Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes

Alysa J. Remsburg[1] AND Monica G. Turner[2]

University of Wisconsin-Madison, Department of Zoology, Madison, Wisconsin 53706 USA

Abstract. The physical structure of vegetation influences diversity, interactions, movement, and thermoregulation of animals. Vegetation structure might be a good indicator of habitat requirements of generalist predators, such as dragonflies and damselflies (order Odonata), and thereby affect species diversity. Odonates use aquatic and terrestrial habitats during larval and adult life stages, respectively, but the relative importance of vegetation in these habitats is poorly understood. We compared how aquatic and riparian habitat variables affected odonate larvae from 41 sites (each 30 m in shoreline length) on 17 lakes in northern Wisconsin. We used principal components analyses to reduce multiple habitat variables to 2 lake-level axes (lake size and development, lake wetlands and predators), 2 site-level littoral axes (littoral macrophytes, littoral muckiness), and 2 site-level riparian axes (riparian structural complexity, riparian tall wetland plants). Most (61.6%) of the variance in larval species richness occurred at the site level. Density of the most abundant family, Gomphidae, was positively related to riparian tall wetland plants, whereas species richness was positively correlated with abundance of littoral macrophytes (on the basis of multiple linear regression with an information theoretic approach). Surveys in 18 paired littoral microsites in 9 lakes indicated that larvae from the clasper and sprawler behavioral guilds were most abundant in microsites with submerged macrophytes. However, predation risk, assessed by tethering larvae in patches of submerged macrophytes, did not differ between habitats with and without macrophytes. We tested whether shoreline plants affected recruitment from the adult stage by comparing adult odonate behaviors in response to 2 riparian vegetation treatments. Adult damselfly abundance was higher where we placed potted wetland plants than at manicured lawns without tall vegetation. Our results indicate that odonate larvae might be influenced by vegetation structure in both aquatic and riparian habitats and demonstrate how animals with complex life histories link aquatic and terrestrial communities.

Key words: dragonflies, damselflies, riparian plants, habitat selection, insect behavior, vegetation structure, predator habitat, aquatic macrophytes, lakeshore development, complex life history, benthic insects.

Understanding how vegetation structure affects animal abundance and diversity has long been a fundamental objective in ecology (e.g., MacArthur 1965, Karr and Roth 1971). The physical structure of vegetation influences predator–prey interactions, thermoregulation, landscape permeability (ease of movement), and mate detection (McCoy and Bell 1991). Vegetation structure can successfully describe habitat suitability for predacious species on land (e.g., Pianka 1967, Brose 2003, De Souza and Martins 2005, Muntifering et al. 2006) and in the water (e.g., Werner et al. 1983, Carr 1991, Tupper and Boutilier 1995, Cheruvelil et al. 2002, Sass 2004, Milner and Gloyne-Phillips 2005).

Animals that use multiple habitats for different behaviors or life stages might respond to vegetation structure in each of the habitats they occupy. Studies comparing the importance of aquatic and terrestrial habitat features for animals that inhabit both of these ecosystems generally have focused on amphibians (Marnell 1998, Scribner et al. 2001, Ficetola et al. 2004, Becker et al. 2007). Research investigating how Odonata (dragonfly and damselfly) species respond to both aquatic and terrestrial habitat structure is lacking, particularly for their larval phase. The long aquatic phase (1–4 y) of many odonates in temperate regions might increase the importance of aquatic habitat features for odonates relative to amphibians and other aquatic insects with shorter aquatic phases.

Land–water ecotones are often structurally complex and provide critical habitat for many animals (De-

[1] Present address: Biodiversity Center, Unity College, Unity, Maine 04988 USA. E-mail: aremsburg@unity.edu
[2] E-mail address: turnermg@wisc.edu

camps et al. 2004). Structural complexity arises from the combination of abiotic characteristics (e.g., substrate, slope), littoral vegetation, and riparian vegetation. Human activity also interacts with natural drivers of structural complexity. Housing development is expanding rapidly in many riparian areas (Burger 2000, Hansen et al. 2005), leading to simplification of vegetation structure by removal of the shrub layer (Racey and Euler 1982, Elias and Meyer 2003), floating macrophytes (Jennings et al. 2003, Radomski and Goeman 2001), and coarse wood (Marburg et al. 2006). Those structural changes might have consequences for a variety of animals in both the riparian and littoral (near-shore aquatic) zones (Bryan and Scarnecchia 1992, Schindler et al. 2000, Lindsay et al. 2002, Woodford and Meyer 2003, Butler and DeMaynadier 2008, Henning and Remsburg, in press). The relative influence of natural and anthropogenic drivers on Odonata communities is not well known.

Odonates generally show little response to particular plant species (terrestrial or aquatic) (Buchwald 1992, Foote and Hornung 2005), but adult odonate diversity and abundance often are correlated positively with local abundance of vegetation (reviewed in Remsburg 2007). Vegetation provides adults with perching structures for thermoregulation, foraging, territory defense, mate attraction, copulation, nocturnal roosting, and protection from adverse weather (Buchwald 1992, Wildermuth 1993, McKinnon and May 1994, Rouquette and Thompson 2007), thereby potentially affecting their density and diversity.

Vegetation and other physical structures can interact with top-down controls on odonate larvae or on odonate tenerals (immature adults that have recently emerged from the water) to influence population sizes. Riparian vegetation, for example, might harbor both emerging odonates and their predators (Duffy 1994, Whitaker et al. 2000). Mesocosm experiments have shown that odonate larvae find refuge from predators in aquatic macrophytes (Crowder and Cooper 1982, Thompson 1987, Dionne et al. 1990, Diehl 1992). However, local predator densities in lakes also tend to increase where macrophytes offer protection or higher prey densities (Werner et al. 1983, Weaver et al. 1997, Gamboa-Perez and Schmitter-Soto 1999). Littoral coarse wood or mucky substrates also might provide refugia from predators for some larval odonate species (Schmude 1998, Alzmann et al. 1999, Burcher and Smock 2002). In addition, predation on odonates can vary among water bodies as a result of differences in water chemistry or fish communities (Johnson and Crowley 1980, McPeek 1990, Johansson and Brodin 2003). For example, if littoral fish diversity and densities are lower in lakes than in streams (Willis

and Magnuson 2000), fish predation might exert less control on lacustrine odonate populations than is suggested by stream studies. Among lakes, we expected that odonate abundance and species richness would decline with increasing fish abundance, lake depth, and water clarity (Aksnes and Giske 1993, Davies-Colley and Smith 2001).

We used surveys of larval odonates at a variety of lake and site conditions and field experiments to address 3 questions: 1) How do abundance and community composition of larval odonates vary with habitat structure among and within lakes? 2) Does local macrophyte abundance within lakes affect predation on odonate larvae? 3) Does presence of tall riparian vegetation influence use of riparian sites by adult dragonflies?

Methods

Study area

We conducted our study in Vilas County in northeastern Wisconsin, USA, in the center of the Northern Highlands Lake District (NHLD). Curtis (1959) classified the vegetation as northern wet forest and boreal forest. The forested landscape is interrupted by a high density of glacial lakes (>1300 lakes in the 2639-km^2 county), which cover 13% of the NHLD surface area (Martin 1965). Lakeshores in the area have experienced unprecedented housing development (Schnaiberg et al. 2002, Gonzalez-Abraham et al. 2007).

We surveyed larval Odonata assemblages at 41 lake sites. We defined sites as 30-m segments along the shoreline, including the adjacent littoral zone to a water depth of 1 m and the riparian zone 6 m inland from the ordinary high water mark. We distributed sites among 17 lakes in Vilas County, Wisconsin; the number of sites/lake ranged from 1 to 5. We selected sites with qualitative differences in littoral or riparian vegetation structure when sites were on the same lake. We selected ½ of the sites from developed areas and the rest from undeveloped forested areas. All sites were at least somewhat sandy, had only moderate riparian slopes (<20°), and were separated from each other by ≥120 m (with only 2 pairs of sites <500 m apart).

Aquatic and terrestrial drivers of Odonata larval density and richness

At each site, we collected odonate larvae with a D-frame net by scooping 12 m^2 of benthic material (0.6 m^2/scoop) on 1 d/site during June to July 2004. Samples were collected along four 16-m-long transects that paralleled the shore. We centered transects along

the 30-m site shoreline and placed them at 0.25-, 0.50-, 0.75-, and 1.00-m water depths; transect distance from shore depended on littoral slope. Pilot studies suggested that odonate densities were highest in water >0.50 m deep, so we took 6 scoops along the 0.75- and 1.00-m transects and 4 scoops along the 0.25- and 0.50-m transects. Larvae of most species (except some Zygoptera and smaller Libellulidae) were present throughout the summer because odonates generally are semivoltine in northern Wisconsin lakes (R. DuBois, Wisconsin Department of Natural Resources, personal communication). We sorted larvae from benthic material by hand, preserved them in 70% ethanol, and identified them to species or family (for suborder Zygoptera) using the keys of Needham et al. (2000) and Westfall and May (1996).

We characterized 12 lake-level variables, including fish abundance, human activity, vegetation, and water chemistry in each lake. We recorded 9 littoral and 10 riparian habitat variables at each site (Table 1). We conducted separate principal components analyses (PCA; PC-ORD, version 4; MjM, Gleneden Beach, Oregon) on lake, littoral, and riparian variables to reduce these predictor variables to a smaller set of orthogonal variables (Remsburg 2007). We based PCAs on centered, standardized matrices of Pearson correlation coefficients. We examined PCA eigenvalues and habitat variable correlations with the PCA scores, and chose to use the first 2 PCA axes from each category of variables in mixed-effects multiple linear regressions of larval densities.

We used mixed-effects multiple linear regression models to compare the effects of lake-level and littoral and riparian site-level habitat variables on odonate density, density of the most common family (Gomphidae), and species richness ($\sqrt{[x]}$ transformed to meet normality assumptions) across the 41 sites. We assigned lake as a random effect because specific lakes were not of interest, but sites on the same lakes were not independent. We used similar mixed-effects logistic models, including a fixed-effects term for area sampled, to compare habitat effects on presence or absence of the less-abundant Zygoptera suborder and the 4 other Anisoptera families observed. We present R^2 values for linear regressions using the most influential single independent variable. All analyses were completed using R software (version 2.4.1; R Core Development Team, Vienna, Austria).

We used an information theoretic approach, which avoids arbitrary cutoff values (e.g., $\alpha = 0.05$) and Bonferroni problems of multiple tests (Burnham and Anderson 2002), to compare alternative linear models containing 0 to 6 PCA scores. The 64 candidate models (permutations for all possible combinations) were ranked by 2nd-order criterion Akaike's information criterion values (Sugiura 1978). Strength of evidence for each candidate model can be compared using Akaike weights, w_i, the log likelihood of model i divided by the sum of log likelihoods for all candidate models (Burnham and Anderson 2002). We used all candidate models to estimate the relative importance of each predictor by summing the Akaike weights (Σw) over all models in which a variable appeared (Burnham and Anderson 2002).

Macrophyte effects on larval densities within sites

Submerged macrophtye biomass effects.—To evaluate effects of submerged macrophytes on odonate larval densities at a finer scale than the site-level surveys, we sampled larvae at 18 microsites (5–10 m^2) in 9 lakes in July 2006. In each lake, we chose 1 microsite with dense submerged macrophytes and 1 adjacent microsite with no macrophytes. The macrophyte and non-macrophyte microsites were separated by ≥ 4 m within each lake. Paired microsites had similar substrates and distances from man-made structures. Within each microsite, we used a D-net to collect benthos enclosed by a cylinder (diameter $= 0.55$ m) at 5 adjacent subsampling locations at 0.3-m depth and 5 adjacent subsampling locations at 0.5-m depth. We pooled the 10 subsamples and counted all larvae in 2.4 m^2 of benthos at each microsite as replicates.

We used a paired Wilcoxon test to compare densities of 3 larval behavioral guilds between microsites with and without macrophytes. Behavioral guilds provided more informative response variables than families because densities of some families were very low within the microsites. Guilds included burrowers, which hide in detritus or under the sand; sprawlers, which lie on top of detritus; and claspers, which climb on the leaves, stems, and roots of macrophytes (Appendix).

Tethering experiment.—In August 2006, we conducted a predation experiment at 42 microsites from 21 lakes (including the 18 microsites used for surveys). We paired microsites within lakes. Macrophytes varied among lakes, so we recorded macrophyte species and designated macrophyte biomass categories (none, low, moderate, or high). At each microsite, we used Superglue® to attach monofilament fishing lines (30–40 cm in length) onto the abdomens of 8 live larvae (in later instars) collected from nearby lakes or ponds. We used a variety of Anisoptera species and larval instars, but most larvae were *Cordulia shurtleffi* (2 cm long). We controlled for variations in larval behavior and vulnerability to predation by matching larval species and sizes (range: 15–30-mm length) for paired micro-

TABLE 1. Pearson correlation coefficients between habitat variables and the best 2 axes generated by 3 separate principal components analysis (PCA) procedures on lake-level, site-level littoral, and site-level riparian habitat descriptors at 17 lakes in Vilas County, Wisconsin (Remsburg 2007). Littoral sites consisted of 30 m along the lakeshore contour and the adjacent littoral zone with water depth <1 m. Riparian sites were 30 m along the shore × 6 m inland, but % cover variables were measured within 0.5 m of the ordinary high water mark. Descriptive labels provided for each axis and analysis refer to the major habitat features captured by the axis. CPUE = catch per unit effort.

Habitat descriptors	Pearson correlation coefficients	
	PCA axis 1	PCA axis 2
Lake-level	Lake size and development	Lake wetlands and predators
Insectivorous fish CPUE[a]	0.20	−0.73
Total fish CPUE[a]	0.24	−0.34
Conductance (μS/cm)[b]	0.67	−0.18
Secchi depth (m)[b]	−0.16	0.07
Morphometry[b]	0.60	0.54
Area (ha)[b]	0.75	−0.14
Maximum depth (m)[b]	0.49	0.22
Perimeter (km)[b]	0.87	0.30
Length of wetlands (m)[c]	0.15	0.85
% perimeter with wetlands[c]	−0.15	0.78
Building density (/km)[d]	0.56	−0.40
Number of buildings[d]	0.89	−0.03
Site-level littoral	Littoral macrophytes	Littoral muckiness
Sand (ordinal variable: 0, 1, 2)[e]	−0.23	−0.77
Rock (ordinal variable: 0, 1, 2)[e]	−0.44	0.21
Gravel (ordinal variable: 0, 1, 2)[e]	−0.63	−0.10
Muck (ordinal variable: 0, 1, 2)[e]	0.53	0.64
Mean macrophyte richness[f]	0.90	−0.09
Mean macrophyte % cover[f]	0.86	0.03
Mean frequency of emergent macrophytes[f]	0.66	−0.28
Coarse wood (number/50 m)[e]	−0.03	0.60
Slope (°)	−0.48	0.47
Site-level riparian	Riparian structural complexity	Riparian tall wetland plants
Canopy (ordinal variable: 1, 2, 3)	0.70	0.03
Slope (°)	0.35	−0.10
Length of shore with shrubs (m)	0.86	0.04
Length of shore with tall wetland plants (m)[g]	0.17	−0.84
Vegetation distance from water (m)	0.46	0.26
Maximum understory foliage height (m)	0.68	−0.25
Mean structural diversity (number of structure types intersected)	0.73	<0.01
Mean foliage height diversity (number of layers intercepted)	0.92	−0.08
% shore herbaceous	0.12	−0.82
% shore shrubs	0.56	0.58

[a] CPUE based on electrofishing, minnow traps, and crayfish traps in 2001 to 2004 (Carpenter et al. 2006)
[b] Data collected 2001 to 2003 (Carpenter et al. 2006)
[c] Gergel (1996)
[d] Schnaiberg et al. (2002)
[e] Littoral substrate dominance and coarse wood abundance estimated at 0.5-m water depth in 2001 to 2004 (Marburg et al. 2006)
[f] Macrophyte species richness and % cover estimated in 2001 to 2003 along a transect extending 0 to 2-m depth (Alexander 2005)
[g] *Carex*, *Typha*, or *Iris* species

sites within the same lake. Laboratory observations indicated that fish predation occurred on tethered larvae. We assumed that empty lines indicated predation on odonates because larvae never became unglued from fishing lines in the laboratory. We attached tethered larvae just above the benthos by tying fishing lines to submerged metal stakes. We retrieved tethered larvae remaining after 3.5 to 6 h of exposure to predation at all microsites (timing paired by lake). We did all tethering experiments during the afternoon (between 1200 and 1900 h), when fish densities in macrophytes are probably greatest (Hall et al. 1979, Gliwicz et al. 2006). We used larval mortality (proportion of larvae missing after exposure) to estimate relative predation rates.

We used analysis of variance (ANOVA) with lake as

a random effect to compare mortality of tethered larvae among 42 microsites with different macrophyte biomass categories. Variance partitioning indicated that a large portion of the variance occurred at the lake level. Therefore, we also used mixed-effects linear regressions to test effects of secchi depth and conductance at the lake level on larval mortality (fish catch per unit effort for these lakes was not available).

Effects of riparian vegetation on adult abundance

We experimentally investigated whether riparian vegetation affects adult site use, which could help explain larval distributions within lakes. We recorded adult Odonata behavioral responses to riparian vegetation treatments in 2 blocks of lakeshore home sites. One block had very dense aquatic macrophytes (dense-macrophyte block), whereas the other had very few (sparse-macrophyte block). Both blocks were on bays in the same lake (Little Saint Germain), had stone seawalls separating trimmed lawns from the water, similar aspect, and riparian slope ≈ 0. Ten meters separated the 2 treatment plots; plots were 15 m along the shoreline × 2 m inland.

The 2 riparian vegetation treatments applied to each block were: 1) trimmed lawns with 20 dwarf cattail (*Typha minima*) plants in pots added at the shoreline (*Typha* plots), and 2) trimmed lawns without potted or other tall plants (no-*Typha* plots). We chose the dwarf cattails because they closely resembled the height (0.6 m) and rigidity of native sedges. We replicated both treatments on 21 d at the dense macrophyte block and on 19 d at the sparse macrophyte block. This design might have allowed repeated observations of some individuals, but we treated separate observation days as replicates because adults from the genera we observed move away from the shoreline to roosting sites each evening (Askew 1982, Bried and Ervin 2006) and probably do not demonstrate site fidelity across multiple days (Jacobs 1955, Logan 1971). At both blocks, we alternated the 2 treatments each day between the 2 plots to separate *Typha* treatment effects from littoral or location-specific influences.

On each observation day, we set up the *Typha* treatments ≥3 h before recording odonate behaviors in both treatments within the same block. To capture the period of greatest odonate activity, we made observations from 25 June to 18 August 2006 between 1200 and 1600 h on days with relatively low wind and cloud cover. A single observer (AJR) stood at 1 corner of the plot to survey odonates, including those over the water adjacent to the riparian plot (within ~5 m of shore), in the whole plot simultaneously. The observer also walked slowly across the plot twice per observa-tion period to improve detection of the less active odonates perched on shore. We recorded the total number of individuals present within the plot during 10 min of observation. We estimated instantaneous odonate abundance within the plot by counting all individuals visible at the end of 10 min.

We used blocked mixed-effects ANOVAs to compare Zygoptera and Anisoptera abundance estimates among treatments, where observation day was treated as a random effect. We pooled responses by suborder because odonate abundances were low overall, and the major differences in behaviors corresponded with suborder.

Results

Aquatic and terrestrial drivers of Odonata larval density and richness

We found larvae from 23 Odonata species at the 41 survey sites (Appendix). Species richness ranged from 0 to 10 species per site (mean = 5.2 species). *Gomphus spicatus* was the most abundant (0.45 ± 0.86 [SD] larvae/m^2) and frequently occurring species (present at 67% of the sites). *Gomphus*, which included 3 other species (*Gomphus exilis, Gomphus lividus,* and *Gomphus fraternus*), was by far the most prevalent genus (occurring at 86% of the sites). The family Gomphidae occurred at 87.8% of sites, whereas Zygoptera, Macro-minae, Cordulinae, Libellulinae, and Aeshnidae oc-curred at 44, 34, 22, 20, and 17% of sites, respectively.

Correlations of habitat variables with the 6 PCA axes used in the multivariate regressions had straight-forward interpretations (Table 1). Total variance of the 12 lake-level variables summarized by the first 2 axes of the PCA was 52.4% (axis 1 = 30.4% [lake size and development]; axis 2 = 22.0% [lake wetlands and predators]). The first 2 axes of the PCAs from the 9 site-level littoral and 10 site-level riparian variables captured 53.9% (axis 1 = 34.9% [littoral macrophytes]; axis 2 = 19.0% [littoral muckiness]) and 56.4% (axis 1 = 37.8% [riparian structural complexity]; axis 2 = 18.6% [riparian tall wetland plants]) of the variance, respec-tively. The 3rd lake-level axis represented 14.6% of the variance (more of the variance than the 3rd site-level axes represented) and was correlated almost exclu-sively with secchi depth ($r = -0.9$). However, we did not add the 3rd lake-level axis to the set of candidate models because secchi depth was not correlated with odonate density or diversity. Scores from the 3 separate PCAs generally were not correlated with each other (Pearson correlation coefficients < 0.3), except for the 1st lake axis and 1st riparian axis ($r = -0.41$).

More of the variance in density and richness of

TABLE 2. Relative importance (sums of Akaike weights) of lake- and site-level summary habitat descriptors in predicting Odonata larval densities at 41 Wisconsin lake sites. The 6 predictors are synthetic axes derived from 3 separate principal components analyses of 12 lake-level, 9 site-level littoral, and 10 site-level riparian variables (see Table 1). Bold font indicates statistical significance ($p < 0.05$).

| | Sums of Akaike weights from all candidate models with the predictor | | | | | |
| | Lake | | Littoral | | Riparian | |
Model type/ dependent variable	Size and development	Wetlands and predators	Macrophytes	Muckiness	Structural complexity	Tall wetland plants
Linear regression						
Odonata density	0.33	0.20	**0.54**	0.20	0.21	**0.63**
Species richness	0.29	0.22	**0.60**	0.21	0.26	0.28
Gomphidae density	0.40	0.20	0.42	0.20	0.22	**0.73**
Logistic regression						
Zygoptera presence	0.23	0.22	**0.73**	0.33	0.31	0.34
Libellulinae presence	0.38	0.23	**0.58**	0.22	0.32	0.21
Macrominae presence	0.25	0.45	0.25	0.34	**0.59**	0.25
Cordulinae presence	**0.73**	0.23	0.24	**0.87**	0.32	0.25
Aeshnidae presence	0.34	0.20	0.35	**0.95**	0.45	**0.65**

odonates occurred at the site level (56.5 and 61.6%, respectively) than at the lake level (34.6 and 29.4%, respectively), and all of the variance in Gomphidae densities occurred at the site level. The information theoretic approach for model selection enabled us to assess the importance of predictor variables across all possible models, rather than only from a somewhat-arbitrary best model. Density of all odonates combined was best explained by increasing riparian tall wetland plants, followed by increasing littoral macrophytes (Table 2). Importance of the riparian tall wetland plant axis was even greater for the Gomphidae family, and the model fit was better than that of all odonates. The strongest predictor for Odonata species richness was

FIG. 1. Rank-abundance curves showing mean (±1 SE) number of individual larvae for each odonate species found in 2.4 m² lake microsites with and without dense submerged macrophytes.

increasing littoral macrophyte abundance, which was also the best predictor for presence of Zygoptera and Libellulinae (Table 2). Littoral muckiness was the best predictor for presence of Aeshnidae and Cordulinae (Table 2).

Macrophyte effects on larval densities within sites

Macrophyte biomass effects.—At the 18 paired microsites, we found most of the same species as in our 2004 survey and 3 new Libellulids: *Leucorhinia hudsonica*, *Leucorhinia proxima*, and *Tramea carolina*. Unlike in the initial survey, the most abundant species was *Epitheca cynosura* (0.45 ± 1.0 larvae/m²), even though it occurred only at macrophyte microsites (Fig. 1). *Gomphus* species occurred at 67% of the microsites.

We found many more odonates in microsites with submerged macrophytes (5.2 ± 3.8 larvae/m²) than in microsites without (0.8 ± 1.0 larvae/m²; Wilcoxon rank sum test, $W = 74$, $p = 0.004$). Clasper and sprawler larval behavioral guilds were significantly more abundant in microsites with than without submerged macrophytes (claspers: $W = 66$, $p = 0.02$; sprawlers: $W = 65$, $p = 0.03$), whereas the burrower larval behavioral guild did not differ significantly between microsites with and without submerged macrophytes ($p > 0.1$; Fig. 2). We observed higher Anisoptera species richness at microsites with (5.22 ± 3.35) than without submerged macrophytes (2.11 ± 1.83; Wilcoxon rank sum test $W = 63$, $p = 0.05$).

Tethering experiment.—Tethered larvae mortality ranged from 0 to 100% among the 42 microsites (53% ± 32%). On separate occasions, we observed 2 bluegills and 1 small painted turtle feeding on tethered
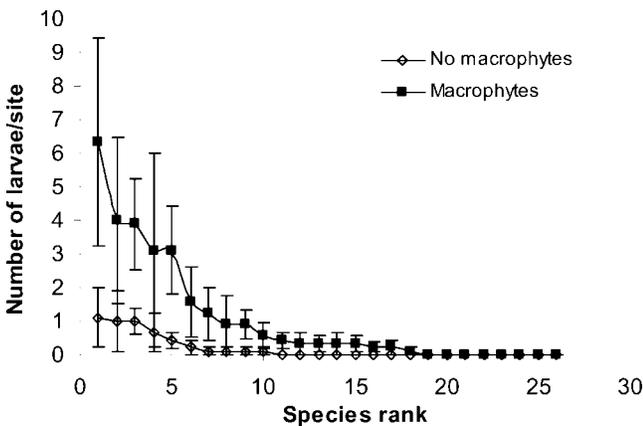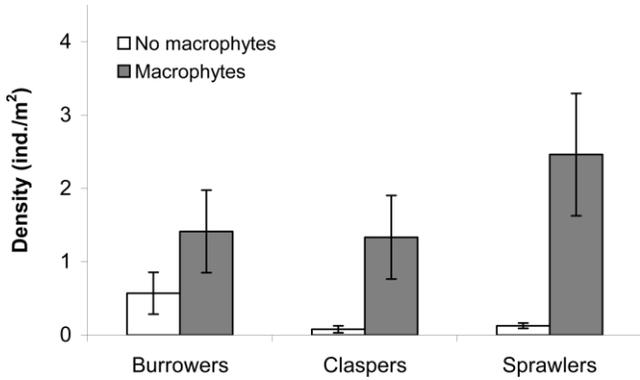
FIG. 2. Mean densities (±1 SE) of 3 larval behavioral guilds among paired 7-m² lake microsites with and without submerged macrophytes.

larvae in the field. Mortality did not vary with submerged macrophyte biomass category ($F_{1,20} = 1.19$, $p = 0.3$) or with macrophyte presence (paired t-test: $t_{20} = -1.13$, $p = 0.3$). Mean larval mortality was 47% (± 32%) at microsites with submerged macrophytes and 56% (± 35%) at microsites without submerged macrophytes. Much of the total variance in mortality (39.1%) occurred at the lake level, but mortality was not correlated significantly with lake clarity or conductance ($p > 0.1$).

Effects of riparian vegetation on adult abundance

We observed adult odonates from 15 different genera at the experimental plots but only *Enallagma* (Zygoptera:Coenagrionidae), *Leucorrhinia*, and *Libellula* spp. (Anisoptera:Libellulinae) were present on >50% of the observation days (96%, 65% and 56%, respectively). Abundances of Gomphidae adults at these plots were much lower than those of Libellulidae adults, probably because Gomphidae spend more time perched in treetops than do Libellulidae. Anisoptera abundance was greatest at the dense-macrophyte block and did not differ significantly between *Typha* treatments ($p > 0.1$; Fig. 3A). Zygoptera abundance was significantly higher at the *Typha* than at the no-*Typha* treatment ($F_{1,51} = 9.2$, $p = 0.004$; Fig. 3B).

Discussion

Riparian vegetation influenced larval odonate assemblages in the adjacent aquatic ecosystem. Previous studies on ecological links between riparian landscapes and aquatic communities have focused primarily on detrital, nutrient, and structural subsidies (Wallace et al. 1997, Nakano et al. 1999, Bastow et al. 2002, Sass 2004, Baxter et al. 2005, Roth et al. 2007). Our results suggest that adult habitat selection by
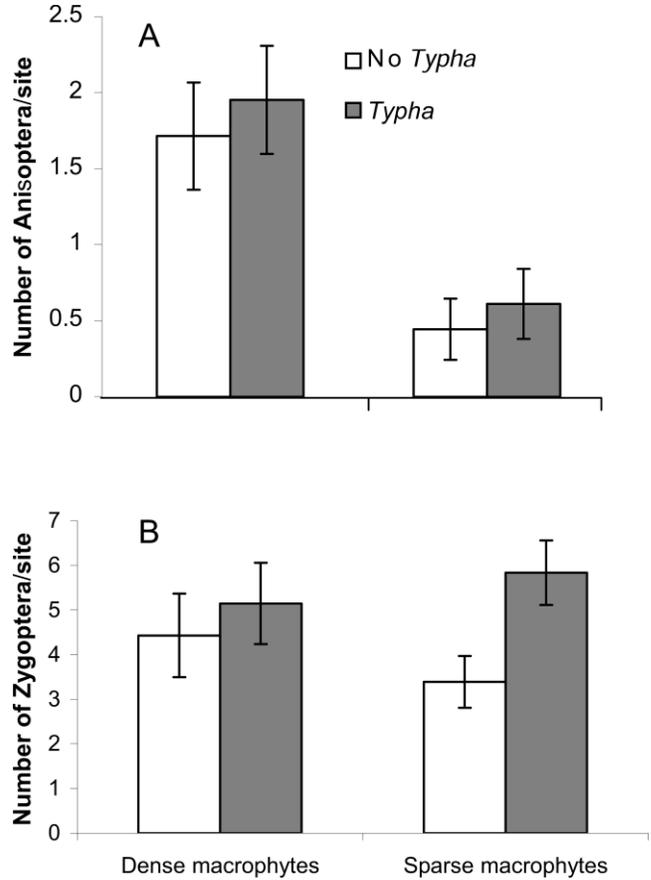

FIG. 3. Mean (±1 SE) number of adult Anisoptera (A) and Zygoptera (B) within 15- × 7-m experimental plots at 2 blocks of lakeshore home sites in northern Wisconsin (1 with sparse and 1 with dense emergent macrophytes in the littoral zone). *Typha* treatments consisted of 20 potted *Typha minima* placed on the seawalls. *Typha* treatments were rotated between 2 plots/site on 21 d during June to August 2006.

animals with complex life histories provides an additional link between terrestrial and aquatic ecosystems. A growing body of research on agricultural systems has demonstrated that vegetation structure in one ecosystem affects insect abundances in an adjacent system (Langellotto and Denno 2004, Tscharntke et al. 2005, Bianchi et al. 2006). In our study, site-level riparian vegetation was a better predictor of total larval Odonata density, Gomphidae density, and Macrominae presence than site- or lake-level aquatic habitat features. In particular, larval density of the most abundant family, Gomphidae, increased with the amount of riparian tall wetland plants adjacent to—but not in—the lakes. Previous studies have linked abundance of *adult* odonates to riparian sedge or rush abundance (Van Buskirk 1986, Clark and Samways 1996, Foote and Hornung 2005, Hofmann and Mason 2005b, Rouquette and Thompson 2007, Butler and

DeMaynadier 2008), but our study shows that the abundance of *larval* odonates is correlated with abundance of terrestrial herbaceous vegetation.

The stronger relationship between larval abundance and riparian tall wetland plants than with riparian structural complexity might reflect the role of the plant structure. Riparian tall wetland plants (*Carex, Typha,* and *Iris* spp.) are rigid and provide stable vertical structures on which emerging larvae complete hardening of the wings (Corbet 1999). However, Gomphidae (unlike most other Anisoptera families) also can emerge on horizontal surfaces (Eda 1963). A cause–effect relationship between the availability of suitable emergence structures and odonate population abundances remains to be demonstrated. Adult odonates might prefer rigid plants for perching because their height and open structure facilitate thermoregulation (May 1976, Pezalla 1979) or mate attraction (McKinnon and May 1994). Riparian vegetation also could affect adult abundances if it were correlated with terrestrial prey densities (Baird and May 1997, Whitaker et al. 2000, Garono and Kooser 2001, Henning and Remsburg, in press).

The correlations we observed between larvae and riparian vegetation also might reflect adult selection for oviposition sites with highest survivorship of eggs and larvae (Storch and Frynta 1999). Adults cannot assess all aspects of aquatic habitat suitability for larvae (Wildermuth 1993). However, adult odonates might use emergent aquatic plants or riparian plants as proximate cues of macrophyte, substrate, prey availability, or predator conditions for larvae in littoral sites (Buchwald 1992, Wildermuth 1992, McKinnon and May 1994). Adult riparian site use generally corresponds with oviposition locations (Corbet 1999), and larvae are unlikely to move >20 m from the littoral site where eggs were laid (Ubukata 1984, Schaffner and Anholt 1998, but see Alzmann et al. 1999), so adult habitat use could help explain larval distributions. Other studies have demonstrated indirectly that adding artificial perches can lead to higher adult odonate densities (Wolf and Waltz 1988, Rehfeldt 1990, Baird and May 1997, May and Baird 2002, De Marco and Resende 2004). Our field experiment provides some support for a link between adult site selection and larval densities at sites with riparian wetland plants, but more observations of Gomphidae oviposition are needed to resolve the question directly.

Aeshnidae, which are endophytic species, were most likely to occur at sites with greater littoral muckiness and riparian tall wetland plants; but their presence was not predicted by littoral macrophytes, possibly because we observed so few Aeshnidae larvae in surveys. As the strongest fliers of all odonates,

Aeshnidae also might respond to littoral macrophytes at a larger spatial or temporal scale than do other odonates.

High species richness at sites with more littoral macrophytes can be attributed to more Zygoptera and Libellulinae occurrences at those sites, consistent with previous studies showing the strongest associations of odonate richness with macrophyte biomass (Weatherhead and James 2001, Michaletz et al. 2005, Osborn 2005, Butler and DeMaynadier 2008). Zygopterans require emergent macrophytes for endophytic oviposition, and both Zygoptera and Libellulinae larvae use macrophytes. Last, all Zygoptera and Libellulinae species are perchers as adults, so emergent macrophytes also might serve as important perching structures for adults at oviposition sites (McKinnon and May 1994, Switzer and Walters 1999, De Marco and Resende 2004).

Predation risk for tethered larvae did not help explain why larval densities were highest at microsites with dense macrophytes. Our results differ from those of mesocosm predation experiments in other systems that have shown the importance of macrophytes in predator avoidance by odonate larvae (Crowder and Cooper 1982, Thompson 1987, Dionne et al. 1990, Diehl 1992). Tethering can interfere with predator avoidance behaviors (Curran and Able 1998, Kneib and Scheele 2000), but field and aquarium observations gave us no reason to suspect that effects of tethering on larval behavior differed among microsite treatments. Nevertheless, unnaturally high predation rates resulting from tethering might have overwhelmed the effects of vegetation in our experiment. Differences among fish communities among lakes also might have obscured the predator avoidance effect in our field experiment. Alternatively, competition or foraging behaviors of odonate larvae might better explain their associations with macrophytes than predator avoidance (Johansson 1991, Schmude 1998, Elkin and Baker 2000, Hofmann and Mason 2005a), potentially because of higher predator densities inside than outside macrophyte beds (Werner et al. 1983, Weaver et al. 1997, Gamboa-Perez and Schmitter-Soto 1999). Additional field experiments, such as fish exclusion cages, will be necessary to clarify the specific role of macrophytes for odonate larvae.

Our findings that both riparian and littoral vegetation structure influence lentic Odonata assemblages have several implications for conservation. Odonate abundances and diversity could decline as a consequence of the vegetation simplification and removal of macrophytes and coarse wood that often accompanies lakeshore development (Racey and Euler 1982, Radomski and Goeman 2001, Elias and Meyer 2003,

Marburg et al. 2006). Our observation that site-level vegetation structure affects abundance and diversity of charismatic insects potentially could motivate home-owners to maintain or restore wetland and littoral vegetation. Furthermore, invasion by rusty crayfish (*Orconectes rusticus*) leads to severe macrophyte reduction in north-temperate lakes (Wilson et al. 2004) and might indirectly reduce odonate diversity and density.

Last, Odonata abundances can influence many other components of aquatic and riparian communities because Odonata are predators of smaller inverte-brates throughout their complex life cycle (Thorp and Cothran 1984, Johnson et al. 1987, Van Buskirk 1988). High predation by adult odonates on terrestrial pollinators, including bees, moths, and flies, might even alter riparian plant reproduction (Knight et al. 2005). At critical times, odonates make up a significant portion of the diets of fish (Crowder and Cooper 1982, Johnson et al. 1995, Sass 2004) and birds (Orians and Horn 1969, Wissinger 1988), so habitat variables that drive odonate abundances could lead to widespread changes in both aquatic and terrestrial food webs.

Acknowledgements

Literature Cited

Aksnes, D. L., and J. Giske. 1993. A theoretical model of aquatic visual feeding. Ecological Modelling 67:233–250.

Alexander, M. L. 2005. Lake ecosystem variation across landscape position and human development gradients in Vilas County, Wisconsin. PhD Thesis, University of Wisconsin, Madison, Wisconsin.

Alzmann, N., B. Kohler, and G. Maier. 1999. Spatial distribution, food and activity of *Gomphus pulchellus* Selys 1840 (Insecta; Odonata; Gomphidae) from a still water habitat. International Review of Hydrobiology 84: 299–313.

Askew, R. 1982. Roosting and resting site selection by coenagrionid damselflies. Advances in Odonatology 1: 1–8.

Baird, J. M., and M. L. May. 1997. Foraging behavior of *Pachydiplax longipennis* (Odonata: Libellulidae). Journal of Insect Behavior 10:655–678.

Bastow, J. L., J. L. Sabo, J. C. Finlay, and M. E. Power. 2002. A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. Oecologia (Berlin) 131:261–268.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Becker, C. G., C. R. Fonseca, C. F. B. Haddad, R. F. Batista, and P. I. Prado. 2007. Habitat split and the global decline of amphibians. Science 318:1775–1777.

Bianchi, F., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society of London B: Biological Sciences 273:1715–1727.

Bried, J. T., and G. N. Ervin. 2006. Abundance patterns of dragonflies along a wetland buffer. Wetlands 26:878–883.

Brose, U. 2003. Bottom-up control of carabid beetle commu-nities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia (Berlin) 135:407–413.

Bryan, M. D., and D. L. Scarnecchia. 1992. Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. Environmental Biology of Fishes 35:329–341.

Buchwald, R. 1992. Vegetation and dragonfly fauna—characteristics and examples of biocenological field studies. Vegetatio 101:99–107.

Burcher, C. L., and L. A. Smock. 2002. Habitat distribution, dietary composition and life history characteristics of odonate nymphs in a blackwater coastal plain stream. American Midland Naturalist 148:75–89.

Burger, J. 2000. Landscapes, tourism, and conservation. Science of the Total Environment 249(1–3):39–49.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York.

Butler, R. G., and P. G. DeMaynadier. 2008. The significance of littoral and shoreline habitat integrity to the conser-vation of lacustrine damselflies (Odonata). Journal of Insect Conservation 12:23–36.

Carpenter, S. R., T. K. Kratz, J. Kitchell, J. J. Magnuson, and M. J. Vander Zanden. 2006. Biocomplexity; coordinated field studies. National Biological Information Infra-structure Metadata Clearinghouse. (Available from: http://mercury.ornl.gov/metadata/lter/html/lter/ metacat.lternet.edu_knb_metacat_action_read_qformat_ xml_docid_knb-lter-ntl.126.2_5.html)

Carr, M. H. 1991. Habitat selection and recruitment of an

assemblage of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 146:113–137.

CHERUVELIL, K. S., P. A. SORANNO, J. D. MADSEN, AND M. J. ROBERSON. 2002. Plant architecture and epiphytic macro-invertebrate communities: the role of an exotic dissected macrophyte. Journal of the North American Benthological Society 21:261–277.

CLARK, T. E., AND M. J. SAMWAYS. 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. Journal of Applied Ecology 33:1001–1012.

CORBET, P. S. 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca, New York.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813.

CURRAN, M. C., AND K. W. ABLE. 1998. The value of tethering fishes (winter flounder and tautog) as a tool for assessing predation rates. Marine Ecology Progress Series 163:45–51.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

DAVIES-COLLEY, R. J., AND D. G. SMITH. 2001. Turbidity, suspended sediment, and water clarity: a review. Journal of the American Water Resources Association 37:1085–1101.

DECAMPS, H., G. PINAY, R. J. NAIMAN, G. E. PETTS, M. E. MCCLAIN, A. HILLBRICHT-ILKOWSKA, T. A. HANLEY, R. M. HOLMES, J. QUINN, J. GIBERT, A. M. P. TABACCHI, F. SCHIEMER, E. TABACCHI, AND M. ZALEWSKI. 2004. Riparian zones: where biogeochemistry meets biodiversity in management practice. Polish Journal of Ecology 52:3–18.

DE MARCO, P., AND D. C. RESENDE. 2004. Cues for territory choice in two tropical dragonflies. Neotropical Entomology 33:397–401.

DE SOUZA, A. L. T., AND R. P. MARTINS. 2005. Foliage density of branches and distribution of plant-dwelling spiders. Biotropica 37:416–420.

DIEHL, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661.

DIONNE, M., M. BUTLER, AND C. FOLT. 1990. Plant-specific expression of antipredator behavior by larval damselflies. Oecologia (Berlin) 83:371–377.

DUFFY, W. G. 1994. Demographics of Lestes disjunctus disjunctus (Odonata, Zygoptera) in a riverine wetland. Canadian Journal of Zoology 72:910–917.

EDA, S. 1963. Emergence of Epophlebia superstes Selys. Tombo 5:1–3 (in Japanese) (reviewed by Corbet 1999).

ELIAS, J. E., AND M. W. MEYER. 2003. Comparisons of undeveloped and developed shorelands, northern Wisconsin, and recommendations for restoration. Wetlands 23:800–816.

ELKIN, C. M., AND R. BAKER. 2000. Lack of preference for low-predation-risk habitats in larval damselflies explained by costs of intraspecific interactions. Animal Behaviour 60:511–521.

FICETOLA, G. F., E. PADOA-SCHIOPPA, A. MONTI, R. MASSA, F. DE BERNARDI, AND L. BOTTONI. 2004. The importance of aquatic and terrestrial habitat for the European pond turtle (Emys orbicularis): implications for conservation planning and management. Canadian Journal of Zoology 82:1704–1712.

FOOTE, A. L., AND C. L. R. HORNUNG. 2005. Odonates as biological indicators of grazing effects on Canadian prairie wetlands. Ecological Entomology 30:273–283.

GAMBOA-PEREZ, H. C., AND J. J. SCHMITTER-SOTO. 1999. Distribution of cichlid fishes in the littoral of Lake Bacalar, Yucatan Peninsula. Environmental Biology of Fishes 54:35–43.

GARONO, R. J., AND J. G. KOOSER. 2001. The relationship between patterns in flying adult insect assemblages and vegetation structure in wetlands of Ohio and Texas. Ohio Journal of Science 101:12–21.

GERGEL, S. E. 1996. Scale-dependent landscape effects on north temperate lakes and rivers. MS Thesis, University of Wisconsin, Madison, Wisconsin.

GLIWICZ, Z. M., J. SLON, AND I. SZYNKARCZYK. 2006. Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. Freshwater Biology 51:823–839.

GONZALEZ-ABRAHAM, C. E., V. C. RADELOFF, R. B. HAMMER, T. J. HAWBAKER, S. I. STEWARD, AND M. K. CLAYTON. 2007. Building patterns and landscape fragmentation in northern Wisconsin, USA. Landscape Ecology 22:217–230.

HALL, D. J., E. E. WERNER, J. F. GILLIAM, G. G. MITTELBACH, D. HOWARD, C. G. DONER, J. A. DICKERMAN, AND A. J. STEWART. 1979. Diel foraging behavior and prey selection in the Golden Shiner (Notemigonus crysoleucas). Journal of the Fisheries Research Board of Canada 36:1029–1039.

HANSEN, A. J., R. L. KNIGHT, J. M. MARZLUFF, S. POWELL, K. BROWN, P. H. GUDE, AND A. JONES. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893–1905.

HENNING, B. M., AND A. J. REMSBURG. Effects of lakeshore vegetation structure on avian and amphibian abundance in northern Wisconsin. American Midland Naturalist (in press).

HOFMANN, T. A., AND C. F. MASON. 2005a. Competition, predation and microhabitat selection of Zygoptera larvae in a lowland river. Odonatologica 34:27–36.

HOFMANN, T. A., AND C. F. MASON. 2005b. Habitat characteristics and the distribution of Odonata in a lowland river catchment in eastern England. Hydrobiologia 539:137–147.

JACOBS, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology 36:566–586.

JENNINGS, M. J., E. E. EMMONS, G. R. HATZENBELER, C. EDWARDS, AND M. A. BOZEK. 2003. Is littoral habitat affected by residential development and land use in watersheds of Wisconsin lakes? Lake and Reservoir Management 19:272–279.

JOHANSSON, F. 1991. Foraging modes in an assemblage of odonate larvae—effects of prey and interference. Hydrobiologia 209:79–87.

JOHANSSON, F., AND T. BRODIN. 2003. Effects of fish predators

and abiotic factors on dragonfly community structure. Journal of Freshwater Ecology 18:415–423.

Johnson, D., and P. Crowley. 1980. Habitat and seasonal segregation among coexisting odonate larvae. Odonatologica 9:297–308.

Johnson, D. M., T. H. Martin, M. Mahato, L. B. Crowder, and P. H. Crowley. 1995. Predation, density dependence, and life histories of dragonflies: a field experiment in a freshwater community. Journal of the North American Benthological Society 14:547–562.

Johnson, D. M., C. L. Pierce, T. H. Martin, C. N. Watson, R. E. Bohanan, and P. H. Crowley. 1987. Prey depletion by odonate larvae—combining evidence from multiple field experiments. Ecology 68:1459–1465.

Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. American Naturalist 105:423–435.

Kneib, R. T., and C. E. H. Scheele. 2000. Does tethering of mobile prey measure relative predation potential? An empirical test using mummichogs and grass shrimp. Marine Ecology Progress Series 198:181–190.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880–883.

Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia (Berlin) 139:1–10.

Lindsay, A. R., S. S. Gillum, and M. W. Meyer. 2002. Influence of lakeshore development on breeding bird communities in a mixed northern forest. Biological Conservation 107:1–11.

Logan, E. R. 1971. A comparative ecological and behavioral study of two species of damselflies, *Enallagma boreale* (Selys) and *Enallagma carunculatum* Morse (Odonata: Coenagrionidae). PhD Thesis, Washington State University, Pullman, Washington.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Reviews 40:510–533.

Marburg, A. E., M. G. Turner, and T. K. Kratz. 2006. Natural and anthropogenic variation in coarse wood among and within lakes. Journal of Ecology 94:558–568.

Marnell, F. 1998. Discriminant analysis of the terrestrial and aquatic habitat determinants of the smooth newt (*Triturus vulgaris*) and the common frog (*Rana temporaria*) in Ireland. Journal of Zoology 244:1–6.

Martin, L. 1965. The physical geography of Wisconsin. 3rd edition. University of Wisconsin Press, Madison, Wisconsin.

May, M. L. 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecological Monographs 46:1–32.

May, M. L., and J. M. Baird. 2002. A comparison of foraging behavior in two "percher" dragonflies, *Pachydiplax longipennis* and *Erythemis simplicicollis* (Odonata: Libellulidae). Journal of Insect Behavior 15:765–778.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure. Pages 3–27 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky (editors). Population and community biology series. Chapman and Hall, New York.

McKinnon, B., and M. L. May. 1994. Mating habitat choice and reproductive success of *Pachydiplax longipennis* (Burmeister) (Anisoptera: Libellulidae). Advances in Odonatology 6:59–77.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71:83–98.

Michaletz, P. H., K. E. Doisy, and C. F. Rabeni. 2005. Influences of productivity, vegetation, and fish on macroinvertebrate abundance and size in Midwestern USA impoundments. Hydrobiologia 543:147–157.

Milner, A. M., and I. T. Gloyne-Phillips. 2005. The role of riparian vegetation and woody debris in the development of macroinvertebrate assemblages in streams. River Research and Applications 21:403–420.

Muntifering, J. R., A. J. Dickman, L. M. Perlow, T. Hruska, P. G. Ryan, L. L. Marker, and R. M. Jeo. 2006. Managing the matrix for large carnivores: a novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. Animal Conservation 9:103–112.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Needham, J. G., M. J. Westfall, and M. L. May. 2000. Dragonflies of North America. Scientific Publishers, Gainesville, Florida.

Orians, G. H., and H. S. Horn. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50:930–938.

Osborn, R. 2005. Odonata as indicators of habitat quality at Lakes in Louisiana, United States. Odonatologica 34:259–270.

Pezalla, V. M. 1979. Behavioral ecology of the dragonfly *Libellula pulchella* Drury (Odonata:Anisoptera). American Midland Naturalist 102:1–22.

Pianka, E. R. 1967. Lizard species diversity. Ecology 48:333–351.

Racey, G. D., and D. L. Euler. 1982. Small mammal and habitat response to shoreline cottage development in central Ontario. Canadian Journal of Zoology 60:865–880.

Radomski, P., and T. J. Goeman. 2001. Consequences of human lakeshore development on emergent and floating-leaf vegetation abundance. North American Journal of Fisheries Management 21:46–61.

Rehfeldt, G. E. 1990. Anti-predator strategies in oviposition site selection of *Pyrrhosoma nymphula* (Zygoptera: Odonata). Oecologia (Berlin) 85:233–237.

Remsburg, A. J. 2007. Aquatic and terrestrial vegetation influence lacustrine dragonfly (order Odonata) assemblages at multiple life stages. PhD Thesis, University of Wisconsin, Madison, Wisconsin.

Roth, B. M., I. C. Kaplan, G. G. Sass, P. T. Johnson, A. E. Marburg, A. C. Yannarell, T. D. Havlicek, T. V. Willis, M. G. Turner, and S. R. Carpenter. 2007. Linking terrestrial and aquatic ecosystems: the role of woody habitat in lake food webs. Ecological Modelling 203:439–452.

Rouquette, J. R., and D. J. Thompson. 2007. Roosting site selection in the endangered damselfly, *Coenagrion mer-*

curiale, and implications for habitat design. Journal of Insect Conservation 11:187–193.

SASS, G. G. 2004. Fish community and food web responses to a whole-lake removal of coarse woody habitat. PhD Thesis, University of Wisconsin, Madison, Madison, Wisconsin.

SCHAFFNER, A. K., AND B. R. ANHOLT. 1998. Influence of predator presence and prey density on behavior and growth of damselfly larvae (*Ischnura elegans*) (Odonata: Zygoptera). Journal of Insect Behavior 11:793–809.

SCHINDLER, D. E., S. I. GEIB, AND M. R. WILLIAMS. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems 3:229–237.

SCHMUDE, K. L. 1998. Effects of habitat complexity on macroinvertebrate colonization of artificial substrates in north temperate lakes. Journal of the North American Benthological Society 17:73–80.

SCHNAIBERG, J., J. RIERA, M. G. TURNER, AND P. R. VOSS. 2002. Explaining human settlement patterns in a recreational lake district: Vilas County, Wisconsin, USA. Environmental Management 30:24–34.

SCRIBNER, K. T., J. W. ARNTZEN, N. CRUDDACE, R. S. OLDHAM, AND T. BURKE. 2001. Environmental correlates of toad abundance and population genetic diversity. Biological Conservation 98:201–210.

STORCH, D., AND D. FRYNTA. 1999. Evolution of habitat selection: stochastic acquisition of cognitive clues? Evolutionary Ecology 13:591–600.

SUGIURA, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics: Theory and Methods 7:13–26.

SWITZER, P. V., AND W. WALTERS. 1999. Choice of lookout posts by territorial amberwing dragonflies, *Perithemis tenera* (Anisoptera: Libellulidae). Journal of Insect Behavior 12:385–398.

THOMPSON, D. J. 1987. Regulation of damselfly populations: the effects of weed density on larval mortality due to predation. Freshwater Biology 17:367–371.

THORP, J., AND M. COTHRAN. 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. Ecology 65:1546–1555.

TSCHARNTKE, T., T. A. RAND, AND F. BIANCHI. 2005. The landscape context of trophic interactions: insect spillover across the crop–noncrop interface. Annales Zoologici Fennici 42:421–432.

TUPPER, M., AND R. G. BOUTILIER. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52:1834–1841.

UBUKATA, H. 1984. Oviposition site selection and avoidance of additional mating by females of the dragonfly, *Cordulia aenea amurensis* Selys (Corduliidae). Researches on Population Ecology 26:285–301.

VAN BUSKIRK, J. 1986. Establishment and organization of territories in the dragonfly *Sympetrum rubicundulum* (Odonata: Libellulidae). Animal Behaviour 34:1781–1790.

VAN BUSKIRK, J. 1988. Interactive effects of dragonfly predation in experimental pond communities. Ecology 69:857–867.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

WEATHERHEAD, M. A., AND M. R. JAMES. 2001. Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. Hydrobiologia 462:115–129.

WEAVER, M. J., J. J. MAGNUSON, AND M. K. CLAYTON. 1997. Distribution of littoral fishes in structurally complex macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 54:2277–2289.

WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

WESTFALL, M. J., AND M. L. MAY. 1996. Damselflies of North America. Scientific Publishers, Gainesville, Florida.

WHITAKER, D. M., A. L. CARROLL, AND W. A. MONTEVECCHI. 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. Canadian Journal of Zoology 78:740–747.

WILDERMUTH, H. 1992. Habitate und Habitatwahl der grossen Moosjungfer (*Leucorrhinia pectoralis*) Charp. 1825 (Odonata, Libellulidae). Zeitschrift fur Okologie und Naturschutz 1:3–21.

WILDERMUTH, H. 1993. Habitat selection and oviposition site recognition by the dragonfly *Aeshna juncea* (L.): an experimental approach in natural habitats (Anisoptera: Aeshnidae). Odonatologica 22:27–44.

WILLIS, T. V., AND J. J. MAGNUSON. 2000. Patterns in fish species composition across the interface between streams and lakes. Canadian Journal of Fisheries and Aquatic Sciences 57:1042–1052.

WILSON, K. A., J. J. MAGNUSON, D. M. LODGE, A. M. HILL, T. K. KRATZ, W. L. PERRY, AND T. V. WILLIS. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences 61:2255–2266.

WISSINGER, S. A. 1988. Spatial distribution, life history and estimates of survivorship in a fourteen-species assemblage of larval dragonflies (Odonata: Anisoptera). Freshwater Biology 20:329–340.

WOLF, L. L., AND E. C. WALTZ. 1988. Oviposition site selection and spatial predictability of female white-faced dragonflies (*Leucorrhinia intacta*) (Odonata: Libellulidae). Ethology 78:306–320.

WOODFORD, J. E., AND M. W. MEYER. 2003. Impact of lakeshore development on green frog abundance. Biological Conservation 110:277–284.

APPENDIX. Odonata species collected as larvae from 59 littoral sites during a broad-scale survey of 41 sites (12 m² of littoral benthos sampled per site) in 2004 and a fine-scale survey of 18 microsites (½ with macrophytes, ½ without macrophytes; 2.4 m² of littoral benthos sampled per microsite) in northern Wisconsin lakes in 2006. Behavioral guild classifications are shown for larval and adult stages. Three Libellulinae species (*Leucorrhinia hudsonica, Leucorrhinia proxima, and Tramea carolina*) were observed only in 2006; all other species were found in both years.

Taxon	Larval behavior				Adult behavior	
	Clasper	Sprawler	Burrower		Flier	Percher
Aeshnidae						
Basiaeschna janata	X				X	
Boyeria vinosa	X				X	
Gomphidae						
Arigomphus furcifer			X			X
Dromogomphus spinosus			X			
Gomphus spicatus			X			X
Gomphus exilis			X			X
Gomphus lividus			X			X
Gomphurus fraternus			X			X
Hagenius brevistylus		X	X			
Libellulinae						
Celithemis elisa	X					X
Ladona julia	X	X				X
Leucorrhinia hudsonica		X				X
Leucorrhinia proxima		X				X
Somatachlora cingulata		X				X
Tramea carolina		X				X
Cordulinae						
Cordulia shurtleffli		X			X	
Drorocordulia libera		X			X	
Epitheca cynosura		X			X	
Epitheca princeps		X			X	
Epitheca spinigera		X			X	
Macrominae						
Didymops transversa		X	X		X	
Macromia illinoiensis		X	X		X	
Coenagrionidae spp.	X					X