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AN ASSESSMENT OF FISH ASSEMBLAGE STRUCTURE IN A LARGE RIVER

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ABSTRACT

The Penobscot River drains the largest watershed in Maine and once provided spawning and rearing habitats to 11 species of diadromous fishes. The construction of dams blocked migrations of these fishes and likely changed the structure and function of fish assemblages throughout the river. The proposed removal of two main-stem dams, improved upstream fish passage at a third dam, and construction of a fish bypass on a dam obstructing a major tributary is anticipated to increase passage of and improve habitat connectivity for both diadromous and resident fishes. We captured 61 837 fish of 35 species in the Penobscot River and major tributaries, through 114 km of boat electrofishing. Patterns of fish assemblage structure did not change considerably during our sampling; relatively few species contributed to seasonal and annual variability within the main-stem river, including smallmouth bass *Micropterus dolomieu*, white sucker *Catostomus commersonii*, pumpkinseed *Lepomis gibbosus*, and golden shiner *Notemigonus crysoleucas*. However, distinct fish assemblages were present among river sections bounded by dams. Many diadromous species were restricted to tidal waters downriver of the Veazie Dam; *Fundulus* species were also abundant within the tidal river section. Smallmouth bass and pumpkinseed were most prevalent within the Veazie Dam impoundment and the free-flowing river section immediately upriver, suggesting the importance of both types of habitat that supports multiple life stages of these species. Further upriver, brown bullhead *Ameiurus nebulosus*, yellow perch *Perca flavescens*, chain pickerel *Esox niger*, and cyprinid species were more prevalent than within any other river section. Our findings describe baseline spatial patterns of fish assemblages in the Penobscot River in relation to dams with which to compare assessments after dam removal occurs. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS: fish; assemblage; rivers; dams; biomonitoring

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INTRODUCTION

Dams affect the distribution and abundance of fishes through fragmentation and alteration of habitat. They fragment habitat by impeding movements of fishes within a river system (Gehrke *et al*., 2002; Burroughs *et al*., 2010), potentially restricting access to spawning, rearing, feeding, or refuge habitat. One of the most publicized effects is restricted passage of spawning anadromous fishes (Beasley and Hightower, 2000; Maret and Mebane, 2005; Sprankle, 2005), which affects not only the distribution and abundance of those species but also food web dynamics and nutrient cycling within freshwater ecosystems (Saunders *et al*., 2006; MacAvoy *et al*., 2009). Resident fish movements are impeded by dams as well, resulting in changes to assemblage structure through isolation of populations and restriction of access to habitats essential to fish at different life stages (Porto *et al*., 1999; Lienesch *et al*., 2000; Burroughs *et al*., 2010). Dams convert lotic habitat to lentic habitat (Kanehl *et al*., 1997; Santucci *et al*., 2005), which favours generalist and piscivorous species (Guenther and Spacie, 2006) and could result in the invasion of riverine areas from impoundments by these species (Erman, 1973; Martinez *et al*., 1994). They also alter flow and thermal regimes, along with water chemistry, further altering fish assemblages (Bain *et al*., 1988; Lessard and Hayes, 2003; Quinn and Kwak, 2003).

Historically, 11 species of diadromous fishes were native to the Penobscot River and could access hundreds of kilometres of river, stream, and lake habitat for spawning and/or juvenile rearing (Saunders *et al*., 2006). The construction of more than 100 dams on the river and tributaries has limited the distribution of many diadromous species to lower portions of the river; these species have subsequently declined in abundance, and some are nearly extirpated (Saunders *et al*., 2006). Resident fish assemblages above and below the dams likely have changed as well, as suggested by results of several other studies (Quinn and Kwak, 2003; Guenther and Spacie, 2006; Catalano *et al*., 2007), although overall changes to fish assemblage structure due to dams on the Penobscot River are unknown. The Penobscot River Restoration Project (PRRP) is anticipated

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to increase passage of anadromous and resident fish and improve connectivity among currently fragmented habitats within the Penobscot River watershed through the removal of the two farthest downstream dams coupled with the installation of a fish lift at the third main-stem dam and a fish bypass around a dam on a major tributary (Opperman *et al.*, 2011; PRRT, 2011).

Despite widespread damming of rivers (Dynesius and Nilsso, 1994), the effects of dams and dam removal projects on large rivers are understudied, with most research focused on smaller rivers and streams or upper-watershed areas of large rivers (e.g. Connolly and Brenkman, 2008; Burroughs *et al.*, 2010; Gardner *et al.*, 2011). Additionally, evaluations of the effects of dam removal for recent projects on large rivers have relied on anecdotal evidence rather than scientific assessment because often, few data are available before and/or after dam removal (Babbitt, 2002). The PRRP provides a valuable opportunity to study the effects of dams, and eventually dam removal, on fish assemblage structure within a large river. Our goal was to characterize fish assemblage structure in the Penobscot River and major tributaries prior to dam removal by focusing on the distribution and abundance of fishes, along with variability of fish assemblage patterns among years and seasons.

STUDY AREA

The Penobscot River watershed is the largest in Maine, and the second largest in New England, draining 2.2 million primarily forested hectares through more than 8800 km of river and streams (Opperman *et al.*, 2011). Our study focused on the lower 70 km of the river (Figure 1), which ranges from 170 to 600 m wide with an average annual discharge of ~440 $m^3 s^{-1}$ during recent years (USGS, 2012). This river reach contained approximately 257 km of shoreline and included freshwater tidal, impounded, and free-flowing areas. Excluding relatively small impoundments, most areas were heterogeneous in shoreline habitat and flow types. The river was impounded at the head of tide by the Veazie Dam (Figure 1); two other main-stem dams (Great Works and Milford) were also included in the main-stem study area, which was bounded on the upstream end by the West Enfield Dam and Howland Dam. Major tributaries were also sampled, some of which drain into the Penobscot River within the main-stem study area; others drain into the river farther upstream in the watershed (Figure 1).

METHODS

Sampling designs

Fixed-station sampling design. The fixed-station design had been implemented as part of an earlier study for 2 years prior to our data collection (Kleinschmidt Associates, 2009a, 2009b); we sampled along transects that were chosen and sampled previously by Kleinschmidt Associates (2009b). The fixed-station sampling design included 11 transects on the main-stem river and eight transects along major tributaries (Figure 1), all of which were approximately 1000 m in length. Six of the main-stem transects were concentrated in areas above and below dams scheduled for removal (Kleinschmidt Associates, 2009b). During the summer 2011 sampling, we divided each fixed transect in half when feasible, to yield data comparable with that collected with the stratified random design (described later).

Stratified random sampling design. The stratified random sampling design was implemented to improve spatial coverage and account for heterogeneity within the main-stem river and was not conducted on any tributaries. We divided the river longitudinally into nine strata (Figure 1), the bounds of which were based on dam locations, broad-scale habitat types, and boat access. Using ArcGIS 9.3 (Redlands, California), we delineated the river shoreline, including shoreline around large islands, into 219 transects approximately 500 m in length. We selected multiple transects at random from within each stratum; a prioritized list in random order was created to select alternate transects if that area of river was inaccessible by boat.

River sections

For describing fish assemblage structure in relation to dam locations, we divided the river into four sections: Tidal, Orono, Milford, and Argyle (Figure 1). All river sections were bounded on both ends by dams except for the Tidal section, which was only bounded on the upriver end, and there were no dams obstructing the main-stem river within any section. Each river section contained between one and three strata (Figure 1). The Tidal river section contained all three tidal strata, the Orono section contained one impounded and one free-flowing strata, the Milford section contained one impounded stratum, and the Argyle section contained three free-flowing strata. Tributaries were grouped by general drainage locations and the presence of dams. Tributary transects were considered 'lower' if the tributary drained directly into our main-stem strata with no dams between the transect and our strata. All lower tributary transects were located three dams above the head of tide; these included transects on Pushaw Stream, Sunkhaze Stream, and the Passadumkeag River. Tributary transects were considered 'upper' if the tributary drained into the main-stem river higher in the watershed, or if dams were present between a tributary transect and the main-stem strata. All upper tributary transects were located four or five dams above the head of tide; these included transects on the Piscataquis River, Mattawamkeag River, and East Branch Penobscot River.

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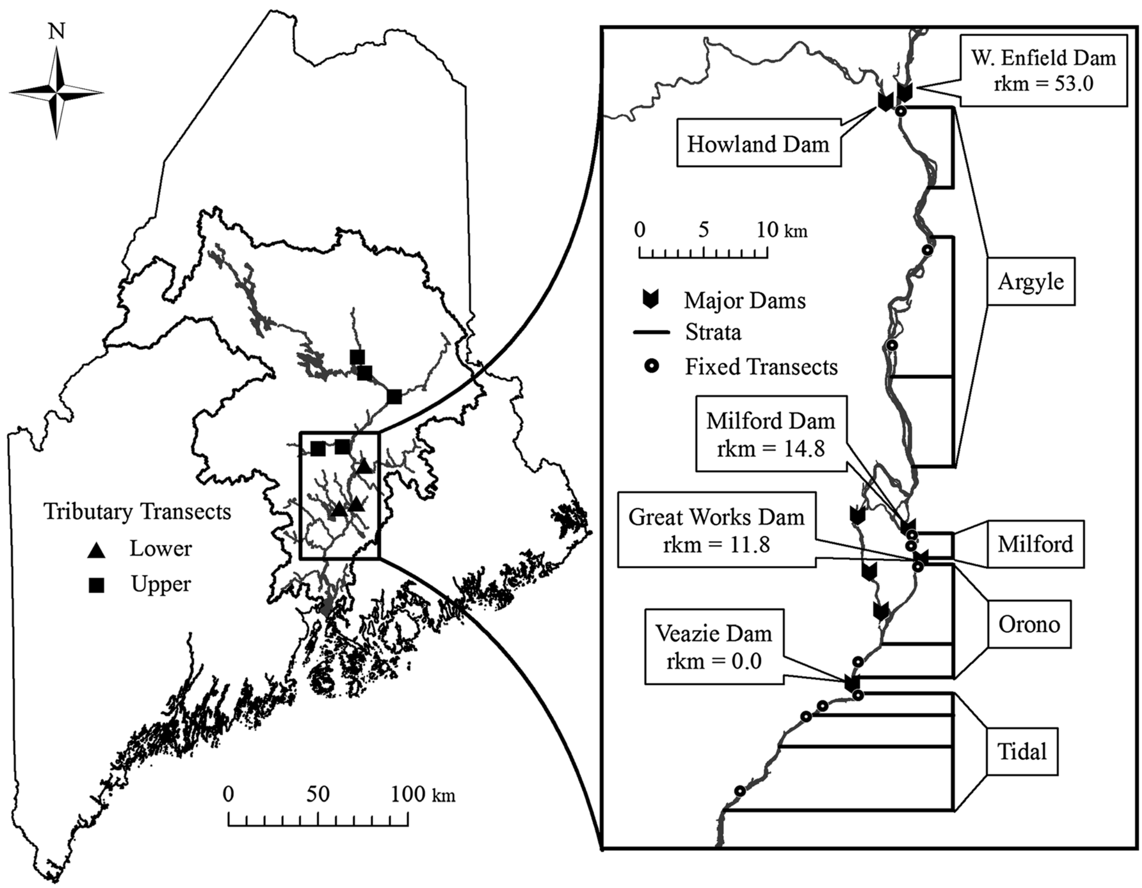

Figure 1. The Penobscot watershed, including the locations of major dams, main-stem stratum boundaries, river sections, and fixed transects. Tributary transects are indicated on a State of Maine map

Fish collection

Prior to sampling, we measured water temperature and specific conductivity and recorded global positioning system coordinates at the start and end of each transect, along with seconds of electrofishing after sampling was complete. Single-pass daytime boat electrofishing surveys (Curry *et al.*, 2009) were conducted in the summer (June) and the fall (September–October) during 2010 and 2011, for a total of four discrete sampling events. We electrofished on the Penobscot River only if discharge was less than 425 $m^3 s^{-1}$ at West Enfield, Maine (USGS gauge 01034500), and when water temperatures were below 22 °C as measured at the start of each transect.

On the Penobscot River and the largest tributaries, we used a 17.5-ft (5.5-m) Lowe (Lebanon, Missouri) Roughneck aluminium boat equipped with Smith Root (Vancouver, Washington) electrofishing equipment, including two booms with six-dropper anode arrays, and a generator powered pulsator (GPP) 5.0 electrofishing system. On smaller tributaries, we used a 14-ft (4.3-m) Sea Eagle (Port Jefferson, New York) inflatable raft equipped with a Smith Root (Vancouver, Washington) GPP 2.5 electrofishing system and a custom anode array similar to that used by Maine Department of Inland Fisheries and Wildlife biologists (J. Dembeck, Maine Department of Inland Fisheries and Wildlife, personal communication). On both vessels, we installed custom cathode dropper arrays near and along the bow of the boat. Metal conduit encased half of the droppers in order to increase the cathode surface area and homogenize the electric field in order to reduce fish injury and mortality. The electrofishing units were operated using pulsed direct current at 60 Hz and 30–40% of power, as required to capture fish successfully while limiting injury; settings were chosen to maximize power transfer. Two netters captured shocked fish with Duraframe (Viola, Wisconsin) dip nets of multiple designs; all net bags were constructed of 4.8-mm delta mesh. Surveys were conducted by manoeuvring the boat parallel and close to shore and fishing in a downstream direction, at a speed equal to or slightly greater than the current. Pockets, eddies, and shoreline were sampled thoroughly by manoeuvring the boat

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perpendicular or at an angle to the shore. Habitat structure (e.g. boulders, large woody debris, and vegetation) were fished thoroughly as well.

All fishes that were captured were identified to species and measured to the nearest millimetre and tenth of a gramme. If age 0 or small fishes (length < 80 mm) of any species were captured in high abundance ($n > 50$), these fishes were separated by size class and counted, and mass was measured for batches, with length taken to the nearest millimetre for the smallest and largest specimens in a batch. This method was implemented to collect required data from these specimens while reducing mortality and processing time. Because of endangered species permitting restrictions, we did not attempt to net adult Atlantic salmon *Salmo salar*, Atlantic sturgeon *Acipenser oxyrhynchus*, or shortnose sturgeon *Acipenser brevirostrum* but rather noted their occurrence visually and considered each encounter as a 'capture' for later data analysis. Estimated mass for Atlantic salmon observed in 2010 was calculated by approximating size and year class (Dube *et al*., 2010) and using historical (Baum, 1997) and recent (Bacon *et al*., 2009) length–mass data. Similar methods were used to estimate mass of Atlantic salmon in 2011, but using fish captured in the Penobscot River during that year (O. Cox, Maine Department of Marine Resources, unpublished data). Sturgeon mass was estimated using length–frequency and length–mass data (G. Zydlewski and M. Altenritter, University of Maine, unpublished data).

Data analysis

Dataset. Age 0 smallmouth bass *Micropterus dolomieu* (length < 30 mm) and white sucker *Catostomus commersonii* (length < 40 mm) were removed from the summer sampling data prior to analyses. The growth of these specimens necessary to recruit to our gear (length > 25 mm) appeared to be inconsistent among strata for the duration of the summer sampling; by fall, these fish were large enough to be captured reliably within all strata. Previous analyses by Kiraly *et al*. (in press) indicated that species richness and proportional abundance results from fixed-station and stratified random sampling were similar; therefore, we combined data from both sampling designs in further calculations (described later) by considering fixed transects as part of the stratified random design.

Catch and mass per unit effort. Both catch per unit effort (CPUE) and mass per unit effort (MPUE) were analysed to explore potential differences in patterns that may exist between the two measurements. Analyses for CPUE pertain to species that are most abundant, often small fish, whereas those for MPUE pertain to larger fish that are usually less abundant but are also important within aquatic ecosystems. We calculated CPUE and MPUE of each species for each stratum and each tributary classification by dividing the total catch or mass by the total length of shoreline electrofished, as measured between start and end global positioning system coordinates using orthoimagery in ArcGIS 9.3. The sample mean and variance were also calculated for total CPUE and MPUE within each stratum and tributary classification by averaging sampling seasons (i.e. summer and fall samplings). To identify longitudinal patterns, we plotted total CPUE and MPUE against river kilometre using the midpoint of each stratum for the main-stem river. Because tributary transects varied in relative location within the watershed, we did not attempt to identify longitudinal patterns in CPUE and MPUE among tributaries; thus, tributary data remain categorical (lower and upper).

Multivariate ordination. Fish assemblage structure was analysed using a variety of multivariate methods; all multivariate analyses were performed with PC ORD software (McCune and Mefford, 1999; McCune and Grace, 2002) after a fourth-root transformation of CPUE and MPUE. Fourth-root transformations reduce the effects of numerically large values and increase the contribution from rare species, focusing attention on the whole assemblage rather than on species dominating abundance or mass (Clarke, 1993; Goodsell and Connell, 2002). Nonmetric multidimensional scaling (NMS) was performed using Bray–Curtis dissimilarity, which is considered to be the most reliable distance measure for NMS ordination of assemblage structure (Clarke, 1993). Dimensionality was determined by following the procedure of McCune and Grace (2002): performing the analysis with a random start and a stability criteria of 1.0×10^{-5} and incorporating 40 runs of real data with 50 runs of randomized data. After a stable solution was found, the ordination was conducted with one run of real data; we determined the number of ordination axes by balancing reduction in stress with ease of interpretation (Clarke, 1993; McCune and Grace, 2002). We incorporated all sampling events into one NMS ordination each for CPUE and MPUE in order to identify variability in spatial patterns among sampling events; PC ORD provided Kendall's tau coefficients (T) with which we determined the direction and strength of correlations between each species and both axes.

Multiresponse permutation procedures and indicator species analysis. We used multiresponse permutation procedures (MRPP) based on rank-transformed Bray–Curtis dissimilarity to identify significant ($\alpha = 0.05$) differences of fish assemblages among sampling events and also among river sections within the Penobscot River. When comparing sampling events, we considered all strata from a given sampling event as a group (i.e. all nine strata during summer 2010 vs all nine strata during summer 2011) regardless of location in relation to

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dams, whereas when comparing river sections, we considered all strata within a given river section for all sampling events as a group (i.e. Tidal = three tidal strata from each of the four sampling events analysed together as a group). Tributary data were not included in MRPP analyses because many tributary transects were not sampled during every sampling event due to flow and time constraints. MRPP is a nonparametric method that tests for differences in assemblages among groups; it calculates a *p*-value and an *A*-statistic, both of which must be used to assess dissimilarity (McCune and Grace, 2002). The *p*-value is the likelihood that an observed difference is due to chance, whereas the chance-corrected within-group agreement (*A*), also known as the effect size, describes within-group homogeneity compared with the random expectation (McCune and Grace, 2002). When all items within groups are identical, $A = 1$, whereas if heterogeneity equals expectation by chance, then $A = 0$; however, $A < 0$ if there is less agreement within groups than expected by chance (McCune and Grace, 2002). A rank transformation of the distance matrix was performed so that results were analogous to our NMS ordinations (McCune and Grace, 2002). All seasonal groups within CPUE and MPUE were analysed simultaneously, followed by subsequent pairwise comparisons given a significant result. For comparisons among river sections, groups were analysed simultaneously without subsequent pairwise comparisons.

Indicator species analysis (Dufrene and Legendre, 1997) is a method often used in conjunction with MRPP (McCune and Grace, 2002) and was performed given significant MRPP results. Indicator species are more abundant or frequent within a group when compared with other groups and thus describe differences among groups. Rare species are not typically indicators; however, it is not necessary for an indicator species to be dominant within a group. Indicator species analysis provides an indicator value ($IV = 0–100$), along with *p*-values, which were calculated using a Monte Carlo test of significance based on 1000 permutations and were considered significant if $p \leq 0.05$.

RESULTS

Catch and mass

Over all four sampling events, 61 837 fish of 35 species (Table I) were captured; 45 874 of these fish were captured in the main-stem Penobscot River (88 km of electrofishing), whereas 15 963 were captured in tributaries (26 km of electrofishing). Sampling within the Penobscot River accounted for 34 species, with slimy sculpin as the only species captured within tributaries (one transect) but not in the main-stem river. The most numerically abundant species captured were fallfish and common shiner, whereas smallmouth bass and white sucker contributed the most to total mass (Table I). Of all species captured, seven were anadromous, making up 1.4% of the total catch by numbers and 4.4% of the total catch by mass. The single catadromous species captured, American eel, accounted for 1.8% of the total catch by numbers but 12.8% of catch by mass. There were also seven introduced species, making up 13.8% of catch by numbers and 36.3% of catch by mass; of these species, smallmouth bass was dominant for catch by both numbers and mass. The majority of species (22) were captured both above and below the Veazie Dam. Seven species were captured downriver of Veazie Dam but at no locations upriver: American shad, alewife, blueback herring, striped bass, sturgeon, mummichog, and black crappie. Six species were captured upriver of Veazie Dam (tributaries included), but at no locations downriver: burbot, finescale dace, longnose sucker, ninespine stickleback, northern redbelly dace, and slimy sculpin. Finescale dace, ninespine stickleback, and slimy sculpin were captured only above Milford Dam.

The CPUE was relatively low within strata downstream of Great Works Dam and was similar between seasons (Figure 2). We recorded relatively high CPUE within the three strata above Milford dam; two of these strata exhibited high seasonal variability, with greater CPUE during fall sampling. CPUE was low within the Milford stratum during the summer but relatively high during the fall. Total MPUE increased from downriver to upriver within the tidal strata but was relatively low within the impounded stratum immediately upriver of Veazie Dam (Figure 2); this pattern was evident during both summer and fall samplings. The greatest MPUE was recorded within the free-flowing stratum upriver of the Veazie Dam impoundment but declined upriver of Great Works Dam, within another impoundment. MPUE was moderate and similar among strata and season above Milford Dam, including lower and upper tributary transects (Figure 2).

Multivariate ordination

We obtained stable, two-dimensional NMS ordinations (Figure 3) for CPUE (final stress = 15.7) and MPUE (final stress = 16.3) in 46 and 56 iterations, respectively. The solution for CPUE explained 87.9% of the variance. Axis 1 accounted for 47.9% of the variance and was correlated most positively with brown bullhead ($T = 0.54$), yellow perch ($T = 0.48$), white sucker ($T = 0.46$), and chain pickerel ($T = 0.44$) (Figure 4); it was correlated most negatively with alewife ($T = -0.40$), blueback herring ($T = -0.28$), and mummichog ($T = -0.27$). Axis 2 accounted for 40.0% of the variance and was correlated most positively with burbot ($T = 0.45$), smallmouth bass ($T = 0.30$), and longnose sucker ($T = 0.23$) (Figure 4); it was correlated most negatively with

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Table I. Fish species captured in the Penobscot River and major tributaries prior to dam removal

Species	Abbreviation	*n*	Mass (kg)	Frequency	Origin	Life history
Common shiner *Luxilus cornutus*	CSH	18 554	27.3	0.68	N	R
Fallfish *Semotilus corporalis*	FF	15 717	50.5	0.90	N	R
Smallmouth bass *Micropterus dolomieu*	SMB	6733	303.4	0.96	I	R
Golden shiner *Notemigonus crysoleucas*	GSH	5211	9.8	0.47	N	R
Redbreast sunfish *Lepomis auritus*	RBS	3923	82.5	0.92	N	R
White sucker *Catostomus commersonii*	WS	3465	212.7	0.74	N	R
Pumpkinseed *Lepomis gibbosus*	PS	3056	24.3	0.68	N	R
American eel *Anguilla rostrata*	EEL	1140	133.9	0.85	N	C
Yellow perch *Perca flavescens*	YP	961	23.3	0.49	I	R
Chain pickerel *Esox niger*	CHP	698	53.7	0.61	I	R
Brown bullhead *Ameiurus nebulosus*	BBH	567	65.1	0.43	N	R
Banded killifish *Fundulus diaphanus*	BKF	517	1.2	0.29	N	R
Sea lamprey *Petromyzon marinus*	LAM	429	5.5	0.44	N	A
Alewife *Alosa pseudoharengus*	ALE	224	26.6	0.15	N	A
Blueback herring *Alosa aestivalis*	HER	192	7.7	0.12	N	A
Burbot *Lota lota*	CSK	166	11.3	0.24	N	R
Eastern silvery minnow *Hybognathus regius*	ESM	68	0.1	0.08	I	R
Mummichog *Fundulus heteroclitus*	MUM	52	0.1	0.03	N	R
White perch *Morone americana*	WP	40	0.5	0.08	N	R
Atlantic salmon *Salmo salar*	ATS	27	81.5[a]	0.08	N	A
Largemouth bass *Micropterus salmoides*	LMB	19	0.3	0.07	I	R
Black crappie *Pomoxis nigromaculatus*	CRA	18	0.2	0.07	I	R
Creek chub *Semotilus atromaculatus*	CRC	16	<0.1	0.06	N	R
Ninespine stickleback *Pungitius pungitius*	NSS	9	<0.1	0.03	I	R
Blacknose dace *Rhinichthys atratulus*	BND	6	<0.1	0.04	N	R
Three-spined stickleback *Gasterosteus aculeatus*	TSS	6	<0.1	0.03	N	R
Slimy sculpin *Cottus cognatus*	SSC	5	<0.1	<0.01	N	R
Blacknose shiner *Notropis heterolepis*	BNS	4	<0.1	0.02	N	R
American shad *Alosa sapidissima*	SHD	3	2.5	0.02	N	A
Longnose sucker *Catostomus catostomus*	LNS	3	1.5	0.02	N	R
Brook trout *Salvelinus fontinalis*	BKT	2	0.1	0.01	N	R
Northern redbelly dace *Phoxinus eos*	RBD	2	<0.1	0.01	N	R
Striped bass *Morone saxatilis*	STB	2	4.2	<0.01	N	A
Finescale dace *Phoxinus neogaeus*	FSD	1	<0.1	<0.01	N	R
Sturgeon spp. *Acipenser* spp.	SGN	1	3.4[a]	<0.01	N	A

The abbreviations, number (*n*), mass (kg), and frequency (proportion of transects occupied) of fish captured by electrofishing during 2010 and 2011, along with the origin and life history of each species.
N, native; I, introduced; A, anadromous; C, catadromous; R, resident.
[a]Mass was an estimate and not a direct measurement.

golden shiner ($T = -0.65$), brown bullhead ($T = -0.49$), pumpkinseed ($T = -0.43$), and eastern silvery minnow ($T = -0.41$).

The solution for MPUE explained 87.8% of the variance. Axis 1 accounted for 54.6% of the variance and was correlated most positively with brown bullhead ($T = 0.73$), yellow perch ($T = 0.58$), golden shiner ($T = 0.57$), and chain pickerel ($T = 0.39$) (Figure 5); negative correlations with axis 1 were relatively weak, but the most negative species correlations were mummichog ($T = -0.19$) and alewife ($T = -0.17$). Axis 2 accounted for 33.2% of the variance and was correlated most positively with burbot ($T = 0.59$), white sucker ($T = 0.33$), common shiner ($T = 0.24$), and fallfish ($T = 0.23$) (Figure 5); it was correlated most negatively with alewife ($T = -0.46$), banded killifish ($T = -0.42$), blueback herring ($T = -0.38$), and pumpkinseed ($T = -0.38$).

The CPUE and MPUE ordinations show similar patterns, where there was a clear progression in the assemblage structure longitudinally and large differences among the various tributary types. Strata within the Tidal section of the river grouped together but were relatively variable and distant in ordination space from strata within the Argyle river section. Strata within the Orono and Milford sections were grouped relatively tightly and positioned between the Tidal and Argyle river sections in ordination space, which corresponds to their spatial position in the landscape. Lower river tributaries were consistently grouped tightly (Figure 3) and were separated from main-stem strata, characteristic of warm-water species (Figures 4 and 5), with the exception of one lower tributary that grouped with the Argyle river section (Figure 3); the only tributary transect that was above

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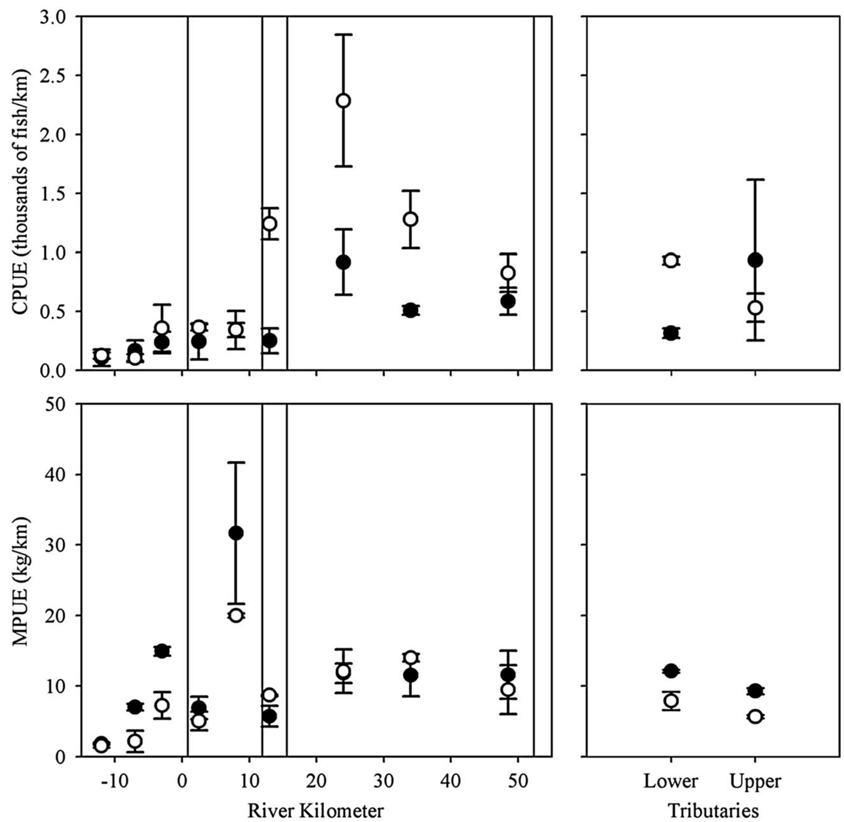

Figure 2. Mean ± standard error catch per unit effort (CPUE; top panels) and mass per unit effort (MPUE; bottom panels) of all fishes captured by boat electrofishing during 2010 and 2011 on the Penobscot River and major tributaries. Closed circles represent summer, whereas open circles represent fall sampling. Locations of dams are indicated by vertical bars within the Penobscot River panels; river kilometre 0 is located at Veazie Dam and the head of tide (Figure 1)

four dams but was relatively close to the study area grouped consistently within the Argyle river section, whereas other upper tributary transects grouped together (Figure 3) and were separated from the main-stem strata in the opposite direction from lower tributaries, characteristic of a cool-water assemblage (Figures 4 and 5).

Multiresponse permutation procedure and indicator species analysis

A comparison among all sampling events on the Penobscot River yielded significant MRPP results for CPUE ($A = 0.064$; $p = 0.02$), whereas analysis of MPUE did not ($A = 0.012$; $p = 0.26$) Pairwise MRPP comparisons of CPUE were significant when summer 2010 sampling was compared with any other sampling event; no other comparisons produced significant differences (Table II). Indicator species analysis revealed only one significant indicator of CPUE for the comparison between summer 2010 and fall 2010: smallmouth bass ($IV = 61.2$; $p = 0.008$) occurred within all strata during both sampling events, but the relative CPUE of this species was much higher during fall 2010. A comparison of summer 2010 and 2011 sampling events yielded four significant indicator species: golden shiner ($IV = 71.9$; $p = 0.003$), smallmouth bass ($IV = 57.5$; $p = 0.006$), sea lamprey ($IV = 68.1$; $p = 0.011$), and pumpkinseed ($IV = 64.1$; $p = 0.011$). Smallmouth bass and pumpkinseed were captured within all strata, and indicator values were based on increases in relative CPUE between summer 2010 and 2011. Golden shiner and sea lamprey were captured within six and five strata, respectively, during summer 2010, but within all nine strata during summer 2011; both of these species also increased in relative abundance between these sampling events.

Three significant indicator species described differences between summer 2010 and fall 2011: pumpkinseed ($IV = 61$; $p = 0.001$), smallmouth bass ($IV = 63$; $p = 0.001$), and white sucker ($IV = 62$; $p = 0.049$). Similar to comparisons with other seasons, pumpkinseed and smallmouth bass were captured within all strata during both sampling events but exhibited greater CPUE during fall 2011 relative to summer 2010. White sucker exhibited the opposite pattern, declining in CPUE from 2010 to 2011; the relative frequency of white sucker also decreased, having been captured within all strata during summer 2010 and seven out of nine strata during fall 2011.

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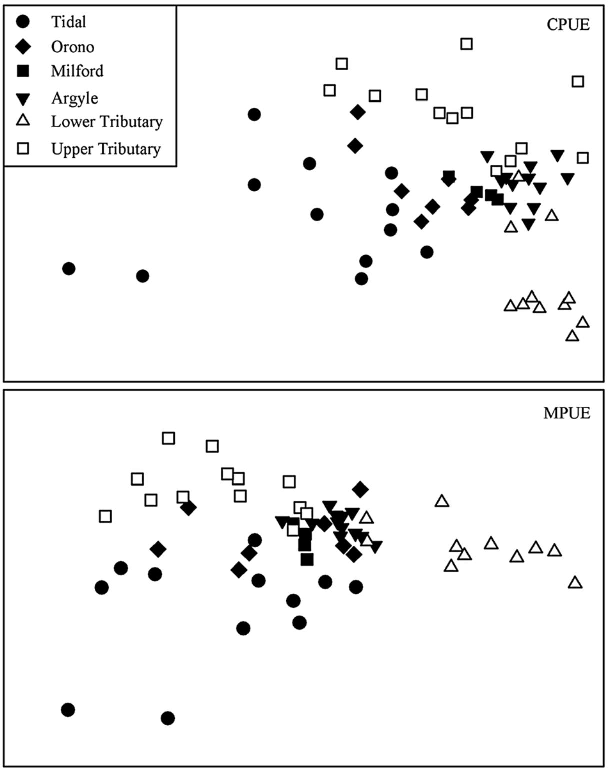

Figure 3. Nonmetric multidimensional scaling ordinations of catch per unit effort (CPUE) and mass per unit effort (MPUE) for all fishes captured by boat electrofishing on the Penobscot River and major tributaries during 2010 and 2011. Ordinations were based on Bray–Curtis dissimilarity. Symbols represent river sections and tributary transects presented in Figure 1

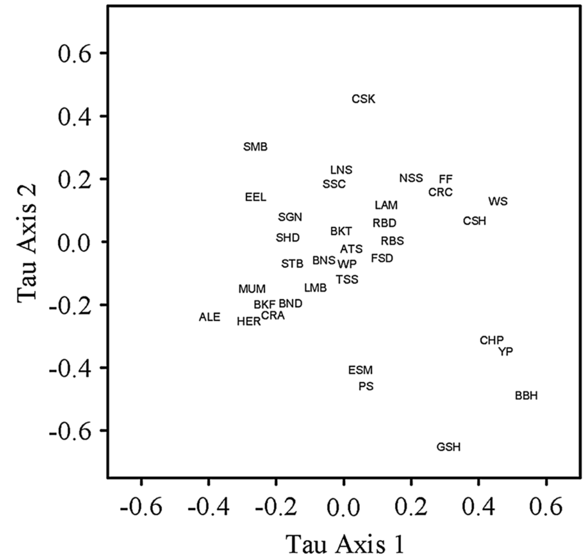

Figure 4. Kendall's tau correlations with nonmetric multidimensional scaling ordination axes for catch per unit effort on the Penobscot River and major tributaries during 2010 and 2011. ALE, alewife; ATS, Atlantic salmon; BBH, brown bullhead; BKF, banded killifish; BKT, brook trout; BND, blacknose dace; BNS, blacknose shiner; CHP, chain pickerel; CRA, black crappie; CRC, creek chub; CSH, common shiner; CSK, burbot; EEL, American eel; ESM, eastern silvery minnow; FF, fallfish; FSD, finescale dace; GSH, golden shiner; HER, blueback herring; LAM, sea lamprey; LMB, largemouth bass; LNS, longnose sucker; MUM, mummichog; NSS, ninespine stickleback; PS, pumpkinseed; RBD, northern redbelly dace; RBS, redbreast sunfish; SGN, sturgeon spp.; SHD, American shad; SMB, smallmouth bass; SSC, slimy sculpin; STB, striped bass; TSS, three-spined stickleback; WP, white perch; WS, white sucker; YP, yellow perch

Results from MRPP indicated that the fish assemblage differed among all river sections for CPUE ($A = 0.303$; $p = 0.000$) and MPUE ($A = 0.241$; $p = 0.000$). Indicator species analysis results were similar for CPUE and MPUE (Table III). Alewife and blueback herring were indicators of the Tidal section of the river, whereas pumpkinseed and smallmouth bass were indicators for the Orono river section between Veazie Dam and Great Works Dam. No indicators were present for the Milford river section between Great Works Dam and Veazie Dam; all species recorded in this river section were captured in greater abundance and mass elsewhere. Many indicator species were present within the Argyle river section between Milford Dam and West Enfield Dam (Table III), which included brown bullhead, sea lamprey, yellow perch, chain pickerel, common shiner, white sucker, and fallfish.

DISCUSSION

Considerable differences were present among river sections. Most species that we captured within tidal waters but at no locations upriver were anadromous. Adults of these species once migrated up the Penobscot River to spawn in great abundance (Saunders *et al.*, 2006), potentially driving ecosystem function through the delivery of marine-derived nutrients (Hicks *et al.*, 2005; Walters *et al.*, 2009) and by altering assemblage interactions either directly or through their progeny (Hanson and Curry, 2005; Kiffney *et al.*, 2009). Alewife and blueback herring were consistent indicators for the Tidal river section; these species were responsible for distinguishing the Tidal section from all other river sections within our indicator species analyses along with separating tidal strata from those above Veazie Dam in our NMS ordination. Atlantic salmon and sea lamprey were the only anadromous species encountered upstream of Veazie Dam. Although both of these species were distributed throughout the study area and within tributaries, passage through dams by these species was likely restricted as well. Atlantic salmon were rarely encountered, and most adults were observed in areas below Veazie Dam and Great Works Dam. Sea lampreys were primarily immature individuals and contributed to CPUE to a greater extent than MPUE; the number of adult sea lamprey accessing spawning habitats upriver is unknown. It is possible that

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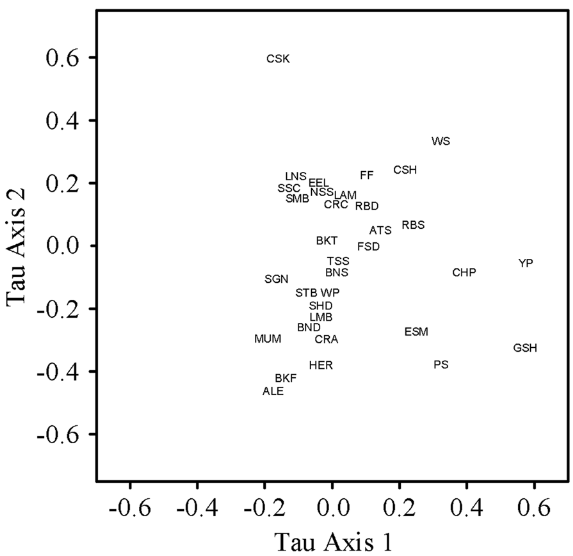

Figure 5. Kendall's tau correlations with nonmetric multidimensional scaling ordination axes for mass per unit effort on the Penobscot River and major tributaries during 2010 and 2011. ALE, alewife; ATS, Atlantic salmon; BBH, brown bullhead; BKF, banded killifish; BKT, brook trout; BND, blacknose dace; BNS, blacknose shiner; CHP, chain pickerel; CRA, black crappie; CRC, creek chub; CSH, common shiner; CSK, burbot; EEL, American eel; ESM, eastern silvery minnow; FF, fallfish; FSD, finescale dace; GSH, golden shiner; HER, blueback herring; LAM, sea lamprey; LMB, largemouth bass; LNS, longnose sucker; MUM, mummichog; NSS, ninespine stickleback; PS, pumpkinseed; RBD, northern redbelly dace; RBS, redbreast sunfish; SGN, sturgeon spp.; SHD, American shad; SMB, smallmouth bass; SSC, slimy sculpin; STB, striped bass; TSS, three-spined stickleback; WP, white perch; WS, white sucker; YP, yellow perch

our capture methods are ineffective (either in location or timing) for adult sea lamprey or that relatively few adults are accessing upriver areas but are able to produce moderate numbers of juveniles.

Fish assemblages in the main-stem Penobscot River exhibited distinct longitudinal patterns in structure; tributary fish assemblages were nearly always distinct from the main-stem river. The pattern of increasing total CPUE with distance upriver coincides with greater abundance of common shiner,

Table II. Multiresponse permutation procedure results for pairwise catch per unit effort comparisons among fish assemblages from all sampling events on the Penobscot River

Comparison	*A*	*p*
1 vs 2	0.058	0.04
1 vs 3	0.064	0.04
1 vs 4	0.074	0.03
2 vs 3	0.045	0.07
2 vs 4	−0.008	0.51
3 vs 4	0.006	0.34

1, summer 2010; 2, fall 2010; 3, summer 2011; 4, fall 2011.

fallfish, brown bullhead, yellow perch, and chain pickerel. Increasing MPUE up to Veazie Dam, especially during the summer sampling, likely resulted from increased concentrations of anadromous fish such as alewife and blueback herring attempting to pass the dam. We found low MPUE within the two impounded strata, both of which were characterized by low habitat heterogeneity, with the greatest MPUE observed within the free-flowing river section upriver of the Veazie impoundment.

It should be noted that we captured smallmouth bass and chain pickerel frequently; these non-native predators were widely distributed throughout the Penobscot River and were likely influencing fish assemblages through top-down effects (Van den Ende, 1993; Weidel *et al*., 2007). Adult smallmouth bass were most prevalent in the Orono river section, which was characterized by two distinct but connected habitats: a relatively small impounded area and a longer, free-flowing reach immediately upriver where relatively large numbers of adult bass were captured. Smallmouth bass may have been spawning within the impoundment and moving into free-flowing reaches after rearing (Erman, 1973; Penczak *et al*., 2012). Additionally, adult smallmouth bass may have moved between lotic and lentic habitats, utilizing the impoundment during the winter and the free-flowing section during the summer (Langhurst and Schoenike, 1990). The presence of Great Works Dam at the upriver boundary of this river section could also concentrate adult fish and result in high MPUE owing to the inability of these fishes to distribute throughout upriver reaches. The next section upriver, the Milford river section, was impounded by Great Works Dam but was not connected to a large amount of lotic habitat upriver because of obstruction by Milford Dam and did not yield high MPUE for smallmouth bass. Abundance and mass patterns in relation to dams were not evident for chain pickerel, although effects of the presence of dams on this species could emerge after dam removal.

Overall, we observed similar spatial patterns in fish distribution between years and seasons. We observed some variability of species composition among sampling events for CPUE on the main-stem river, which resulted from fluctuating CPUE within certain strata for relatively few species: smallmouth bass, pumpkinseed, golden shiner, white sucker, and sea lamprey (Figure 6). Annual variability in environmental conditions combined with interspecific interactions may account for these fluctuations.

The one-season lag between the increase in CPUE for smallmouth bass and increases in CPUE for pumpkinseed and golden shiner may be attributed to sampling effects; age 0 smallmouth bass were catchable via boat electrofishing during the fall 2010 sampling, whereas the other two species were not large enough to recruit to our gear until the following year's summer sampling event. Alternatively,

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Table III. Indicator species for river sections delineated by dams on the Penobscot River, 2010–2011

River section	CPUE indicator species	MPUE indicator species
Milford Dam to West Enfield Dam	BBH (46), LAM (42), YP (41), CHP (39), CSH (39), WS (37), FF (35)	BBH (46), YP (43), CSH (41), CHP (39), FF (33)
Great Works Dam to Milford Dam	None	None
Veazie Dam to Great Works Dam	PS (34)	PS (34), SMB (31)
Tidal (below Veazie Dam)	ALE (75), HER (50)	ALE (75), HER (50)

Indicator values are shown in parentheses; only significant results ($p \leq 0.05$) are shown.
ALE, alewife; BBH, brown bullhead; CHP, chain pickerel; CPUE, catch per unit effort; CSH, common shiner; FF, fallfish; HER, blueback herring; LAM, sea lamprey; MPUE, mass per unit effort; PS, pumpkinseed; SMB, smallmouth bass; WS, white sucker; YP, yellow perch.

white sucker declined after fall 2010. The reasons for this are unknown, although environmental conditions during 2011 may have been unfavourable for juvenile survival or large numbers of smallmouth bass could have reduced the abundance of this species through predation (Weidel *et al*., 2007). Although sea lamprey CPUE varied between summer samplings, these fish were primarily juveniles that reside within the substrate for multiple years (Beamish, 1980), and results from this species may be unreliable owing to capture difficulties.

Although it is natural for river systems to exhibit longitudinal gradients in ecosystem structure and function (Naiman *et al*., 1987), the Penobscot River has been impacted by large, main-stem dams that are impeding passage and fragmenting habitat for a variety of fish species. Our assessment of fish assemblage structure describes the longitudinal patterns and current indicators of seasonal variability within the Penobscot River and major tributaries prior to dam removal; data collected after dam removal can be compared with our findings in order to evaluate success of the PRRP. Dams and associated impoundments on the Penobscot River encompass a relatively small area within the ecosystem, but their effects are considerable and likely reach far upriver and even into marine ecosystems. The effects of removing these dams and improving fish passage in the Penobscot River will not be known until after the PRRP has been completed; however, with improved habitat connectivity (both within freshwater and between marine and freshwater habitats) and reduced lotic–lentic interactions, patterns of fish assemblage structure could change considerably.

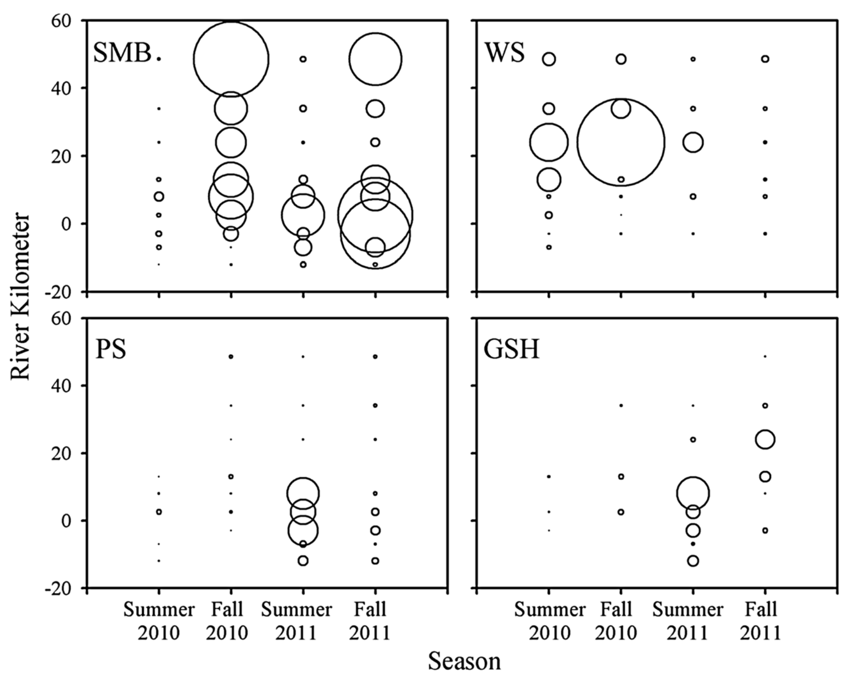

Figure 6. Longitudinal patterns of boat electrofishing catch per unit effort (CPUE) for fish species that were indicators for assemblage differences between summer 2010 and any other sampling events on the Penobscot River. Larger bubbles indicate greater CPUE. GSH, golden shiner; PS, pumpkinseed; SMB, smallmouth bass; WS, white sucker

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