29	42
W. Bibon	—	29.1	7.3	0.87	0.10	2.06	2.93	97
W. Fish	0.60	10.9	7.9	2.26	0.23	1.77	4.03	39

Table 5. Logistic regression results relating status of plant growth forms to wetland segment type (Back-bay, Channel, or Lake-like), position along the tributary flow path (on or off), and size of typical seiche and tributary inputs. Growth form data are ordinal, so the terms inc. (increase), dec. (decrease), and > or < refer to relative frequency of presence or dominance. Only model terms having chi-square p-values < 0.10 are reported (for SegType, the smaller p-value of the two for B vs. C and B vs. L is given).

Growth form	Model McFadden rho ²	Significant terms (chi-square p, nature of relationship)		
		SegType (B, C, L)	FlowPath (on, off)	SegFlow (m³/s)
		Emergent Forms		
Slender stem	0.13	0.004 W > C > B	0.03 on > off	0.007 dec.
Broad-leaf	0.11	0.08 L < B & C	0.06 off > on	
Stout stem	no significant terms			
		Submerged/Floating Forms		
Small-leaf pondweed	0.27		0.001 off > on	0.000 dec.
Ribbon	0.22	0.001 C > L & B		0.000 dec.
Ground cover	0.10	0.004 L < C < B		0.02 dec.
Floating disc	0.17	0.01 C < B & L	0.007 off > on	0.001 dec.
Dissected	0.11	0.09 C < B & L	0.004 off > on	
Large-leaf pondweed	no significant terms			

floating forms was quite low. Ribbon forms and small-leaf pondweeds were present or dominant at flows up to 3 m³/s in off-flow-path segments but only at flows < 1 m³/s in on-flow segments, suggesting that they may be prone to scouring during floods. Concordance among emergent growth forms and emergent cover and complexity was weaker. Stout-stemmed emergents were present in 95% of segments, were unrelated to logistic predictors (Table 5), and probably drove the lack of response of emergent fringe cover to the ANCOVA predictors (Table 3). Slender-stem forms responded to segment water inputs (less likely present and dominant at higher flows) even though aggregate emergent variables did not and, unlike other growth

forms, were more likely present and dominant on the flow path and in lake-like segments (Table 5).

Wetland-Scale Patterns in Aquatic Habitat Variables

The three groups of habitat variables identified by analyses at the segment scale remained somewhat distinct when examined at the whole-wetland scale, but associations also emerged that had not been evident at the segment scale. Water agitation, temperature, and dissolved oxygen had responded only to segment water inputs in the ANCOVAs, and their wetland median and range generally correlated best with wetland seiche and tributary descriptors (Table 6). Median and

Table 6. Correlation structure among wetland hydrology and morphology descriptors and median and range of habitat variables.

Descriptor	Significantly Correlated Habitat Variables (all r ² > 0.25; bold if r ² > 0.5, in parentheses if negative correlation)	
	Median	Range
Hydrology Descriptors		
TribFlow	DO , (T), (ZMax)	WaterAgit, ECplx, SCov
SechAmp	WaterAgit , SCov	
SechFlow	WaterAgit , ECCov	DO
CombFlow	WaterAgit , DO	WaterAgit, DO
ShedArea	(ZMax)	ECplx, SFCplx, SCov
AreaRatio	(ZMax), (Scov)	EFCov, (DO), (T)
Morphology Descriptors		
WetArea	(ECplx)	(ECCov)
%Off	ZMax, (ECplx)	(FCov), (ECCov)
%Lakelike	FCov , SCov, SFCplx, (ECplx)	DO
%Channel	ECplx, (FCov)	ECCov
%Bay	ZMax, (SFCplx)	
ShapeFac	WaterAgit, SCov, (T), (ECplx)	T , DO , WaterAgit

range of submerged/floating vegetation variables correlated with both wetland water inputs and morphology (Table 6), paralleling their response in ANCOVAs. Maximum water depth and emergent vegetation also correlated with both wetland water input and morphology descriptors (Table 6), in contrast to their lack of response to segment water inputs in ANCOVAs.

A principal components ordination (whose first and second axes explained 28% and 18% of the among-wetland variance in habitat variables) illustrates that wetland-scale associations among variables that were independent at the segment scale arose because wetland water inputs and morphology are themselves correlated (Figure 5). Variables describing size of seiche (amplitude, flow) were essentially orthogonal to variables describing tributary inputs (base flow, watershed area). Wetland inundated area and percent of the wetland in channels, lake-like segments, and off the flow path generally aligned with the vertical PC axis (Figure 5), as did emergent vegetation variables and submerged cover, which had been related to segment type and position in the ANCOVAs (Table 3). Wetland shape factor increased to the right in Figure 5, along with combined water inputs, explaining why it was the only morphology descriptor significantly correlated with water agitation, temperature, and dissolved oxygen (Table 6). Submerged vegetation complexity and floating cover responded to a combination of segment flow and type in ANCOVAs and ordinated in a direction reflecting both decreasing seiche and tributary inputs and less area in channels (Figure 5). Range in emergent fringe cover plotted to the upper left in the ordination despite a lack of pattern in the ANCOVAs because the few cases of low fringe cover (hence high range) occurred in Sioux, Amnicon, and Middle wetlands.

The utility of classifying aquatic habitat patterns according to position of wetlands in the principal components ordination is explored in Figure 6. Classification by position left or right along principal components axis 1 was sufficient to identify those wetlands having high levels of and range in water agitation, although it failed to single out those wetlands having very low levels of water agitation (Figure 6, top panel). Classification by the quadrant of the ordination in which wetlands plotted provided some organization of patterns in submerged/floating vegetation structure, with those wetlands that ordinated to the upper or lower right having low median and small range in submerged/floating plant complexity, those ordinating to the lower left having generally high median and small range in submerged/floating complexity, and those ordinating to the upper left having the largest ranges in submerged/floating complexity (Figure 6, bottom panel). Attempts to distill the ordination-based classifica-

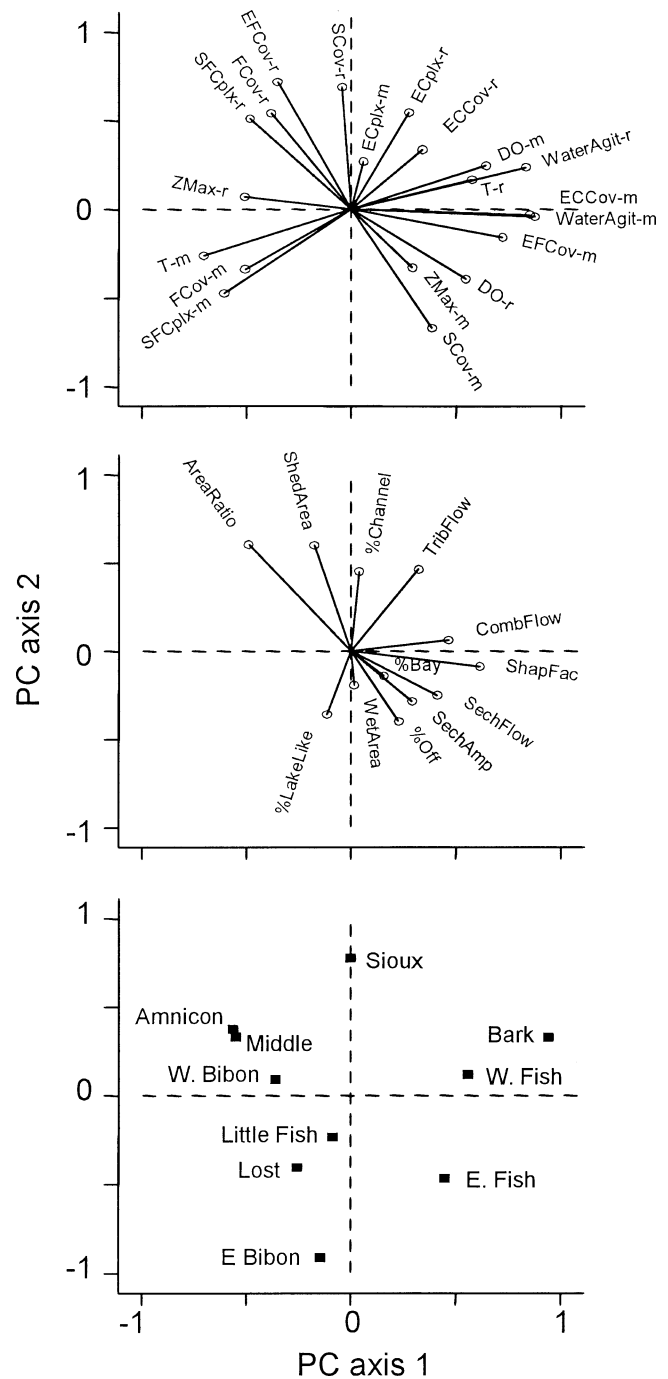


Figure 5. Principal components ordination of habitat variables summarized by their median and range within wetlands (top), correlation of wetland hydromorphology to the PC axes (middle), and position of the wetlands in PC components space (bottom). See Table 1 for variable names (appended "m" or "r" indicate median or range).

tion down to a minimal set of wetland water input and morphology parameters (e.g., those in Table 4) were only partially successful. Using wetland shape factor as a classifier (highly correlated with PC axis 1) appropriately grouped W. Bibon with Bark, E. Fish, and

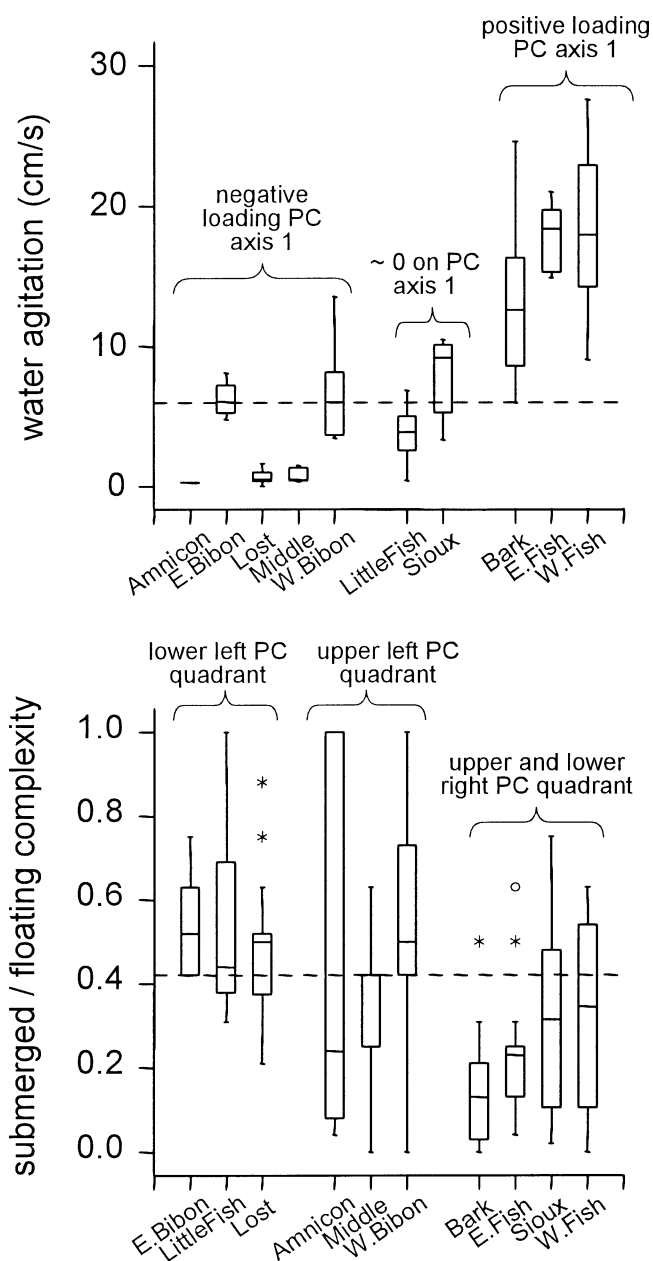


Figure 6. Patterns in water agitation and submerged/floating vegetation complexity resulting from sorting wetlands into groups according to position in the principal components ordination (Figure 5). Dashed horizontal lines depict grand median across wetlands. There is only one water agitation data point for Amnicon.

W. Fish as having large water agitation levels, but Lost wetland was completely mis-classified by this scheme due to its large shape factor (Table 4). Separation of wetlands according to submerged/floating complexity patterns (Figure 6, bottom) could be largely reproduced by grouping wetlands with tributary flow <0.1 m^3/s and seiche flow <1 m^3/s (E. Bibon, Little Fish, Lost), those with tributary flow >0.1 m^3/s but seiche

flow <1 m^3/s (Amnicon, Bark, Middle, Sioux), and those with seiche flow >1 m^3/s (E. Fish, W. Bibon, and W. Fish), but this seems a somewhat arbitrary set of criteria.

DISCUSSION

Importance of Tributary and Seiche

Our results emphasize that there is considerable variability in aquatic habitat elements of western Lake Superior coastal wetlands at both within- and among-wetland spatial scales. Factors that structure habitat differences among broad wetland classes are recognized, as are biogeographic and anthropogenic factors structuring wetland communities on broad spatial scales (e.g., Smith et al. 1991, Brazner and Beals 1997, Minc 1997, Keough et al. 1999, Loughheed et al. 2001, Wilcox et al. 2002). However, the ten wetlands we sampled are in relatively close proximity in the same lake and ecoregion and ecotype (Albert 1995), and we made comparisons only among the inundated, herbaceous vegetation portions of the wetlands, yet differences in aquatic habitat patterns among them were substantial. Historical road construction has substantially modified the original extent and drainage pattern of several of these wetlands, but current human impacts on their aquatic habitat and water quality are relatively minor compared to elsewhere in the Great Lakes.

Magnitudes of seiche and tributary inputs seem to be key factors influencing wetland habitat patterns observed in this study. Increasing seiche and tributary inputs both increased mixing of wetland water and mitigated tendencies towards temperature elevation and oxygen depression but had different effects on habitat patterns. Larger tributary flows tended to suppress development of submerged vegetation, while larger seiche flows did not. Tributary inputs created within-wetland spatial variability by affecting primarily those segments along their flow path (joint significance of flow path and segment flow ANCOVA terms). In contrast, seiche-driven water oscillations affected all wetland segments and tended to homogenize habitat elements (seiche amplitude and flow did not generally correlate with range in habitat variables). Seiche action can establish water quality gradients in the vicinity of wetland mouths due to the limited distance of intrusion of lake water (Trebitz et al. 2002), but such effects were not seen at the segment spatial scale. The difference between seiche and tributary is not simply a volume effect, as typical seiche flows exceeded tributary base flows in several of the wetlands. Because of variation in tributary size, natural habitat differences among wetlands are likely to be

expressed more strongly in channel and lake-like areas than in sheltered back-bays. Conversely, human impacts on vegetation structure and water quality may be more evident when comparing back-bays.

We focused on tributary base flows and typical summer seiche amplitude, but unusually large tributary flows (floods) and seiche events (storm surges) no doubt also drive habitat patterns. Amnicon and Middle wetlands have flashy tributaries, and their large channel vs. back-bay differences in water depth and plant structure may be due to flood scouring. The study wetlands are relatively sheltered, but wind and waves can inhibit development of submerged macrophytes in open-coast wetlands (Keddy and Reznicek 1985, Minc 1997). Periodic closing of wetland outlets can have strong influences on water quality and fish (Jude and Pappas 1992, Vorwerk 2003), and some of the study wetlands do have occasional mouth closures (Trebitz et al. 2002), but such effects were not investigated here. Inter-annual variability in tributary flows and lake water levels also play an important role in structuring habitat (Poff and Allen 1995, Wilcox and Meeker 1992, Keough et al. 1999), but our comparisons are among wetlands subject to the same temporal hydrologic regime, as they were sampled in the same year and are all connected to the same lake.

Regardless of whether we characterize typical or unusual conditions, bulk tributary and seiche flows may be less important in structuring habitat than actual water velocities, which vary locally with water depth, substrate, channel morphology, and wind and wave exposure. However, the strong relationship between wetland habitat variables and segment seiche and tributary inputs reassures us that bulk inputs, which are much more easily measured than velocity patterns, are useful predictors of wetland habitat. Principal component and correlation results suggest that habitat predictions can also be made from Map/GIS-based measures such as watershed area. Wetlands having low ratios of watershed to wetland area (large wetlands in small drainage basins) were those having large ranges in dissolved oxygen and temperature. Shape factor seems to be a promising index of wetland habitat variability, as it was well-correlated with combined water inputs and range in physical habitat parameters.

Habitat Metrics and Assessment Techniques

Division of the inundated portions of the wetlands into a moderate number of spatial units (segments) represented a useful conjunction of sampling effort and interpretable spatial scale. Analyses on the segment scale produced meaningful insights into habitat patterns, previously collected point data (water depth) could easily be assigned to segments, and plant sur-

veys that characterized cover and composition over the inundated portion of entire wetlands in a manner that integrated small-scale spatial variability in segment units could be completed in a reasonable time frame. Our results do not necessarily apply to other portions of these wetlands such as wet meadows and peat bogs. Additional work on how best to classify segments would be helpful, as distinctions among back-bays, channels, and lake-like areas were blurred in some wetlands, and position on or off the tributary flow path is complicated by alternate or high-water flow patterns. Regardless of how they are categorized, aspects of segment morphology and position relative to the tributary flow path organized many habitat patterns and should be covariates or design elements in future studies.

Water agitation inferred from gypsum plug dissolution was a strong indicator of wetland hydrologic activity and a good predictor for temperature and dissolved oxygen patterns. Temperature and dissolved oxygen are of course easily measured directly, while gypsum plug deployment requires some effort, but the plugs integrate over time, while early morning sampling is needed to capture oxygen depressions. Maximum water depth was not a particularly informative habitat descriptor in this study, as the only clear pattern was the expected one of back-bays being shallower than channel and lake-like segments. Given that we collected at least 45 depth measurements per wetland (a not insignificant effort), more detailed and data-intensive analyses of bathymetry at the segment scale (e.g., average depth, depth variability) might be prohibitive (the wetlands are too shallow for rapid survey methods like sonar). Depth measurements do support calculation of wetland volume and water residence time, a potentially important aspect of hydrologic characterization.

Spatial patterns in emergent vegetation were quite different than patterns in submerged/floating vegetation. There was considerable concordance among submerged/floating vegetation descriptors, suggesting that submerged and floating plants can be broadly aggregated, although finer-scale responses among growth forms provided additional resolution. In contrast, emergent vegetation fringing wetland banks clearly differed in composition and spatial patterns from emergents growing in the center of segments. We could not compute separate fringe and center emergent complexity indices because we had tallied taxa across the fringe and center combined, but future studies might benefit from separating data for these two zones. Simply recording whether emergent plants grow in the center of inundated wetland segments might also be a useful habitat indicator. Homogeneity of emergent fringe vegetation (similar taxa and cover in all segments) suggests that it does not usefully define habitat

differences among these relatively intact wetlands, but practices that prevent establishment of the typical emergent fringe (e.g., shoreline hardening) represent a substantial alteration of coastal wetland habitat elsewhere in the Great Lakes.

Wetland Patterns and Classification

Our results emphasize that understanding coastal wetland aquatic habitat patterns requires a multi-factor and multi-scalar approach. At the segment scale, there was a distinction between habitat elements that appeared to be structured by seiche and tributary (size of inputs and position relative to the tributary flow path), those that responded to wetland morphology (segment type) regardless of flow, and those that responded to both water inputs and morphology. When aggregated to the wetland scale, habitat elements continued to separate into groups structured primarily by wetland morphology versus water inputs, but for the practical purpose of predicting difference among wetlands, distinctions among wetland morphology and seiche and tributary inputs as structuring elements were blurred by their co-variation.

We are aware of only a handful of other studies that report on spatial patterns within Great Lakes coastal wetlands. Johnston *et al.* (2001) found that sediments and water quality differed between riverbed and backwater sites of wetlands in Lake Superior's St. Louis Bay (higher nutrient levels, sedimentation rates, and ratios of sand to silt and organic matter in channels). Meeker (1996) likewise found higher sedimentation rates in channel than backwater areas of Lake Superior's Kakagon Slough. Suzuki *et al.* (1995) and Cardinale *et al.* (1998) documented gradients of increasing submerged plant cover/complexity and decreasing dissolved oxygen, turbidity, chlorophyll, epiphytic invertebrate biomass/diversity, and fish abundance/richness with distance from the open lake in heavily seiche-influenced wetlands fringing Lake Huron's Saginaw Bay. MacKenzie *et al.* (2004) reported patterns in dissolved oxygen, primary productivity, and invertebrate abundance relating to distance from the main channel in Peshtigo wetland, Lake Michigan. The interaction of hydrology and wetland morphology seem to be the common factor generating these patterns, and these studies, like ours, show that differences among locations within wetlands can be as large or larger than differences among wetlands. The importance of tributary and seiche is analogous to the structuring role of tidal amplitude, size of freshwater inputs, and flushing time identified for marine estuaries (e.g., Edgar *et al.* 2000, Roman *et al.* 2000, Kelly 2001, Uncles *et al.* 2002).

The existence of within-wetland spatial patterns in

aquatic habitat is not a new finding, but it remains relatively undiscussed in the wetland assessment literature. Assessment schemes for habitat and the associated wetland fishes must recognize and account for natural causes of within-wetland variability. Loughheed *et al.* (2001) reported that turbid, nutrient-rich wetlands are characterized by a fringe of emergents with only sparse submerged vegetation, while high quality wetlands have a mix of emergent and floating-leaf taxa and a diverse and dense submerged community. Loughheed *et al.* (2001) sampled only sheltered locations within wetlands, but the pattern they described is the same as that distinguishing back-bay from channel segments in our relatively unimpacted wetlands. Similarly, finding oxygen levels low enough to stress fish (Suthers and Gee 1986) in backwater areas will come as no surprise to wetland ecologists (e.g., Murkin *et al.* 1992, Rose and Crumpton 1996) but emphasizes that assessment schemes for detecting adverse human impacts (e.g., hypoxia resulting from eutrophication) must consider wetland hydrology and spatial aspects of the sampling design. Classification by morphology and the intensity of seiche and tributary inputs holds promise for organizing habitat patterns (Figure 6), but different classification schemes may be required to capture different aspects of habitat. Eventually, studies analogous to those currently being published in the stream literature (e.g., Lammert and Allan 1999, Wang *et al.* 2003) relating changes in fish habitat to land use and cover at various spatial scales would be informative for coastal wetlands but in the context of an understanding of natural habitat variability and spatial arrangement.

CONCLUSIONS

Patterns in aquatic habitat elements within and among ten coastal wetlands of western Lake Superior were strongly associated with wetland morphology and water inputs. Increasing tributary inputs tended to increase within-wetland variability in fish habitat, while increasing seiche inputs tended to homogenize habitat among segments. Differences among wetlands were expressed more strongly in channel and lake-like areas than in back-bays sheltered from lake and tributary influences. Spatial patterns in emergent vegetation differed from patterns in submerged/floating vegetation, and different metrics for describing patterns may be appropriate for different plant zones. Sampling schemes targeting a spatial scale like the segment scale used in this study have the potential to elucidate habitat patterns within inundated portions of wetlands with a reasonable level of sampling effort. Wetland assessment and classification schemes explicitly need to link expectations for aquatic habitat to wetland mor-

phology and the absolute and relative size of seiche and tributary inputs in order to separate human impacts from natural conditions.

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