

The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish

Michael D. Rennie and Leland J. Jackson

Abstract: Relationships between littoral habitat complexity and invertebrate distributions in fishless lakes are not well understood compared with well-documented relationships in lakes with fish. We examined littoral invertebrate distributions over fine-scale gradients of weed-bed habitat complexity and contrasted these patterns in four shallow prairie lakes — two with fish and two without. The above-sediment portion of submerged macrophytes and associated invertebrates was sampled from three littoral microhabitats: weed-bed centres (highly complex), weed-bed edges (moderately complex), and single plants that grew apart from distinct weed beds (least complex). Total invertebrate densities in fishless lakes did not differ between littoral microhabitats, nor were they correlated with macrophyte biomass. In contrast, total invertebrate densities in lakes with fish increased with microhabitat complexity and were positively correlated with macrophyte biomass. Weed-bed complexity also affected littoral invertebrate community structure; in all lakes, the proportion of filter-feeders decreased with increasing microhabitat complexity, but the proportion of predatory invertebrates was greater overall in fishless lakes than in lakes with fish. Our results demonstrate that small-scale variation in littoral microhabitat complexity can lead to specific patterns of invertebrate distribution that systematically differ between lakes with and without fish, and that these systematic differences may be mediated through top-down mechanisms.

Résumé : Les relations entre la complexité de l'habitat littoral et la répartition des invertébrés dans les lacs sans poissons sont mal comprises, alors qu'elles sont bien étudiées dans les lacs qui ont des poissons. Nous avons examiné les répartitions des invertébrés littoraux le long de gradients à échelle fine de complexité de l'habitat des herbiers et comparé ces patrons dans quatre lacs peu profonds des prairies, deux avec des poissons et deux sans poissons. Nous avons échantillonné les macrophytes et les invertébrés associés dans la partie supérieure aux sédiments dans trois microhabitats littoraux, soit le centre des herbiers (très complexe), le bord des herbiers (moyennement complexe) et les plantes qui poussent isolément de tout herbier défini (le moins complexe). Les densités totales d'invertébrés dans les lacs sans poissons ne diffèrent pas d'un microhabitat littoral à un autre et elles ne sont pas corrélées à la biomasse des macrophytes. En revanche, la biomasse totale des invertébrés dans les lacs avec poissons augmente en fonction de la complexité du microhabitat et est en corrélation positive avec la biomasse des macrophytes. La complexité des herbiers affecte aussi la structure des communautés d'invertébrés : dans tous les lacs, la proportion des organismes filtreurs décroît à mesure que la complexité des microhabitats augmente; globalement, la proportion d'invertébrés prédateurs est plus grande dans les lacs sans poissons que dans les lacs avec poissons. Nos résultats démontrent que la variation à petite échelle de la complexité des microhabitats littoraux peut entraîner l'établissement de patrons spécifiques de répartition des invertébrés qui diffèrent systématiquement dans les lacs avec et sans poissons; ces différences systématiques s'expliquent peut-être par les mécanismes à action descendante.

[Traduit par la Rédaction]

Introduction

The relationship between ecosystem structure and function is a fundamental issue in ecology. The variety of resources available to organisms (e.g., food, nesting sites, and refugia) is dictated by the physical structure and complexity

of their habitats. Compared with nonvegetated areas of lakes, sections of the littoral zone that harbour aquatic macrophytes are structurally more complex and typically support a greater abundance, biomass, and diversity of macroinvertebrates (Pardue and Webb 1985; Beckett et al. 1992; Blindow et al. 1993). Traditional sampling techniques have assumed

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Table 1. Physical and chemical attributes of lakes near Strathmore, Alberta, Canada.

	Dawson Lake	Mushroom Lake	SGC	SPA
Secchi depth (m)	1.4	1.2	1	1.3
Turbidity (NTU) ^a	3.49 ± 0.68	2.32 ± 0.14	7.70 ± 0.27	7.57 ± 0.58
Total phosphorus (µg·L ⁻¹) ^a	937.3 ± 391.0	547.7 ± 468.0	67.36 ± 33.39	75.66 ± 16.44
DOC (mg·L ⁻¹) ^a	31.12 ± 2.42	26.05 ± 6.34	11.72 ± 2.18	23.48 ± 11.79
pH ^a	9.44 ± 0.25	9.01 ± 0.55	8.71 ± 0.21	8.26 ± 0.17
Conductivity (mS·cm ⁻¹) ^a	3.937 ± 0.006	0.597 ± 0.030	0.558 ± 0.006	0.732 ± 0.004
Temperature (°C) ^a	22.5 ± 0.8	22.2 ± 0.7	20.3 ± 0.8	20.0 ± 1.5
Area (km ²)	0.314	0.117	0.103	0.02
Maximum depth (m)	1.7	1.3	1.3	3.3

Note: SGC, Strathmore Golf Course; SPA, Strathmore Picnic Area; NTU, nephelometric turbidity units; DOC, dissolved organic carbon.

^aValues are given as the mean ± standard deviation and are summer averages from June, July, and August samples.

plant density and invertebrate distributions within a weed bed to be homogeneous (Cyr and Downing 1988a, 1988b; Zimmer et al. 2000). Realistically, variability in growth form and density of plants likely contributes to significant structural heterogeneity within weed beds. The density and complexity of weed beds can directly interfere with the foraging efficiency of both fish and invertebrate predators (Crowder and Cooper 1982; Tokeshi and Pinder 1985; Dibble et al. 1996). Therefore, fine-scale habitat complexity (within weed beds) may directly contribute to differences in the distribution and abundance of littoral invertebrates and thus the flow of energy through littoral food webs (Lillie and Budd 1992).

Previous research in lakes with fish has shown that total invertebrate abundance, biomass, and diversity are strongly influenced by a variety of measures describing macrophyte habitat complexity. These include the type and number of plant species present (Keast 1984; Dionne and Folt 1991), the degree of substrate dissectedness (Hacker and Steneck 1990; Kershner and Lodge 1990; Jeffries 1993), plant biomass (Downing 1986; Cyr and Downing 1988a; Paterson 1993), plant biomass density (Duarte and Kalff 1990), plant surface area (Brown et al. 1988; Taniguchi et al. 2003), and the complexity of the immediate surrounding environment (Sloey et al. 1997). In contrast to this relatively large body of evidence, the effect of macrophyte habitat complexity — according to any of the measures described above — on invertebrate communities in fishless lakes remains unknown.

Many fish species preferentially forage among aquatic weed beds (Mittlebach 1981; Tompkins and Gee 1983; Trebitz et al. 1997). The primary mode of prey detection by many littoral fish is visual (Croy and Hughes 1991). Thus, it is likely that fish play an important role in shaping observed relationships between macrophytes and littoral invertebrate assemblages. Because fish feed most efficiently where they can best see and access prey (Crowder and Cooper 1982; Engel 1988; Manatunge et al. 2000), negative effects of predation by fish on littoral invertebrate communities should be most pronounced in less complex habitats such as low-density weed beds or along the edges of dense weed beds. Very dense patches of macrophytes can reduce both foraging success and efficiency of littoral fish (Dibble et al. 1996). Foraging preferences of fish could in turn affect preferential feeding habitats of invertebrate predators, either through predation (by fish on predatory invertebrates) or through competition for shared prey, resulting in trophic cascades or

more complex trophic interactions through intraguild predation (Hart 2002). Thus, the effects of fish predation on littoral invertebrate abundance and community structure likely vary over small spatial scales in aquatic weed beds and may be correlated with fine-scale gradients of weed-bed structural complexity.

Our objective was to examine the degree to which the structure of aquatic weed beds affect their function as invertebrate habitat across the range of macrophyte structural complexity typically encountered in shallow prairie lakes, while examining the role that fish presence or absence might play in shaping these relationships. We selected three operational levels of habitat complexity over which to compare invertebrate assemblages — individual plants, weed-bed edges, and weed-bed centres — and contrasted these patterns in two lakes with fish and two lakes without fish. This design allowed us to examine in detail littoral invertebrate distributions across gradients of microhabitat complexity within a few lakes with contrasting food-web structure, as opposed to comparing habitats of a single type over a greater number of lakes. Previous studies have examined broad-scale patterns of invertebrate distributions across lakes with and without fish (Zimmer et al. 2000). Because predator impacts in open ecosystem experiments have been shown to be scale-dependent (Englund et al. 2001), our sampling design was purposely chosen to assess littoral invertebrate distributions across gradients of macrophyte complexity smaller than those typically considered in lake studies. This allowed us to investigate differences at spatial scales relevant to the fish and invertebrates occupying these habitats. To assess the generality of our findings, we compared our results from lakes with fish with published patterns observed elsewhere.

Materials and methods

Site description

During the summer of 1998 we sampled four shallow prairie lakes in and around the town of Strathmore, Alberta, Canada (51°2.5'N, 113°24.5'W). The lakes in Strathmore Picnic Area (SPA) and Strathmore Golf Course (SGC) both contained naturally occurring brook stickleback (*Culaea inconstans*). SPA is stocked annually with rainbow trout (*Oncorhynchus mykiss*) by the town of Strathmore. Mushroom Lake and Dawson Lake were deemed fishless after random transects were swum with SCUBA once a month

Table 2. Food-web characterization of the lakes under study.

	Dawson Lake	Mushroom Lake	SGC	SPA
Dissolved phosphorus concentration ($\mu\text{g}\cdot\text{L}^{-1}$) ^a	928 \pm 348	338 \pm 198	20.5 \pm 7.3	35.4 \pm 14.7
Chlorophyll <i>a</i> concentration ($\mu\text{g}\cdot\text{L}^{-1}$) ^a	0.5 \pm 0.18	2.57 \pm 1.54	0.35 \pm 0.06	2.89 \pm 3.62
Total macrophyte biomass ($\text{kg}\cdot\text{m}^{-2}$)	11.80	2.05	5.78	6.98
Invertebrate abundance ($\text{no}\cdot\text{m}^{-2}$) ^a				
Weed-bed centre	51 734 \pm 7 466	31 789 \pm 8 123	95 066 \pm 18 105	287 150 \pm 64 548
Weedbed edge	54 700 \pm 11 906	34 201 \pm 7 374	46 203 \pm 9 380	72 161 \pm 23 513
Individual plants	36 253 \pm 6 060	31 557 \pm 8 029	23 901 \pm 13 649	12 622 \pm 3 078
Fish species present	Fishless	Fishless	<i>Culaea inconstans</i>	<i>Oncorhynchus mykiss</i> , <i>C. inconstans</i>

Note: SGC, Strathmore Golf Course; SPA, Strathmore Picnic Area.

^aValues are given as the mean \pm standard deviation. Dissolved phosphorus and chlorophyll *a* concentrations are summer averages from June, July, and August samples. Standard deviations for invertebrate abundance are based on a sample size of five from samples collected in late August.

from July to early September. No fish were observed in these lakes during this period. Data on physical lake attributes and water chemistry (Table 1) were collected, analyzed, and reported by Jackson (2003).

The four lakes selected for this study differed systematically based on biological attributes measured over the summer (e.g., presence or absence of fish; Table 2). Lakes with fish appeared to be slightly more turbid and held lower concentrations of total phosphorus than lakes without fish (Table 1). All lakes were alkaline, with similar light penetration and dissolved organic carbon concentrations, and only SPA had a maximum depth greater than 2 m. SPA was smaller than the other three lakes, and conductivity in Dawson Lake was slightly higher than in other lakes.

Sample collection

All lakes were sampled in late August, when plants and their associated invertebrates were at or near their maximum seasonal biomass (Carpenter and Lodge 1986; Kornijów 1989). Macrophytes and epiphytic invertebrates were collected by a diver using SCUBA and a sampling device modified from Wollheim and Lovvorn (1995, 1996). The device was a plastic cylinder approximately 0.5 m tall, designed to capture aquatic macrophytes and associated invertebrates occurring within an area of 638 cm². The open end of the cylinder was gently lowered over the macrophytes being sampled. The opposite end was attached to a tapered canvas bag that led to a removable collection cup with a mesh size of 253 μm . Floats were attached to the cup end to ensure that the sampler remained vertical in the water column during sampling. Three legs extended from the bottom of the cylinder to the lake bottom to allow a space of 10–15 cm above bare lake sediments. The open end of the sampler was equipped with a removable lid covered with 253- μm mesh to aid movement through the water column when the lid was attached. The lid was removed just above the top of the plants to minimize capture of organisms not associated with the macrophytes, then lowered carefully over plants until the sampler legs contacted the sediments. Plants were gently severed just above the sediments and the lid of the sampler was replaced. Care was taken to exclude sediments and associated benthic invertebrates from samples. The sampler was then inverted and brought to the surface, where water was

drained through the collection cup. The plant material was removed by hand and placed in a sealable freezer bag. The sides of the sampler were rinsed with deionized water into the collection cup and the contents backwashed into the freezer bag containing the plants. A small amount of water was added to the sample, which was then placed on ice in a dark cooler for transport to the laboratory. Samples were stored in a refrigerator at 4 °C for up to 48 h before processing.

Distinct weed beds to be sampled in our lakes were identified as clear, continuous masses of aquatic macrophytes a minimum of 3 m across at the narrowest point, surrounded entirely by either open water or a combination of open water and shoreline. As all our lakes were relatively shallow (Table 1), distinct weed-bed patches were distributed throughout the entire lake and not limited to areas bordering the shoreline. This allowed the selection of independent weed beds for sampling from within our lakes.

We sampled three distinct littoral microhabitats — individual aquatic plants, weed-bed edges, and weed-bed centres — chosen to reflect the complexity of the surrounding environment in relation to the plants being sampled. An individual plant was defined and selected as a single macrophyte standing on bare sediment at least 2 m away from distinct weed beds. Weed-bed edges consisted of plants sampled on the edges of distinct weed beds. Weed-bed centres were defined as plants sampled from the middle of a dense weed bed, at least 1 m in from all edges to minimize edge effects. Five samples were taken in each habitat across the entire lake between the hours of 1000 and 1400. Weed beds were sampled only once, so that disturbance from taking a centre sample would not influence edge samples taken from the same weed bed, or vice versa. The positions of edge samples from around distinct weed beds were chosen randomly by an observer from a boat.

In the laboratory, samples were poured into a basin with a small amount of tap water. Plants were shaken free of invertebrates, spun in a salad spinner to remove excess moisture, and frozen for later analysis. The remaining debris and invertebrates were concentrated on a 253 μm mesh screen, transferred to containers, and preserved in 70% ethanol. Invertebrates were later sorted from debris and identified to order, suborder, family, or genus (following Clifford (1991)

and Merritt and Cummins (1996)), enumerated, and then categorized according to functional feeding groups (following Merritt and Cummins (1996)).

Plants were thawed, separated, and identified to species following Fassett (1957), Burland (1994), and Moss (1983). Species names were then cross-referenced against the Integrated Taxonomic Information System (ITIS) online database (http://www.cbif.gc.ca/pls/itisca/taxaget?p_ifx=plgt) to report accepted scientific nomenclature. In cases where the ITIS nomenclature was different, we listed the more commonly employed scientific names in brackets behind the currently accepted ITIS conventions, as these may be more familiar to many of our readers. Any remaining invertebrates found on the macrophytes were categorized and enumerated. Plants were spun once more in a salad spinner to remove excess moisture and wet mass was measured.

Surface areas were estimated for plants from SPA and Dawson Lake. Representative plant shoots, stems, and leaves were measured to the nearest 1 mm on a minimum of 20 individual plants for each species. A digital image analyzer was used to measure leaf surface areas of broad-leaved species such as *Potamogeton richardsonii* (*Potamogeton richardsonii*). Averages for stem area and leaf area were calculated for each plant species. Stems and leaves were enumerated and surface area was calculated for the plants in each sample.

Defining measures of littoral habitat complexity

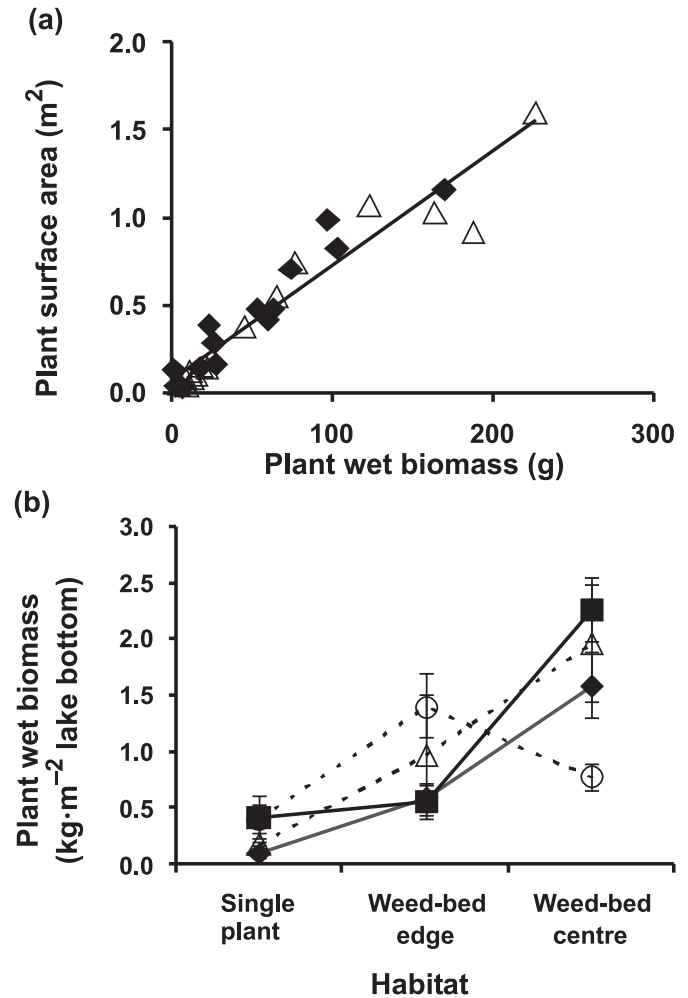
Aquatic macrophytes sampled typically reached the water surface, where they occurred in all our lakes. All samples were taken at depths of approximately 1.3 m (±0.2 m). Care was taken to ensure consistency of depth across samples taken within a lake, which was made easy by the highly regular bathymetry within our lakes: all sloped gently from their maximum depth to shoreline in a parabolic manner. Therefore, we assumed that the volume of the water column sampled was constant across all sampling sites in our lakes.

Plant surface area is a direct measure of the available substrate that littoral invertebrates can occupy within the volume of water sampled. Plant surface area was found to be strongly correlated with plant wet biomass in our study (Fig. 1a; $r = 0.957, p < 0.001, df = 28$). Based on the consistency of this relationship over two lakes and multiple plant species, and the relative ease with which plant wet biomass is measured relative to plant surface area, we chose plant wet biomass per square metre of lake bottom as our quantitative measure of habitat complexity. Thus, we used two independent measures of plant-habitat complexity in this study: microhabitat complexity and plant wet biomass per square metre of lake bottom. The first is defined categorically to describe the complexity of the plants sampled relative to their surrounding environment (i.e., individual plants versus weed-bed edges versus weed-bed centres). The second is defined continuously as wet plant biomass per square metre of lake bottom, which closely reflects plant surface area available to littoral invertebrates.

Statistical analyses

Total invertebrate abundance was log₁₀-transformed to normalize distributions and homogenize variance among fac-

Fig. 1. Measures of aquatic macrophyte complexity in shallow prairie lakes (Strathmore Golf Course (■); Strathmore Picnic Area (◆); Mushroom Lake (○); Dawson Lake (△)). Open symbols represent fishless lakes and solid symbols indicate lakes with fish. (a) Correlation between macrophyte surface area (m²) and macrophyte wet biomass (g) over 30 samples from two lakes. (b) Increase in plant biomass (kg·m⁻² lake bottom) with habitat complexity (qualitative classification) for all lakes but Mushroom Lake. Error bars are ±1 standard error.



tors. The effects of fish (presence or absence; fixed effect), lake (SPA, SGC, Mushroom Lake, or Dawson Lake; random effect), and microhabitat complexity (individual plants, weed-bed edges, or weed-bed centres; fixed effect) on the total numbers of invertebrates encountered per square metre of lake bottom were tested categorically with a nested analysis of variance (ANOVA). Lake was nested within fish status, and we considered all higher order interaction terms. Sheffé's tests were used to evaluate significant terms among fixed effects in the ANOVA. We also used the same nested ANOVA model to test patterns of plant biomass across our qualitative determinations of habitat complexity. Plant biomass was fourth-root-transformed to satisfy assumptions of normality and homogeneity of variance among factors.

We also regressed invertebrate abundance against wet plant biomass for all lakes to examine patterns in total inver-

Table 3. Taxonomic relationships among identified organisms that contributed more than 1% (on average) to their respective functional feeding group (FFG).

Taxonomy of identified specimens						Average frequency of occurrence in FFG (%)	
Phylum and subphylum	Class and subclass	Order and suborder	Family	Tribe and genus	FFG		
Arthropoda							
Crustacea	Branchiopoda	Cladocera	Bosminidae		Filterers	9.12 ^S	
			Daphnidae		Filterers	12.3 ^{T,S}	
			Chydoridae		Filterers	18.2 ^S	
	Maxillopoda Copepoda	Ostracoda			Detritivores	62.4 ^{S^a}	
					Filterers	59.7 ^{T,S^a}	
Malacostraca	Amphipoda		<i>Hyalella</i> sp., <i>Gammarus</i> sp.	Detritivores	23.6 ^T		
Uniramia	Insecta	Diptera	Chironomidae	Non-Tanytopodinae ^b	Scrapers	58.0 ^{T,S^a}	
				Tanytopodinae ^b	Predators	7.2 ^{T,S}	
			Ceratopogonidae	<i>Bezzia</i> sp.	Predators	3.4	
		Ephemeroptera	Baetidae	<i>Baetis</i> sp., <i>Caenis</i> sp.	Scrapers	2.7 ^T	
		Odonata					
		Zygoptera				Predators	32.1 ^{T^a}
Cheliceriformes	Chelicerata						
	Arachnida	Acari	Acara		Predators	15.5 ^{T,S}	
Annelida	Oligochaeta	Lumbriculidae			Detritivores	11.8 ^S	
	Hirudinea				Predators	3.0	
Cnidaria	Hydrozoa	Hydroidea					
		Anthomedusae		<i>Hydra</i> sp.	Predators	17.3	
Mollusca					Scrapers	31.7	

Note: A superscript "T" denotes an item from the trout (*Oncorhynchus mykiss*) diet (Hodgson et al. 1991; MacNeil et al. 1999), and a superscript "S" denotes an item from the brook stickleback (*Culaea inconstans*) diet (Tompkins and Gee 1983) as determined by previous diet studies.

^aThe dominant taxa for each FFG.

^bChironomids were sorted only to this level of taxonomic separation. Though there is a diversity of FFGs at the genus and species levels within both groups of chironomids defined here, the FFGs assigned to these taxonomic divisions indicate the majority representation of species within each group (Paterson 1993; Merritt and Cummins 1996).

tebrate abundance against a continuous measure of habitat complexity. We compared the slopes and intercepts of the regressions between lakes with and without fish, and between lakes within a treatment. We corrected critical α values of our tests for the number of comparisons made. Effect sizes (defined here as the slope of \log_{10} invertebrate abundance with plant biomass) were also compared between lakes to determine the maximum effect size of plant biomass on invertebrate abundance from fishless lakes in our study (Hoenig and Heisey 2001; Colegrave and Ruxton 2003; Di Stefano 2004).

To test the effects of lake and microhabitat on invertebrate community composition, invertebrates were sorted into zooplankton and other algal filter-feeders (hereinafter referred to as filterers), scrapers (feed on epiphyton), shredders (live on plant material), detritivores, and predators (Table 3). Functional feeding groups were represented as numerical proportions of the total invertebrate community to control for variation in total invertebrate abundance between samples. Proportional data often violate the assumption that groups are independent, and distributions of proportional data are frequently not normally distributed and therefore not appropriate for analysis by traditional parametric statistics (Jackson 1997). Arcsine square-root transformations normalized

our proportional data. For each functional feeding group, we used the same nested ANOVA approach described previously to investigate differences among lakes and habitats (shredders, consisting largely of *Halplius* spp. or trichopteran larvae, were extremely rare in our samples and were thus excluded from this particular analysis).

Despite transformations, distributions of some functional feeding groups were found to be heteroscedastic. However, it has been argued that ANOVA is a robust statistical test and that even large departures from the parametric assumptions do not have a great impact on the results of the test, particularly when sample sizes are equal among groups (Zolman 1993; Zar 1999). Comparisons that were found to be heteroscedastic are indicated as such.

Results

Habitat complexity

Generally, plant biomass was best explained by microhabitat complexity (Fig. 1b, Table 4), although a high-order interaction term in the nested ANOVA model was significant (Table 4). With the exception of Mushroom Lake, all lakes demonstrated significant increases in plant biomass with increasing habitat complexity from individual plants to

Table 4. Statistical results for individual factors in statistical ANOVA models examining patterns of invertebrate abundance and plant biomass across littoral habitats (single plants, weed-bed edges, weed-bed centres) and lakes, according to model 1.

Dependent variable	Statistical results for models	Habitat	Fish	Habitat × fish	Lake within fish	Habitat × lake within fish
Log ₁₀ invertebrate abundance	$F_{[11,48]} = 9.64$ $p < 0.0001^a$ $r^2 = 0.69$	0.022 ^a	0.473	0.035 ^a	0.312	0.086
Plant wet biomass	$F_{[11,48]} = 9.29$ $p < 0.0001^a$ $r^2 = 0.68$	0.020 ^a	0.736	0.432	0.613	0.019 ^a

^aSignificant at the 0.05 level.

weed-bed centres (Sheffé’s test, between mean squared error (MSE) = 0.77697, df = 48; individual plants vs. weed-bed centres: Dawson Lake, $p = 0.021$; SPA, $p = 0.002$; SGC, $p = 0.038$; Mushroom Lake, $p > 0.05$).

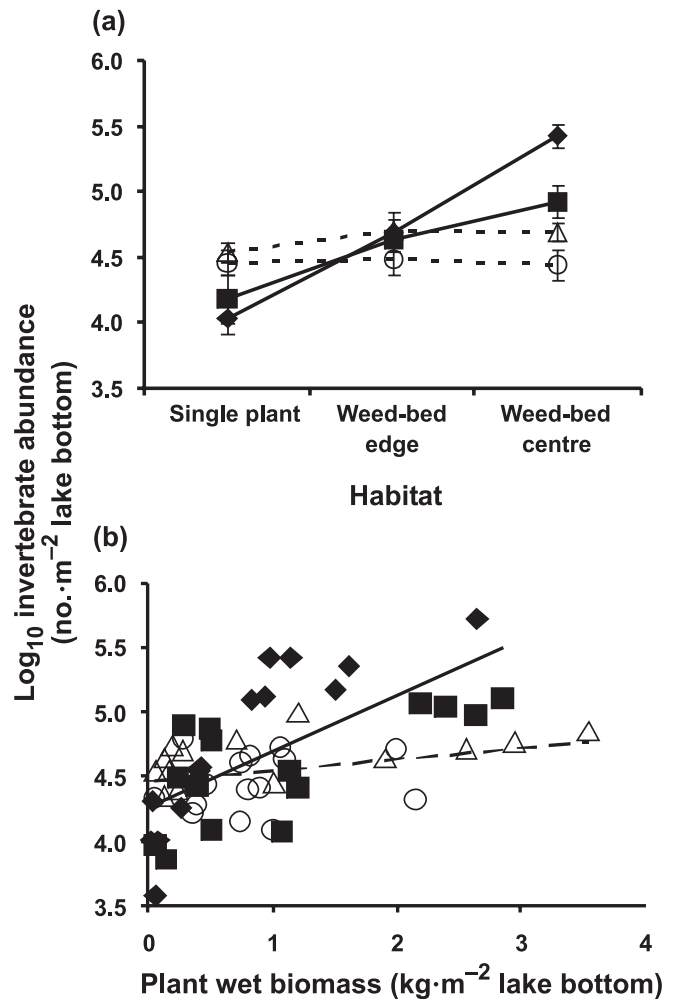
Dawson Lake was dominated by *Ruppia maritima* and *Stuckinia pectinatus* (*Potamogeton pectinatus*); *Myriophyllum sibiricum* (*Myriophyllum exalbescens*), *S. pectinatus*, and *Potamogeton pusillus* dominated SGC and Mushroom lakes; and *S. pectinatus*, *P. richardsonii*, and *Myriophyllum sibiricum* were dominant in SPA. Plant condition, based on visual inspection, was similar in all samples. Systematic differences between plant species composition from one habitat to the next within lakes were not apparent. Owing to the number of samples examined from each habitat within a lake (5) relative to the number of plant species encountered (6), we were unable to assess statistically the effect of plant species composition on invertebrate abundance within habitats. It is not likely that changes in plant species composition and architecture across habitats contributed to our observations, since plant biomass typically increased by an order of magnitude between microhabitats in lakes (Fig. 1b). We assume that these large changes in plant biomass, and therefore surface area (Fig. 1), between microhabitats would have a much greater effect on the amount of substrate available to invertebrate assemblages than minute changes in plant architecture that may have occurred over this gradient because of differences in plant species assemblage.

Total invertebrate abundance

Invertebrate abundance per square metre of lake bottom increased significantly with increasing microhabitat complexity in lakes with fish only (Fig. 2a). A significant interaction found between fish presence and habitat type in the statistical model (Table 4) demanded further exploration with post-hoc comparisons. Invertebrate abundance did not differ significantly between habitat types in fishless lakes (a posteriori comparison of weed-bed centres = weed-bed edges = individual plants, Sheffé’s test, MSE = 0.06516, df = 48, all $p > 0.05$). In contrast, invertebrate abundance increased significantly from individual plant habitats to weed-bed centres in lakes with fish ($p < 0.001$ for individual plants vs. weed-bed edges; $p = 0.009$ for weed-bed edges vs. weed-bed centres).

We used regression and analysis of covariance (ANCOVA) to explore relationships between our continuous measure of littoral habitat complexity (plant biomass) and invertebrate abundance (Fig. 2b), independent of our qualita-

Fig. 2. Log₁₀ invertebrate abundance (no.·m⁻² lake bottom) plotted against habitat complexity in shallow prairie lakes (Strathmore Golf Course (■); Strathmore Picnic Area (◆); Mushroom Lake (○); Dawson Lake (△)). Habitat complexity is represented (a) categorically by sampling location or (b) continuously by wet plant biomass. Open symbols represent fishless lakes and solid symbols represent lakes with fish. Error bars are ±1 standard error.



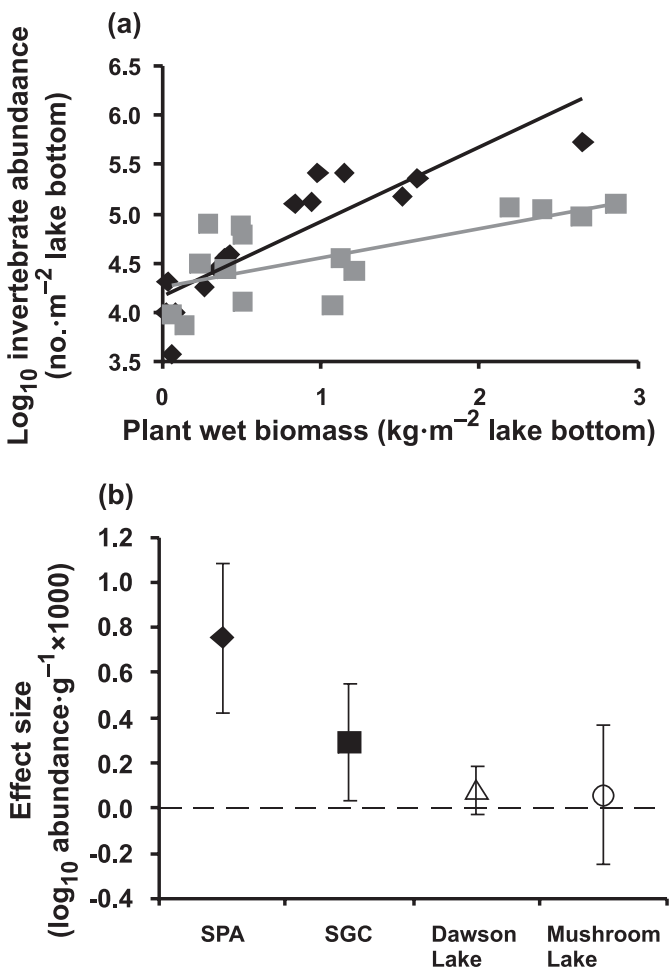
tive designations of microhabitat complexity. Lakes with fish demonstrated a significantly different slope from those without fish (test for heterogeneity of slopes, $F_{[1,56]} = 13.17$, $p = 0.0006$; $p_{crit} = 0.0073$ for seven comparisons). The

Table 5. *P* values for factors in significant statistical models examining littoral invertebrate community patterns.

Dependent variable	Habitat	Fish	Habitat × fish	Lake within fish	Habitat × lake within fish
Filterer community	0.019 ^a	0.884	0.272	<0.001 ^a	0.149
Detritivore community	0.041 ^a	0.444	0.196	<0.001 ^{a,b}	0.580
Scraper community	0.127	0.892	0.218	0.022 ^{a,b}	0.103
Predator community	0.307	0.143	0.172	0.037 ^{a,b}	0.522

^aSignificance at 0.05.^bHeteroscedastic variance among factors.

Fig. 3. (a) \log_{10} invertebrate abundance (no.·m⁻² lake bottom) plotted against habitat complexity in lakes with fish only (Strathmore Picnic Area (SPA; solid symbols and line); Strathmore Golf Course (SGC; shaded symbols and line)). (b) Slopes \pm 98.75% confidence intervals for effect size of plant biomass on \log_{10} invertebrate abundance.



slopes of invertebrate abundance on plant biomass in lakes without fish were not significantly different from zero, nor were the intercepts different from one another (test: slope = 0; $p = 0.8700$ for Mushroom Lake, $p = 0.2000$ for Dawson Lake; test for equal intercepts, $p = 0.1062$; $p_{\text{crit}} = 0.0073$). In contrast, lakes with fish exhibited slopes significantly different from zero ($p = 0.0001$ for SPA, $p = 0.003$ for SGC; $p_{\text{crit}} = 0.0073$) and also differed from one another (test for

heterogeneity of slopes, $F_{[1,52]} = 14.51$, $p = 0.0004$; Fig. 3a; $p_{\text{crit}} = 0.0073$).

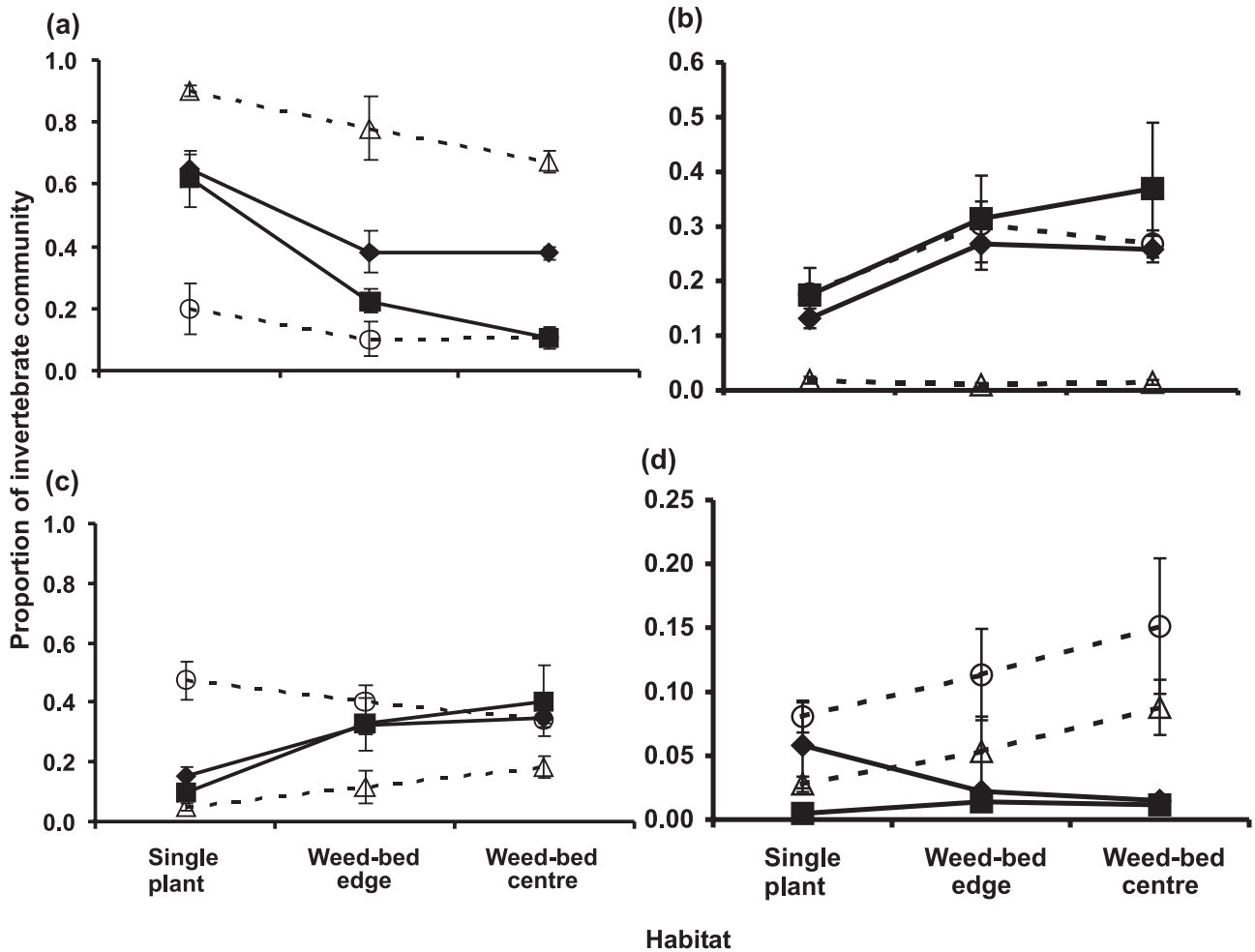
To determine the maximum effect size of plant biomass on invertebrate abundance in fishless lakes, we examined confidence intervals around the slope of \log_{10} total invertebrate abundance with plant biomass (Fig. 3b). We used 98.75% confidence intervals to correct for the number of comparisons made ($\alpha = 0.05/4 = 0.0125$; $\alpha_{\text{one-tailed}} = 0.00625$; confidence interval = $100 \times (1 - 2\alpha_{\text{one-tailed}}) = 98.75\%$) as recommended by Hoenig and Heisey (2001). Based on the largest confidence interval for fishless lakes (Mushroom Lake; Fig. 3b), we would not expect an effect of plant biomass on invertebrate abundance greater than 0.000364 \log_{10} invertebrates/g wet plant biomass. This value overlaps considerably the 95% confidence intervals for both Dawson Lake and SGC, but is smaller than the lower confidence interval for SPA.

Invertebrate functional feeding groups

The proportion of invertebrate predators present in samples was best explained by variation in habitat and lake-specific effects (Table 5). Across all lakes, filterer communities were negatively influenced by increased habitat complexity (Table 5, Fig. 4a; Sheffé's test, MSE = 0.017, df = 48; individual plants < weed-bed edges = weed-bed centres). In lakes with fish, both detritivores and scrapers appeared to increase as a proportion of the invertebrate community as habitat complexity increased (Fig. 4). In fishless lakes, predators appear to make a more significant contribution to invertebrate communities in more complex habitats (Fig. 4d), even though total invertebrate abundance in fishless lakes did not differ between habitats (Fig. 2). This observation is of ecological interest because of the consistency of this pattern in both lakes without fish, and the clear absence of this pattern in lakes with fish (Fig. 4d).

To better understand the significance of this observation, and therefore the role of predators in the invertebrate community of dense weed beds, we performed a randomization test on the relative abundance of predators from weed-bed centres only to examine differences in this particular habitat among lakes. A randomization test was chosen for this analysis because it tests results against the actual distribution from which the data are sampled, and is therefore not sensitive to violations of normality or homoscedasticity. We compared the absolute value of the observed *t* statistic from the comparison of lakes with and without fish ($t = -3.67$) with 10 000 simulated *t* statistics generated from randomly sampling the observed values of transformed relative predator abundance. To account for the fact that these data were a subset of a larger set of data, we corrected our randomiza-

Fig. 4. Invertebrate community composition in shallow prairie lakes with and without fish (Strathmore Golf Course (■); Strathmore Picnic Area (◆); Mushroom Lake (○); Dawson Lake (△)). Open symbols represent fishless lakes and solid symbols represent lakes with fish. Patterns for (a) filterers, (b) detritivores, (c) scrapers, and (d) predators are shown. Error bars are ±1 standard error. Note the differences in scale on the y axis in b and d.



tion critical probability to $p_{crit} = 0.05/12 = 0.004$. The randomized p value from this procedure was 0; of 10 000 simulations, no single t value exceeded that of the observed test (the maximum t value obtained over 10 000 simulations was 3.18).

Discussion

Invertebrate abundance in fishless lakes was unrelated to either macrophyte microhabitat complexity or plant biomass. In contrast, over a similar range of plant species, plant biomass, and microhabitats, abundance of littoral invertebrates in lakes with fish was positively and strongly associated with gradients of habitat complexity. Positive relationships between invertebrate abundance and large-scale habitat complexity in lakes with fish are well documented in the literature (Cyr and Downing 1988a; Zimmer et al. 2000; Tolonen et al. 2001). Our data supported these previous findings and revealed that these patterns occur at much finer spatial scales than was previously considered. Addressing patterns of invertebrate distribution at this scale of investigation may be important when considering scales relevant to

organisms occupying the littoral zone. For instance, some species of fish have been shown to prefer weed-bed edges to other littoral habitats when foraging for littoral invertebrates and (or) forage fish (Trebitz et al. 1997). It has also been suggested that fish foraging is maximized in weed beds of intermediate macrophyte density (Crowder and Cooper 1982). Experimental data have shown that high densities of artificial macrophytes significantly impeded fish foraging (Manatunge et al. 2000). Thus, the ability to accurately describe variation in invertebrate abundance at scales we consider here may have important consequences for modeling littoral invertebrates as prey for fish occupying the littoral zone.

Our study examines how invertebrates distribute themselves in weed beds when fish are absent — a condition that previous studies have not considered. Our findings suggest that trends in littoral invertebrate abundance in fishless lakes differ dramatically from the well-established positive relationship between total invertebrate density and habitat complexity in lakes with fish. The patterns we observed were consistent across both the fishless lakes we considered, and are supported by the limited experimental work that has

been conducted on the topic. For example, Uiblein et al. (1996) reported that ostracods spent a significantly greater amount of time visiting aquatic macrophytes and less time in open water in the presence of a chemical fish cue than when it was absent. Thus, littoral invertebrates may be more closely associated with aquatic macrophytes in the presence of fish, but disperse more widely when this particular predation threat is absent. In contrast to the results of our study, Crowder and Cooper (1982) reported an increase in invertebrate density with increasing weed-bed density in fishless littoral enclosures. However, their results may reflect the movement of invertebrates across their fish-exclusion curtain (4.8 mm mesh) from areas with fish into fishless habitats.

A number of considerations suggest that the potential effect of macrophyte habitat complexity on invertebrate abundance in fishless lakes in this study is ecologically insignificant compared with effects observed in lakes with fish. First, our "fish" effect is likely conservative because both our lakes with fish had higher turbidity than those lacking fish. Rainbow trout and stickleback both rely on visual cues to detect prey (Croy and Hughes 1991; Flamarique and Browman 2001). However, increased turbidity can impair the predatory efficiency of fish (Utne-Palm 2002; De Robertis et al. 2003) and reduce their ability to detect littoral invertebrates in less complex habitats. We detected significant effects of fish presence despite this possibility.

Second, we detected a significant "fish" effect in two lakes with very different fish communities. The dietary preferences of stickleback and rainbow trout overlap considerably, though species-specific differences in body size are likely to generate differences in size-selective preferences for invertebrate prey. The relationship between invertebrate abundance and plant biomass had a shallower slope in SGC than in SPA, possibly reflecting the difference in fish community structure between lakes. Nonetheless, both relationships with habitat complexity were positive, and significantly different from those in fishless lakes. Additionally, the largest confidence interval for our fishless lakes suggests that the largest effect size supported by our data is 0.000364, which is lower than the lower bound of the confidence interval for SPA. Confidence intervals overlapped between SGC and our fishless lakes, which further supports the idea that the strength of fish effects on littoral invertebrate distributions likely depends on fish community structure.

Last, the narrow confidence intervals around the effect size (slope estimate) of plant biomass on invertebrate abundance in Dawson Lake, which includes zero, provides our best evidence that the null hypothesis of no effect between plant biomass and invertebrate abundance in fishless lakes is true. In other words, the inclusion of zero in the error around the slope estimate is not due simply to high variation in invertebrate density between sites sampled in this lake. Despite a consistent increase in plant biomass with habitat complexity in Dawson Lake, mean invertebrate densities were very similar among habitats. This suggests that our inability to detect an effect of habitat complexity on invertebrate abundance in Dawson Lake is less likely to be due to random variation masking a true effect. Our study suggests that the capacity for habitat complexity to affect invertebrate abundance in fishless lakes is too weak to be observable in

fishless lakes at the scale of investigation in this study. However, it remains possible that habitat complexity may structure invertebrate communities in fishless lakes at spatial scales even finer than those investigated here.

In the most complex habitats, predators made up a greater proportion of the littoral invertebrate community in fishless lakes than in lakes with fish. Fishless lakes appeared to support a greater proportion of predators in more complex macrophyte habitats than in less dense habitats. This trend was significant, as evidenced by our randomization test. In lakes with fish, predators appeared to represent an equal proportion of the community across all habitats (SGC), or actually appeared to decrease as a proportion of the community as habitat complexity increased (SPA).

Significant differences in the contribution of predators to invertebrate communities between lakes with and without fish may be due to differences in invertebrate behaviour resulting from differential predation by fish. Like ostracods, some other invertebrates display alternative behaviour depending on whether fish are present or absent. Damselflies, the most common predatory invertebrate in our samples, display a "sit-and-wait" foraging behaviour in the presence of fish (McPeck 1990; Johnson 1991; Wellborn et al. 1996). This behaviour is adaptive for catching prey and avoiding predators. In environments that lack fish, damselflies are more active predators (Johnson 1991). Blois-Heulin et al. (1990) reported similar shifts between "cryptic appearance" and more active behaviour in damselflies from environments with and without fish, respectively. Damselflies are awkward swimmers (M. Rennie, personal observation) and in fishless lakes may find the pursuit of prey more effective across dense weed bed habitats.

The uniformity of invertebrate abundance among habitats in fishless lakes may be due to predation effects of invertebrate predators on nonpredatory invertebrates. Among the growing evidence of predatory effects of littoral invertebrate predators includes a report by Burks et al. (2001) that odonate nymphs were capable of reducing pelagic prey abundance (*Daphnia* sp.) in laboratory and field environments. Odonate nymphs and *Hydra* sp. have also been reported to significantly reduce rotifer abundance in laboratory experiments (Walsh 1995). In a fish removal experiment, Prejs et al. (1997) found depressed numbers of nonpredatory epiphytic invertebrates and more than a doubling of predatory invertebrates 2 years after fish removal. These studies support the hypothesis that in the absence of fish, invertebrate predators are capable of exerting strong negative predatory effects on nonpredatory littoral invertebrate communities. If this is so, predation — whether by fish or invertebrates — may be an important top-down mechanism in shaping the littoral invertebrate communities of shallow prairie lakes. This is particularly true for numerous shallow prairie lakes that harbour dense stands of macrophytes and are subject to high rates of oxygen depletion under ice and winter fish kills (Meding and Jackson 2001, 2003; Jackson 2003).

Proportions of filterers (primarily zooplankton) decreased as microhabitat complexity increased in all lakes. Other studies have shown similar negative relationships between zooplankton and aquatic macrophytes (Cyr and Downing 1988a; but see also Lauridsen and Buenk 1996). Given that

samples were taken from each lake at similar times of the day, horizontal migration patterns of zooplankton would not result in any bias that could generate these results. This negative relationship between the relative abundance of filterers and habitat complexity might be a response to a reduction in suspended algal concentrations in macrophyte beds, brought about by shading from macrophytes (Carpenter and Lodge 1986). Aquatic macrophytes may also reduce water velocity (wind-generated currents in this case), causing algae to settle out into the sediment rather than remain suspended in the water column (Carpenter and Lodge 1986; Hamilton et al. 1990).

Distribution patterns of scrapers and detritivores in lakes with fish increased with littoral habitat complexity. No consistent trend for these two groups was apparent in fishless lakes. The pattern observed for scrapers and detritivores in lakes with fish may be a function of both top-down structuring via predation by fish and bottom-up energetic constraints. A number of the major taxa of scrapers and detritivores found in our samples are typical prey of both brook stickleback and rainbow trout. Mancinelli et al. (2002) found that the exclusion of large predatory fish resulted in an increase in the biomass and abundance of detritivores in experimental leaf packs (interestingly, those authors defined detritivores to include the scraper guild as well, though scrapers, considered on their own, showed no significant treatment effect in their study). However, scrapers feed primarily on epiphytic algae, which require a substrate to grow on (i.e., plants). As a result, scrapers may prefer dense macrophyte habitats with a large plant surface area per square metre of lake bottom. Likewise, detritivores are likely to find greater concentrations of decaying matter in dense weed beds than in open water because of deposition due to macrophyte senescence and the physical properties of weed beds on suspended particulate matter discussed above (Carpenter and Lodge 1986; Hamilton et al. 1990).

It is possible that other factors besides fish presence or absence generated the gradients of invertebrate distributions we measured. It could be argued that differences in water chemistry might generate the patterns we observed. For this to be true, however, chemical differences among lakes would need to also translate into persistent chemical gradients between habitats (i.e., water chemistry by habitat interactions). Additionally, these chemical gradients would have to occur in lakes with fish but not in lakes without fish (a three-way interaction between fish presence, water chemistry, and habitat). We suggest that this scenario is unlikely, since many shallow lakes, including those in our study, undergo frequent and thorough mixing (Blindow et al. 1993; Scheffer et al. 1993). Thus, horizontal chemical gradients between habitats are unlikely to persist long enough to form structural gradients in invertebrate distributions. Additionally, these lakes all occur within a few kilometres of one another and experience similar wind patterns and weather. Therefore, wind-generated mixing should also be similar between all lakes, and not differ between lakes with and without fish. The fact that our measured patterns in invertebrate distributions occur not just between lakes with and without fish, but across habitats within those lakes, suggests that there is a selectively structuring force (i.e., predators) in our study system.

In two recent mesocosm studies, water temperature, nutrient concentrations, and dissolved inorganic carbon have been shown to have positive effects on invertebrate abundance (Jones et al. 2002; McKee et al. 2003). However, both studies were only able to maintain these nutrient gradients by using mesocosm enclosures, which does not reflect the situation in shallow lake habitats in nature. Additionally, both studies demonstrated significant effects of fish (stickleback in one study, rainbow trout in the other) as large and as frequent as water-chemistry effects, and fish effects that were often more pronounced under high-nutrient and warm conditions (i.e., fish by warming or fish by nutrient interactions) — conditions that are consistent with those in the lakes in our study. Therefore, because shallow prairie lakes mix frequently, and all lakes in this study experience similar weather and climate, we believe that chemical gradients in these lakes are unlikely to persist over the time scales required to influence invertebrate abundance patterns directly, and that complex three-way interactions between water chemistry, habitat complexity, and fish presence are an unlikely and unparsimonious alternative explanation for our trends.

Though our study does not directly address how fish presence and habitat complexity interact to affect invertebrate biomass, our results, when considered alongside other findings, may offer some speculative insights. In lakes with fish, total invertebrate abundance increased by one order of magnitude or more with increasing habitat complexity. Other studies in lakes with fish have shown that more complex littoral habitats typically house larger bodied invertebrates than less complex habitats (Hanson 1990; Rasmussen 1993; Tolonen et al. 2003). If invertebrates in our lakes followed a similar pattern, it is very likely that total invertebrate biomass in lakes with fish follows a pattern similar to abundance, i.e., increasing with habitat complexity. In fishless lakes, though we did not observe differences in invertebrate abundance across gradients of habitat complexity, the proportion of predatory invertebrates increased by about 5% over the range of habitat complexity we measured. The dominant predatory invertebrates in this study were damselflies, and this may have resulted in increases in total invertebrate biomass with habitat complexity in fishless lakes; however, it is unclear whether a 5% increase in relative abundance, even in a relatively large-bodied predator, would be significant enough to cause a substantial increase in overall invertebrate biomass.

The functional assemblage of invertebrate communities changed with habitat complexity in each lake we studied. This implies that trophic linkages among invertebrates, and therefore ecosystem function, may also vary substantially across similar gradients of habitat complexity. Macrophyte beds are often assumed to be homogeneous with respect to the invertebrate communities they support (Cyr and Downing 1988a, 1988b; Zimmer et al. 2000). Yet our data suggest that variation in littoral invertebrate community and abundance patterns should be considered at smaller spatial scales — which are perhaps more relevant to the organisms ecologists wish to describe — to better understand patterns of energy flow through these heterogeneous systems. In particular, variability in predation pressure in the littoral zones

of highly productive shallow lakes (via invertebrates or fish) and systematic differences in habitat complexity (and thus prey availability) appear to interact significantly. In doing so, these factors may regulate invertebrate abundance patterns in the littoral zones of lakes and may also play an important role in diversifying the ecological function of the invertebrate community across variably complex habitats.

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