

Biogeography of Stream Fishes in Connecticut: Defining Faunal Regions and Assemblage Types

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Abstract - Stream fish survey data were analyzed to describe patterns of fish distributions in wadeable streams (primarily 1st–4th order) in Connecticut. Species occurrence within the United States Geological Survey 8-digit hydrologic unit code watersheds were used to aggregate similar watersheds into stream fish faunal regions. Within each identified region, multivariate analyses were used to identify major fish assemblage types and associate stream habitat with assemblage types. The analyses revealed an eastern and western faunal region defined primarily by distribution of a few native species. Native species associated with the western watersheds were: *Semotilus atromaculatus* (Creek Chub), *Exoglossum maxillingua* (Cutlips Minnow), and *Cottus cognatus* (Slimy Sculpin). Native fishes associated with the eastern watersheds were: *Erimyzon oblongus* (Creek Chubsucker), *Esox niger* (Chain Pickerel), and *Esox americanus* (Redfin Pickerel). Inclusion of non-indigenous species in the analyses resulted in a similar east–west grouping of watersheds. Five and four assemblage types were identified in the eastern and western faunal regions, respectively. Both regions harbored 3 fluvial assemblages defined longitudinally from headwater streams to larger wadeable streams and a macro-habitat generalist assemblage inhabiting streams with proportionately more pool habitat, but taxonomic membership and indicator species rankings among assemblages were not necessarily identical between the regions. A distinct assemblage dominated by Redfin Pickerel was recognized only in the eastern region. Streams in the western region were generally higher in elevation and colder in water temperature. The discovery and description of eastern and western fish faunal regions and their fish assemblage types will be useful in stratifying the biological monitoring of streams and other aquatic resource management actions in Connecticut.

Introduction

The presence of a fish species or an assemblage of fish species within a particular stream reach is a result of past and current influences operating across hierarchical spatial scales (Frissell et al. 1986, Poff 1997). Physiography, climate, basin geomorphometry, and human introductions influence the composition of regional-scale species pools, but stream fish distribution also is influenced by many local factors including stream size (Lyons 1996, Maret et al. 1997, Newall and Magnuson 1999, Zorn et al. 2002), elevation (Fausch et al. 1994), stream gradient (Lyons 1996, Maret et al. 1997, Waite and Carpenter 2000), water temperature (Lyons 1996, Waite and Carpenter 2000), and hydrological variability (Taylor and Warren 2001, Zorn et al. 2002). Typically, stream habitat and the organisms it supports change predictably as streams increase in size (Goldstein and Meador 2004, Vannote

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et al. 1980), and in some systems, stream fishes may show a longitudinal pattern of coldwater–coolwater–warmwater transitions from headwater to downstream segments (Herlihy et al. 2006, Rahel and Hubert 1991).

Documenting and inventorying stream fish distributions and their habitat hierarchically are useful for aquatic conservation planning. Herlihy et al. (2006) hierarchically classified fish assemblages across the conterminous United States and related the assemblage types to environmental variables such as stream size, nutrient level, and water temperature. At a smaller geographic scale, Pfieger (1989) divided Missouri into 3 physiographic regions (Lowland, Ozark, and Prairie), subdivided each physiographic region into a cluster of similar drainages based on stream fish species and assemblages, and further described faunal changes from headwater creeks to large streams in each drainage cluster. Sowa et al. (2005) recently expanded Pfieger's faunal classification into even finer spatially nested hierarchical levels including segment- and reach-scale information. Zorn et al. (2002) used a hierarchical classification of stream assemblages that describes the stream size-hydrology gradient in Michigan's lower peninsula, and their work led to a valley-segment classification which incorporated landscape variables and assemblage distributions (Seelbach et al. 2006).

We believe that an aquatic classification system in Connecticut will be useful and necessary for aquatic resource management. The state harbors a dense network of wadeable streams, and spatially-extensive sampling has occurred in these streams, but knowledge of stream fish distributions remains largely qualitative. Our objectives were twofold. First, we aggregated watersheds based on species occurrence to define stream fish faunal regions. Second, in each faunal region, we quantitatively defined the major fish assemblage types and described differences in stream habitat among assemblage types.

Methods

Defining fish faunal regions

Fish data. Stream fish survey data on wadeable streams were assembled to examine species occurrence within major watersheds. Given connectivity of watersheds beyond political boundaries, analysis extended beyond Connecticut to include adjoining portions of New York, Massachusetts, and Rhode Island (Fig. 1). The data were obtained from the Connecticut Department of Environmental Protection, New York State Department of Environmental Conservation, Massachusetts Department of Fish and Game, and Rhode Island Department of Environmental Management. Most of the stream surveys were conducted between 1990 and the present, but some samples were taken in the 1980s. Sampling periods primarily ranged from June to September, and stream lengths sampled varied by state agency and stream size.

Stream survey datasets were screened by several criteria. Wadeable stream samples were limited to those collected with backpack or tote-barge electro-fishers and generally corresponded to 1st–4th order streams at the 1:24,000 scale. Records from larger streams collected with boat electrofishing were not available in all watersheds and were excluded. Hybrids, unidentified

individuals, and samples with ≤ 10 total individuals were deleted from analysis. When repeat visits were made to the same sampling location, all visits were used to score whether a species was present or absent at the site. Species present in fewer than 5% of the sites were excluded to reduce potential effects of rare species on multivariate analysis (McCune and Grace 2002), but *Erimyzon oblongus* (Creek Chubsucker) was retained because it is known to occur in eastern Connecticut (Whitworth 1996)—its presence is a zoogeographical signal, rather than noise. Diadromous species, *Anguilla rostrata* Lesueur (American Eel) and *Salmo salar* Linnaeus (Atlantic Salmon), also were excluded from analyses. The resultant dataset contained 2218 stream sites with 25 native and non-indigenous species ($n = 1184$ for Connecticut, $n = 391$ for New York, $n = 481$ for Massachusetts, and $n = 162$ for Rhode Island; Table 1).

Statistical analysis. Species occurrence was evaluated to group similar watersheds in Connecticut and adjoining areas. Given the small size of the study area, the landscape was assumed to be relatively homogeneous terrestrially, being defined by regionally operating factors such as physiography and climate (Omernik 1987). Our intent in the first series of analyses was to

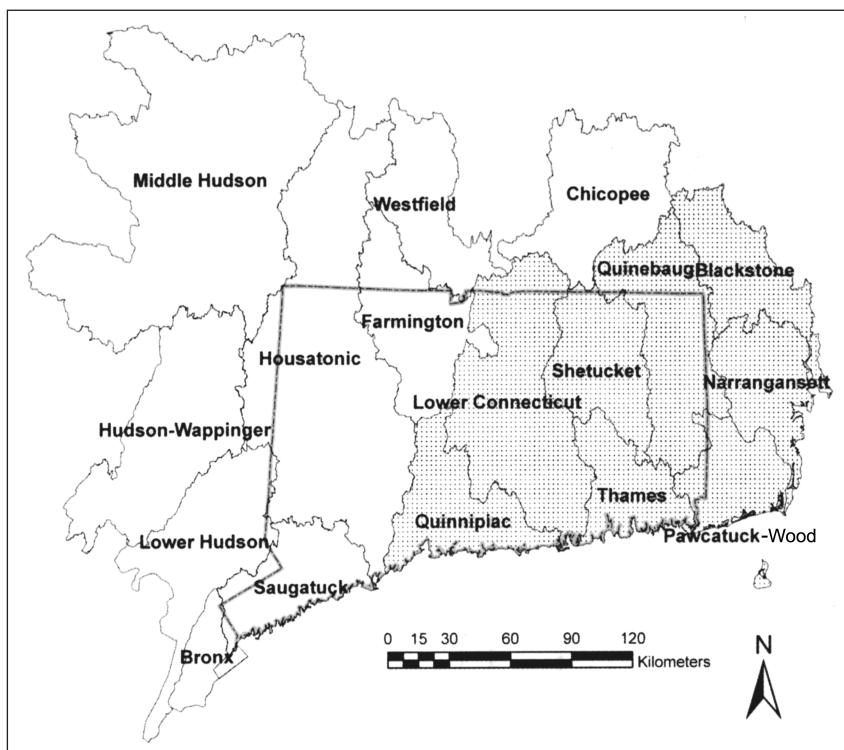


Figure 1. A map of the USGS 8-digit hydrologic units (HUC) watersheds and two faunal regions recognized in this study for Connecticut and its adjacent watersheds. The HUC watersheds are encircled by solid lines with watershed names. The western and eastern faunal regions are indicated by open and stippled polygons, respectively. Dashed lines are the state boundaries of Connecticut.

divide the study region into clusters of similar watersheds based on stream fish occurrence, corresponding approximately to the drainage-level classification of Pfleiger (1989).

Sixteen watersheds were delimited using the United States Geological Survey's National hydrography dataset 8-digit hydrologic unit code (HUC). The study area encompassed 17 HUC watersheds (Fig. 1), but because of its small size, the Bronx watershed in New York was joined with the adjacent Saugatuck watershed. Relative occurrence of each fish species in each watershed was calculated as the total number of sites where the species was present divided by the total number of sites in the watershed, resulting in a species occurrence by HUC watershed matrix. Occurrence values were arcsine square-root transformed for use in multivariate analyses and Mantel tests.

Cluster and ordination analyses were conducted separately for native species only and native plus non-indigenous species using PC-ORD version 5 (MJM Software, Gleneden Beach, OR). The distributions of native species may represent historical biogeographic patterns of occurrence. A

Table 1. Twenty-five native and non-indigenous fish species used to define stream fish faunal regions in Connecticut and adjoining watersheds. Species are listed in descending order of occurrence among 2218 stream sites across the study region. Ecological characteristics of fish species are from regional references (Armstrong et al. 2001, Halliwell et al. 1999, Whitworth 1996). Abbreviations are: % = percent occurrence in Connecticut and others; Temp (temperature): C = cold water, C-W = cool water, W = warm water; SF (stream flow): FS = fluvial specialist, FD = fluvial dependent, MG = macro-habitat generalist; To (tolerance): I = intolerant, M = intermediate, T = tolerant; Fe (feeding): GF = generalist feeder (e.g., omnivorous fishes), BI = benthic insectivore, TC = trophic carnivore.

Common name	Scientific name	Species coding	%	Temp	SF	To	Fe
Blacknose Dace	<i>Rhinichthys atratulus</i> Hermann	BL	68.3	C-W	FS	T	GF
White Sucker	<i>Catostomus commersoni</i> Lacepède	WS	64.2	C-W	FD	T	GF
Brook Trout	<i>Salvelinus fontinalis</i> Mitchell	BK	51.8	C	FS	I	TC
Brown Trout*	<i>Salmo trutta</i> Linnaeus	BN	42.2	C	FD	I	TC
Pumpkinseed	<i>Lepomis gibbosus</i> Linnaeus	PS	39.0	W	MG	M	GF
Tessellated Darter	<i>Etheostoma olmstedi</i> Storer	TD	37.9	C-W	FS	M	BI
Longnose Dace	<i>Rhinichthys cataractae</i> Valenciennes	LD	36.9	C-W	FS	M	BI
Bluegill*	<i>Lepomis macrochirus</i> Rafinesque	BG	33.1	W	MG	T	GF
Largemouth Bass*	<i>Micropterus salmoides</i> Lacepède	LM	31.3	W	MG	M	TC
Common Shiner	<i>Luxilus cornutus</i> Mitchell	CS	31.0	C-W	FD	M	GF
Creek Chub	<i>Semotilus atromaculatus</i> Mitchell	CR	28.2	C-W	MG	T	GF
Fallfish	<i>Semotilus corporalis</i> Mitchell	FF	27.1	C-W	FS	M	GF
Golden Shiner	<i>Notemigonus crysoleucas</i> Mitchell	GS	20.1	W	MG	T	GF
Brown Bullhead	<i>Ameiurus nebulosus</i> Lesueur	BB	19.7	W	MG	T	GF
Chain Pickerel	<i>Esox niger</i> Lesueur	CP	17.1	W	MG	M	TC
Redbreast Sunfish	<i>Lepomis auritus</i> Linnaeus	RS	14.7	W	MG	M	GF
Redfin Pickerel	<i>Esox americanus</i> Gmelin	RF	14.3	W	MG	M	TC
Yellow Perch	<i>Perca flavescens</i> Mitchell	YP	12.7	C-W	MG	M	TC
Cutlips Minnow	<i>Exoglossum maxillingua</i> Lesueur	CM	11.1	W	FS	I	BI
Rock Bass*	<i>Ambloplites rupestris</i> Rafinesque	RB	9.6	C-W	MG	M	TC
Smallmouth Bass*	<i>Micropterus dolomieu</i> Lacepède	SM	9.5	C-W	MG	M	TC
Rainbow Trout*	<i>Oncorhynchus mykiss</i> Walbaum	RW	9.2	C	FD	I	TC
Slimy Sculpin	<i>Cottus cognatus</i> Richardson	SC	9.0	C	FS	I	BI
Yellow Bullhead*	<i>Ameiurus natalis</i> Lesueur	YB	5.4	W	MG	T	GF
Creek Chubsucker	<i>Erimyzon oblongus</i> Mitchell	CH	2.8	W	FS	I	GF

*Non-Indigenous to the study region.

parallel analysis, which might help in understanding patterns in the current distribution of stream fishes, was performed with inclusion of non-indigenous species, many of which are naturalized and widespread in the study watersheds that. The Sorenson distance measure with the flexible beta linkage method (beta = -0.25) was used in the cluster analysis (McCune and Grace 2002). Nonmetric multidimensional scaling (NMS), an ordination technique unencumbered by assumptions of multivariate linearity, was used with Sorenson distance to simultaneously ordinate watersheds and fish species in fish-occurrence space. NMS extracts major gradients in the data structure by iteratively searching for positions that minimize departures of an ordination structure from the original data. It graphically presents (dis)similarities of sampling entities, such that watersheds plotted close together in the ordination space are more similar in their fish occurrence than those far apart. The general guidelines provided by McCune and Grace (2002) were followed to execute NMS. Specifically, a preliminary run was executed to identify the best dimensionality of the data. A scree plot also was examined to help determine dimensionality. Then, a final run was executed with the number of dimensions set and the starting configuration that worked best in the preliminary run.

The influence of non-indigenous species on watershed groupings was tested by a Mantel test, which evaluates the congruence between two distance matrices (Sorenson distance, Monte Carlo randomization test, 10,000 permutations). If the addition of non-indigenous species exerts a major influence on watershed aggregation, distance matrices derived from native species only and the native species plus non-indigenous species will not be significantly associated.

Characterization of fish assemblage types and stream habitat

Fish data. Characterization of fish assemblage types was limited to a subset of stream fish data in Connecticut, which was collected by the Connecticut Department of Environmental Protection between 1988 and 1994 and incorporated a number of stream habitat variables including stream width, depth, gradient, elevation, water temperature, and pool/riffle ratio (Hagstrom et al. 1989, 1990, 1991, 1992, 1995, 1996). Sampling occurred from June to October, and all fish samples were taken using 3-pass electro-fishing depletions of block-netted sections. Fish catch was calculated as the proportional abundance of each species at each stream site. In each faunal region delineated as previously described, rare species (<5% occurrence in each region) were excluded from analyses. In addition, 2 diadromous species, the American Eel and *Petromyzon marinus* Linnaeus (Sea Lamprey), and 2 non-indigenous trout species, *Salmo trutta* (Brown Trout) and *Oncorhynchus mykiss* (Rainbow Trout), were excluded from analyses. Migrations of diadromous fishes are often obstructed by numerous dams in Connecticut, and the presence of a diadromous species in a stream may primarily indicate current access to the ocean. The 2 trout are stocked widely across Connecticut; each spring hundreds of thousands of individuals of these species are released in publicly accessible streams. Their presence in a stream primarily reflects current stocking practices. The final dataset contained 24 fish species and 891 sites (Table 2).

Table 2. Results of indicator species analysis for 4 fish assemblage types identified in the western faunal region and 5 fish assemblage types identified in the eastern faunal region in Connecticut. Assemblage type was used as the grouping variable, and in each faunal region the largest indicator value for each species is listed with its associated P -value. Indicator values > 10 with P -value < 0.05 are marked with an “*”.

Western faunal region in Connecticut			Eastern faunal region in Connecticut		
Assemblage type	Species	Indicator values (%)	Assemblage type	Species	Indicator values (%)
Assemblage A (n = 76)	Brook Trout	72.9 ($P = 0.0001$)*	Assemblage A (n = 103)	Brook Trout	62.8 ($P = 0.0001$)*
Assemblage B _w (n = 150)	Blacknose Dace	53.3 ($P = 0.0001$)*	Assemblage B _E (n = 135)	Blacknose Dace	66.1 ($P = 0.0001$)*
Assemblage C _w (n = 163)	Creek Chub	38.5 ($P = 0.0001$)*	Assemblage C _E (n = 168)	Fallfish	54.7 ($P = 0.0001$)*
	White Sucker	47.0 ($P = 0.0001$)*		Redbreast Sunfish	42.1 ($P = 0.0001$)*
	Longnose Dace	38.3 ($P = 0.0001$)*		Tessellated Darter	39.1 ($P = 0.0001$)*
	Common Shiner	34.5 ($P = 0.0001$)*		White Sucker	35.0 ($P = 0.0002$)*
	Tessellated Darter	29.5 ($P = 0.0003$)*		Common Shiner	34.4 ($P = 0.0003$)*
	Redbreast Sunfish	20.8 ($P = 0.0017$)*		Longnose Dace	30.3 ($P = 0.0003$)*
	Fallfish	19.7 ($P = 0.0036$)*		Largemouth Bass	23.5 ($P = 0.0122$)*
	Cutlip Minnow	19.5 ($P = 0.0004$)*		Bluegill	22.5 ($P = 0.0149$)*
	Rock Bass	11.3 ($P = 0.0140$)*		Spatial Shiner	20.2 ($P = 0.0018$)*
	Smallmouth Bass	8.9 ($P = 0.0267$)		Smallmouth Bass	18.5 ($P = 0.0025$)*
	Fathead Minnow	5.3 ($P = 0.1165$)		Green Sunfish	4.4 ($P = 0.3727$)
Assemblage D _w (n = 26)	Pumpkinseed	70.8 ($P = 0.0001$)*	Assemblage D _E (n = 52)	Brown Bullhead	38.5 ($P = 0.0001$)*
	Brown Bullhead	40.5 ($P = 0.0001$)*		Chain Pickerel	33.1 ($P = 0.0010$)*
	Golden Shiner	36.1 ($P = 0.0001$)*		Pumpkinseed	21.6 ($P = 0.0483$)*
	Bluegill	35.2 ($P = 0.0001$)*		Golden Shiner	17.5 ($P = 0.0551$)*
	Chain Pickerel	34.0 ($P = 0.0001$)*		Yellow Perch	14.5 ($P = 0.0485$)*
	Largemouth Bass	33.3 ($P = 0.0001$)*		Creek Chubsucker	7.0 ($P = 0.0811$)
	Yellow Perch	23.2 ($P = 0.0001$)*			
	Redfin Pickerel	22.9 ($P = 0.0001$)*			
			Assemblage E (n = 13)	Redfin Pickerel	87.9 ($P = 0.0001$)*

Statistical analysis. Within faunal regions, analyses were conducted to identify fish assemblage types and species that typified each assemblage. Similar stream sites were grouped using arcsine square-root transformed proportional abundance of fish species in a cluster analysis (PC-ORD, Sørensen distance, flexible beta linkage, beta = -0.25). Several criteria were used to define the number of fish assemblage types in the resultant cluster dendrogram (i.e., “pruning” the dendrogram into meaningful groups). First, indicator species analysis was used as a quantitative criterion (PC-ORD; McCune and Grace 2002). Indicator species analysis combines a measure of ubiquity of a species in a particular group and a measure of fidelity of a species to the particular group, and calculates indicator values that range from 0% (no indication) to 100% (perfect indication). As such, a species that is exclusively found in an assemblage type and is ubiquitous among sampling sites of that particular type receives a high indicator value, identifying it as indicative of that particular fish assemblage. Fish species with an indicator value of $\geq 10\%$ and an associated P -value < 0.05 were considered good indicators of an assemblage type (Herlihy et al. 2006). P -values of indicator values (Monte Carlo method, 10,000 permutations) were averaged across all species when the cluster dendrogram was pruned at 2, 3, 4, 5, and 6 levels of division, and the minimal average was used as a guide in determining the number of meaningful fish assemblages types (McCune and Grace 2002). Second, canonical discriminant analysis (CDA; SAS version 9.1, SAS Institute Inc., Cary, NC) was used to visualize relations between fish assemblage types and as a dimension-reduction technique to contrast among-group differences. Fish assemblage type was used as an a priori categorical variable in the CDA to construct linear combinations of the quantitative variables that maximize among-group separation while minimizing within-group dissimilarity. Bi-variate plots from this analysis were examined for the presence of noticeable separation among fish assemblage types. Additionally, spatial distributions of assemblage types were examined to see if finer pruning of the cluster dendrogram supported recognition of additional assemblage types.

Habitat characteristics (stream width, depth, gradient, elevation, water temperature, and pool/riffle ratio) were compared among the fish assemblage types in each faunal region. Kruskal-Wallis tests (SAS) were used to test for differences among habitat and fish assemblages because the raw data were non-normal and heteroscedastic; transformations did not improve the data structure. When a significant difference ($P < 0.05$) among fish assemblages was detected for a habitat characteristic, a post-hoc two-tailed t-test was applied for all possible pair-wise comparisons using a contrast statement in PROC MULTTEST (permutation adjusted P -value < 0.05 for each pair-wise comparison).

Results

Defining fish faunal regions

Both cluster and NMS analyses indicated an east–west pattern of watershed alignment based on native fish species (Fig. 2a, b). The division in the cluster analysis generally separated eastern watersheds (Narragansett to

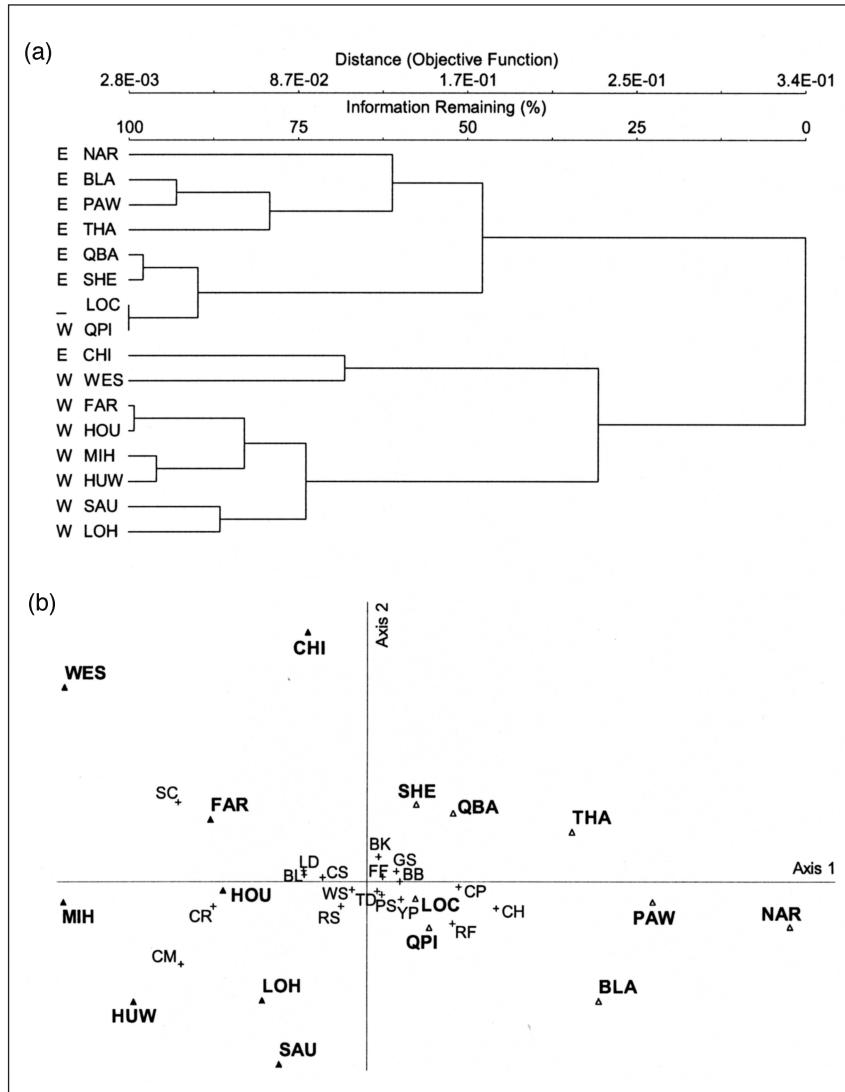


Figure 2. Cluster analysis dendrogram (a) and nonmetric multidimensional scaling (NMS) ordination (b) of 18 native stream fish species. Codes located to the left of each watershed in the dendrogram indicate watersheds located to the east (E) or west (W) of the Lower Connecticut watershed. The NMS graph was rotated to highlight the east–west pattern of watershed grouping. Open and filled triangles indicate eastern and western faunal regions, respectively (see Fig. 1), and crosses denote fish species (see species coding in Table 1). Watershed abbreviations are: BLA = Blackstone, NAR = Narragansett, PAW = Pawcatuck-Wood, QBA = Quinebaug, SHE = Shetucket, THA = Thames, LOC = Lower Connecticut, QPI = Quinnipiac, CHI = Chicopee, WES = Westfield, FAR = Farmington, HOU = Housatonic, SAU = Saugatuck, MIH = Middle Hudson, HUW = Hudson-Wappinger, and LOH = Lower Hudson.

Quinnipiac) from western watersheds (Chicopee to Lower Hudson) (Fig. 2a). NMS yielded a 2-dimensional best-fit solution (50 iterations, final stress = 7.661, instability = 0.00048), and grouped watersheds across an east to west gradient (Fig. 2b, Axis 1: $r^2 = 0.761$, Axis 2: $r^2 = 0.185$). The gradient placed western watersheds to the left on Axis 1, which was associated with *Exoglossum maxillingua* (Cutlips Minnow), *Semotilus atromaculatus* (Creek Chub), and *Cottus cognatus* (Slimy Sculpin). Eastern watersheds were primarily located to the right on Axis 1, which was associated with Creek Chubsucker, *Esox niger* (Chain Pickerel), and *Esox americanus* (Redfin Pickerel). However, as evidenced by their more central positions in the ordination space, the associations of these species were not as strong as those of Cutlips Minnow, Creek Chub, and Slimy Sculpin in the western region. Axis 2 appeared to represent a north–south gradient in the western faunal region. Northern inland watersheds (Chicopee and Westfield) were contrasted with more southern coastal watersheds (Saugatuck, Lower Hudson, and Hudson-Wappinger). Other native fish species, such as *Luxilus cornutus* (Common Shiner), *Catostomus commersoni* (White Sucker), and *Etheostoma olmstedi* (Tessellated Darter), showed no distinctive distribution patterns, being placed near the center of the ordination space (Fig. 2b).

The addition of non-indigenous species did not change the east–west pattern of watershed aggregation (Fig. 3a, b). The Mantel test yielded a strong correlation between the natives only and natives plus non-indigenous distance matrices (Mantel $r = 0.98$, $P = 0.0001$), indicating that non-indigenous species had little effect on the structure of watershed aggregation. Cluster analysis produced the east–west grouping of watersheds similar to the native-only analysis. NMS also showed the east–west gradient (66 iterations, final stress = 7.76, instability = 0.00006, 2 dimensional best-fit solution): eastern and western watersheds were plotted at the upper and lower ends of Axis 1 ($r^2 = 0.776$), respectively. Axis 2 ($r^2 = 0.171$) again appeared to represent a north–south gradient in the western faunal region: northern Chicopee and Westfield watersheds were contrasted with southern Saugatuck, Lower Hudson, and Hudson-Wappinger watersheds. Non-indigenous species generally were plotted near the center of the NMS ordination, indicating no strong associations with particular watersheds and/or widespread distributions across the study area.

The strong east–west patterns observed in cluster and NMS analyses support recognition of eastern and western faunal regions. The differences in the 2 regions resulted from distributional patterns of a few species (i.e., associations of Cutlips Minnow, Creek Chub, and Slimy Sculpin with the western region, and associations of Creek Chubsucker, Chain Pickerel, and Redfin Pickerel with the eastern region). In fact, the 2 regions shared most species.

Characterization of fish assemblage types

In the eastern region, analyses supported recognition of 5 assemblage types. The average P -value of indicator values across all species from indicator species analysis was minimal when the eastern cluster dendrogram (chaining = 0.49%) was pruned at 4 clusters (average P -values, 0.1067,

0.0343, 0.0140, 0.0320, and 0.0442 for 2, 3, 4, 5, and 6 clusters, respectively). The *P*-value at 4 clusters was less than half of those at the neighboring 3 and 5 clusters, conferring statistical support for 4 fish assemblage types. In addition, CDA suggested the presence of a fifth distinct fish assemblage type dominated by Redfin Pickerel (Fig. 4a). Streams belonging to this assemblage type were typically found in the southeastern corner of Connecticut and the Connecticut River floodplain and valley (Fig. 5). Indicator

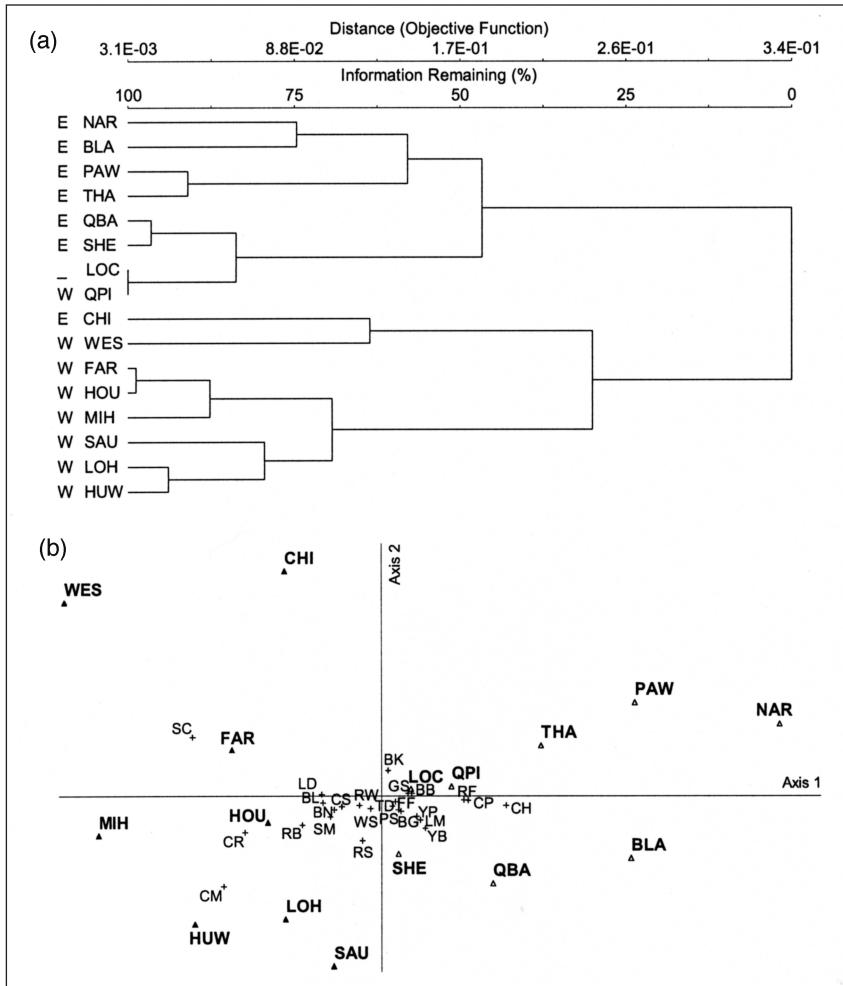
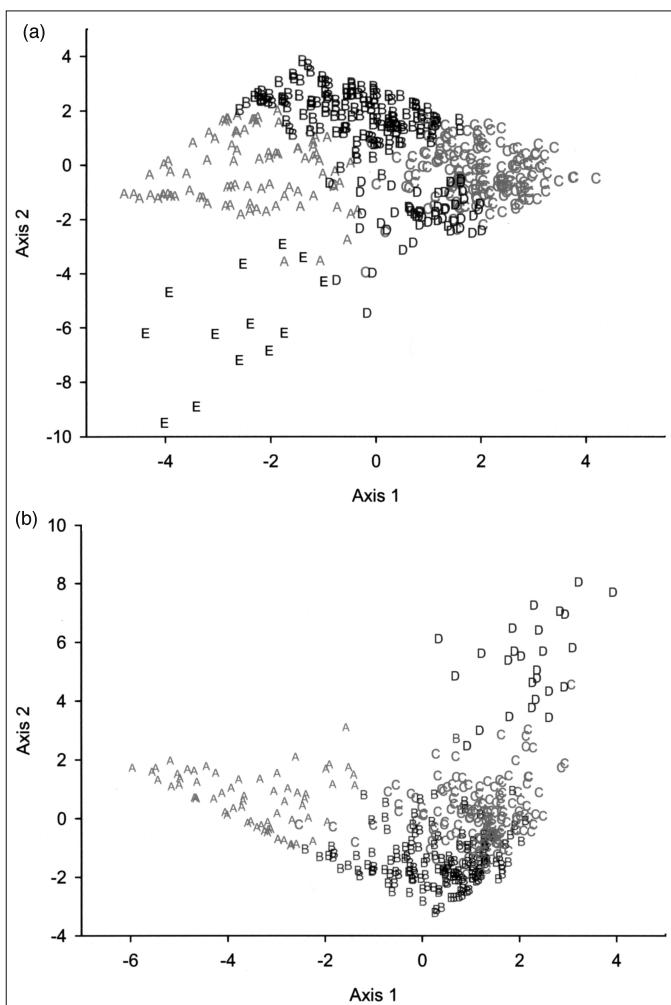


Figure 3. Cluster analysis dendrogram (a) and nonmetric multidimensional scaling (NMS) ordination (b) of 18 native and 7 non-indigenous stream fish species. Codes located to the left of each watershed in cluster analysis dendrogram indicate watersheds located to the east (E) or west (W) of Lower Connecticut watershed. The NMS graph was rotated to highlight the east–west pattern of watershed grouping. Open and filled triangles indicate eastern and western faunal regions, respectively (see Fig. 1), and crosses denote fish species (see species coding in Table 1). Watershed abbreviations follow those in Figure 2.

values characterized typical taxonomic membership of each assemblage type (Table 2). Given the species compositions and ecological characteristics (Table 1), the 5 assemblage types in the eastern faunal region were termed (1) *Salvelinus fontinalis* (Brook Trout) dominated assemblage (Assemblage A), (2) *Rhinichthys atratulus* (Blacknose Dace) dominated assemblage (Assemblage B_E), (3) eastern mixed fluvial assemblage (Assemblage C_E), (4) eastern mixed macro-habitat generalist assemblage (Assemblage D_E), and (5) Redfin Pickerel dominated assemblage (Assemblage E). Assemblages A, B_E, and E were taxonomically simple; Brook Trout, Blacknose Dace, and Redfin Pickerel were the only dominant species, respectively. In contrast, Assemblages C_E and D_E were more diverse. Assemblage C_E, with 10 species, was the most diverse stream fish community in terms of the number of statistically significant indicator species. It was best characterized by fluvial specialists or fluvial dependents, since 5 of the first 6 indicator species were fluvial

Figure 4. Discriminant canonical analysis of the eastern faunal region (a) and the western faunal region (b) in Connecticut. Letters in the graphs indicate stream fish assemblage-type designations in Table 2. Taxonomic compositions differ between the two faunal regions for Assemblages B_(E-W), C_(E-W), and D_(E-W).



species including *Semotilus corporalis* (Fallfish), Tessellated Darter, White Sucker, Common Shiner, and *Rhinichthys cataractae* (Longnose Dace). An exception was *Lepomis auritus* (Redbreast Sunfish), a macro-habitat generalist, which had the second highest indicator value in Assemblage C_E. Three other macro-habitat generalists, *Micropterus salmoides* (Largemouth Bass), *Lepomis macrochirus* (Bluegill), and *Notropis hudsonius* (Spottail Shiner), also were indicator species of assemblage C_E, although their indicator values were lower. Assemblage D_E was composed of 4 statistically significant indicator species of macro-habitat generalists: *Ameiurus nebulosus* (Brown Bullhead), Chain Pickerel, *Lepomis gibbosus* (Pumpkinseed), and *Perca flavescens* (Yellow Perch). Proportionately, Assemblage C_E dominated the sites (36%), followed by Assemblage B_E (29%), Assemblage A (22%), Assemblage D_E (11%), and Assemblage E (3 %) in the eastern region. Assemblage E was constrained geographically, but other assemblages were distributed throughout the eastern region (Fig. 5).

Analyses of the western region supported recognition of 4 assemblage types. The average p-value of indicator values from indicator species analysis across all species was minimal when the cluster dendrogram (chaining = 0.66%) was pruned at 5 clusters (averaged p-values were 0.0121, 0.0166, 0.0078, 0.0032, and 0.0076 for 2, 3, 4, 5, and 6 levels of divisions, respectively). The p-value at 5 clusters was less than half that of the neighboring 4 and 6

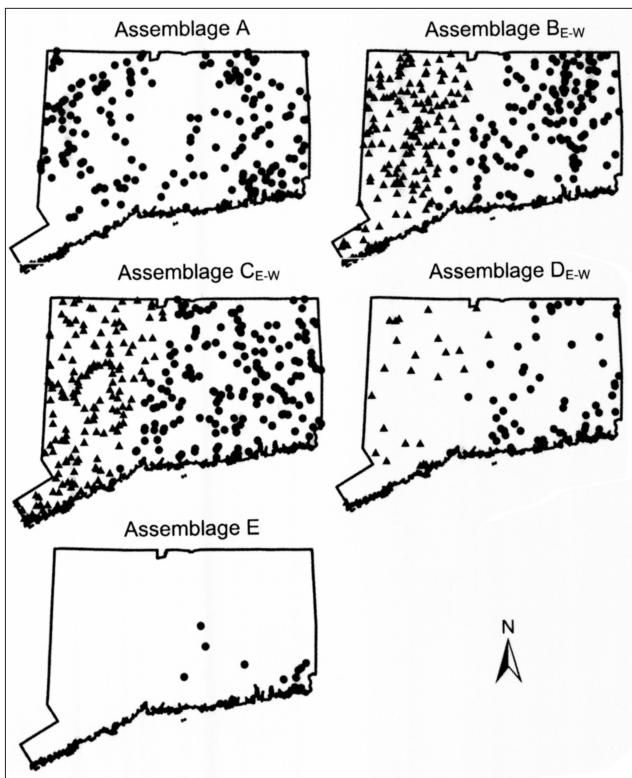


Figure 5. Distributions of the fish assemblage types in two faunal regions within Connecticut. Assemblage-type designations follow those in Table 2. Where taxonomic compositions differ between the two faunal regions (Assemblages B_{E-W}, C_{E-W}, and D_{E-W}), stream sites in the eastern region and the western region are represented by circles and triangles, respectively.

clusters. However, when pruned at 5 groups, assemblages showed substantial overlap in the CDA, and none showed discrete spatial distributions. Recognition of 4 groups reduced the overlap in the CDA and produced more meaningful separation in multivariate space (Fig. 4b). Indicator values characterized typical taxonomic membership of each of the 4 assemblage types (Table 2). The 4 assemblage types were ecologically similar to Assemblages A, B_E, C_E, and D_E in the eastern faunal region: (1) Brook Trout dominated assemblage (Assemblage A), (2) Blacknose Dace-Creek Chub dominated assemblage (Assemblage B_W), (3) western mixed fluvial assemblage (Assemblage C_W), and (4) western mixed macro-habitat generalist assemblage (Assemblage D_W). Assemblage A was taxonomically identical to that in the eastern region, and Brook Trout was the only statistically significant indicator. Creek Chub, in addition to Blacknose Dace, characterized Assemblage B_W in the western region. Assemblages C_W and D_W were best represented by fluvial species and macro-habitat generalists, respectively, but their taxonomic composition and indicator value rankings differed from the eastern region. Specifically, Assemblage C_W was almost exclusively dominated by fluvial species, and Redbreast Sunfish and *Ambloplites rupestris* (Rock Bass), the only macro-habitat generalists belonging to this assemblage type, had smaller indicator values. Interestingly, the first 6 indicator species were identical between Assemblages C_W and C_E, but the rankings of their indicator values showed an inverse relationship between the assemblages, such that Fallfish shifted from rank 1 in the east to rank 6 in the west; Redbreast Sunfish, from 2 to 5; Tessellated Darter, from 3 to 4; White Sucker, from 4 to 1; Common Shiner, from 5 to 3; and Longnose Dace, from 6 to 2. Assemblage D_W was again exclusively dominated by macro-habitat generalists, but more species (8 statistically significant indicator species) represented the assemblage than its counterpart in the eastern region (4 significant indicator species). Species rankings also differed between Assemblages D_W and D_E, and Pumpkinseed had a notably high indicator value (70.8%) in the western region. In the western region, Assemblage C_W was again the most numerically abundant (39%), followed by Assemblage B_W (36%), Assemblage A (18%), and Assemblage D_W (6%). The 4 assemblage types were distributed across all drainages in the western region (Fig. 5).

Habitat characterization

The 2 faunal regions shared similar patterns of fish assemblage-habitat associations related primarily to longitudinal transitions in stream size and secondarily to a subdivision between fluvial species and macro-habitat generalists. In each region, stream width, depth, gradient, elevation, water temperature, and pool/riffle ratio were all significantly different among the assemblage types (Kruskal-Wallis test: $P < 0.0001$ for all habitat variables in each region; Table 3). Both regions showed a longitudinal transition of fluvial species from Assemblage A to Assemblage B_E or B_W, and finally to Assemblage C_E or C_W, with increasing width, depth, and water temperature and with decreasing stream gradient and elevation. Assemblages D_E and especially D_W were associated with habitat characteristics that were intermediate with regard to stream size, and inhabited streams with high pool/riffle

Table 3. Stream habitat characteristics in eastern and western faunal regions in Connecticut. Numbers reported are median values. In both regions, all habitat variables are significantly different among assemblage types (Kruskal-Wallis test at $P < 0.05$), and for each habitat variable in each region values followed by the same alphabetical letters are not significantly different according to a post-hoc two-tailed t-test at $P < 0.05$ (permutation adjusted) for each pairwise comparison.

Assemblage	Community characteristics	Width (m)	Depth (cm)	Water temp (°C)	Gradient (%)	Discharge (m³/s)	Elevation (m)	Pool/riffle ratio
(a) Eastern faunal region in Connecticut								
Assemblage A	Brook Trout dominated (n = 103)	2.64 a	9.30 a	18 a	1.70 a	0.06 a	79 a	1.00 ab
Assemblage B _E	Blacknose Dace dominated (n = 135)	3.75 b	10.25 ab	19 a	1.60 ab	0.15 b	82 a	0.85 a
Assemblage C _E	Eastern mixed fluvial (n = 168)	6.96 c	20.70 c	21 b	0.40 c	0.29 c	43 b	2.21 c
Assemblage D _E	Eastern mixed macro-habitat generalist (n = 52)	3.40 b	12.15 abd	21 b	0.85 d	0.09 ab	69 ab	2.06 bc
Assemblage E	Redfin Pickerel dominated (n = 13)	2.80 ab	15.65 bcd	18 a	0.50 bcd	0.11 ab	47 ab	12.51 c
(b) Western faunal region in Connecticut								
Assemblage A	Brook Trout dominated (n = 76)	2.46 a	9.41 a	16 a	3.1 a	0.02 a	181 a	0.56 a
Assemblage B _W	Blacknose Dace-Creek Chub dominated (n = 150)	3.23 b	9.78 a	18 b	1.9 a	0.04 b	166 ab	0.81 a
Assemblage C _W	Western mixed fluvial (n = 163)	5.71 c	17.11 b	19 b	0.8 b	0.12 c	125 c	1.30 b
Assemblage D _W	Western mixed macro-habitat generalist (n = 26)	4.05 b	13.69 b	19 b	0.3 b	0.04 b	119 bc	2.33 b

ratios (i.e., abundant pools). In the eastern region, Assemblage E inhabited cold, small, low-gradient streams with numerous pools.

The CDA spatially reflected differences across assemblages revealed in the habitat comparisons (Fig. 4). In the eastern region, 3 fluvial assemblages (Assemblages A, B_E , and C_E) were aligned along the first canonical axis to suggest the effect of increasing stream size ($r^2 = 0.775$). This pattern contrasted headwater Brook Trout streams with relatively species-diverse larger streams in the dataset. On the second canonical axis ($r^2 = 0.717$), riffle-associated Assemblage B_E was juxtaposed with pool-associated Assemblages D_E and E. Assemblage E formed a distinct group, concentrated in the lower left quadrant of the plot. Generally, the western region shared similar patterns. Stream sites transitioned from Assemblage A to B_W to C_W along the first axis ($r^2 = 0.784$), corresponding to increasing stream size. On the second axis ($r^2 = 0.729$), Assemblage D_W was separated from the other 3 assemblages, emphasizing a shift across the macro-habitat generalist assemblage to the fluvial assemblages.

Despite the generally shared patterns, the two regions showed some differences in observed habitat variables. Streams in the western region were generally higher in elevation and colder in water temperature (Table 3). Median values of elevation among the 5 assemblage types in the eastern region ranged from 43 m to 82 m, and those in the western region were between 119 m and 181 m. Coincidentally, Assemblage A had a colder median water temperature (16 °C) in the western region than in the eastern region (18 °C), and inhabited higher-gradient streams in the western region (3.1%) than in the eastern region (1.7%).

Discussion

The east–west zoogeographical pattern resulted from characteristic distributions of relatively few native species at the geographic scale of the study region. Most other native stream fishes were distributed widely across the study region. However, assemblage-level differences also were recognized between the two faunal regions as evidenced by differences in indicator species rankings within mixed fluvial and macro-habitat generalist assemblages. Furthermore, a fifth assemblage type dominated by Redfin Pickerel was recognized only in the eastern region. These assemblage-level differences additionally support the validity of two faunal regions in our study area. Our analyses were limited to wadeable streams, and the effect of the inclusion of large streams on our classification is unknown. But we believe that our classification of the two faunal regions is robust since it can be supported by the colonization history of native fishes to the study region.

Our data support that present-day distributions of stream fishes in the study region are generally explained by 3 possible pathways of postglacial colonization from Pleistocene refugia (Schmidt 1986, Whitworth 1996). First, most stream fishes are widely distributed in the study area, and they probably originated from the Northeastern Coastal Refugium located to the south of today's northeastern coast (Schmidt 1986, Whitworth 1996). Second, two eastern species (Creek Chubsucker and Redfin Pickerel) are hypothesized to have entered the region from the Atlantic Coastal Plain Refugium and proceeded

through glacial Lake Ronkonkoma (present Long Island Sound) from the lake outlet located on its east (Schmidt 1986). The presence of this refugium also explains the eastern distributions of two lentic species (*Etheostoma fusiforme* Girard [Swamp Darter] and *Enneacanthus obesus* Girard [Banded Sunfish]; Schmidt 1986, Whitworth 1996), neither of which were included in the current study because of their rarity in streams. The third pattern is dispersal from the south and/or west. Whitworth (1996) suggested that the Cutlips Minnow and Creek Chub invaded from the south, a refugia located south of the current western third of Connecticut. However, Schmidt (1986) suggested that Cutlips Minnow dispersed from the Atlantic Coastal Uplands Refugium (i.e., entered Connecticut from the west), and Creek Chub colonized the study area from the Northeastern Coastal Refugium. Our data indicated that Cutlips Minnow was most abundant in Hudson River watersheds, became less common in western Connecticut, and was absent in eastern Connecticut; thus the dispersal route of this species may have been from the west (Schmidt 1986). The western distribution of Creek Chub in our study area is difficult to explain. If Creek Chub invaded from Northeastern Coastal Refugium like many other widespread species of this study (Schmidt 1986), then its current distribution might be expected to be more extensive. The species might have invaded from a refugia located south of the current western third of Connecticut (Whitworth 1996), but its extensive distribution pattern across North America makes it difficult to identify post-glacial dispersal pathways to a particular region. Indeed, the complexity of colonization history in the western region may explain why Axis 2 of NMS (Figs. 2b, 3b) depicts a north–south distributional gradient within the western faunal region but not the eastern region.

Interestingly, Schmidt (1986) reported high assemblage resemblance between Housatonic, Connecticut, and Thames watersheds, but our analyses separated these watersheds into two faunal regions. High resemblance was attributed to the ancient connections of these watersheds to glacial Lake Ronkonkoma. However, the relatively fine resolution of our analyses may support patterns that reflect colonization from other sources, such as Cutlips Minnow from the Atlantic Coastal Uplands Refugium. The historical connection of the major watersheds of Connecticut to the glacial lake was not sufficient alone to explain present-day distributions of stream fishes in our study area.

The extent and validity of the two faunal regions outside the study region is not known. The east–west pattern also is observed among native fishes of Massachusetts (Hartel et al. 2002). The Creek Chub is mostly restricted to the western one third of the state, and the distributions of Redfin Pickerel and Creek Chubsucker are skewed toward the eastern coastal watersheds. In addition, species such as Slimy Sculpin, Longnose Dace, and Blacknose Dace, are distributed primarily in the western half of Massachusetts, and their eastern distribution extent appears to be delimited approximately by the drainage divide between the Connecticut and Merrimack rivers (Hartel et al. 2002). This pattern also may relate to the classification of the Chicopee watershed into the western faunal region despite its geographic location in the eastern half of our study region. Given the fish assemblage similarity between Merrimack River watersheds and coastal watersheds in Connecticut (Schmidt 1986), the eastern

faunal region might extend north along the coast into the Merrimack River watershed, including part of New Hampshire. However, the western faunal region might not extend as far north, since a group of species with Mississippi Valley affinity, such as *Couesius plumbeus* Agassiz (Lake Chub) and *Phoxinus eos* Cope (Northern Redbelly Dace) are found in the northwestern part of Massachusetts (Schmidt 1986, Hartel et al. 2002). The western extent of the western faunal region might be similarly limited by the presence of species originating from the Mississippi Valley Refugium. Smith (1985) described the occurrence of eastern and western species in New York, which corresponded to affinity with the Atlantic Coastal Refugium and Mississippi Valley Refugium, respectively.

Our analyses described fish distributions at two spatially hierarchical levels (i.e., faunal regions and assemblages within them); finer levels of spatially nested classifications warrant further research. This analysis requires integration of geomorphic channel types, surficial materials, and groundwater interactions (Seelbach et al. 2006, Wehrly et al. 2006). Given the habitat differences between the two regions, particular attention may be paid towards understanding if there are inter-regional differences in the relative importance of major environmental variables controlling species and assemblage distributions. The longitudinal replacement patterns among species and assemblages typically differ regionally (Fausch et al. 1994, Torgersen et al. 2006).

Results of our analyses provide useful information for aquatic resource management in Connecticut. The fish assemblage types identified here can help stratify inventories of aquatic resources in the state. From the viewpoint of biodiversity conservation, some assemblages may require more attention than others. Assemblages B_{E-W} and D_{E-W} were composed mainly of tolerant and/or macro-habitat generalists, which are not only likely secure from endangerment but also may become more common as human perturbations continue across the landscape. In contrast, the Brook Trout dominated assemblage (A) and the mixed fluvial assemblages (C_{E-W}) likely will be more prone to declines from human disturbances and thus merit more active management. Brook Trout are vulnerable to a multitude of human disturbances including habitat degradation (Lyons et al. 1996, Steedman 1988), exotic species (Larson and Moore 1985, Waters 1983), and global warming (Meisner 1990).

Identifying high-quality stream habitat inhabited by Assemblage C_{E-W} warrants further inventory efforts. This process could be facilitated by developing a tool that assesses the health of stream environments such as an index of biotic integrity (IBI) (Karr 1981). Given the number of fluvial assemblage types identified, it might be necessary to use more than one IBI to accurately assess stream conditions in Connecticut streams. In Vermont, for example, 3 categories of streams exist for biomonitoring: (1) Brook Trout only streams, (2) coldwater streams containing 2–5 species, and (3) streams containing 5 or more species (Vermont Department of Environmental Conservation 2004). While no IBI exists for the Brook Trout only streams, different IBIs are applied to the other 2 categories. Connecticut may benefit from a similar approach. Our results indicated that an equivalent of Vermont's second stream category would include some streams in Assemblages A and B_{E-W} , and the

third category would mostly correspond to Assemblage C_{E-W}. As a result, in Connecticut, a coldwater IBI (Jacobson 1994) may be applicable primarily to smaller streams, while another IBI (mixed-water IBI) may need to be developed for more diverse fish assemblages in relatively larger wadeable streams.

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