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EFFECTS OF DAM REMOVAL ON ASSEMBLAGE COMPOSITION AND THE INTERACTIONS OF FISHES IN THE PENOBSCOT RIVER, MAINE

By Jonathan Watson

B.S. College of Charleston 2010

A THESIS

Submitted in Partial Fulfillment of the
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Advisory Committee:

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An Abstract of the Thesis Presented
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Dams and their impoundments disrupt river habitat connectivity to the detriment of migratory fishes. Removal of dams improves riverine connectivity and lotic habitat which benefits these fishes along with resident fluvial specialist species. Restoration efforts on the Penobscot River (Maine, USA) are among the largest recently completed in the United States, and include the removal of the two lower-most dams and improvements to fish passage at several remaining barriers. Here we describe initial and potential future changes to fish communities in the Penobscot River associated with these restoration efforts.

We assessed fish assemblages in the mainstem river and several major tributaries before (2010-2012) and after dam removal (2014-2016) using boat electrofishing surveys and a stratified-random sampling design. In total, we sampled 303 km of shoreline and captured 107,335 individual fish from 39 species. Similarity indices suggest that the most pronounced changes in fish assemblage composition occurred in reaches that underwent both habitat and connectivity changes (i.e. directly above removed dams). The newly connected reaches became more compositionally similar, as demonstrated by an average increase of 31% in similarity scores. The similarity score changes in these reaches were driven by increasing access for anadromous fish and decreasing abundances of slow-water specialist species. For example, we observed a marked reduction in lacustrine species in former impoundments. We also found all anadromous species in greatest abundance below lower-most dam during each respective sampling period. River herrings *Alosa* spp. passed through the new fish elevator at the new lower-most dam and spawned in newly available habitat upstream, as evidenced by presence of juveniles in our samples. Our results demonstrate the potential for large dam removal projects to restore both fluvial and anadromous fish assemblages.

We also examined the current and future impacts of rebounding river herring populations on Smallmouth Bass. Here we describe the diet and growth of Smallmouth Bass collected from different areas of the Penobscot River watershed and project changes to annual growth associated with increasing access to juvenile river herring prey using bioenergetics modeling. We collected 765 Smallmouth Bass throughout 2015, examined the stomach contents of 573 individuals, and found notable differences in diet between river reaches with common seasonal trends. Juvenile river herring composed an average of 19% (SE = ±6%) of stomach contents by mass from Smallmouth Bass collected in the freshwater tidal area but were observed only rarely in the diets upstream. We used von Bertalanffy growth models to examine potential difference in growth among reaches and found overlapping 95% credible intervals for all estimated growth parameters in each area, with the exception of the freshwater tidal reach where the average asymptotic length was the largest (425 mm TL). Results from bioenergetics models suggest that increasing consumption of juvenile river herring will likely lead to increases in seasonal growth throughout the watershed as river herring populations continue to rebound. Our results provide new insight to both the predator-prey dynamic of these fish in a large river and the implications of anadromous river herring population recovery in systems where Smallmouth Bass has been introduced.

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1.1 Introduction

Dams allow humans to store water and harness the power of the hydrologic cycle to produce electricity with relatively low-carbon emissions. They also provide a reliable source of water for human use by storing 15% of global annual runoff in impoundments (Bukaveckas 2009). Their utility is also evident by their ubiquity on the landscape. In the contiguous United States, there are only 42 large rivers (> 200 km) without major impoundments (Benke 1990).

Dams fundamentally alter the flow, temperature, sediment dynamics, and connectivity of rivers, which results in changes to aquatic and riparian biota (Petts 1980, Poff et al. 1997). Such biotic changes include reduced biodiversity in impoundment habitat (Santucci et al. 2005, Guenther and Spacie 2006, Slawski et al. 2008), reduction in habitat quality for riverine fishes (Santucci et al. 2005), and shifts in fish assemblage structure (Hayeset al. 2008). The impoundments created by dams convert riverine habitat from lotic to lentic which favors fluvial generalist fish species (Guenther and Spacie 2006) and facilitates establishment of invasive species (Heinz Center 2003).

An obvious impact of barriers is reduced connectivity in a riverine systems through the introduction of both physical and physio-chemical barriers, which restrict movements of diadromous and potamodromous fishes (reviewed by Pringle et al. 2000). This can ultimately impede the flow of organisms and energy / nutrients from areas of high to relatively lower productivity (Hall 1972).

Many studies have shown that dams restrict movements for many aquatic organisms including freshwater mussels (Vaughn and Taylor 1999), amphidromous shrimps (Pringle 1997), and suckers *Catostomus spp.* (Chart and Bergersen 1992, Cooke et al. 2005). Though these studies illustrate the taxa-specific impacts of barriers, collectively they suggest that dams restrict freshwater biota from essential habitats. Previous studies have also shown that impoundments genetically isolate populations in both large rivers (Bessert and Ortí 2008, Leclerc et al. 2008) and headwater streams (Hudman and Gido 2013) which increases likelihood of localized extirpation (e.g., as described by Winston et al. 1991 for several species in a prairie stream after dam construction).

The migrations of diadromous fish populations are greatly impeded by the presence of dams (see review by Freeman et al. 2003). Such situations are especially prevalent in the Eastern United States where mill dams are common (Walter and Merritts 2008) and diadromous fishes are currently at historically low abundances (Limburg and Waldman 2009). In New England, many local populations of anadromous fishes, including Alewife *Alosa pseudoharengus*, Blueback Herring *A. aestivalis* (collectively known as river herring), American Shad *A. sapidissima*, and Atlantic Salmon *Salmo salar*, have been extirpated from their natal rivers by the construction of dams in the 19th and 20th centuries (Brown et al. 2013). Similar problems have been created by the construction of dams throughout the world. In the Pacific Northwest for example, Nehlsen et al. (1991) described over 100 salmon and steelhead populations or stocks that have already been extirpated and many more that face future threats due to the presence of dams and other anthropogenic stressors.

The decline of anadromous fish populations impacts fish food webs directly through the loss of forage fish (Hall et al. 2012) and indirectly through the exclusion of an annual subsidy of marine derived nutrients and energy (Gresh et al. 2000). One notable impact of dams in large coastal rivers is a reduction of marine nutrients and energy reaching oligotrophic headwater streams. In the Pacific Northwest, the construction of dams along with commercial exploitation and other anthropogenic stressors has resulted in only 5%-7% of the marine-derived nitrogen and phosphorous returning annually to those streams in the form of adult salmon carcasses (Gresh et al. 2000).

There are many approaches to mitigate impacts of reduced connectivity, all of which have variable efficacy. Many dams include fishways; however, these structures may not be effective for passing all target species of fish (Noonan et al. 2012, Brown et al. 2013). An alternative approach to addressing connectivity and water quality problems created by dams is to remove the structures entirely. Dam removal is gaining traction throughout the United States in an attempt to improve water quality and restore native, lotic fish communities. One of the major challenges of this approach is that existing regulatory frameworks tend to result in fish passage improvements or dam removals at the individual impoundment level (Owen and Apse 2014) rather than across an entire watershed. Thus, it is particularly important to study the effects of dam removals on a large system where several large dams remain that may confound restoration efforts. Furthermore, because dams affect riverine ecosystems differently depending on size and river morphology (Poff and Hart 2002), there is a definitive need for studies to provide a larger perspective concerning dam removal as a management tool in different settings (Babbitt 2002).

Dam removals have immediate and often profound impacts on riverine fish communities. These changes have been studied recently in, for example, Pine River in Michigan (Burroughs et al. 2010), Baraboo River in Wisconsin (Catalano et al. 2007), Rappahannock River in Virginia (Hitt et al. 2012), Eightmile River in Connecticut (Poulos et al. 2014) and Sedgeunkedunk Stream in Maine (Gardner et al. 2013, Hogg et al. 2015). These studies and others have highlighted changes common among dam removals such as recolonization of diadromous fishes in newly available habitat (Hitt et al. 2012, Weigel et al. 2013, Hogg et al. 2015), increased fish diversity upstream of former dams (Burroughs et al. 2010, Hogg et al. 2015), and the incorporation of newly available marine derived nutrients and energy in stream food webs (Tonra et al. 2015). Such case studies are important for describing commonalities among dam removals which will inform similar projects in the future (Bednarek 2001, Poff and Hart 2002).

The Penobscot River Restoration Project (PRRP) is one of the largest river restoration efforts recently completed in the United States (Trinko Lake et al. 2012). The goal of this project was to restore the connectivity of the watershed through both dam removal and enhanced fish passage at remaining barriers (see review by Opperman et al. 2011). Most of the 11 species of diadromous fishes once abundant in the Penobscot watershed before dams were constructed in the 19th and early 20th centuries are currently at historically low levels (Saunders et al. 2006). The PRRP is anticipated to greatly increase the ability of these diadromous species to access critical habitat (Trinko Lake et al. 2012). It is important to remember that though we describe these actions as a "restoration project", the resulting assemblages will almost certainly be different than that which existed before the anthropogenic perturbation of dam construction (i.e. a new "state" sensu Dufor and Piegay 2009).

Prior to the PRRP, we completed multiple years of electrofishing surveys to characterize baseline metrics of species richness, relative abundance, and assemblage structure. The results from those survey include finding distinct assemblages associated with lentic habitat in former impoundments and evidence of habitat fragmentation between dammed sections of the river (Kiraly et al. 2014a).

The objective of this study is to describe immediate changes to fish assemblages at the watershed scale associated with the PRRP. Specifically, we ask: i) Has the PRRP resulted in immediate changes to species occurrence and richness in different areas of the watershed? ii) Did changes in connectivity associated with dam removal and fish passage improvement result in different distributions of migratory fishes? iii) To what extent did conversion of river conditions from lentic to lotic in former impoundments result in changes to resident fish assemblages?

1.2 Methods

1.2.1 Study area and river modification

The Penobscot River watershed in the largest in Maine and the second largest in New England, draining approximately 22,455 km^2 and containing more than 8,800 km of riverine habitat (Opperman et al. 2011). At the time of publication, there are seven dams on the main-stem river with the Milford Dam as the lowest, located on a natural falls at river kilometer (rkm) 63. Four of the dams constitute the Marsh Island hydropower complex, where water flows either through Milford Dam and into the mainstem Penobscot River or through a flow-control dam into the Stillwater Branch, through two hydroelectric dams, and then into the mainstem river (Figure 1.1). These three hydroelectric dams have been retrofitted with increased generation capacity to compensate for the removal of two hydroelectric dams lower on the mainstem river (Opperman et al. 2011). Great Works Dam (rkm 60) and Veazie Dam, formerly located at the head of tide (rkm 48), were removed in 2012 and 2013, respectively. In 2014 a new fish lift was completed and operational at Milford, the new lower-most mainstem dam. Also, in 2016 a rock-ramp fishway was completed and operational at the Howland Dam (rkm 100), located at the mouth of the Piscataquis River, a major tributary. Before fish passage modification, there was either a

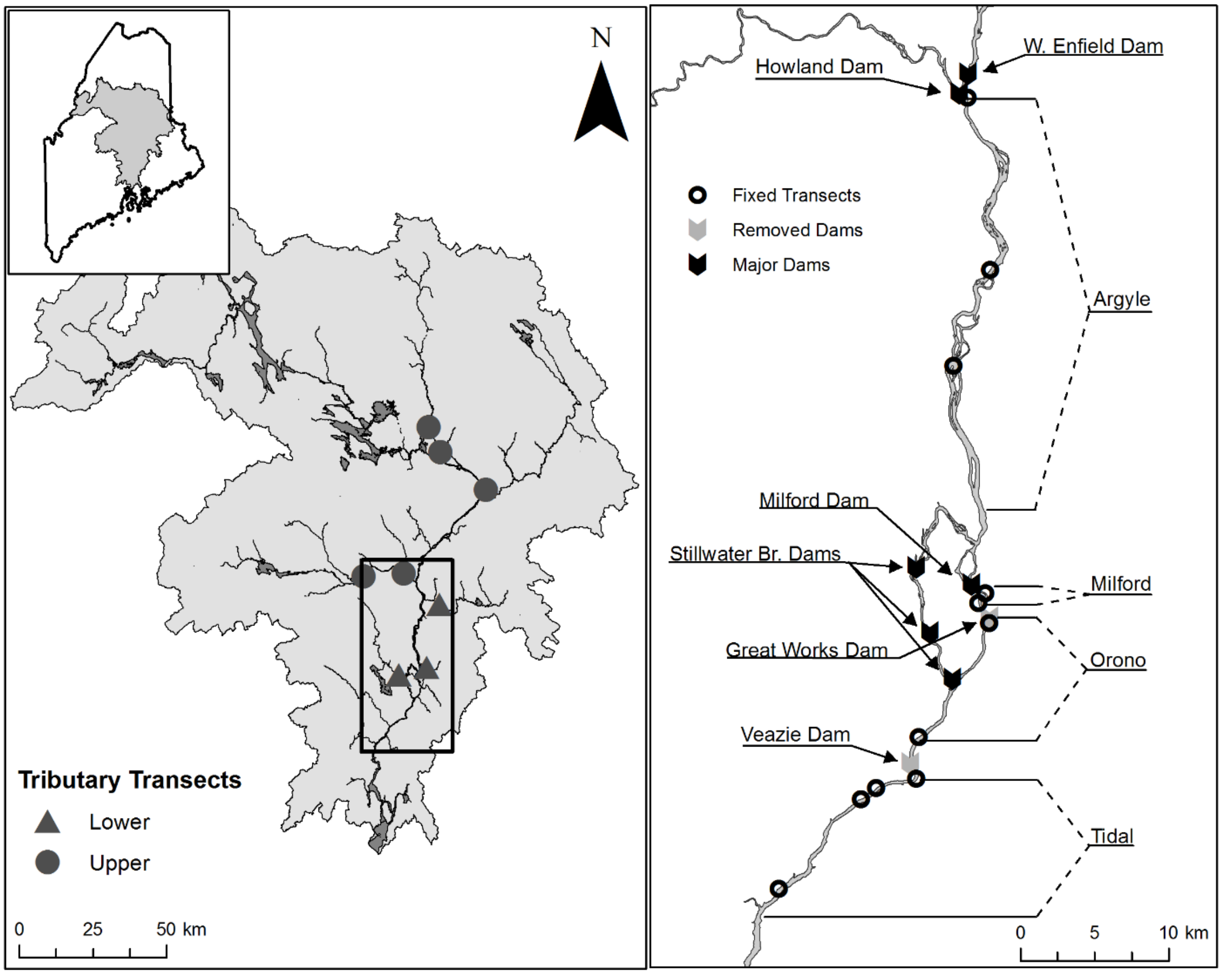

Figure 1.1: The Penobscot River Watershed and fixed tributary transects (left), the mainstem Penobscot River (inset), major mainstem dams, removed mainstem dams, locations of fixed transects (circles) and strata (lines) on the mainstem Penobscot River.

vertical slot or denil fishway at each of these dams, which were used by some anadromous species such as Atlantic Salmon, but were largely impassible to others such as alosines (Opperman et al. 2011, Grote et al. 2014a).

1.2.2 Sampling design

We established and tested our sampling design prior to dam removals (described in detail by Kiraly et al. 2014a; 2014b). We adhered to this design during post-removal surveys and review it here briefly to provide context for our analyses. Our sampling design included both fixed sites and sites selected randomly. We used a stratified random sampling design to account for large-scale habitat heterogeneity on the mainstem river (Kiraly et al. 2014b). Kiraly et al. (2014b) determined that sampling both fixed and random sites were sufficient to describe over 90% of the species richness in the mainstem Penobscot River, as long as a minimum of 5 km of shoreline was sampled during each sampling season.

We divided our sampling efforts among four sections (strata) of the mainstem river (Figure 1.1) described here from upstream to downstream: (a) “Argyle” stratum which consists of 32 km of mainstem river between West Enfield Dam and Milford Dam. (b) “Milford” stratum which consists of 3 km of mainstem river located between Milford Dam and the former Great Works Dam. (c) “Orono” stratum which consists of 9 km of mainstem river between the former Great Works Dam and former Veazie Dam at the head of tide. (d) “Freshwater Tidal” stratum which consists of 15 km of mainstem river below the head of the tide and above the area of saltwater intrusion.

Each stratum was further divided into reaches that reflect their location relative to dams (former and existing) and general accessibility. Accessible shoreline in each reach was then delineated into 500m transects from which two to four were chosen randomly for sampling in each season. We report results at the stratum level here for the sake of simplicity.

We also sampled eight fixed sites on major tributaries to the Penobscot River. Tributaries were classified as "lower" if they joined the mainstem river in the Argyle stratum and "upper" if they joined the mainstem upstream of that stratum. No tributaries were sampled below the Argyle stratum for this study.

We sampled twice annually in both early summer (late May – early July) and fall (September-October) from the spring of 2010 until the summer of 2012 and again from the spring of 2014 until the summer of 2016. The dams of interest were removed during the interim between these sampling periods (2012-2013).

1.2.3 Sampling via boat electrofishing

We used the same electrofishing equipment and sampling approach described in detail by Kiraly et al. (2014a) and we briefly review the details here. In all possible sampling situations, we deployed a 5.5m-long Lowe (Lebanon, MO) Roughneck aluminum boat equipped with a Smith Root (Vancouver, WA) 5.0 GPP electrofishing system and two anode droppers. In situations where boat access was not possible (most tributary sites), we deployed a 4.3m-long Sea Eagle (Port Jefferson, NY) inflatable raft with a Smith Root 2.5 GPP electrode fishing system and a custom single-boom anode dropper. We initiated sampling at the upstream boundary of each transect, positioned the vessels parallel to shore, and operated at the same rate or slightly faster than stream flow, proceeding in a downstream direction. Where feasible, we returned to all accessible structure (e.g. woody debris, boulder fields, vegetation) and pocket water areas contained in each transect and systematically sampled these areas thoroughly by probing them with the anode boom arrays.

We identified all captured fish to species, measured for total length (TL; nearest mm), measured mass to the nearest tenth of a gram, and returned near point of capture. Any fish that were difficult to identify were euthanized in buffered MS-222, preserved in 10% formalin, and brought back to the lab for confirmation. Because of permitting restrictions, adult Atlantic Salmon, Shortnose Sturgeon *Acipenser brevirostrum,* and Atlantic Sturgeon *A. oxyrhinchus* were not netted, but sightings were considered a "capture", noted, and size was visually estimated. We estimated mass of these fishes using the procedures described by Kiraly et al. (2014a).

1.2.4 Catch and mass per unit effort and species richness

In this study we use both catch (*n*) and mass (kg) per unit effort (CPUE and MPUE, respectively) to describe the structure and changes to fish assemblages. Effort is defined by the length (km) of each transect, which was determined using field global positioning system coordinates recorded at the start and end points for each transect and measured using orthoimagery in ArcGIS. We also evaluated the relationship for our indices of relative abundance (CPUE) and biomass (MPUE) standardized by transect length and total sampling time (see Figure A.1, Figure A.2). We used the doBy package (Højsgaard and Halekoh 2016) to calculate the groupwise mean and standard error for these indices in Program R 3.2.3 (R Core Team 2016). We calculated the mean CPUE/MPUE and standard errors for each species, within each stratum, and for each sampling period (i.e. pre-removal and post-removal)

We calculated percent occurrence to describe the ubiquity of species throughout the sampled area and species incidence data to describe changes in observed distribution of commonly occurring species. We also calculated observed species richness (*s*) as the total number of species collected in each stratum during each sampling period. Changes in observed species richness (Δs) were calculated by subtracting pre-removal richness from post-removal richness.

1.2.5 Indices of similarity

We used both the Morisita-Horn index and Sørensen index to describe similarity among strata during each sampling period and between the same strata in each period. We calculated both indices using Program R 3.2.3 (R Core Team 2016) and the vegan package (Oksanen et al. 2016). Both calculations result in a value on a scale of 0-1, where 0 indicates no similarity and 1 indicates compositionally identical assemblages.

In order to assess changes in species composition, we used the Sørensen index, described by Jost et al. (2016). We used incidence data for each species, in each stratum, during each sampling period. We calculated the index as:

$$S = 2c / (a + b)$$

Where c was the number of species in common between two sites and a and b were the total number of species in each of the sites.

In order to compare relative abundance data at the assemblage level, we used the Morisita-Horn index, derived by Morisita (1959) and modified by Horn (1966). This index was calculated using mean CPUE for each species during each sampling period, and was defined:

$$C_{jk} = 2 \sum X_{ij} X_{ik} / (\lambda_j + \lambda_k) N_j N_k$$

Where C was the similarity between assemblage j and k. X_{ij} and X_{ik} were the relative abundance of a species i in assemblages j and k, and N_j and N_k were the summed relative abundance of all species in assemblage j and k. Lambda j was calculated using equation 3, and lambda i calculated in the same manner with appropriate subscripts:

$$\lambda_j = \sum X_{ij}^2 / N_j^2$$

1.2.6 Non-metric multi-dimensional scaling

In order to examine changes in assemblage composition graphically, we analyzed relative abundance data with non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity. For this analysis, we used the metaMDS routine in the vegan package (Oksanen et al. 2016) in Program R 3.2.3 (R Core Team 2016). We chose to use mean CPUE from each sampling period. We transformed CPUE values by taking the fourth root which reduces the influence of abundant species and better reflects differences in the entire assemblage (Clarke 1993). The metaMDS function posteriorly rotates the NMDS axes using Principle Component Analysis so that Axis-1 reflects the primary sources of variation followed by Axis-2 (Oksanen et al. 2016).

1.2.7 Relative abundance and biomass for indicator species

We chose to examine changes in CPUE and MPUE by stratum for all fish as well as several indicator species identified from the Tidal and Orono strata during pre-removal surveys (Kiraly et al. 2014a). Indicator species analysis identifies species that are more abundant within a group (in this case, stratum) relative to other groups in order to describe among-group differences (Dufrêne and Legendre 1997). Kiraly et al. (2014a) found that Alewife were a significant indicator species in the Tidal stratum and Smallmouth Bass and Pumpkinseed Sunfish were both significant indicator species in the Orono stratum. We also examined the spatial distribution of American Eel *Anguilla rostrata* due to its status as a species of concern and its ubiquity in the watershed.

1.3 Results

1.3.1 Abundance, richness, and occurrence

We captured a total of 107,335 individuals representing 39 species through all years of electrofishing surveys. During pre-removal surveys we captured 69,393 individuals from 38 species. During post-removal surveys we captured 37,942 individuals from 35 species. The distance of shoreline sampled in each stratum was roughly equal between periods (Table 1.1, Table A.1), which facilitates comparison of observed species occurrence and richness.

Table 1.1: Observed species richness (s) and km shoreline sampled (km) in each stratum during pre-removal and post-removal periods.

	s		km	
	Pre	Post	Pre	Post
Tidal	32	31	42.0	42.3
Orono	21	21	23.3	24.1
Milford	16	22	13.3	15.9
Argyle	24	25	34.4	41.8
Lower Tributary	20	19	14.1	13.7
Upper Tributary	24	20	17.1	20.9

Twelve species occurred frequently (> 40% relative occurrence) in our samples during both periods including Smallmouth Bass *Micropterus dolomieu*, Fallfish *Semotilus corporalis*, and White Sucker *Catostomus commersonii* (Table 1.2). Of the frequently observed species, four exhibited large decreases (>20%) in relative occurrence between sampling periods. These were species associated with slow-water habitats and we observed the largest decrease in their relative abundances in former impoundments. Sea Lamprey *Petromyzon marinus* was the only one of these frequently captured species to exhibit and increase in relative occurrence. Among the species that were less frequently observed in our samples (< 30% relative occurrence) only Banded

Killifish *Fundulus diaphanus* exhibited a large decrease (20%) in relative occurrence. In contrast, the frequency of occurrence for two of these less common species, Alewife and Largemouth Bass *Micropterus salmoides*, increased moderately (9% and 11%, respectively).

Spatial patterns of observed richness remained largely consistent between both pre-removal and post-removal sampling periods with the highest observed richness in the Tidal stratum (Table 1.1). The most notable exception was the Milford stratum. Observed species richness in this stratum increased from a pre-removal total of 16 species, the lowest number found in any stratum, to a total of 22 species observed during post-removal sampling. Several strata exhibited declines in observed species richness between sampling periods. These declines occurred in the Upper Tributary stratum (Δs = -4), Lower Tributary stratum (Δs = -1), and Tidal stratum (Δs = -1) and likely reflect the failure to detect rare species during post-removal sampling.

We did not encounter four species during post-removal sampling that we captured during the pre-removal period (Blacknose Shiner *Notropis heterolepis*, Spottail Shiner *N. hudsonius*, Ninespine Stickleback *Pungitius pungitius*, and Sturgeon *Acipenser spp.*). Also, we captured one species during post-removal sampling (Atlantic Tomcod *Microgadus tomcod*) that we did not capture during pre-removal sampling. All of these species were captured in low abundance ($n \leq$ 20) during either survey period.

Table 1.2: Species caught during electrofishing surveys and their relative occurrence in all electrofishing surveys. Species information includes abbreviations, life histories (R = resident, A= anadromous, C = catadromous, E = estuarine), Origins (N = native, I = introduced), and each species is listed in order of its pre-removal relative occurrence.

					Relative Occurrence (%)	
Common Name	Scientific Name	Abbreviation	Life History	Origin	Pre-removal (*n*= 202)	Post-removal (*n*= 226)
Smallmouth Bass	*Micropterus dolomieu*	SMB	R	I	96	93
Redbreast Sunfish	*Lepomis auritus*	RBS	R	N	92	69
Fallfish	*Semotilus corporalis*	FF	R	N	88	85
American Eel	*Anguilla rostrata*	EEL	C	N	85	75
White Sucker	*Catostomus commersonii*	WS	R	N	74	69
Common Shiner	*Luxilus cornutus*	CSH	R	N	69	52
Pumpkinseed Sunfish	*Lepomis gibbosus*	PS	R	N	68	30
Chain Pickerel	*Esox niger*	CHP	R	I	61	41
Golden Shiner	*Notemigonus crysoleucas*	GSH	R	N	52	23
Yellow Perch	*Perca flavescens*	YP	R	I	49	40
Brown Bullhead	*Ameiurus nebulosus*	BBH	R	N	45	34
Sea Lamprey	*Petromyzon marinus*	LAM	A	N	44	50
Banded Killifish	*Fundulus diaphanus*	BKF	R	N	27	7
Burbot	*Lota lota*	CSK	R	N	23	21
Alewife	*Alosa pseudoharengus*	ALE	A	N	15	24
Blueback Herring	*Alosa aestivalis*	HER	A	N	11	15
Largemouth Bass	*Micropterus salmoides*	LMB	R	I	9	21
Atlantic Salmon	*Salmo salar*	ATS	A	N	9	10
Creek Chub	*Semotilus atromaculatus*	CRC	R	N	9	11
White Perch	*Morone americana*	WP	R/A	N	9	8
Eastern Silvery Minnow	*Hybognathus regius*	ESM	R	I	6	3
Black Crappie	*Pomoxis nigromaculatus*	CRA	R	I	5	0.4
Blacknose Dace	*Rhinichthys atratulus*	BND	R	N	3	3
Mummichog	*Fundulus heteroclitus*	MUM	E	N	3	1
American Shad	*Alosa sapidissima*	SHD	A	N	2	4
Threespine Stickleback	*Gasterosteus aculeatus*	TSS	R/E	N	2	0.4
Ninespine Stickleback	*Pungitius pungitius*	NSS	R	I	2	0
Fathead Minnow	*Pimephales promelas*	FHM	R	I	1	3
Northern Redbelly Dace	*Phoxinus eos*	RBD	R	N	1	2
Longnose Sucker	*Catostomus catostomus*	LNS	R	N	1	1
Blacknose Shiner	*Notropis heterolepis*	BNS	R	N	1	0
Spottail Shiner	*Notropis hudsonius*	STS	R	I	1	0
Brook Trout	*Salvelinus fontinalis*	BKT	R/A	N	1	2
Sturgeon spp.	*Acipenser* spp.	SGN	A	N	1	0
Finescale Dace	*Phoxinus neogaeus*	FSD	R	N	0.5	4
Striped Bass	*Morone saxatilis*	STB	A	N	0.5	3
Central Mudminnow	*Umbra limi*	CMM	R	I	0.5	2
Slimy Sculpin	*Cottus cognatus*	SSC	R	N	0.5	2
Atlantic Tomcod	*Microgadus tomcod*	ATC	E	N	0	1

1.3.2 Similarity indices

Patterns of assemblage composition analyzed using the Sørensen and Morisita-Horn indices suggest that assemblages within each stratum remained largely similar between sampling periods (i.e. pre-removal vs. post-removal), with a few notable exceptions. Strata that were determined to be least similar between sampling periods were those directly upstream of former dams (i.e. Orono and Milford). In contrast, all other strata (i.e. Tidal, Argyle, tributaries) exhibited largely similar assemblages between sampling periods.

Table 1.3: Similarity indices calculated for each stratum during pre-removal vs. post-removal periods.

	Sørensen	Morisita-Horn
Tidal	0.92	0.71
Orono	0.81	0.89
Milford	0.74	0.40
Argyle	0.86	0.99
Lower Tributary	0.87	0.73
Upper Tributary	0.77	0.91

Sørensen index values were relatively high when comparing the same strata between sampling periods (Table 1.3). Milford had the lowest species composition similarity (S = 0.74), primarily due to the new detection of anadromous fish in the post-removal sampling period. The Tidal stratum had the highest similarity score (S = 0.92) which reflects the consistent detection of over 30 species of fish in this area in both sampling periods. These results suggest that the species found in every stratum remained largely consistent (S ≥ 74%) between sampling periods.

Sørensen similarity index values were relatively high when comparing among different strata within each respective sampling period (Table 1.4). During the pre-removal sampling period, the Tidal stratum consistently exhibited the lowest similarity scores when compared to other strata, due to the occurrence of anadromous fish in this area. In contrast, when we compared strata during the post-removal sampling period, both upper and lower tributary strata exhibited the lowest similarity relative to other strata due to differences in connectivity or general habitat characteristics.

When we examined shifts in among strata similarity between sampling periods, we found the largest the Sørensen index increases between the Tidal stratum and the Milford and Argyle strata (+17% and +14%, respectively; Table 1.4). The largest decrease in Sørensen similarity index values was observed between the Upper Tributary stratum and the Orono and Milford strata (-21% and -13%, respectively; Table 1.4). These differences reflect both the increased occurrence of anadromous species upstream of the former Veazie Dam and the failure to detect a few relatively rare species in the Tidal and Upper Tributary strata during post-removal survey

Table 1.4: Sørensen similarity index values comparing assemblage composition (CPUE) between strata. Values range from 0 (no similarity) to 1 (identical). Values above the diagonal compare strata before dam removal. Values below the diagonal compare strata after dam removal.

	Tidal	Orono	Milford	Argyle	Lower Tributary	Upper Tributary
Tidal	--	0.72	0.63	0.71	0.69	0.71
Orono	0.77	--	0.86	0.89	0.83	0.84
Milford	0.79	0.88	--	0.80	0.83	0.80
Argyle	0.86	0.83	0.81	--	0.77	0.83
Lower Tributary	0.68	0.80	0.83	0.77	--	0.77
Upper Tributary	0.67	0.63	0.67	0.76	0.67	--

The Morisita-Horn similarity index values were also relatively high comparing the same stratum between sampling periods (Table 1.3). The most notable exception was the Milford stratum for which similarity was 40% (C = 0.40). This suggests that the Milford stratum underwent the largest assemblage composition change associated with its change from a lentic impoundment to a lotic habitat and increasing connectivity for migratory fish. The Orono stratum exhibited similar shifts but the effects were not as pronounced due to the occurrence of both impoundment and free-flowing river reaches present in this stratum prior to dam removal. The highest Morisita-Horn index value (C = 0.99) occurred in the Argyle stratum which indicates that the assemblage composition remained nearly identical during both sampling periods.

Table 1.5: Morisita-Horn similarity index values comparing relative abundance (CPUE) between strata. Values range from 0 (no similarity) to 1 (identical). Values above the diagonal compare strata before dam removal. Values below the diagonal are compare strata after the dam removal.

	Tidal	Orono	Milford	Argyle	Lower Tributary	Upper Tributary
Tidal	--	0.81	0.33	0.37	0.35	0.43
Orono	0.78	--	0.53	0.58	0.27	0.66
Milford	0.83	0.96	--	0.95	0.12	0.96
Argyle	0.69	0.42	0.52	--	0.11	0.96
Lower Tributary	0.18	0.10	0.12	0.24	--	0.09
Upper Tributary	0.80	0.76	0.82	0.89	0.20	--

Morisita-Horn similarity index values were relatively low comparing among stratum similarity during each period (Table 1.5). During the pre-removal period, this index suggested evidence of fragmentation in the lower river. The two lower-most strata (Tidal and Orono) had consistently low similarity scores ($C \leq 0.66$) when comparing to areas upstream. Among the strata upriver (Milford, Argyle, Upper Tributary) there was high similarity ($C \geq 0.95$). In contrast, during post-removal surveys, strata downstream of the new lowermost dam (Milford, Orono, Tidal) had high similarity scored ($C \geq 0.78$) which reflects greater connectivity between these strata associated with dam removal. Similarity remained high between the Argyle and Upper Tributary strata (C = 0.89). During both sampling periods, the Lower Tributary stratum had consistently low similarity scores relative to all other strata ($C \leq 0.35$) which reflects the lentic characteristics of these tributaries.

Concerning changes to among strata assemblage similarity between sampling periods, there were substantial shifts in the Morisita-Horn index values (Table 1.5). Morisita-Horn similarity scores increased between the three lowest strata (Tidal, Orono, Milford) after the dam removal associated with increased connectivity between these strata and changing river conditions from lotic impoundments to lentic conditions. For example, the Morisita-Horn similarity between the Orono stratum and Milford stratum increased by 43%. Similarity scores also changed for these three strata relative to Argyle, the stratum above the current lower-most dam. Morisita-Horn similarity decreased between Argyle and the next two strata downstream, Milford and Orono by 43% and 16%, respectively. Interestingly, Morisita-Horn similarity increased (+32%) between the Argyle stratum and the Tidal stratum, likely associated with the failure to detect relatively rare fish in the Tidal stratum (e.g. sturgeons) and the detection of anadromous fish in the Argyle stratum.

Collectively, the similarity indices suggest that though the assortment of species (Sørensen) in each stratum has remained largely consistent between sampling periods, there have been some notable changes regarding the relative abundance of different species (Morisita-Horn), especially in the Milford stratum. Both indices indicated that there was little relative change in the similarity among strata above the current lowest-most dam between sampling periods. For example, The Morisita-Horn similarity was high between the Argyle and Upper Tributary strata during and during both sampling periods. Both indices further suggest the Lower Tributary stratum has a distinctly different assemblage composition compared all other strata which remained evident during both sampling periods.

1.3.3 Non-metric multidimensional scaling

The NMDS ordination represented the data (final stress = 0.02). Values < 0.2 indicate that the data are well described in the chosen number of axes (Clarke 1993). Axis-1 ordinated with positive values associated with anadromous and estuarine species (e.g. Atlantic Tomcod) to negative values associated with species only found upstream (e.g. Ninespine Stickleback) or only

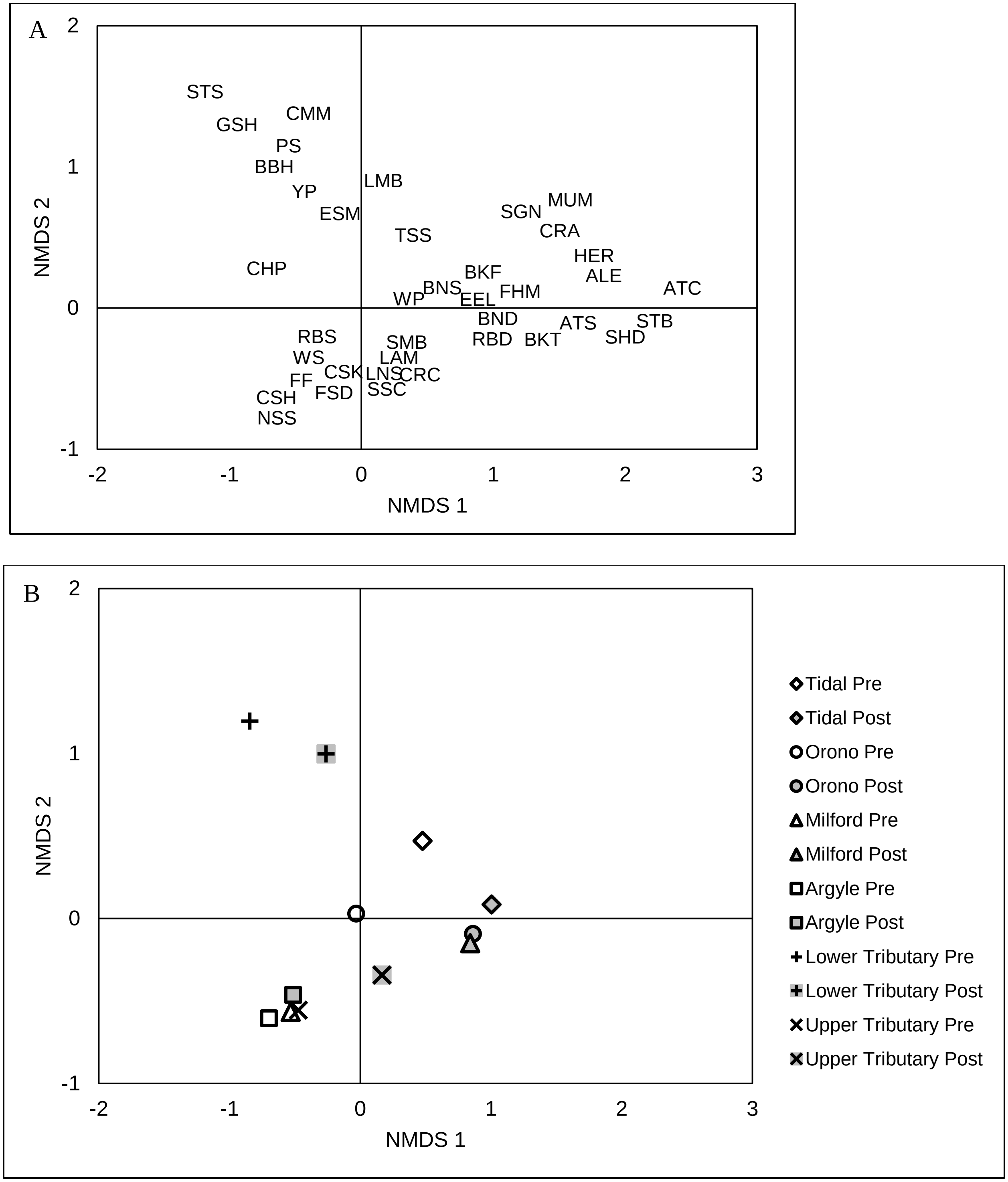

Figure 1.2: NMDS ordination including species leverages (A) and site ordinations (B). Ordinations were computed using averages from each stratum for the pre-removal period (open symbols) and post-removal period (filled symbols). Some species leverage labels are shifted slightly for clarity.

in slack-water reaches (e.g. Golden Shiner *Notemigonus crysoleucas*). Axis-2 ordinated with positive values associated with species only found in slack-water habitats (e.g. Central Mudminnow *Umbra limi*) and negative values associated with species mainly found in fast-water reaches (e.g. Slimy Sculpin *Cottus cognatus*).

Ordination results were consistent with Morisita-Horn similarity index results, though the influence of relatively rare fish was more pronounced in this analysis (Figure 1.2). We observed a consistent increase in Axis-1 values for post-removal averages throughout the mainstem river, with the most pronounced shifts in the strata immediately above the removed dams (Figure 1.2). This is a result of increasing occurrences of anadromous fish upstream of the former Veazie Dam and a decrease in impoundment specialist species. Changes in stratum ordination along Axis-2 tended toward less extreme values during post-removal sampling in all strata. This change is due to a lack of detection of a few, relatively rare species during the post-removal sampling period.

The Milford stratum exhibited the largest shift, relative to other strata followed by the Orono stratum. Interestingly, the post-removal ordination of three strata downstream of the new lower-most dam (Tidal, Orono, Milford) grouped very closely, indicating increasing similarity, increasing influence of anadromous fish, and decreasing lentic specialist fishes in all three strata. The three strata upstream of these areas ordinated relatively close to their pre-removal values which further suggests little assemblage changes upstream of the new lower-most dam.

1.3.4 Distribution of selected species

Patterns of combined relative abundance (CPUE) for all species of fish were similar during both periods except in former impoundments, in which we observed lower relative abundance post-removal. For example, in the Milford stratum (i.e. former Great Works Impoundment), CPUE decreased from an average of 631 fish per km (SE = ± 133 fish) to an average of 101 fish per km (SE = ±11 fish). This change was associated with decreasing capture of young-of-year (YOY) centrarchids (e.g. Redbreast Sunfish *Lepomis auritus*) and slow-water specialists (e.g. Golden Shiner) in this stratum.

Patterns of relative biomass (MPUE) for all species of fish were similar between both sampling periods. We consistently found the highest average fish biomass in the Orono stratum, relative to other mainstem strata. Average MPUE in this stratum ranged from 15.5 kg of fish per km (SE = ±2.1 kg) during pre-removal sampling to 12.4 kg of fish per km (SE = ±1.8 kg) during post-removal sampling. These similarities in reflect the persistence of adult macro-habitat generalist (e.g. Smallmouth Bass) and fluvial dependent (e.g. White Sucker) species which continue to dominate the biomass in the mainstem Penobscot River.

When we examined longitudinal patterns of distribution for selected species, we found patterns associated with increasing connectivity for migratory fish and decreasing relative abundance of macrohabitat generalist species. In addition to the species discussed in detail here, we present the average CPUE and MPUE data for all species in Table A.2 and Table A.3 of Appendix A.

Smallmouth Bass continues to dominate the biomass of the mainstem Penobscot River, but we observed a decrease in relative abundance in the Orono stratum from 110 fish per km (SE = ±86 fish) during pre-removal surveys to 45 fish per km (SE = ±9 fish) during post-removal surveys (Figure 1.3). This decline in CPUE was not also observed in MPUE, which indicates that the decreases in abundance were largely due to low CPUE of YOY Smallmouth Bass.

We observed a large decline in the relative abundance of Pumpkinseed Sunfish in the Orono and Tidal strata (Figure 1.3), resulting from the loss of impoundment habitat. In the Orono stratum for example, CPUE decreased from an average of 32 fish per km (SE = ± 12 fish) to 0.1

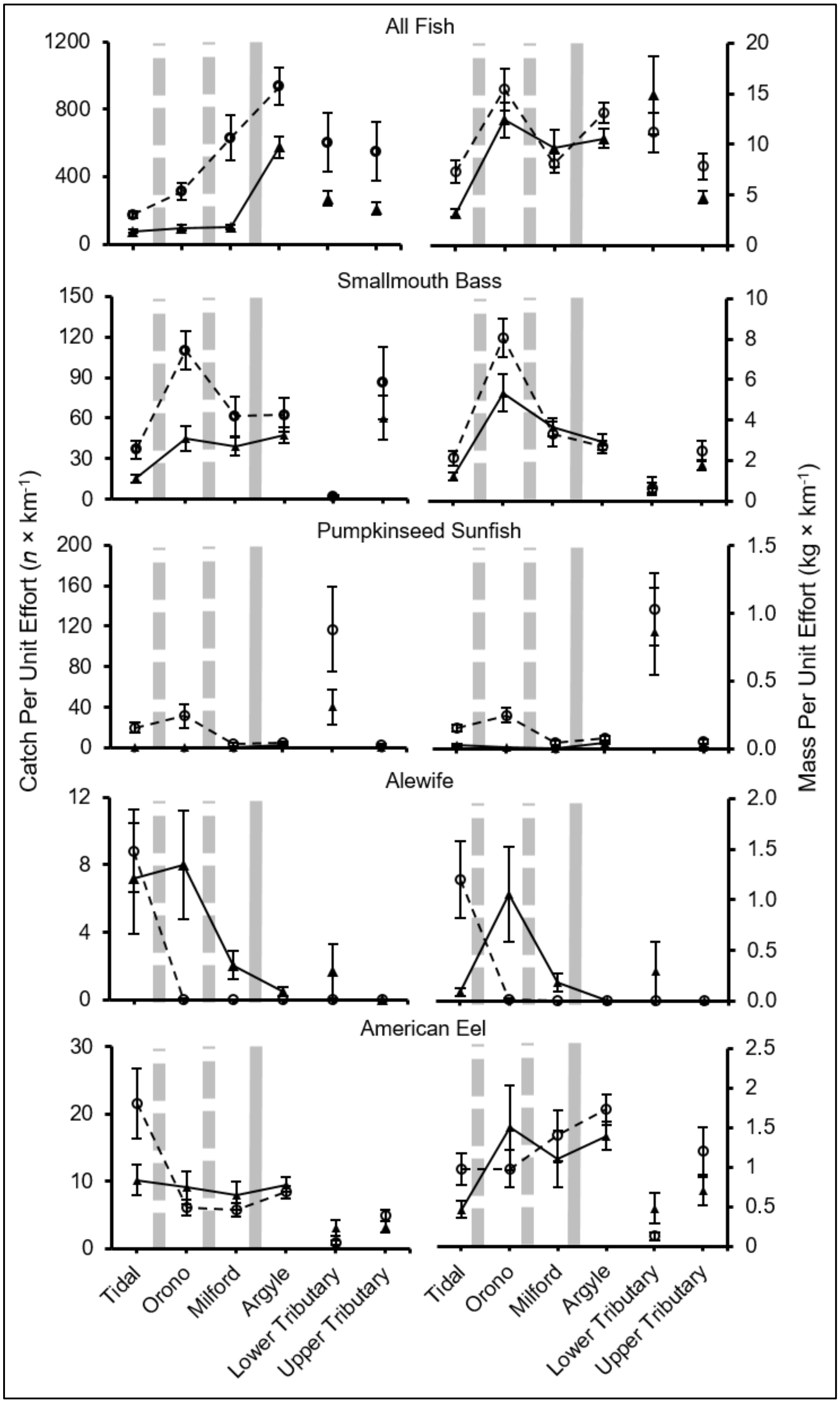

Figure 1.3: Mean CPUE (n × km^{-1} ± 1 SE) and MPUE (kg × km^{-1} ± 1 SE) for pre-removal (open circle, dashed line) and post-removal (triangle, solid line) sampling periods for several indicator species. Values are presented from downstream to upstream along the x-axis. Vertical grey bars indicate the relative location of removed dams (dashed) and existing dams (solid).

fish per km (SE = ± 0.07 fish). This decline is associate with the loss of impoundment habitat upstream of the former Veazie Dam. Similar declines were observed in other slow-water fishes (e.g. Golden Shiner). We did not observe such declines in the Lower Tributary stratum, where they were found in the highest biomass during both sampling periods.

The relative abundance and biomass of Alewife, a pre-removal indicator species in the Tidal stratum, shifted upstream subsequent to dam removal (Figure 1.3). Only one Alewife was captured in the Orono stratum, immediately upstream of the Veazie Dam, prior to its removal. In contrast, we found the highest average relative biomass of Alewife in this stratum during post-removal surveys (CPUE = 8 fish/km, SE = ± 3 fish). We also captured adult Alewife while sampling one of the Lower Tributary fixed transects in 2016 and YOY Alewife in the Argyle stratum each year, indicating that successful reproduction occurred upstream of Milford, the new lower-most dam.

American Eel, the only catadromous species present in the Penobscot River Watershed, exhibited relatively little change in longitudinal patterns of CPUE and MPUE between sampling periods (Figure 1.3). There was, however, a slight decrease in their mean relative abundance in the Tidal stratum from 22 fish per km (SE = ± 5 fish) to 10 fish per km (SE = ± 2 fish). This may suggest that upstream movement of this species was formerly restricted by the Veazie Dam.

1.4 Discussion

Our collective results suggest that dam removal has caused the most pronounced changes in strata in the immediate vicinity of removed dams and that the new lower-most dam (Milford) still causes fragmentation within the mainstem Penobscot River. Patterns of species occurrence and richness remained largely consistent, as indicated by observed richness values and the Sørensen similarity index. The only exception was the Milford stratum, in which more anadromous species were present during post-removal sampling. Collective patterns of relative abundance and biomass, as measured by the Morisita-Horn similarity index, indicate that the assemblages were most changed in former impoundments and that strata in the lower river became more compositionally similar during the post-removal period. This is due to a shift in the longitudinal distribution of certain fish species. Anadromous species have shifted upstream, whereas the relative abundance of slow-water specialist and, to a lesser extent, macro-habitat generalist species has decreased substantially in former impoundments. Strata above the new lower-most dam (Milford) exhibited largely similar assemblage composition and we did not observe any major changes in the relative abundance or biomass of common species in these areas.

We observed the largest increase in diversity in the Milford stratum which is more connected to areas downstream post-dam removal and is bounded on the upstream end by the new lower-most dam. Other studies (e.g. Dodd et al. 2003, Stoller et al. 2016) have described similar peaks in fish species richness below dams resulting from restrictions in upstream movement. Collectively, this result indicates that there is greater connectivity among the lowest three strata and that Milford Dam still acts as a barrier to the movement of fish in the mainstem Penobscot River.

We chose to use both the Sørensen and the Morisita-Horn similarity indices because changes in connectivity and, in some cases, habitat in each stratum may result in differences in species composition (Sørensen), proportional species abundance (Morisita-Horn), or both aspects of the assemblage composition. They have also been used in previous studies examining the impact of connectivity on fish assemblages (e.g. Dodd et al. 2003, Hayes et al. 2006, Gardner et al. 2013, Stoller et al. 2016) and their use here facilitates comparison across studies. For example, Hayes et al. (2006) found that, when comparing fish assemblages in upstream and downstream reaches, 23 un-dammed streams in the Laurentian Great Lakes basin had average Sørensen and Morisita similarity scores of 0.69 and 0.75, respectively.

The NMDS ordination (Figure 1.2) corroborated results from the Morisita Horn similarity indices by demonstrating increasing similarity between strata where connectivity was improved through dam removal. The two formerly impounded strata (Orono and Milford) displayed the largest ordinal shifts which indicates a greater influence of diadromous fishes and a reduction in relative abundance of lacustrine fishes. These two adjacent strata ordinated closely to each other during both sampling periods. However, during pre-removal surveys they grouped more closely with the Argyle and Upper Tributary strata and during post-removal surveys exhibited scores associated with diadromous fish ordination. These ordinal shifts along with the Morisita-Horn index suggest that the dam removals made these two strata more similar to areas downstream (i.e. Tidal stratum) and less similar to areas upstream (i.e. Argyle stratum). These results are consistent with other dam removal studies (e.g. Poulos et al. 2014, Hogg et al. 2015) which have shown increasing ordinal similarity in sites where connectivity has been restored.

The relative abundance and relative biomass data collected for this study reflect high annual assemblage variability, heterogeneous shoreline habitats, and variable sampling conditions. As such, it is important to note that there are limitations to the inferences one can draw from these data. Unfortunately, it was impractical to generate estimates of true abundance for each species in each sample. However, the magnitude of changes relative to average pre-removal abundance and biomass for several species is greater than the variability observed in the data. Such large signals are a result of the PRRP rather than a result of annual, seasonal, or sampling variability. Similarly, Catalano et al. (2007) observed high variability in index of biotic integrity (IBI) scores following dam removal, though the magnitude of changes in former impoundments were well above the observed magnitude of annual variability.

Concerning anadromous fishes, we found evidence of both increasing connectivity and increasing relative abundance and relative biomass for most species. We observed an increase in the number of YOY river herring during the post-removal period, most noticeably in the Tidal stratum. We also captured both adult and juvenile river herring above the current lower-most dam (Milford Dam) in both the Argyle stratum and several lower tributaries during the post-removal surveys (Figure 1.3). Notably, in the final sampling season for this study (early summer 2016) we captured several adult river herrings in Sunkhaze Stream, where they had not been previously detected. It is important to note that three years prior to the first dam removal a program was initiated whereby several lakes within the watershed were annually stocked with adult river herrings that were trapped-and-trucked from the Kennebec and Union rivers in Maine (Mitch Simpson, Maine Dept. of Marine Resources, pers. comm.). Similar efforts occurred prior to the dam removal on the Kennebec River in Maine (Pess et al. 2014). Such pre-emptive stocking confounds our ability to attribute new upstream occurrences of river herring to increased connectivity but, regardless, our sampling documents successful reproduction either from new colonizers or previous stocked spawners. In contrast, American Shad were not actively stocked before dam removal and we also found evidence of successful recolonization of this species including detection of adults throughout the mainstem study area and the capture of one YOY individual during fall 2014 sampling surveys.

While alosines exhibited the most pronounced changes, post-removal distributions of other migratory fishes also changed. For example, American Eel exhibited a more even longitudinal distribution in the mainstem river (Figure 1.3) during post-removal surveys, which suggests that these fish are no longer concentrating below the former Veazie Dam. Hitt et al. (2012) also described a relatively fast (<4 years) increase in American Eels abundance upstream of a mainstem dam removed from the Rappahannock River.

Based on the observed changes after their removals, the former dams on the Penobscot River seem to have influenced resident fish assemblage composition in several ways. First, localized absence of lacustrine fishes (e.g. Golden Shiner, Pumpkinseed, Banded Killifish) during post-removal surveys indicate that impoundments provided artificial habitat suitable to these fishes. Also, we rarely observed YOY centrarchids (Redbreast Sunfish, Pumpkinseed Sunfish, and Smallmouth Bass) during our post-dam removal fall surveys in the former impoundments which suggests that these habitats no longer provide suitable spawning habitat for these species. Furthermore, we observed a decline in relative biomass of adult Smallmouth Bass in the Orono stratum (Figure 1.3), which suggests that the former Veazie impoundment served as suitable winter refugia habitat for adult fish, as was suggested by Kiraly et al. (2014a). Finally, many lacustrine or generalist species were found below Veazie, the lower-most dam during pre-removal surveys, which suggests that the impoundment provided source populations for these fishes in the freshwater Tidal stratum downstream. These observed changes to resident fish assemblages illustrate the principles described by Pringle (1997) who also described both upstream and downstream effects of dams.

Finally, It is important to note that several studies (e.g. Quinn and Kwak 2003, Kruk et al. 2016) have illustrated that the effects of river modification on fish assemblages are revealed over long time scales (i.e. > 10-20 years) and initial observations may be specific to the period immediately following the dam removal. However, long-term studies associated with dam removals are rare. In this study, the most substantial fish assemblage changes after dam removal occurred in former impoundments. While we found evidence that connectivity has been enhanced for migratory fishes throughout much of the Penobscot River Watershed, these ramifications will likely be revealed over longer timescales (i.e. several generations of fish) than those described here.

CHAPTER 2 : IMPLICATIONS OF RECOVERING RIVER HERRING *ALOSA* SPP. POPULATIONS ON SMALLMOUTH BASS *MICROPTERUS DOLOMIEU* DIET AND GROWTH

2.1 Introduction

Growth and life history patterns of predatory fishes are influenced by prey availability (Adams et al. 1982a, Boisclair and Leggett 1989, Dunlop et al. 2005), prey size (Michaletz 1997, Pazzia et al. 2002), and prey energy density (Rand et al. 1994). Diet composition can influence growth (Boisclair and Leggett 1989) and size at maturity (Shuter et al. 2016) of predators. Differences in diet can result in growth differences across spatial (Yako et al. 2000, Glover and DeVries 2013) and temporal (Martin 1970, Shuter et al. 2016) scales. Therefore, the introduction or, in this case, restoration of forage fish in freshwater systems should result in changes to predator diet and growth.

One such piscivorous fish, the Smallmouth Bass *Micropterus dolomieu*, native to the St. Lawrence and Mississippi drainages (Werner 2004), has been introduced widely throughout the world (Jackson 2002) and has been implicated in declines of abundance and diversity of native minnows, salmonines, and other sensitive taxa (Whittier and Kincaid 1999, Weidel et al. 2007). They also prey upon anadromous fishes in areas outside of their native range such as the Pacific Northwest (e.g. Fritts and Pearsons 2004, Tabor et al. 2007). In Maine, Smallmouth Bass were commonly introduced in the late 19th century and since have spread throughout most of the watersheds in the state (Warner 2005). Also during this period, construction of many large dams fragmented habitat and contributed largely to the decline or extirpation of anadromous fish populations (Saunders et al. 2006). Recently, Maine’s Penobscot River has been the focus of a restoration project, including two large dam removals and upgraded fish passage facilities at several remaining dams. This project is collectively known at the Penobscot River Restoration Project – PRRP (see Opperman et al. 2011 for description). These efforts have increased connectivity for sea-run fishes, resulting in substantial recent population growth for anadromous river herring *Alosa* spp. in this system. Of interest here are the dietary shifts and potential impacts to growth of Smallmouth Bass associated with recently rebounding alosine populations in the Penobscot River.

Anadromous river herring, collectively alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*, once abundant in the Penobscot River watershed (Saunders et al. 2006) are currently at historically low abundance in Maine and throughout their range. River herring populations declined drastically after the mid-20th century (Brown et al. 2013) due primarily to dams and overfishing (ASMFC 2012, Hall et al. 2012). In 2006 they were listed collectively as species of concern by the National Marine Fisheries Service (USDOC 2006). These fishes spawn in coastal rivers and lakes on the Atlantic coast of the United States and Canada (Werner 2004). When connectivity to spawning grounds in fragmented watersheds is restored, anadromous river herring can repopulate river systems relatively quickly, often over a few generations (Lichter et al. 2006, Hall et al. 2011). Recently, river herring returns to the Penobscot River, Maine have increased dramatically coincident with enhanced connectivity associated with the PRRP. These efforts were also accompanied by stocking of adult river herring within the watershed to aid their recovery beginning in 2010; subsequently, adult river herring passage through Milford Dam, the current lower-most mainstem dam, has increased from approximately 187,000 in 2014, the first year after dam removal, to over 1.2 million in 2016 (Mitch Simpson, Maine Department of Marine Resource, pers. comm.).

Anadromous river herring are important prey across fresh and saltwater systems (Hall et al. 2012). In freshwater they are preyed upon heavily by piscivores including Largemouth Bass

Micropterus salmoides (Yako et al. 2000) and Blue Catfish *Ictalurus furcatus* (MacAvoy et al. 2000). Landlocked populations are important prey for Salmonines in the Great Lakes (Stewart and Ibarra 1991, Rand et al. 1994, Savitz 2009), landlocked Striped Bass *Morone saxatilis* (Cyterski et al. 2002), and Chain Pickerel *Esox niger* (Brodersen et al. 2015). Studies similar to ours have examined interactions between piscivorous fishes and juvenile anadromous river herring in their natal lentic environments. Notably, Yako et al. (2000) found that juvenile anadromous alewives constituted a large portion of Largemouth Bass diets in Massachusetts lakes; also, Largemouth Bass in lakes with anadromous river herring attained larger maximum size, which was attributed to the presence of river herring. These studies collectively suggest that *Alosa* spp. are important, energy-dense prey for piscivorous species across many systems. However, previous studies of the interactions between Smallmouth Bass and river herring (e.g. Kircheis et al. 2002, Hanson and Curry 2005, Willis 2009) have focused primarily on interspecific competition between juveniles, thus it is important to define predator-prey interactions in rivers.

Smallmouth Bass have been the focus of conflicting management approaches in the state of Maine. In one regard, they are one of the most popular sportfish in the state, and are managed for recreational fishing by the Maine Department of Inland Fish and Wildlife (Jordan 2001). Paradoxically, MDIFW also designates Smallmouth Bass as an introduced species and discourages further introduction in state waters (Jordan 2001). This presents MDIFW with a challenge to simultaneously preserve native fishes of Maine and maintain popular recreational fisheries. In some cases, advocates for Smallmouth Bass have influenced state management practices in order to preclude anadromous fish passage (Willis 2009).

Interspecific interactions between anadromous river herring and Smallmouth Bass have not been well defined, which has resulted in extensive controversy around river herring restoration elsewhere in Maine. In the St. Croix River, which forms the eastern border between Maine and

New Brunswick, Canada, there was uncertainty over whether juvenile anadromous river herring compete directly with young-of-year (YOY) Smallmouth Bass in nursery lakes and ponds (Hanson and Curry 2005, Willis 2009). Concerns over a perceived decline in Maine's Smallmouth Bass fishery prompted the state to close fish passage structures and exclude river herring from natal spawning grounds, although restoring river herring access to historic habitat is a top priority of Native American tribes and New Brunswick provincial fisheries agencies (Willis 2009).

The extent to which Smallmouth Bass prey upon juvenile anadromous river herring in rivers has not been described previously, though there is great potential for such interaction. Rearing and outmigration of anadromous river herring is protracted throughout the summer and fall in the Northeastern United States (Yako et al. 2000), when water temperatures are optimal for Smallmouth Bass consumption (~22°C; Whitledge et al. 2003). Furthermore, Smallmouth Bass living in freshwater tidal areas may have prolonged access to pulses of juvenile herring exported from lakes and ponds upstream. Though river herring are typically thought to migrate directly to the ocean, two studies (Limburg 1998, Gahagan et al. 2012) have shown extensive movement between salt and freshwater tidal habitats during early life history. Because Smallmouth Bass is the dominant piscivore the lower Penobscot River watershed (Kiraly et al. 2014a) and juvenile river herring prey is available throughout the growing season, these rebounding populations could provide an important prey source for Smallmouth Bass.

The purpose of this study was to assess the importance of river herring as prey in diet and growth of Smallmouth Bass, in the context of watershed-wide efforts towards recovery of river herring populations. We used Penobscot River watershed as a study system to test the extent to which recent increases in river herring populations may have influenced Smallmouth Bass growth and diet. To do so we i) assessed the diet of Smallmouth Bass in several river reaches encompassing variable access to river herring as prey, ii) compared growth of Smallmouth Bass between those reaches and, iii) used a bioenergetics model to explore potential impacts of increasing consumption of anadromous river herring on future Smallmouth Bass growth, coincident with projected river herring population increases.

2.2 Methods

2.2.1 Collection and processing

We captured Smallmouth Bass from May through October 2015 from three mainstem reaches of the Penobscot River (Figure 2.1), corresponding to strata delineated by Kiraly et al. (2014a); i) Argyle, which is above the lower-most dam and has only recently (i.e. 2014) been accessible to river herring through fish passage improvements at that dam, ii) Orono, which is below the lower-most dam and, as of 2014, is accessible to river herring, and iii) the Tidal stratum, which consists of the area below the head of tide and has been historically accessible to a relatively small river herring population (Grote et al. 2014b). We also sampled the Piscataquis River (Piscataquis stratum), a major tributary to the Penobscot River, which became accessible to anadromous river herring through passage improvement in 2016, after the completion of our collections. We chose each area based on river herring presence (both current and historic) and locations relative to several main-stem dams (Kiraly et al. 2014a).

We captured Smallmouth Bass with electrofishing and angling. Electrofishing collections occurred in conjunction with fish community surveys described in Chapter One. When permitting restrictions prohibited electrofishing (water temperature > 22°C), we used angling to capture individuals from July until September. Only individuals captured from three areas were considered for stomach content analysis due to the inconsistent collection of specimens from the

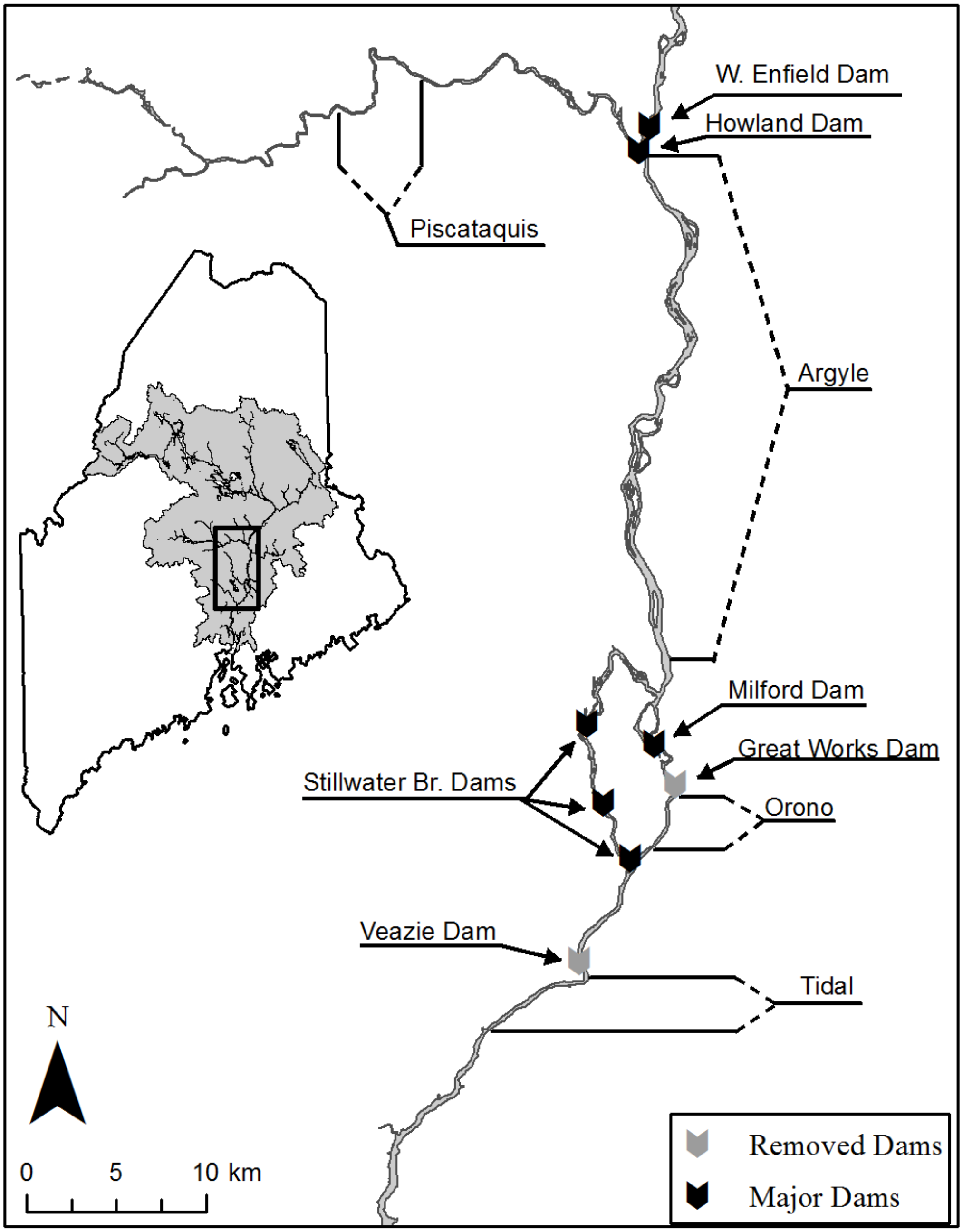

Figure 2.1: The Penobscot River watershed (inset) and lower mainstem river including the Piscataquis River. Also included are the locations of dams both present and former and the delineations of the sample strata.

Argyle stratum. All individuals used in stomach content analysis were captured within four hours of sunrise to decrease the incidence of empty stomachs; the majority (76%) were collected by angling. Angling began at sunrise and continued until capture goals were met or four hours had elapsed, which ever came first. This time was chosen because Smallmouth Bass are crepuscular feeders (Reynolds and Casterlin 1976) and water temperatures are lowest at night, which decreases digestive rates. We attempted to collect ten individual Smallmouth Bass in each 50mm size class, starting at 150mm, in order to obtain a range of ages and diets. For common size classes (i.e. 200-300 mm), we frequently released fish once we met our quota for those size classes. However, for uncommon sizes (e.g. >350 mm) or during periods of low catch due to cool water temperatures (i.e. October sampling), we did not always meet our catch quotas.

Upon capture, fish were measured and, if they were determined to meet our size criteria, placed in buffered MS-222 until cessation of opercular movement and ultimately death. The fish were then placed in a cooler with ice water and brought back to the lab for dissection.

Upon arrival fish were dissected immediately or frozen for later dissection. We measured a subset of fish (n = 75) before and after freezing and confirmed total length measurements were not significantly different (two sample t-test, p = 0.43). During dissection, we removed sagittal otoliths and removed stomachs by cutting the esophageal and pyloric sphincters. Stomachs were wrapped in muslin cloth, preserved in a buffered 10% formaldehyde solution, rinsed with water, and stored in 70% ethanol before further dissection and sorting.

2.2.2 Diet analysis

We removed all preserved contents from each stomach, and sorted into one of five categories: river herring, other fish, insect, crayfish, and other. Each prey type from each stomach was then placed in an aluminum container of known mass and dried at 60°C for 24 hours. Dry mass was recorded to the nearest thousandth of a gram. Items were classified as "other" if the prey was either unidentifiable or did not fit into one of the other four prey categories. The "insect" prey category included both terrestrial (e.g. caterpillar) and aquatic (e.g. stoneflies) insect species. The "other fish" category included all species other than alosines and unidentifiable fish tissue.

We calculated frequency occurrence (Oi) of each prey type, defined as:

$$O_i = \frac{J_i}{P}$$

where J_i was the number of fish containing prey *i* and *P* was the number of fish with food in their stomachs. This measure describes how often each prey type was consumed, though measures of prey mass are more appropriate for determining importance of each prey type to fish diet (Chipps and Garvey 2007). We also calculated the ratio of the total mass of each prey type to the total mass of all stomach contents following the ratio estimation procedure detailed by Hansen et al. (2007):

$$\widehat{R} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i}$$

Where y_i was the mass of prey type *i* and x_i was the total mass of all prey types. We calculated this ratio for the sample population in each stratum and month. The standard error for this ratio (Hansen et al. 2007) was approximated as:

$$\mathrm{SE}\left(\widehat{R}\right) = \frac{1}{\sqrt{n}\,\overline{x}} \sqrt{\frac{\sum_{i=1}^{n} (y_i - \widehat{R}x_i)^2}{n - 1}}$$

2.2.3 Otolith preparation

We chose to use sagittal otoliths for aging as opposed to non-lethal aging structures (e.g. scales) to reduce reader error and increase precision for Smallmouth Bass over age five (Long and Fisher 2011). Otoliths were embedded in Epo-Fix resin and sectioned along the dorsal-ventral axis. Sections were then fixed to a slide using Crystalbond^{TM} adhesive. We then photographed the otolith sections and an external length standard with a Spot 3.1 camera (SPOT Imaging, Sterling Heights, MI) mounted on the trinocular port of a MEIJI Techno EMZ-13TR stereomicroscope. We measured to the distal edge of the most recent annulus along the medial axis and measured total medial radius of each otolith with ImageJ (Schneider et al. 2012) and the ObjectJ plugin (Vischer and Nastase 2015). During digital measuring, we simultaneously viewed the photograph of the sectioned otolith and the corresponding slide of sections from the same otolith using a dissecting microscope to ensure that each annulus was marked appropriately and that the margin of each otolith was marked correctly. Each otolith was aged by two independent reviewers and discrepancies in age determination were corrected prior to measurement. The measurement of each otolith was assigned a confidence level (1 through 10) and only measurements with a confidence level of eight or higher were considered in this analysis.

2.2.4 Back-calculations and growth modeling

To estimate total length at previous ages, we chose the Modified Fry method detailed by Vigliola and Meekan (2009). Because we captured individuals ranging from age-0 through age-20, we were able to determine that the relation between the medial otolith radius and total length for Smallmouth Bass in our study was not linear (i.e. allometric; shown in Figure B.1 in Appendix B). Thus, this method was appropriate to estimate size (Vigliola and Meekan 2009). The Modified Fry back calculation is defined as:

$$L_i = 0.75L_0 + \exp\left(\ln(L_0 - 0.75L_0) + \frac{[\ln(L_c - 0.75L_0) - \ln(L_0 - 0.75L_0)][\ln(R_i) - \ln(R_0)]}{[\ln(R_c) - \ln(R_0)]}\right)$$

where L_i was the estimated length at age i, R_i was the otolith radius at time i, L_0 was the average length at formation of the first increment, R_0 was the average otolith radius at the formation of the first increment, and L_c and R_c were the length at capture and otolith radius at capture, respectively. In the fall of 2015 we collected age-0 Smallmouth Bass from each stratum and used these fish to estimate the length of the fish (L_0) and radius of the otolith (R_0) at the formation of the first annulus. These estimates were then used to set the biological intercept terms in the Modified Fry model.

We fit the von Bertalanffy growth model (VBGM; von Bertalanffy 1938) as a Bayesian hierarchical model with a Markov chain Monte Carlo (MCMC) approach in JAGS (Plummer 2003) using the R2jags package (Su and Yajima 2015) in R (R Core Team 2016). We estimated the VBGM parameters for each stratum independently and used a hierarchical model specification to facilitate information sharing between strata. We assumed that length (Y_i) was a random variable sampled from a normal distribution (N) with a mean of L_i and age-specific precision ($1/\sigma^2$) parameter τ_t:

$$Y_i \sim N(L_i,\ \tau_t)$$

The length of each fish (L_i) at age t_i was estimated using the VBGM as:

$$L_i = L_{\infty j}\left(1 - e^{-K_j\left(t_i - t_{0j}\right)}\right),$$

where $L_{\infty j}$ was the asymptotic length of fish in each stratum j, K_j was the Brody growth coefficient in each stratum, and t_{0j} was age at length zero in each stratum. We chose to fit the VBGM using back calculated sizes for the most recent annulus for each fish, as opposed to size at capture data, to account for the variability in capture dates and corresponding seasonal growth differences.

The prior distributions describing each of the stratum-specific parameters in the VBGM were specified from hyperprior based on global (catchment-wide) hyperparameters. We specified uninformative, hyperpriors for hyperparameters of catchment-wide L_∞, K, and t_0. The prior for $L_{\infty j}$

in each stratum was specified as a log-normal distribution with mean μ_{L_∞} and precision τ_{L_∞} to restrict estimation to values greater than 0 mm. We assigned a flat hyperprior for μ_{L_∞} using a uniform (*U*) distribution on the interval [0.0001, 10] and we assumed a gamma distribution with *r* = 0.001 and λ = 0.0001 for the hyperprior on τ_{L_∞}:

$$L_{\infty j} \sim \text{log-normal}\left(\mu_{L_\infty}, \tau_{L_\infty}\right)$$

$$\mu_{L_\infty} \sim U(0.001, 10)$$

$$\tau_{L_\infty} \sim \text{gamma}(0.001, 0.0001)$$

The prior for each K_j was specified on the logit scale, with mean μ_K and precision τ_K, and was back-transformed before incorporation into the VBGM. This allowed us to specify uninformative hyperpriors on μ_K and τ_K. We specified μ_K as a diffuse normal distribution with a mean of zero and precision of 0.0001, and used a gamma distribution with *r* = 0.001 and λ = 0.0001 for the hyperprior on τ_K such that:

$$\ln\left(\frac{K_j}{1 - K_j}\right) \sim N\left(\mu_K, \tau_K\right)$$

$$\mu_K \sim N(0, 0.0001)$$

$$\tau_K \sim \text{gamma}(0.001, 0.0001)$$

Stratum-specific values of t_{0j} were drawn from a normal distribution with mean μ_{t_0} and precision τ_{t_0}. Because the theoretical age *t* at length zero is negative, we used a uniform hyperprior on the interval [-10, 0] for μ_{t_0}, and a gamma distribution with *r* = 0.001 and λ = 0.0001 for τ_{t_0}.

We ran three Markov chains for each parameter and chose random starting values for each individual chain based on random draws from the prior distributions of each hyperparameter. We used a burn-in of 30 000 samples and then sampled another 160 000 values from the posterior distribution of each parameter, keeping every tenth value to reduce auto correlation between samples and increase the effective sample size (Kruschke 2011). This resulted in a total of 48 000 values from which to construct posterior distributions for each parameter. We assessed convergence of Markov chains using the Gelman-Rubin statistic ($\hat{r}$), and by graphical inspection of mixing among chains. Effective sample size was sufficient to construct posterior estimations of all parameters.

2.2.5 Bioenergetics modeling

To model annual Smallmouth Bass growth we used the Wisconsin mass-balance bioenergetics model (Hanson et al. 1997) and metabolic values reported by Whitledge et al. (2003). We used daily average temperature values from two USGS gauging stations, one on the Piscataquis River and the other on the mainstem Penobscot River (U.S. Geological Survey 2017a, 2017b). All models were run for the period in which average water temperatures were greater than 8°C (May 1 – October 31). Because Smallmouth Bass are largely inactive and presumably not feeding below 10°C (Roell and Orth 1993), we assumed that all annual growth would occur during the modeled period. We also substituted daily average temperature measurements from the two sources to determine whether potential temperature differences could cause differences in growth.

Table 2.1: Diet proportions from Smallmouth Bass 225< TL < 325mm used in bioenergetic models

	Tidal					Orono					Piscataquis				
	May	July	Aug	Sept	Oct	May	July	Aug	Sept	Oct	May	July	Aug	Sept	Oct
Invertebrate	0.55	0.30	0.20	0.01	0.20	0.84	0.71	0.29	0.11	0.03	0.60*	0.37	0.27	0.15	0.10*
Crayfish	0	0.07	0.21	0.05	0	0	0.12	0.36	0.80	0.42	0.02*	0.11	0.45	0.83	0.60*
Fish	0.45	0.21	0.39	0.77	0.80	0.16	0.05	0.35	0.09	0.55	0.38*	0.52	0.29	0.02	0.30*
River Herring	0	0.42	0.20	0.17	0	0	0.12	0	0	0	0*	0	0	0	0*

* = estimated from observed diet proportions in other strata

Modeled diet proportions were taken from individuals with a total length of 225 mm – 325 mm at time of capture to avoid the influence of different feeding strategies employed by the largest and smallest fish in our samples. Because 93% of "Other" diet items by mass were found in only 4% of stomachs, we excluded these prey types from diet composition in bioenergetics analysis. We interpolated diet proportions between sampling events and for two of the modeled months we estimated diet composition in the Piscataquis stratum based on seasonal trends observed in the other two strata (Table 2.1).

We ran all models using average prey energy content values reported by Yako et al. (2000) and energetic content was assumed to be constant throughout the modeling period (Table 2.2). Predator energy content was held constant at 4184 J/g (wet mass) through all models, which is common for models of centrarchid bioenergetics (Whitledge et al. 2003). We chose to model annual growth for individuals ranging from age-2 to age-5 due to the prevalence of those age classes in our samples. We used results from the VBGM and a length-mass relationship (R^2 = 0.99; shown in Figure B.2 in Appendix B) developed for Smallmouth Bass in the Penobscot River watershed based on electrofishing survey data to estimate seasonal growth in grams.

Table 2.2: Prey energy densities used in bioenergetic modelling. Values taken from (Yako et al. 2000).

	Energy Density (kJ/g)
Invertebrate	3.2
Crayfish	3.2
Fish	4.1
River Herring	5.6

We first ran models using observed diet data for each stratum to produce an estimate of the proportion of maximum consumption (% C_{max}) for each age class required to achieve average annual growth. Next, we ran a model with proportions of juvenile river herring observed in Orono diets substituted in the Piscataquis stratum diets to simulate a relatively modest increase in river herring consumption. Finally, we ran two models with proportions of juvenile river herring observed in diets of Smallmouth Bass captured in the Tidal stratum substituted for the diet in both the Orono and Piscataquis strata to simulate large increases in consumption of this prey in these strata. In all instances where diet was manipulated, the proportion of C_{max} was held at the rates previously modeled and the proportion of remaining diet items consisted of the observed diet rescaled to represent the proportion of the diet not composed by juvenile river herring.

2.3 Results

2.3.1 Collections and sample sizes

We captured a total of 765 Smallmouth Bass from four strata of the Penobscot River (Figure 2.1). We captured 372 individuals during our spring and fall electrofishing surveys. We used angling to capture another 393 individuals during the summer, in the interim between electrofishing surveys. We present length and age histograms of Smallmouth Bass collected four our samples in Figure B.3 in Appendix B.

2.3.2 Diet

Of the 765 Smallmouth Bass collected, we used 573 fish for stomach analysis, with 72% of those fish captured during summer angling collections. We used electrofishing to capture all individuals for diet analysis during May and October surveys due to time constraints and potentially low angling success associated with cooler water temperatures. We collected stomachs from the Piscataquis stratum only during angling surveys (July – September) due to time restrictions. The proportion of empty stomachs relative to all stomachs collected during each sampling occasion ranged from 4% to 33%, with an average of 19% across all sampling occasions. We removed empty stomachs for further diet analyses.

Insects were the most frequently consumed prey type in every stratum. On average, we found insects in 76% of stomachs that contained prey (Table 2.3). Fish were, on average, the next most commonly occurring prey type found in 23% of stomachs containing prey.

Table 2.3: Total number of stomachs, number of those which were empty in each stratum, and average frequency of occurrence of each prey type in each stratum.

	Number of Stomachs		Frequency Occurrence (%)				
	Total	Empty	River Herring	Other Fish	Crayfish	Insect	Other
Tidal	162	30	14	30	8	68	20
Orono	274	48	3	18	4	76	19
Piscataquis	136	19	0	15	15	83	15

Table 2.4: The ten largest prey items in the "other" category, the stratum, month, and total length (TL) of Smallmouth Bass in which those items occurred, and the dry mass and percent of the total prey mass they contributed in that month and stratum.

Prey Item	Stratum	Month	TL (mm)	Dry Mass (g)	Total Mass (%)
Rodent	Piscataquis	September	307	12.88	63
Frog	Tidal	October	311	4.39	42
Frog	Orono	October	357	0.94	27
Turtle	Tidal	September	292	3.12	25
Rodent	Piscataquis	August	254	3.16	22
Snake	Tidal	August	284	0.67	11
Turtle	Tidal	September	364	1.06	9
Detritus	Tidal	July	255	0.58	8
Frog	Tidal	October	336	0.76	7
Rodent	Piscataquis	August	430	0.37	3

Average total stomach content mass was highly variable and relatively equal between strata (Figure 2.2). We examined the contribution of each prey category by the relative mass in each stratum per month. The "other" prey category composed a large portion of the diets (>20% by mass) in several months due to the occurrence of several large prey items in relatively few individuals. Ten prey items composed over 95% of the mass for items in that category with the largest item (rodent) composing 63% of the total prey mass in the Piscataquis stratum during the month of September (Table 2.4). We also found one soft plastic fishing lure which was not included in this analysis.

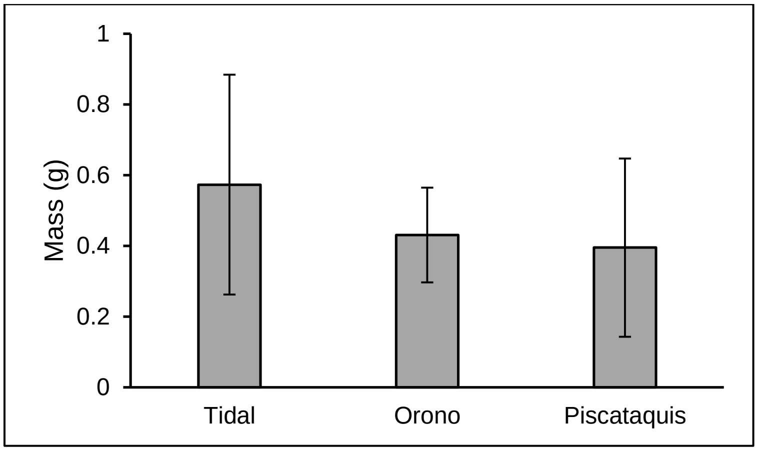

Figure 2.2: Average dried stomach content mass in grams (± 2 SE) calculated for stomachs containing prey, reported by stratum.

River herring were found in the diet during every month sampled in the Tidal stratum and only during July in the Orono stratum. We found river herring in 14% of stomachs containing prey from the Tidal stratum. During the months in which they were available (July-October), juvenile river herring composed an average of 19% (SE = ±6%) of prey by mass in the Tidal stratum, 4% (SE = ±1.9%) in the Orono stratum, and were not found in the stomachs collected in the Piscataquis stratum (Figure 2.3).

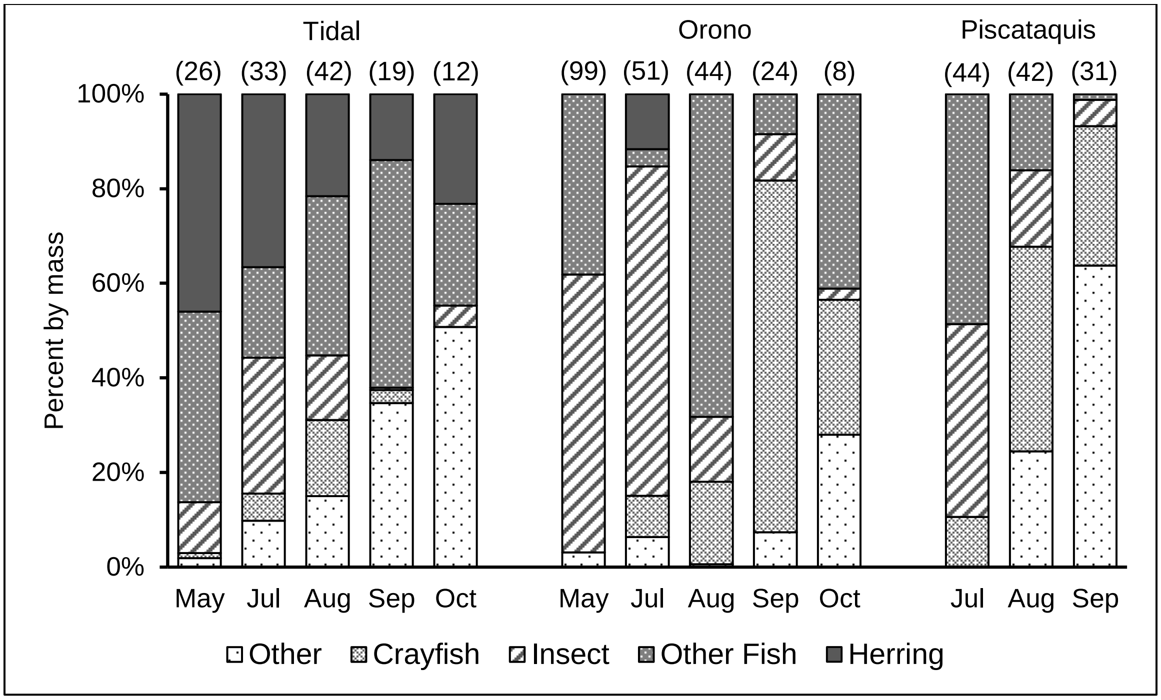

Figure 2.3: Percent diet composition by mass of Smallmouth Bass reported by month in three different areas (top) of the Penobscot River, Maine. Values above bars (in parentheses) indicate number of stomachs containing prey items in each sample.

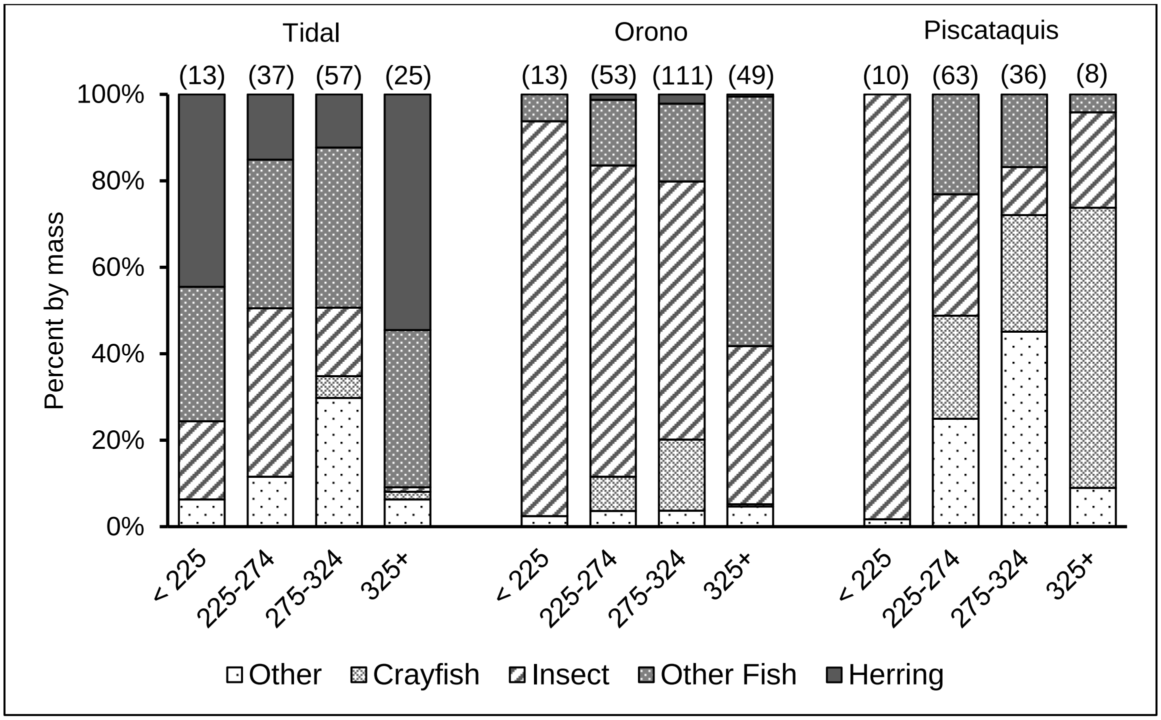

Figure 2.4: Diet composition of Smallmouth Bass in each stratum described in 50 mm (TL) size classes collected in 2015. Values in parentheses denote the number of stomachs containing prey in each group.

When we examined the diets of Smallmouth Bass in the Tidal stratum by size class (Figure 2.4), river herring composed 12% to 55% of the diet by mass in each group. Juvenile river herring composed the largest percent by mass (R= 44%, SE = ±28%) of diet items for our smallest sampled sizes (< 250 mm total length). In contrast, the diet proportion by mass of the smallest sampled size class in the other two strata was dominated by insects, with their contribution decreasing in larger size classes. The contribution of other fish to the diets of different size classes of Smallmouth Bass in the Tidal stratum remained relatively consistent, ranging from 31% (SE = ±20%) to 67% (SE = ±13%). In the Orono stratum, other fish composed the largest portion of the diet by mass (R= 58%, SE = ±13%) for the largest size class (≥325 mm TL). In the Piscataquis stratum, crayfish composed the largest portion of the diet by mass in the largest size class (R= 65%, SE= ±21%).

Finally, we observed seasonal trends in diet. Insects composed the largest observed proportion by mass in July for each stratum and decreased in the proceeding months (Figure 2.3). We also found “other” diet items increasing in relative proportion throughout the sampling period, primarily due to large diet items (Table 2.4) during the September and October sampling periods.

2.3.3 Otolith analysis and growth modeling

We used back calculations from a total of 722 otoliths to fit the hierarchical VBGM. Of a total of 765 otoliths processed, we gave 24 measurements low confidence ratings and they were omitted from further analysis. An additional 19 otoliths were collected from age-0 fish and were only used to inform back-calculations.

All parameters estimates converged as indicated by the Gelman-Rubin statistic calculated for all parameters ($\hat{r} < 1.1$). Though Smallmouth Bass from the Argyle stratum were not considered in diet or bioenergetics analyses, their inclusion here improved VBGM fit.

Two of the estimated VBGM parameters - the Brody growth coefficient (K_j) and the age at which length is 0 (t_{0j}) - were not different between strata based on overlap of 95% credible intervals (CRI) with estimated means (Table 2.5). The parameter estimates of the average asymptotic length (L_∞) in the Tidal stratum (425mm TL) was not within the bounds 95% credible intervals of the other three strata, suggesting that Smallmouth Bass in this stratum grew to larger average asymptotic lengths. All other mean estimates of L_∞ for the Orono, Argyle, and Piscataquis strata were within the 95% credible intervals of at least one other stratum, which suggests that the average asymptotic lengths in these three strata is largely similar (Figure 2.5). The largest difference between mean estimates of L_∞ (3.6 cm) was observed between two adjacent strata, Tidal and Orono.

Table 2.5: von Bertalanffy parameter estimates and 95% credible intervals (CRI) for Smallmouth Bass collected in each of four strata of the Penobscot River watershed.

	L_∞			K			t_0		
	Est.	Lower CRI	Upper CRI	Est.	Lower CRI	Upper CRI	Est.	Lower CRI	Upper CRI
Tidal	425	402	457	0.24	0.20	0.27	-0.52	-0.78	-0.30
Orono	389	377	403	0.25	0.22	0.28	-0.69	-1.04	-0.43
Argyle	409	395	423	0.25	0.22	0.27	-0.61	-0.91	-0.36
Piscataquis	392	371	419	0.24	0.20	0.27	-0.57	-0.84	-0.32

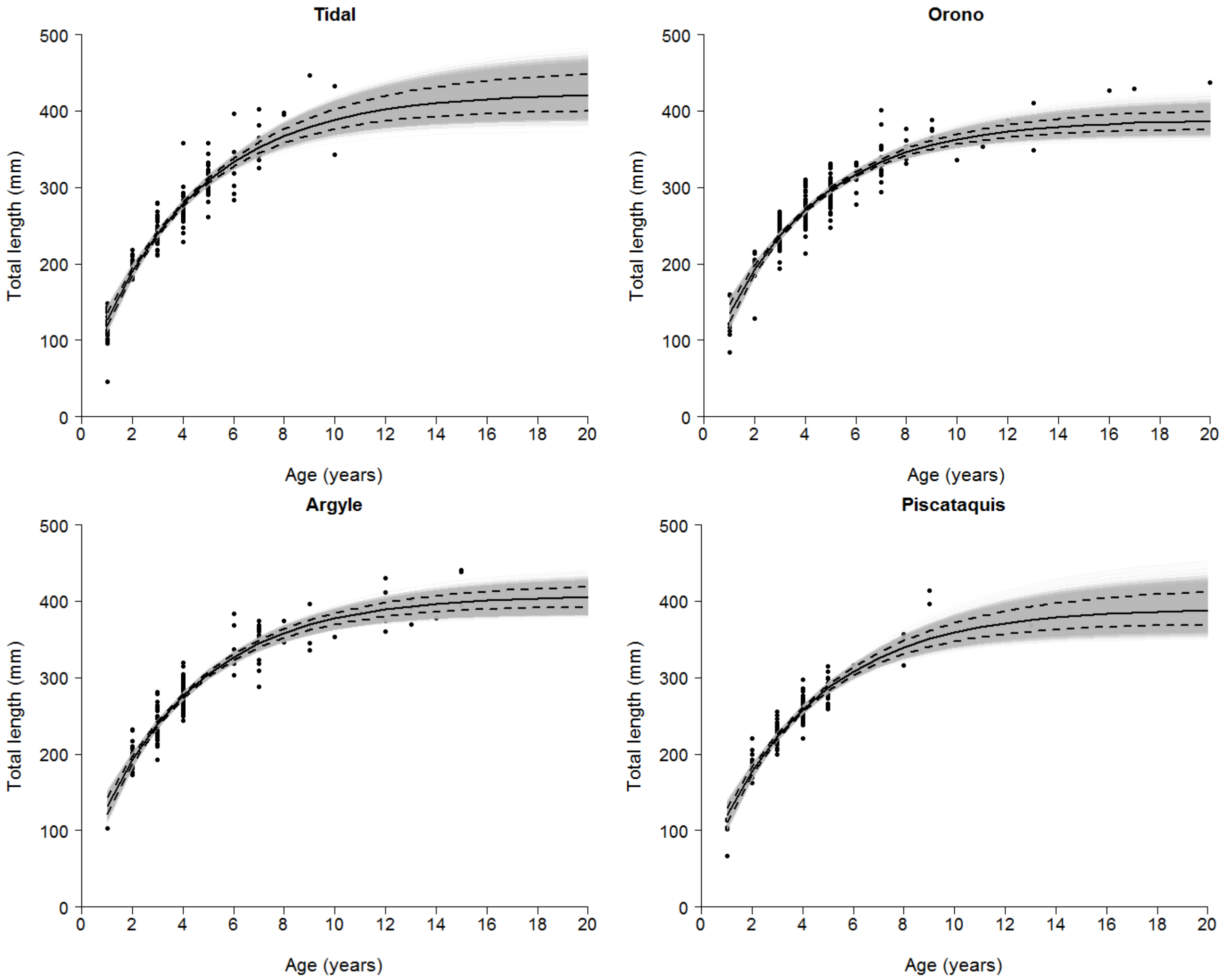

Figure 2.5: Posterior predictions from von Bertalanffy growth models fit to back-calculated size-at-age data for the four sampled strata in the Penobscot River. Points represent raw data, grey lines represent posterior predictive VBGM curves, black solid lines represent posterior predictive VBGM curves, black solid lines represent posterior predictive mean for each stratum, and the dashed lines represent the 95% credible interval.

2.3.4 Bioenergetics modeling

We estimated that the proportion of maximum consumption (P) ranged from 0.4 to 0.9 across modeled ages and strata using observed diet data. Estimates of P decreased with increasing fish age across all strata. Temperature differences did not result in large changes to estimated growth (≤ 5% ending mass difference) when observed temperature data were substituted between strata, with estimated consumption rates held constant.

When we substituted observed river herring prevalence into the diets of strata where less river herring was consumed, we estimated that seasonal growth would increase, with consumption rates held constant (Figure 2.6). Substituting observed prevalence of river herring in the Orono diets to the Piscataquis diets resulted in only a small increase in growth, with an average of 7% by mass across age classes. Substituting observed prevalence of river herring in the Tidal diets to the Piscataquis and Orono strata resulted in an average seasonal growth increase of 35% and 31% by mass, respectively.

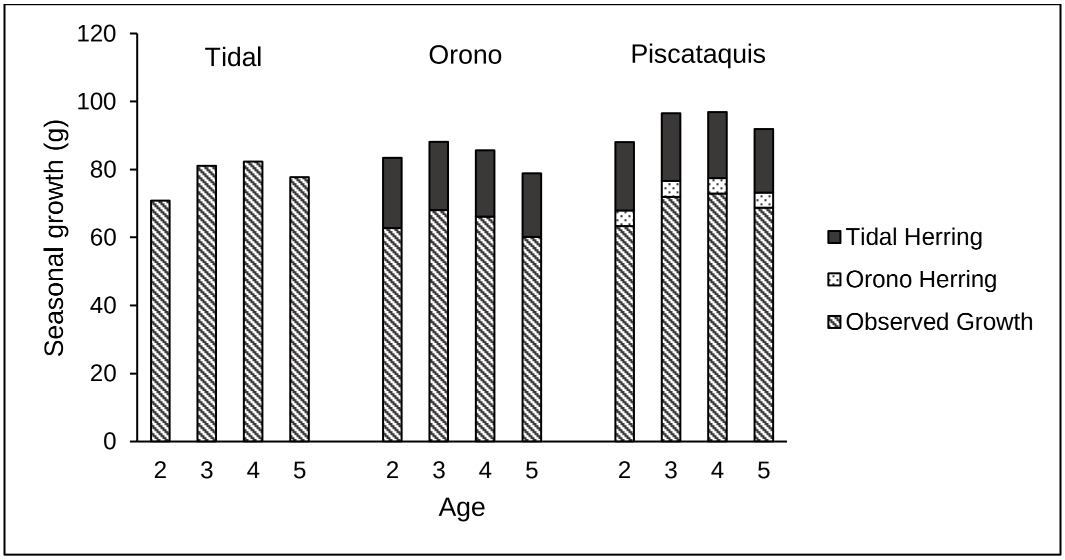

Figure 2.6: Seasonal growth of Smallmouth Bass in the Penobscot River watershed. Observed growth was calculated from the VBGM and length/mass data. River herring proportions observed in lower strata were substituted in the diets of the strata upstream (Tidal Herring and Orono Herring), with the remaining observed diet proportions re-scaled.

Estimates of P were largely driven by fish size and diet. We estimated that fish in the Piscataquis stratum fed at the highest rate, followed by the Orono and Tidal strata, respectively. This is likely influenced by the estimated energy density of prey consumed in each stratum. Smallmouth bass in the Piscataquis stratum ate primarily insects and crayfish, which have a relatively low energy density. In contrast, diets in the Tidal stratum are composed primarily of fish, including river herring, which are more energy-dense. Thus, Smallmouth bass in this stratum are estimated to feed at a lower rate, because they consume more energy dense prey and have similar seasonal growth relative to the other strata.

2.4 Discussion

Our combined results suggest that Smallmouth Bass, feeding upon newly available juvenile anadromous herring, will experience increasing growth throughout the mainstem Penobscot River following recent connectivity increases. Smallmouth Bass consumed juvenile river herring to a variable extent, depending on availability and location in the watershed, with Smallmouth Bass in the Tidal stratum consuming the most river herring across all months and size classes. Smallmouth Bass in that stratum were also estimated to attain the largest average asymptotic size which may be associated with historic access to anadromous river herring prey. The results together with the results from our bioenergetics models suggest that increasing river herring consumption results in proportional increases in seasonal growth. It is therefore likely that because anadromous herring have rebounded only recently in this system, changes in growth upriver of the Tidal stratum are forthcoming.

Because tidal freshwater areas occur at the interface between freshwater rivers and estuaries, they provide unique fish habitats (Rozas and Odum 1987) and present favorable growing conditions for *Micropterus* spp. (e.g. Peterson 1991, Glover and DeVries 2013, Trippel et al.

2015). The results from our diet analyses demonstrate that Smallmouth Bass in the Tidal stratum feed upon river herring throughout the growing season. We also found river herring in the stomachs of every size class of Smallmouth Bass which suggests that they are important prey throughout all adult ages. We observed the highest relative abundance of juvenile river herring in this stratum during shoreline electrofishing surveys in both spring and fall surveys, which indicates that juvenile river herring remain in this area for prolonged periods. Other studies (e.g. Limburg 1998, Gahagan et al. 2012) have suggested that juvenile river herring move extensively between saltwater estuaries and freshwater tidal areas. This protracted presence in the freshwater tidal reaches of the Penobscot River as well as other rivers likely presents predators in these areas with greater forage opportunities throughout the growing season.

Unlike the Tidal stratum, predation of juvenile river herring in the strata sampled further upriver was limited. Smallmouth Bass in the Piscataquis stratum did not have access to river herring as prey until construction of a fish bypass, which was completed the year after our sampling period. We did observe river herring in the diet of Smallmouth Bass captured in the Orono stratum, though this was limited to July diet samples. These observations suggest that river herring may avoid predation by Smallmouth Bass during out-migration through faster flowing sections of the Penobscot River (i.e. Orono stratum) but are susceptible to extensive predation in the freshwater tidal reaches (i.e. Tidal stratum) throughout the summer and early fall.

River herring are an energy dense forage fish, relative to other prey types (Adams et al. 1982b, Cyterski et al. 2002). Other studies have shown that other freshwater piscivores prey on seasonally available, energy dense clupeids in various freshwater systems (Yako et al. 2000, Cyterski et al. 2002, Trippel et al. 2015). Similarly, Brodersen et al. (2015) observed that Chain Pickerel, an apex predator similar to Smallmouth Bass, preyed extensively upon landlocked Alewife and, in result, exhibited greater lipid content. Fish that consume larger or more energy-dense prey grow faster (Martin 1970, Boisclair and Leggett 1989) and have higher winter survival (Shuter and Post 1990). Furthermore, Shuter et al. (2016) demonstrated that shifts in the type of prey consumed and the predator-prey size ratio affects growth and age at maturation of another freshwater piscivore (Lake Trout *Salvelinus namaycush*) over long time scales.

Our growth estimates suggest that Smallmouth Bass in the Tidal stratum attain the largest average asymptotic size of the four sampled strata, which may be associated with diet differences in this stratum. Similarly, Yako et al. (2000) attributed larger asymptotic size reached by Largemouth Bass in lakes to the presence of juvenile anadromous alewife. In our study, we observed a modest difference in average asymptotic size between strata, with the largest difference (3.6 cm) occurring between the Tidal and Orono strata.

Diet is likely a contributing factor to growth differences, though there are other ecological mechanisms that may affect observed differences in growth in the Tidal stratum. For example, population density is a major factor that constrains growth rates of individuals (Lorenzen and Enberg 2002, Dunlop et al. 2005). While we made no direct measure of Smallmouth Bass population densities in this study, Kiraly et al. (2014) observed the highest biomass caught per unit effort in the Orono stratum followed by the Argyle stratum, with lower densities in the remaining two strata. These observed differences in relative biomass may also explain why we observed the largest average asymptotic size in the Tidal stratum.

The strata upstream of the freshwater tidal area exhibited similar growth, which will likely change as a result of increasing river herring abundance throughout the watershed. Bioenergetics models suggest that increasing consumption of river herring by bass should result in proportional increases to seasonal growth in all strata. When we substituted observed river herring prevalence from the Tidal diets into the other two modeled strata, we estimated that growth in every age class would increase by greater than 29%.

River herring populations in the Penobscot River have only recently rebounded following a major effort to restore river connectivity for migratory fish. The year in which we sampled bass diets (2015) was only the second year where adult river herring returns counted at the lowermost dam were above 100 000 individuals (Mitch Simpson, Maine Department of Marine Resources, pers. comm.). That number more than doubled the following year and will likely continue to increase, as the carrying capacity for the Penobscot River was estimated at over 4 million river herring (Opperman et al. 2011). It is important to note that the growth of Smallmouth Bass in the upper three strata (i.e. Orono, Argyle, Piscataquis) occurred when they would not have had access to a substantial amount of river herring prey. Furthermore, changes in growth associated with changing Smallmouth Bass diets upriver will likely take several years to be detectable through length at age analysis.

Increasing abundances of juvenile river herring in the freshwater tidal area present Smallmouth Bass and other piscivores in this area with greater forage opportunities throughout the summer. Such an increase in the availability of energy-dense river herring may be the cause of observed differences in Smallmouth Bass growth in this study. Our collective results indicate that the restoration of anadromous river herring populations may lead to larger maximum sizes attained by riverine sportfish such as Smallmouth Bass. Furthermore, we suggest that any potential competition between river herring and Smallmouth Bass at the juvenile stage (sensu Hanson and Curry 2005) could be compensated by growth and potential reproductive increases associated with increasing consumption of energy-dense juvenile river herring.

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APPENDIX A: SUPPLEMENTAL COMMUNITY SURVEY INFORMATION

Table A.1: Number of random and fixed sites sampled by stratum during each sampling period

	Random		Fixed	
	Pre	Post	Pre	Post
Tidal	44	42	18	20
Orono	27	26	9	10
Milford	10	13	10	10
Argyle	45	59	10	12
Lower Tributary			14	13
Upper Tributary			15	21

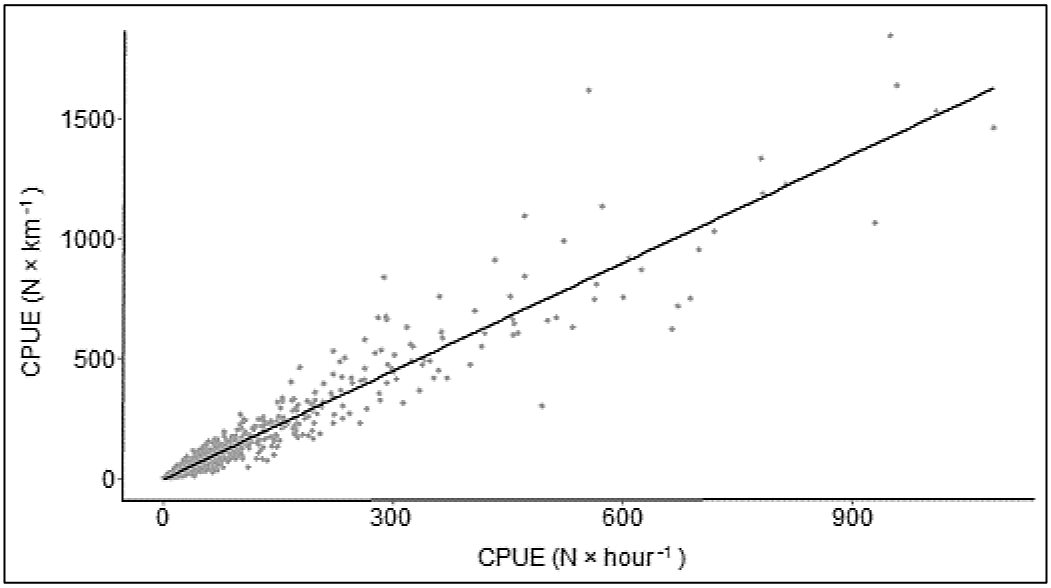


Figure A.1: Linear regression of CPUE standardized by time compared to CPUE standardized by site length. These two indices were highly correlated (R^2 = 0.93). Points indicate individual species values for each sample. Only mainstem river sites were analyzed due to different sampling gear used in tributary sites.

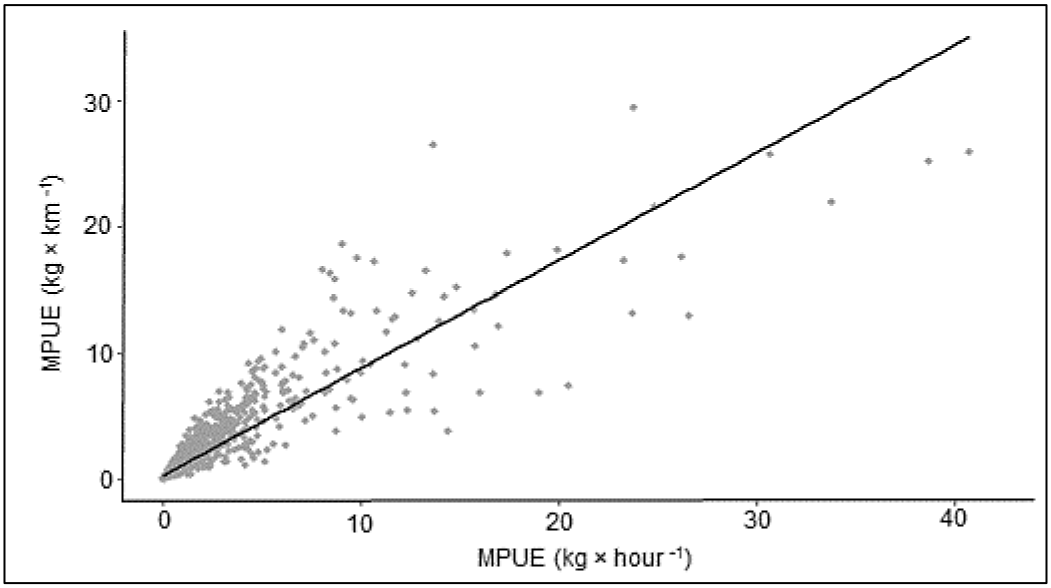
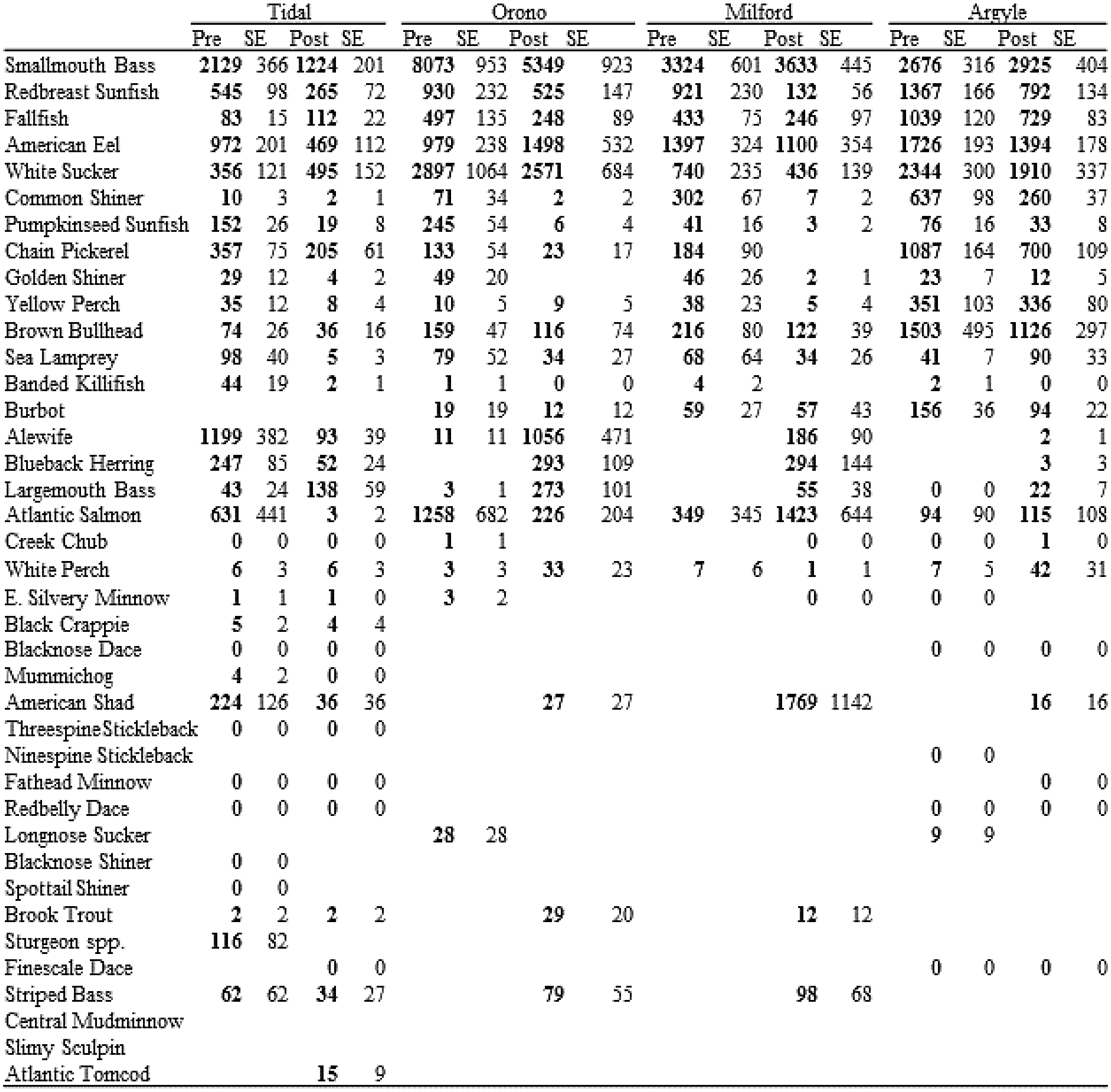


Figure A.2: Linear regression of MPUE standardized by time compared to MPUE standardized by site length. These two indices were highly correlated (R^2 = 0.81). Points indicate individual species values for each sample. Only mainstem river sites were analyzed due to different sampling gear used in tributary sites.

Table A.2: Average CPUE (N × km^{-1} and SE) calculated for each species captured in each mainstem stratum during both sampling periods. Blank spaces indicate no detections.

	Tidal				Orono				Milford				Argyle			
	Pre	SE	Post	SE	Pre	SE	Post	SE	Pre	SE	Post	SE	Pre	SE	Post	SE
Smallmouth Bass	**36.65**	6.71	**15.18**	2.72	**110.1**	14.32	**44.81**	8.95	**61.44**	14.75	**39.14**	6.41	**62.37**	12.80	**47.17**	6.02
Redbreast Sunfish	**12.89**	2.45	**4.01**	0.88	**32.53**	7.69	**5.33**	1.36	**34.43**	9.93	**1.87**	0.56	**68.15**	12.37	**16.26**	2.76
Fallfish	**16.70**	3.44	**25.56**	6.17	**61.38**	16.44	**16.80**	6.99	**153.06**	40.47	**21.24**	3.95	**320.25**	48.57	**225.59**	27.43
American Eel	**21.56**	5.20	**10.18**	2.30	**6.07**	1.12	**9.09**	2.43	**5.74**	1.03	**7.89**	2.13	**8.38**	0.90	**9.52**	1.11
White Sucker	**2.95**	0.76	**1.84**	0.41	**8.80**	2.60	**4.67**	0.97	**25.15**	10.33	**5.90**	1.60	**53.71**	10.76	**25.73**	4.78
Common Shiner	**6.84**	2.08	**2.48**	1.65	**31.23**	12.17	**1.28**	0.98	**322.26**	87.13	**3.32**	1.03	**360.68**	55.17	**202.91**	31.68
Pumpkinseed Sunfish	**19.99**	4.74	**0.37**	0.11	**31.56**	11.52	**0.13**	0.07	**3.58**	1.48	**0.56**	0.19	**5.43**	1.08	**2.73**	0.83
Chain Pickerel	**1.99**	0.40	**0.55**	0.16	**1.08**	0.31	**0.11**	0.08	**2.80**	0.83			**16.77**	3.17	**4.96**	1.02
Golden Shiner	**15.24**	5.55	**0.48**	0.21	**22.80**	13.14			**11.86**	4.98	**0.45**	0.27	**9.40**	3.59	**4.44**	1.60
Yellow Perch	**4.03**	1.52	**0.84**	0.44	**0.65**	0.42	**0.85**	0.48	**2.12**	1.02	**0.27**	0.16	**8.76**	2.12	**12.84**	2.88
Brown Bullhead	**0.56**	0.17	**0.21**	0.09	**1.17**	0.37	**0.50**	0.31	**0.90**	0.26	**0.78**	0.23	**8.31**	1.92	**6.10**	1.43
Sea Lamprey	**1.53**	0.81	**1.40**	0.68	**1.52**	0.52	**1.76**	0.46	**1.11**	0.45	**9.10**	6.94	**8.50**	1.50	**10.68**	1.98
Banded Killifish	**14.79**	5.29	**0.63**	0.19	**0.81**	0.37	**0.05**	0.05	**5.19**	3.22			**1.37**	0.54	**0.03**	0.03
Burbot					**0.05**	0.05	**0.08**	0.08	**0.55**	0.25	**0.30**	0.18	**2.66**	0.57	**1.48**	0.32
Alewife	**8.83**	2.42	**7.17**	3.28	**0.05**	0.05	**8.00**	3.22			**2.04**	0.84			**0.48**	0.28
Blueback Herring	**5.55**	1.55	**4.55**	2.02			**2.83**	0.95			**2.58**	1.28			**0.05**	0.04
Largemouth Bass	**0.33**	0.12	**1.17**	0.67	**0.31**	0.21	**0.62**	0.20			**0.24**	0.12	**0.07**	0.05	**1.39**	0.42
Atlantic Salmon	**0.15**	0.09	**0.08**	0.04	**0.39**	0.18	**0.38**	0.14	**0.20**	0.11	**2.34**	1.37	**0.17**	0.08	**0.04**	0.03
Creek Chub	**0.13**	0.08	**0.02**	0.02	**0.84**	0.61					**0.43**	0.31	**0.21**	0.09	**0.81**	0.25
White Perch	**0.83**	0.54	**0.21**	0.07	**0.06**	0.06	**0.14**	0.08	**0.24**	0.19	**0.09**	0.09	**0.24**	0.12	**0.58**	0.35
E. Silvery Minnow	**0.70**	0.45	**0.32**	0.25	**1.52**	1.32					**0.05**	0.05	**0.21**	0.12		
Black Crappie	**0.46**	0.17	**0.03**	0.03												
Blacknose Dace	**0.14**	0.06	**0.06**	0.04									**0.03**	0.03	**0.03**	0.03
Mummichog	**1.14**	0.66	**0.05**	0.03												
American Shad	**0.24**	0.13	**0.03**	0.03			**0.02**	0.02			**1.91**	1.28			**0.04**	0.03
Threespine Stickleback	**0.12**	0.07	**0.03**	0.03												
Ninespine Stickleback													**0.07**	0.04		
Fathead Minnow	**0.14**	0.10	**0.12**	0.07											**0.09**	0.07
Redbelly Dace	**0.02**	0.02	**0.10**	0.05									**0.06**	0.04	**0.03**	0.03
Longnose Sucker					**0.03**	0.03							**0.02**	0.02		
Blacknose Shiner	**0.06**	0.04														
Spottail Shiner	**0.03**	0.03														
Brook Trout	**0.03**	0.03	**0.02**	0.02			**0.10**	0.07			**0.05**	0.05				
Sturgeon spp.	**0.05**	0.03														
Finescale Dace			**0.03**	0.03									**0.03**	0.03	**0.28**	0.11
Striped Bass	**0.03**	0.03	**0.05**	0.04			**0.20**	0.14			**0.24**	0.17				
Atlantic Tomcod			**0.49**	0.28												

Table A.3: Average MPUE (g × km^{-1} and SE) calculated for each species captured in each mainstem stratum during both sampling periods. Blank spaces indicate no detections, zero values indicate values less than 0.5 grams per kilometer.



	Tidal				Orono				Milford				Argyle			
	Pre	SE	Post	SE	Pre	SE	Post	SE	Pre	SE	Post	SE	Pre	SE	Post	SE
Smallmouth Bass	2129	366	1224	201	8073	953	5349	923	3324	601	3633	445	2676	316	2925	404
Redbreast Sunfish	545	98	265	72	930	232	525	147	921	230	132	56	1367	166	792	134
Fallfish	83	15	112	22	497	135	248	89	433	75	246	97	1039	120	729	83
American Eel	972	201	469	112	979	238	1498	532	1397	324	1100	354	1726	193	1394	178
White Sucker	356	121	495	152	2897	1064	2571	684	740	235	436	139	2344	300	1910	337
Common Shiner	10	3	2	1	71	34	2	2	302	67	7	2	637	98	260	37
Pumpkinseed Sunfish	152	26	19	8	245	54	6	4	41	16	3	2	76	16	33	8
Chain Pickerel	357	75	205	61	133	54	23	17	184	90			1087	164	700	109
Golden Shiner	29	12	4	2	49	20			46	26	2	1	23	7	12	5
Yellow Perch	35	12	8	4	10	5	9	5	38	23	5	4	351	103	336	80
Brown Bullhead	74	26	36	16	159	47	116	74	216	80	122	39	1503	495	1126	297
Sea Lamprey	98	40	5	3	79	52	34	27	68	64	34	26	41	7	90	33
Banded Killifish	44	19	2	1	1	1	0	0	4	2			2	1	0	0
Burbot					19	19	12	12	59	27	57	43	156	36	94	22
Alewife	1199	382	93	39	11	11	1056	471			186	90			2	1
Blueback Herring	247	85	52	24			293	109			294	144			3	3
Largemouth Bass	43	24	138	59	3	1	273	101			55	38	0	0	22	7
Atlantic Salmon	631	441	3	2	1258	682	226	204	349	345	1423	644	94	90	115	108
Creek Chub	0	0	0	0	1	1					0	0	0	0	1	0
White Perch	6	3	6	3	3	3	33	23	7	6	1	1	7	5	42	31
E. Silvery Minnow	1	1	1	0	3	2					0	0	0	0		
Black Crappie	5	2	4	4												
Blacknose Dace	0	0	0	0									0	0	0	0
Mummichog	4	2	0	0												
American Shad	224	126	36	36			27	27			1769	1142			16	16
Threespine Stickleback	0	0	0	0												
Ninespine Stickleback													0	0		
Fathead Minnow	0	0	0	0											0	0
Redbelly Dace	0	0	0	0									0	0	0	0
Longnose Sucker					28	28							9	9		
Blacknose Shiner	0	0														
Spottail Shiner	0	0														
Brook Trout	2	2	2	2			29	20			12	12				
Sturgeon spp.	116	82														
Finescale Dace			0	0									0	0	0	0
Striped Bass	62	62	34	27			79	55			98	68				
Central Mudminnow																
Slimy Sculpin																
Atlantic Tomcod			15	9												

APPENDIX B : SUPPLEMENTAL SMALLMOUTH BASS INFORMATION

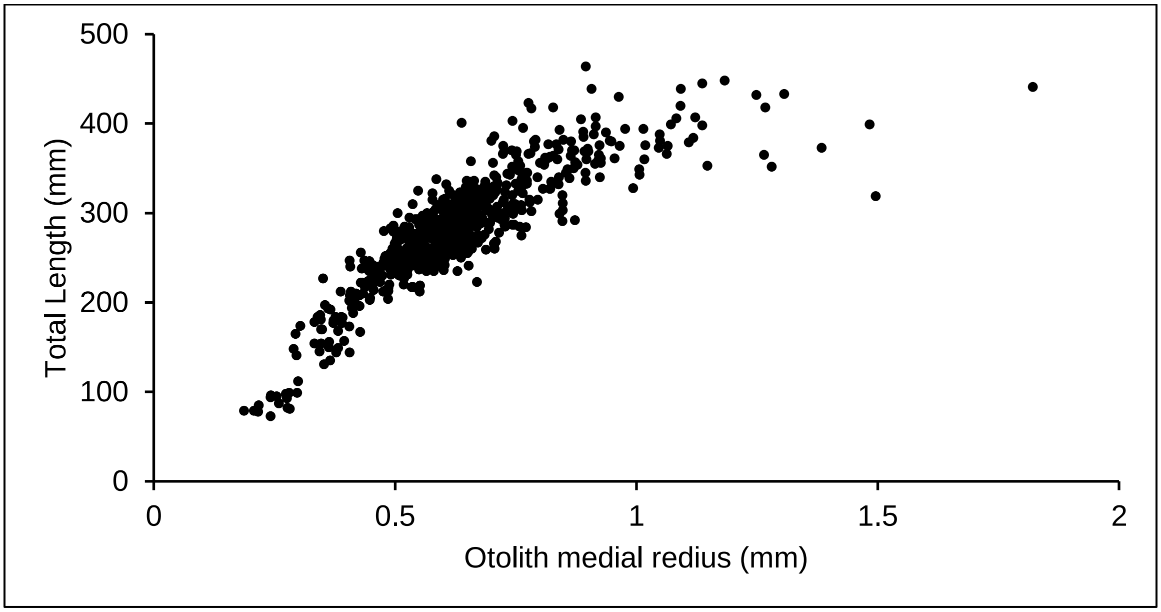


Figure B.1: The relationship between otolith medial radius length and total length measurements from Smallmouth Bass used in growth analysis.

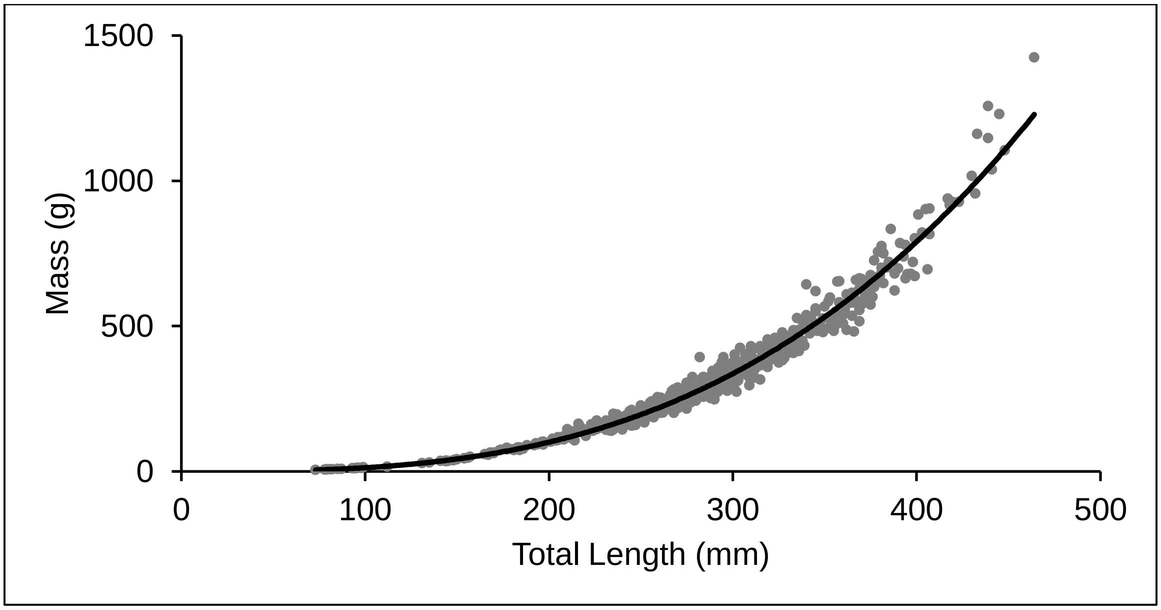


Figure B.2: Length-mass relationship for Smallmouth Bass in the Penobscot River watershed.

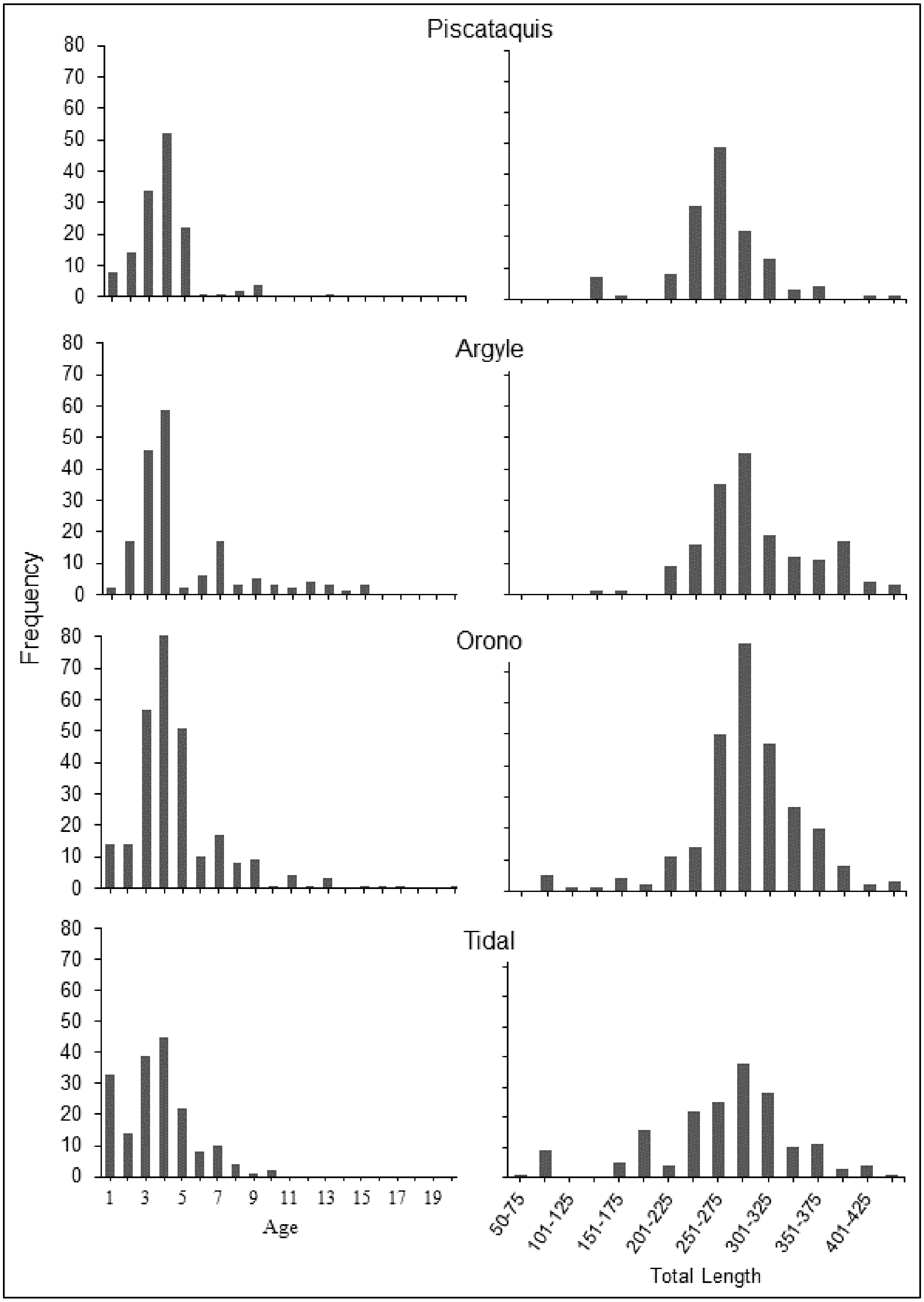


Figure B.3: Age and size distribution of Smallmouth Bass collected in each stratum.

BIOGRAPHY OF THE AUTHOR

Jonathan Watson was born in Atlanta, Georgia and graduated from the now defunct Dreher High School (Columbia, SC) in 2006. He attended the College of Charleston and graduated in May 2010 with a B.S. in Marine Biology. Following his undergraduate degree, Jonathan worked a number of odd jobs first as a commercial fish counter with the NOAA Groundfish Observer Program in the Bering Sea. He then helped establish an off-grid homestead in rural northern Arizona for one year and then returned home to skillfully paint the exterior of his parents' home. He later worked with the South Carolina Department of Natural Resources (SCDNR) for a total of two years, first as a hatchery technician and later as a technician studying diadromous fish in the state. The first position at SCDNR was wholly unrewarding, though he did learn to take care of marine fish in captivity and drive large diesel trucks towing trailers. The period in which he worked as a technician with the Diadromous Fishes Section was formative. He was able to help with a variety of projects including monitoring of endangered sturgeons, sampling commercial catch of American Shad, and monitoring American Eel passage. He then decided to pursue a graduate position at the University of Maine and was accepted to work on the electrofishing survey project under the guidance of Dr. Steve Coghlan and Dr. Joe Zydlewski. During that time, he supervised over a dozen undergraduate technicians and helped out on a variety of projects. Jonathan is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in May 2017.