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Effects of sea lamprey substrate modification and carcass nutrients on macroinvertebrate assemblages in a small Atlantic coastal stream

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ABSTRACT

Aquatic macroinvertebrates respond to patch dynamics arising from interactions of physical and chemical disturbances across space and time. Anadromous fish, such as sea lamprey, *Petromyzon marinus*, migrate from the ocean and alter physical and chemical properties of recipient spawning streams. Sea lamprey disturb stream benthos physically through nest construction and spawning, and enrich food webs through nutrient deposition from decomposing carcasses. Sea lamprey spawning nests support greater macroinvertebrate abundance than adjacent reference areas, but concurrent effects of stream bed modification and nutrient supplementation have not been examined sequentially. We added carcasses and cleared substrate experimentally to mimic the physical disturbance and nutrient enrichment associated with lamprey spawning, and characterized effects on macroinvertebrate assemblage structure. We found that areas receiving cleared substrate and carcass nutrients were colonized largely by Simuliidae compared to upstream and downstream control areas that were colonized largely by Hydropsychidae, Philopotamidae, and Chironomidae. Environmental factors such as stream flow likely shape assemblages by physically constraining macroinvertebrate establishment and feeding. Our results indicate potential changes in macroinvertebrate assemblages from the physical and chemical changes to streams brought by spawning populations of sea lamprey.

Introduction

Aquatic macroinvertebrates are functionally important in stream food webs and provide an intermediate pathway in the cycling of nutrients and transfer of energy (Cummins 1974; Wallace and Webster 1996). Spawning anadromous fish influence freshwater communities through physical disturbance and subsequent delivery of energy and nutrient subsidies (Janetski et al. 2009). These fish may function as ecosystem engineers by physically modifying benthic stream habitat through nest construction and spawning activities (Jones et al. 1994; Moore 2006; Hogg et al. 2014). Additionally, these fish supplement available nutrient pools in the form of metabolic waste, gametes, and post-spawned carcasses (Nislow and Kynard 2009; Flecker et al. 2010). The benthic stream disturbance associated with spawning may influence subsequent nutrient addition effects and therefore affect

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macroinvertebrate community structure and function. The literature describing these mechanisms is replete among salmonids in the Pacific Northwest; however, these effects are not well studied for other anadromous fish.

Macroinvertebrate assemblages may be influenced by the chemical and physical alterations to the benthos from spawning anadromous fish. Research from the Pacific Northwest has demonstrated Pacific salmon (*Oncorhynchus* spp.) carcasses stimulate production (Cederholm et al. 1999; Gende et al. 2002) and increase densities of scrapers, collectors, shredders, and predators (Wipfli et al. 1998, 1999) as well as growth rates and production concurrent with fall migration (Chaloner and Wipfli 2002; Lessard and Merritt 2006). Conversely, salmon spawning and redd construction may disturb and scour the streambed, thus reducing production for some invertebrate species, or create habitat and facilitate colonization for others (Moore and Schindler 2008; Campbell et al. 2012; Hogg et al. 2014). Thus, the physical and chemical disturbances from anadromous fish may create mosaics, or patches of heterogeneous habitat that influence stream communities (Pringle et al. 1988; Townsend 1989). The spatial and temporal scales (i.e. perturbation and timing of migration) that characterize the impact of salmon across the stream landscape may not apply to other anadromous fish.

Anadromous sea lamprey *Petromyzon marinus* are a semelparous species native to Atlantic freshwaters that, like salmon, disturb benthic habitat through the construction of mound and pit nests and deliver pulses of nutrients from carcasses of post-spawned adults (Beamish 1980; Nislow and Kynard 2009; Weaver et al. 2016). During the spring, sea lamprey migrate from the ocean into freshwater, where they construct nests and condition gravel and cobble substrate that create many interstitial spaces free of fine sediment (Sousa et al. 2012; Hogg et al. 2014). After spawning, lamprey die and carcasses may remain in streams for up to three weeks during which the majority of carcass-bound nitrogen and phosphorus is liberated (Weaver et al. 2015). Stream disturbances from spawning fish and subsequent pulses of nutrients from decomposing carcasses may influence macroinvertebrate colonization on these newly cleared substrates.

Among Atlantic coastal streams, Hogg et al. (2014) found benthic invertebrate abundance was higher in sea lamprey spawning mounds versus adjacent reference areas, most notably for Philopotamidae (Trichoptera), a collector/filterer, and Heptageniidae (Ephemeroptera), a scraper. Additionally, carcass nutrients increased periphyton biomass accrual and were assimilated in several macroinvertebrate families including Heptageniidae, Hydropsychidae (Trichoptera), and Perlidae (Plecoptera) (Weaver et al. 2016). However, the role of spawning disturbance and subsequent nutrient enrichment from anadromous sea lamprey on macroinvertebrates was not examined. The coupled effects of these disturbances may demonstrate important patch-dynamic processes that shape stream communities and nutrient cycling (Pringle et al. 1988).

Our objective was to determine the effects of nutrient addition from sea lamprey carcasses on macroinvertebrate colonization on substrate cleared and conditioned by sea lamprey nest construction. We simulated physical and chemical effects of sea lamprey spawning by introducing rock bags, as surrogates for cleared gravel and cobble in nests, and carcasses in a small Atlantic coastal stream to characterize macroinvertebrate colonization, abundance, and biomass.

Study site

We conducted our carcass addition experiment in Sedgeunkedunk Stream, a third-order tributary to the Penobscot River at river kilometer (rkm) 36.5 (Figure 1). Two dams were removed from the stream in 2008 and 2009 restoring connectivity of a 5-km reach to the Penobscot River and ultimately the Atlantic Ocean. Following the dam removals, spawning sea lamprey were observed regularly throughout Sedgeunkedunk Stream (Gardner et al. 2012; Hogg et al. 2013). We selected a 150-m experimental reach with a mean stream width of 6.7 m and mean depth of 0.23 m (Weaver et al. 2016) just upstream of Tannery Falls, a natural barrier in which we observed no spawning sea lamprey, evidence of nest construction, or post-spawned carcasses. We collected sea lamprey for
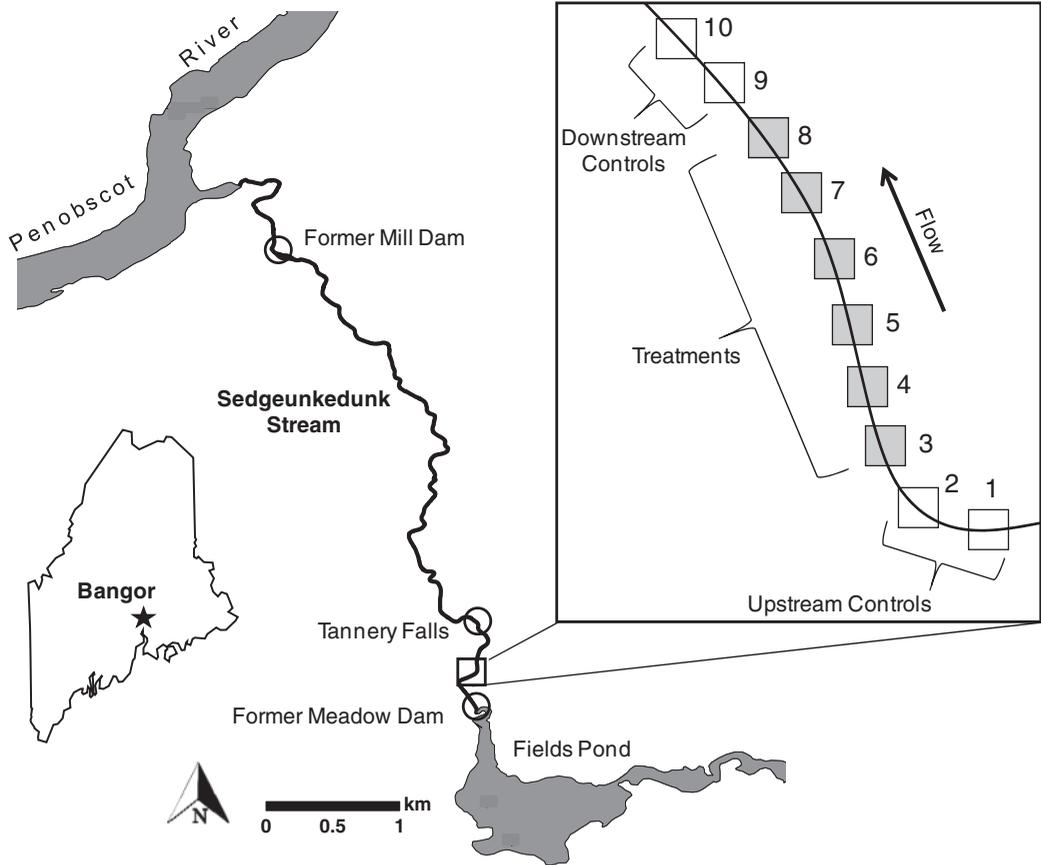
Figure 1. From Weaver et al. (2016). Location of study reach and 10 sites for experimental sea lamprey carcass addition. Inset: shaded boxes indicate sites that received sea lamprey carcass additions. See text for details as well as Weaver et al. (2016) for a detailed description of the study reach.

experimental carcass-addition from Milford Dam (rkm 61.0) on the main-stem Penobscot River. All fish were measured for mass and total length and stored frozen until addition into the experimental reach.

Methods

Experimental design

We delineated 10 sites along an approximate 150-m experimental reach (Figure 1 inset). Each site began at the head of a riffle, extended into a glide, then ended at the next riffle. Sites 1 and 2 served as references (hereafter referred to as 'upstream controls') and received no carcasses. The following six downstream sites (3–8; hereafter referred to as 'treatments') received 20 sea lamprey carcasses each (120 carcasses total). Finally, sites 9 and 10 were the furthermost downstream and received no carcasses (hereafter referred to as 'downstream controls'). Sites ranged from 6–12 m in length. Weaver et al. (2016) determined that stream nutrient concentrations and periphyton biomass accrual from added carcasses invoked localized effects, which allowed us to assume independence between sites. Carcass numbers and spacing were intended to approximate patchy spawning aggregations that typically occur in riffles containing coarse

substrates. Carcasses were placed into 2.5-cm mesh bags and then secured into 2.5-cm mesh metal cages, which were staked mid-channel at each site. See Weaver et al. (2016) for more information on the study design of the current experiment.

At each site, we deployed 10 rock bags that mimicked substrate disturbed and cleaned by sea lamprey now available for macroinvertebrates and provided a means to standardize sampling effort (Maine Department of Environmental Protection 2017). Rock bags were deployed uniformly at each site ≥1 m from the stream bank to ensure substrate immersion, and ≥1 m downstream from the added carcasses. Ten rock bags provided adequate coverage and representation of each site. Rock bags consisted of 2.5-cm mesh filled with 3.17 kg (±0.05 SD) of 3.8–5.1 cm diameter clean rocks. This substrate is similar to the gravel and cobble substrate sea lamprey use to construct nests (Sousa et al. 2012; Hogg et al. 2014). The size range of rocks used in this experiment is classified as 'very coarse gravel' (Bovee and Milhous 1978), and therefore likely mimics the selected sizes of substrate used by sea lamprey to construct nests. The standardized quantity and substrate size of rock bags used allowed us to make inferences between control and treatment sites.

Rock bags were given a unique tag number for identification during retrieval. At the treatment sites, rock bags were placed ≤1 m downstream of the caged carcasses. No rock bags were placed within 0.5 m of either bank to avoid emersion or influences from the bank. The locations of the rock bags in the stream were noted so that upon sampling we could confirm they had remained roughly in their original deployment site. Carcasses and rock bags were deployed on 25 June 2014.

After three weeks incubation, all rock bags were sampled. If bags had been displaced >1 m from their original deployment location, then they were excluded from analysis. Rock bags were washed thoroughly in a bucket of water to extract macroinvertebrates and debris within the rock bag. Contents were sieved into 500-micron mesh and preserved with 70% ethanol.

Abiotic stream variables

Temperature loggers (Hobo Pendant UA-001-08, Onset, Cape Cod, Massachusetts, USA) were deployed in the stream reach and retrieved at the conclusion of the experiment. Loggers continuously recorded temperature at 1-h intervals. We measured total stream depth and mean column velocity at 0.5-m increments along one cross-sectional transect located in the riffle habitat at each site during base flow, and then periodically for three weeks with a top-set wading rod and Swoffer model 2100 current velocity meter (Swoffer Instruments, Seattle, Washington, USA).

Macroinvertebrate subsampling and sorting

Samples were subsampled by mass following the protocol of the Canadian Aquatic Biomonitoring Network (McDermott et al. 2012). Each sample was homogenized by hand-stirring the contents, and then the sample was divided into four trays of equal mass. One tray was selected using a random number table that would serve as the subsample. A trained technician sorted macroinvertebrates to family in the entire subsample. A minimum of 300 total macroinvertebrates in the subsample was necessary to end the sorting after the first subsample. If this first subsample did not contain this minimum number, a second subsample was sorted in its entirety. All macroinvertebrates were identified to family and counted. The total number of subsamples and total subsample mass were recorded.

We observed four macroinvertebrate families common to all samples: Hydropsychidae, Philoptamidae, Simuliidae (Diptera), and Chironomidae (Diptera). These families generally represented >95% of sample abundance and therefore were the focus of this study. Sorted samples were placed into tin trays, measured for mass, then placed into an oven for 24 h at 75 °C. After 24 h, samples

were reweighted to obtain dry mass. Other macroinvertebrate families were present in the samples and noted, but not included in any analyses.

We estimated total macroinvertebrate abundance and total biomass for each of those four families. Based on the dominance of these taxa, we assumed that the macroinvertebrates sorted in each of the four subsamples adequately represented 25% of the entire sample and extrapolated biomass based on the number of samples. We used the subsampled dry mass of each of the four macroinvertebrate families to calculate average dry mass per individual, then extrapolated based on adjusted counts to estimate total sample biomass.

Statistical analysis

We examined the assemblage of the four aforementioned macroinvertebrate families as an index of the taxa colonizing the rock bag samples with nonmetric multidimensional scaling (NMDS; Kruskal 1964). We reduced abundance and biomass estimates from the four families among rock bag samples from each site into two-dimensional space. We used the 'metaMDS' function in the 'vegan package' in the statistical package RStudio (version 0.99.491, RStudio, Boston, MA, USA; Oksanen et al. 2016). The Bray–Curtis dissimilarity distance function was used, which is most appropriate for ecological abundance data collected at different sampling locations from a consistent area (e.g. rock bag volume) (Bray and Curtis 1957). We examined the goodness of fit by calculating stress, which is the sum of squared differences between the ordination distances and distances predicted from the regression. Stress values for the configured plots of abundance and biomass were low (6% and 4%, respectively; Clarke 1993), indicating a low disagreement between the two-dimensional configuration and the predicted values from the regression. We plotted averaged NMDS scores among rock bag samples for each site (±SE).

We analyzed macroinvertebrate abundance, biomass, and individual taxa mass (average mass per individual) as a function of site with a series of analysis of variance (ANOVA) models. We compared abundance and mass estimates among all 10 sites. We tested for spatial autocorrelation among all sites with a Mantel test. We constructed two matrices containing linear distances between each of the sites and distances between abundance values of each taxa. The Mantel test computed the correlation of the two distance matrices and then calculated 1000 permutations to generate p values for the four taxa. For all tests, statistical significance was gauged at $p < 0.05$. ANOVA tests with a significant site main effect were further examined with Tukey's HSD pairwise *post hoc* tests and adjusted family-wise error rates.

Results

Temperatures ranged from 17 to 29 °C, and averaged 24.2 °C (±2.1 SD) during the three-week experiment. We observed mean cross-sectional stream flow (among all transects) increase from 0.18 m/s (±0.05 SD) at baseflow before our experiment to a high of 0.64 m/s (±0.09 SD) during the second week of our experiment (Figure 2). During elevated flows, we observed generally higher mean cross-sectional stream flows at sites receiving sea lamprey carcasses, which ranged 0.61–0.80 m/s compared to the reference sites, which ranged 0.46–0.59 m/s. We attribute elevated flows to precipitation from a tropical depression that arrived during the second week of the experiment.

We retrieved between 6 and 10 rock bag samples from each site that fit the sampling criteria. The remaining rock bags were either displaced >1 m from the original deployment location, and thus were not sampled, or were not recovered because of high flows. During sample sorting and identification, typically only one or two subsamples were required to meet the minimum number of individuals, but this was not the case for three samples, where more than two subsamples were required.
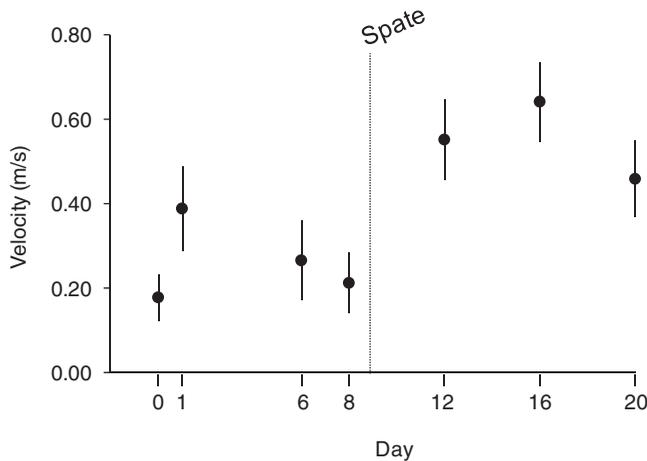
Figure 2. Mean (±SD) cross-sectional mean column velocity (m s^{-1}) over a three-week period. The dashed line indicates the period during which precipitation from a spate elevated stream flows.

Among all samples, we identified 10 families of macroinvertebrates. Hydropsychidae, Philopotamidae, Simulidae, and Chironomidae were present in all samples and comprised ≥95% of the total abundance. Six other families were found infrequently or rarely in low abundance (<5% total abundance) and included Perlidae, Elmidae (Coleoptera), Psephenidae (Coleoptera), Heptageniidae, Aeshnidae (Odonata), and Corydalidae (Megaloptera). The Mantel tests suggested spatial autocorrelation among Hydropsychidae, Philopotamidae, and Chironomidae among sites ($p < 0.05$).

Our NMDS plots for abundance and biomass revealed macroinvertebrate colonization patterns varied among sites. Generally, assemblages in the upstream control sites differed from those in treatment and downstream sites. For abundance, upstream controls were influenced largely by Hydropsychidae, Philopotamidae, and Chironomidae, while treatment and downstream controls were relatively influenced more by Simuliidae (Figure 3). For biomass, upstream controls were not distinctly characterized by Hydropsychidae, Philopotamidae, and Chironomidae. Similar to abundance, biomass in the treatment and downstream controls were influenced most strongly by Simuliidae. Conversely, macroinvertebrate samples among the treatment sites and downstream control sites varied in the indicator taxa that were most influential to the assemblage. Several samples from the treatment sites and additional downstream sites were influenced more by Simuliidae.

We found differences in abundance among Hydropsychidae, Simuliidae, and Chironomidae, and among biomass of all four taxa across all sites ($p < 0.05$; Table 1). Generally, *post hoc* tests revealed higher abundance and biomass estimates among Hydropsychidae and Chironomidae families in the upstream control sites compared to the treatment and downstream control sites (Tables 2 and 3). However, Simuliidae abundance and biomass were generally higher in the treatment sites that received carcasses. These results are consistent with the NMDS analysis, which depicted treatment sites were more influenced by Simuliidae, while the upstream and downstream control sites were influenced more strongly by the abundance and biomass of the other three families.

For individual macroinvertebrate mass among families, we found differences among Hydropsychidae and Philopotamidae among sites (Tables 1 and 4). Hydropsychidae mass at site 7, which was downstream of 100 carcasses, was higher than at upstream sites influenced by fewer carcasses as well as at upstream and downstream control sites that received no carcasses (Table 4). Among individual Philopotamidae mass, we found higher mass per individual in the upstream
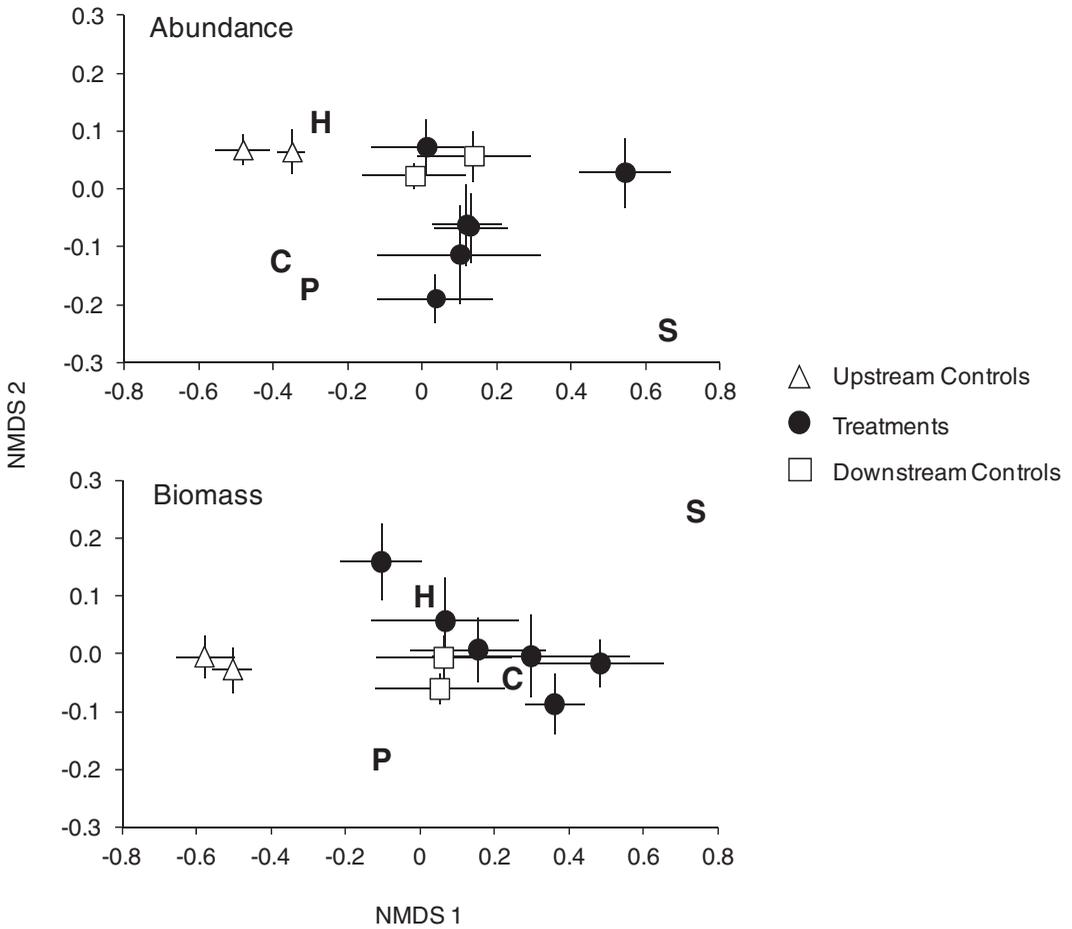
Figure 3. Plots of mean (±SE) NMDS scores from two-dimensional configurations of macroinvertebrate abundance (top) and biomass (bottom) estimates for rock bag samples among sites from the upstream controls (triangles; sites 1 and 2), treatments (circles; sites 3–8), and downstream controls (squares; sites 9 and 10). Letters depict the indicator taxa influencing the sites: Hydropsychidae (H), Philopotamidae (P), Simuliidae (S), and Chironomidae (C).

control sites compared to the treatment and downstream control sites. We found no differences for individual Simuliidae and Chironomidae mass among sites. *Post hoc* tests generally found no differences between sites designated as upstream controls and sites designated as downstream controls (Tables 2 and 3).

Table 1. F and p statistics from ANOVA models among macroinvertebrate taxa tested for differences among sites. Bolded p-values indicate statistically significant differences among sites ($p < 0.05$).

Variable	Taxon	F	p
Abundance	Hydropsychidae	6.547	<**0.001**
	Philopotamidae	1.922	0.0636
	Simuliidae	4.511	<**0.001**
	Chironomidae	4.456	<**0.001**
Biomass	Hydropsychidae	5.129	<**0.001**
	Philopotamidae	3.015	**0.004**
	Simuliidae	3.966	<**0.001**
	Chironomidae	3.135	**0.003**
Average individual mass	Hydropsychidae	3.707	<**0.001**
	Philopotamidae	4.384	<**0.001**
	Simuliidae	1.455	0.183
	Chironomidae	0.755	0.658

Table 2. Mean (±SE) total macroinvertebrate abundance among *N* rock bag samples at each site. Treatment indicates the number of sea lamprey carcasses added to each site. Similar superscript letter combinations depict similarities among sites from pairwise *post hoc* tests. See Figure 1 and text for site locations and descriptions.

Site	Treatment	*N*	Hydropsychidae	Philopotamidae	Simuliidae	Chironomidae
1	Upstream control	10	2111 (229)[a]	555 (62)[a]	38 (11)[a]	141 (23)[a]
2		8	1752 (120)[ab]	492 (45)[a]	19 (6)[a]	82 (13)[ab]
3	Treatments	8	1055 (152)[bc]	432 (122)[a]	199 (44)[b]	109 (20)[abc]
4		7	912 (116)[bcd]	346 (48)[a]	73 (26)[abc]	81 (16)[abcd]
5		6	979 (172)[bcd]	462 (109)[a]	121 (54)[abc]	90 (25)[abcd]
6		9	544 (86)[de]	197 (62)[a]	16 (6)[ac]	45 (16)[bcd]
7		6	994 (87)[bdef]	273 (51)[a]	115 (62)[abc]	30 (9)[bcd]
8		9	1311 (236)[abcdf]	274 (62)[a]	40 (9)[abc]	68 (17)[abcd]
9	Downstream control	8	1096 (162)[bcdef]	269 (63)[a]	20 (3)[ac]	25 (5)[bd]
10		9	1295 (196)[abcdef]	358 (72)[a]	24 (6)[ac]	69 (11)[abcd]

Table 3. Mean (±SE) total macroinvertebrate biomass (mg) among *N* rock bag samples at each site. Treatment indicates the number of sea lamprey carcasses added to each site. Similar superscript letter combinations depict similarities among sites from pairwise *post hoc* tests. See Figure 1 and text for site locations and descriptions.

Site	Treatment	*N*	Hydropsychidae	Philopotamidae	Simuliidae	Chironomidae
1	Upstream control	10	342.1 (31.8)[a]	188.5 (23.6)[a]	3.2 (0.8)[a]	5.8 (1.1)[a]
2		8	169.1 (24.8)[ab]	169.1 (14.2)[a]	1.3 (0.5)[ab]	2.8 (0.6)[ab]
3	Treatments	8	162.3 (28.9)[bc]	76.0 (24.5)[ab]	14.2 (3.7)[c]	4.8 (1.2)[ab]
4		7	112.6 (14.0)[c]	49.7 (7.8)[ab]	3.6 (0.9)[abcd]	3.0 (0.9)[ab]
5		6	141.4 (30.5)[c]	74.2 (29.1)[ab]	8.6 (5.8)[abcd]	3.2 (1.0)[ab]
6		9	101.7 (19.7)[c]	41.1 (14.3)[b]	1.4 (0.5)[abde]	1.4 (0.6)[b]
7		6	225.3 (29.0)[abc]	63.1 (17.9)[ab]	10.3 (6.0)[acdf]	1.3 (0.5)[b]
8		9	199.6 (35.4)[abc]	75.1 (31.0)[ab]	3.2 (0.6)[abcdef]	2.5 (0.5)[ab]
9	Downstream control	8	181.6 (27.1)[abc]	85.5 (23.1)[ab]	2.7 (0.6)[abcdef]	1.0 (0.3)[b]
10		9	180.4 (32.1)[abc]	96.2 (21.0)[ab]	2.1 (0.5)[abdef]	1.9 (0.6)[ab]

Discussion

We simulated physical and chemical effects of sea lamprey spawning on macroinvertebrates by experimentally adding carcasses and monitoring colonization on bare substrate mimicking newly constructed sea lamprey nests. Previous work has indicated that sea lamprey nest construction serves as a physical disturbance that may influence macroinvertebrate assemblages (Hogg et al. 2014). Also, nutrients from sea lamprey carcasses increased periphyton biomass and were assimilated by several macroinvertebrate taxa (Weaver et al. 2016). Collectively, results from this and prior studies indicate that physical and chemical changes brought about from sea lamprey spawning, and subsequent nutrient liberation from carcasses, influence macroinvertebrate colonization on newly

Table 4. Mean individual macroinvertebrate mass (μg) among *N* rock bag samples at each site. Treatment indicates the number of sea lamprey carcasses added to each site. Similar superscript letter combinations depict similarities among sites from pairwise *post hoc* tests. See Figure 1 and text for site locations and descriptions.

Site	Treatment	*N*	Hydropsychidae	Philopotamidae	Simuliidae	Chironomidae
1	Upstream control	10	163.1[a]	334.3[a]	108.7[a]	38.3[a]
2		8	172.0[a]	350.7[a]	78.7[a]	36.3[a]
3	Treatments	8	146.3[a]	167.9[ab]	67.1[a]	42.0[a]
4		7	125.3[ab]	138.7[b]	62.6[a]	36.5[a]
5		6	140.4[ab]	185.5[bc]	96.0[a]	35.2[a]
6		9	188.0[abc]	229.5[abcd]	122.2[a]	33.5[a]
7		6	227.5[acd]	230.2[abcd]	85.1[a]	49.7[a]
8		9	150.4[abce]	228.2[abcd]	105.4[a]	47.0[a]
9	Downstream control	8	167.1[abcde]	286.3[abd]	133.2[a]	42.5[a]
10		9	131.9[abce]	256.0[abcd]	126.7[a]	25.9[a]

cleaned and conditioned substrate. More broadly, the biotic and abiotic effects from migratory fish may influence patch dynamics across interacting spatial and temporal scales.

There is ample research examining the role of migrating and spawning Pacific salmon and corresponding effects on stream ecosystems (Janetski et al. 2009). However, the effects of other anadromous fish species are not well studied, but our results suggest disparate ecological effects. Previous research has demonstrated negative responses of macroinvertebrate abundance and richness to salmon spawning. The large migrations and subsequent redd construction and spawning excavate and scour the stream channel, reducing benthic invertebrate abundance, increasing drift, and offsetting any subsequent increases in productivity from post-spawned carcass nutrients (Moore and Schindler 2008; Honea and Gara 2009; Lessard et al. 2009; Monaghan and Milner 2009; Tiegs et al. 2009). Contrary to these studies, our results and those of Hogg et al. (2014) suggest that sea lamprey spawning disturbance may increase streambed habitat heterogeneity, and therefore create favorable conditions (via increased interstitial spaces) for macroinvertebrate foraging. However, spawning disturbance coupled with nutrient deposition from carcasses and elevated stream flows may elicit taxon-specific responses. While our data are suggestive, future studies could test our hypothesis more rigorously by examining changes in macroinvertebrate assemblages from intact nests with nutrient supplementation from carcasses.

Nutrient deposition from post-spawned fish carcasses may influence macroinvertebrate colonization on newly cleared and conditioned cobble substrate. In the current study, it is plausible that Hydropsychidae, Philopotamidae, Simuliidae, and Chironomidae utilize the cleared substrate for foraging and consume sloughed and drifting tissue from carcass decomposition. Prior research has demonstrated corresponding increases in productivity and macroinvertebrate abundance and biomass in response to added salmon carcasses in Pacific coast systems (Wipfli et al. 1998; Chaloner and Wipfli 2002; Kohler and Taki 2010), and assimilation of sea lamprey carcass nutrients by scrapers (e.g. Heptageniidae) and collectors (e.g. Hydropsychidae) in Atlantic coast systems (Weaver et al. 2016). However, these studies were not subject to the disturbance from migrating and spawning fish. In contrast, we generally observed lower macroinvertebrate abundance and biomass among colonized rock bag samples in sites with added sea lamprey carcasses compared to the control sites. Similar to previous studies with Pacific salmon, the patterns we observed were specific to certain macroinvertebrate taxa. Among treatment sites receiving carcasses, we generally observed higher abundance and biomass of Simuliidae, compared to the control sites, but lower abundance and biomass of Hydropsychidae, Philopotamidae, and Chironomidae.

The physical and chemical disturbances from anadromous fish may further interact with other environmental disturbances enacting on the stream landscape. We observed elevated stream flows, likely at flood-stage levels, associated with precipitation from a spate, which may increase macroinvertebrate drift rates and reduce local abundance (Effenberger et al. 2008). Foraging capabilities unique to macroinvertebrate functional feeding groups, and their response to disturbance, may explain the observed patterns in abundance and biomass. We observed higher abundance of Simuliidae, and lower abundances of Hydropsychidae and Philopotamidae among treatment sites compared to the control sites. These three taxa are largely collector/filterers that capture drifting particles in the water column (Fuller and MacKay 1980; Wallace and Webster 1996). Generally, the net-spinning caddisflies (e.g. Hydropsychidae) prefer swift moving waters (Philipson and Moorhouse 1974). However, Simuliidae are unique in that they occupy a feeding position on substrates that minimizes energy expenditure (Wallace 1980), and demonstrate lower drifting rates with increasing stream flow (Fenoglio et al. 2013). The increased stream flows we observed, which were likely at flood levels, may have affected the treatment sites differently than the control sites through differences in channel architecture (e.g. steeper banks; Naman et al. 2016). These differences in flow rate may have further interacted with the carcass addition treatments, which favored Simuliid colonization. Our work suggests that multiple disturbances (i.e. spawning disturbance, nutrient addition, stream flooding) affect macroinvertebrate colonization among taxa differently. Stream communities

may be influenced by the effects of patch dynamics altered by local resources (i.e. carcasses) and local environmental factors (i.e. flood disturbance).

We used rock bags to mimic the substrate arrangement left from spawning sea lamprey, and we believe they served as a representative surrogate for sea lamprey nests. We used substrate similar in size to that of sea lamprey nests (Sousa et al. 2012; Hogg et al. 2014). Additionally, Hogg et al. (2014) found Philopotamidae and Hydropsychidae were among the most abundant taxa found in sea lamprey nest mounds compared to adjacent reference areas. We observed these two taxa comprise the majority of the macroinvertebrate assemblage among our rock bag samples. Therefore, while we may not have accurately represented changes across the entire macroinvertebrate community, we are confident that our samples reflect the colonization of macroinvertebrate assemblages observed after sea lamprey spawning and nutrient deposition from carcasses.

Our Mantel tests revealed spatial autocorrelation among several macroinvertebrate taxa. Generally, adjacent rock bags contained similar macroinvertebrate assemblages than those farther away. This may limit our ability to draw inferences from the results of our ANOVAs. The carcass nutrients and associated macroinvertebrate assemblages from one treatment site may affect subsequent downstream treatment sites (i.e. a cumulative effect); however, Weaver et al. (2016) did not observe cumulative downstream carcass nutrient effects. We attribute spatial autocorrelation among taxa to the treatments we imposed on the stream and potentially differential effects of increased streamflows in treatment sites relative to upstream control sites.

Among river landscapes, migratory fish may create a mosaic of heterogeneous habitats across interacting spatial and temporal scales (Pringle et al. 1988; Campbell et al. 2012). Sea lamprey migrate into freshwaters during the spring, a period of increasing temperature, and metabolic demand for organisms (Hall 1972), and nutrient limitation (Norris 2012; Weaver et al. 2016). The physical disturbances from sea lamprey spawning alter the benthos (Hogg et al. 2014), and their subsequent death and decomposition supplement available nutrient pools and increase periphyton biomass (Weaver et al. 2015; Weaver et al. 2016). Macroinvertebrates function as an integral component in the cycling of nutrients and transfer of energy (Wallace and Webster 1996), and therefore likely mediate the interaction of the physical and chemical bioengineering characteristics of sea lamprey.

Acknowledgments

Disclosure statement

Funding

Notes on contributors

Dan Weaver has a PhD degree in wildlife ecology from the University of Maine, Orono, Maine. He is broadly interested in aquatic and fish ecology, anadromous fishes, food web processes, nutrient cycling, and cross-ecosystem dynamics.

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Joseph Zydlewski joined the U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit in 2004 as an assistant unit leader, and is a professor of fisheries science in the Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine. Joe's research centers on the study of fish movements and migrations and he explores the three main themes: connectivity and river restoration, physiology and behavior of migration, and the ecological influences of migrants such as the topic of this paper, sea lamprey.

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