Anadromous sea lampreys (*Petromyzon marinus*) are ecosystem engineers in a spawning tributary

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SUMMARY

1. Sea lampreys (*Petromyzon marinus*) disturb the substratum during nest construction and alter the physical habitat, potentially affecting other stream organisms. We quantified differences in depth, velocity, fine-sediment coverage, embeddedness, intragravel permeability and benthic invertebrate assemblages (density and diversity) among nest mounds, nest pits and undisturbed reference locations over a 4-month period after June spawning.

2. In 2010 and 2011, immediate and persistent effects of nest construction were assessed in summer (July) and in autumn (late September to early October), respectively. Randomly selected nests were sampled annually (25 each in summer and autumn).

3. Nest construction increased stream-bed complexity by creating and juxtaposing shallow, swift, rocky habitat patches with deep, slow, sandy habitat patches. Mounds had a 50–143% less cover of fine sediment, and a 30–62% reduction in embeddedness, compared to pits and reference locations. These physical changes persisted into the autumn (almost 4 months).

4. Five insect families contributed 74% of the benthic invertebrate abundance: Chironomidae (27%), Hydropsychidae (26%), Heptageniidae (8%), Philopotamidae (7%) and Ephemerellidae (6%). Densities of Hydropsychidae, Philopotamidae and Heptageniidae were up to 10 times greater in mounds than in pits and adjacent reference habitat. In summer, mounds had twice the density of Chironomidae than did pits, and 1.5 times more than reference habitats, but densities were similar among the habitats in autumn.

5. These results suggest that spawning sea lampreys are ecosystem engineers. The physical disturbance caused by nest-building activity was significant and persistent, increasing habitat heterogeneity and favouring pollution-sensitive benthic invertebrates and, possibly, drift-feeding fish.

Keywords: anadromous fishes, benthic invertebrates, ecosystem engineers, freshwater spawning habitat, sea lampreys

Introduction

Habitat disturbance is an important factor in driving community dynamics and ecosystem processes in streams (Resh *et al.*, 1988). Flooding, for example, can increase aquatic insect mortality (Lytle, 2002) and change food-web dynamics (Wootton, Parker & Power, 1996) or increase in-stream production (Shah & Dahm, 2008). Although abiotic factors are usually considered as agents of disturbance, organisms can also disturb physical habitat and affect community structure (Krantzberg, 1985; Meysman, Middelburg & Heip, 2006). For example, foraging activities of crayfish (*Oronectes limosus*) can change bed-form roughness and modify sediment composition (Statzner *et al.*, 2000). Fish may alter their habitat through feeding (Billheimer & Coull, 1988; Ritvo, Kochba & Avnimelech, 2004), spawning activity (Fuller & Cowell, 1985; DeVries, 1997) and nutrient delivery (Guyette, Loftin & Zydlewski, 2013), affecting ecosystem processes and providing economic benefits (Holmlund & Hammer, 1999).

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The effects of spawning anadromous Pacific salmon (*Onchorhynchus* spp) on the substratum (e.g. Peterson & Foote, 2000; Moore, Schindler & Scheuerell, 2004) and nutrient enrichment (e.g.Tiegs *et al.*, 2009; Rüegg *et al.*, 2012) are perhaps the best studied fish-mediated bioturbations. Pacific salmon excavate, sort and rearrange the substratum during spawning (Montgomery *et al.*, 1996), and salmon nests (redds) have less fine sediment than the adjacent unmodified stream bed (Kondolf, Sale & Wolman, 1993). Interestingly, these actions benefit conspecifics during egg incubation, while young fish are still in the gravel redds, and in subsequent spawning events. Recurring mass spawning alters stream-bed topography which, in turn, influences embryo survival. Spawning coarsens the bed surface and reduces particle mobility, decreasing the likelihood that high-flow events scour redds and dislodge embryos (Montgomery *et al.*, 1996). Thus, a positive feedback between salmon spawning and bed stability favours future spawning success.

While much research has focused on salmonines, other migratory fish influence streams through habitat modification during spawning. Sea lampreys (*Petromyzon marinus*), while reviled in areas outside their native range, have been viewed more recently as a beneficial component of freshwater ecosystems where they are native (Kircheis, 2004; Saunders, Hachey & Fay, 2006). They are of note among the suite of migratory fishes native to the Atlantic coast of North America as they are semelparous and are likely to provide nutrient subsidies in oligotrophic freshwater systems (Guyette *et al.*, 2013, 2014). Similarly, their physical impact from nest excavation and spawning is notable as they construct mound and pit structures qualitatively similar to Pacific salmon redds. Kircheis (2004) and Saunders *et al.* (2006) hypothesise that sea lampreys may 'condition' physical habitat to the benefit of other biota. For example, nest construction by sea lampreys may improve quality of spawning habitat for Atlantic salmon (*Salmo salar*) by removing fine sediment from interstitial spaces, sorting particles and decreasing particle embeddedness.

The degree to which nest building by sea lampreys influences water depth, water velocity, substratum particle size distribution, embeddedness and intragravel permeability has not been characterised. In this paper, we describe a field study in which we tested for the effects of physical disturbance by spawning sea lampreys on stream-bed topography and invertebrate assemblages in Sedgeunkedunk Stream, a tributary of the Penobscot River in Maine. Specifically, we hypothesised that the nesting behaviours of sea lampreys would create habitat patches with reduced fine-sediment coverage, decreased gravel and cobble embeddedness, improved interstitial spacing, increased intragravel permeability, and enhanced depth and velocity heterogeneity relative to neighbouring unmodified patches. We also asked whether any such physical changes would persist into the autumn, when Atlantic salmon spawn, and whether these changes would influence benthic invertebrate assemblages.

Methods

Study area

Sedgeunkedunk Stream is a third-order tributary of the Penobscot River, Maine, USA, draining Fields Pond at (44°44′05″N and 68°45′56″W) and flowing for 5.3 km to its confluence with the Penobscot River near the head of the tidal reach (44°46′08″N and 68°47′06″W). Median wetted width at low flow is *c.* 5 m, with peak discharge of 5 m^3 s^{-1} in spring and base flow of 0.1 m^3 s^{-1} during late summer. Prior to 2009, the lowermost dam (Mill Dam) on Sedgeunkedunk Stream restricted sea lamprey spawning to the lower 0.7 km of the system. Removal of this dam in 2009 allowed sea lampreys to recolonise 5.2 km of lotic habitat that had not been accessible for more than 150 years (Hogg, Coghlan & Zydlewski, 2013). We stratified the stream by delineating three reaches of stream habitat: Habitat Reach 1 (HR1) the lower 0.7 km urbanised portion of stream where sea lampreys spawned prior to dam removal (Gardner, Coghlan & Zydlewski, 2012), HR2 – the middle 1.5 km portion of stream characterised by urban and residential development, early-successional riparian forest and affected substantially by sedimentation and HR3 – the remaining 3.1 km of lotic habitat with little urban development and a mixed forest riparian zone (Fig. 1).

Sea lamprey tracking and nest surveys

Sea lampreys were captured as they entered Sedgeunkedunk Stream using a fyke net located 90-m upstream from the mouth from 15 May to 26 June 2010 and 22 May to 6 July 2011. Upon capture, each sea lamprey was injected with a PIT tag (full duplex, 12 mm) and a T-bar anchor tag into the dorsal musculature on opposite sides (as described in Hogg *et al.*, 2013). We recorded mass, total length and sex (based on morphology) for each fish prior to release upstream of the trap. Daily surveys on foot located tagged individuals and identified sea lamprey nests through the entire study site. Because sea lampreys may abandon nests and seek shelter during the day (Kelso & Gardner, 2000), nest identification was
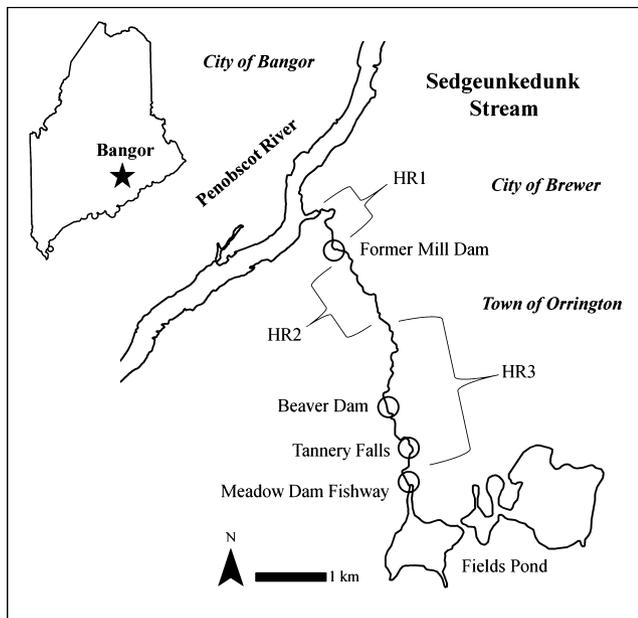
Fig. 1 Locations of Sedgeunkedunk Stream, the former Mill Dam, the Meadow Dam Fishway, Fields Pond, potential barriers to sea lamprey migration (Tannery Falls and a beaver dam), Habitat Reach 1 (HR1), HR2 and HR3, Penobscot County, Maine, U.S.A.

based on substratum disturbances as well as spawning activity. Individual nest location was identified using a shoreline stake, measured distance from shore and a recorded GPS point.

Nest sampling

Twenty-five unique nests were destructively sampled in the summer (just after spawning) and another 25 unique nests in autumn (to determine whether physical changes persisted). Sample sizes were based on power analyses using data from analogous salmonine studies (Chambers *et al.*, 1954; Kondolf *et al.*, 1993) allowing detection of 5–6% changes in fine sediment with a power of 0.80. We allocated random samples to each stratum (i.e. reach of stream, HR-1, 2, 3) proportionally to the abundance of nests within each reach (sampling a minimum of seven and a maximum of 10 nests per reach). Summer sampling began 10 days after spawning activity so that sufficient time had elapsed for lamprey egg incubation, and larval emergence and dispersal, thus minimising our sampling impact. Autumn sampling was conducted from the last week of September to the first week of October in both years.

At the time of sampling, three 'treatments' were assessed (measured) for each nest: the excavated pit ('pit'), the associated gravel-cobble mound ('mound') and an unmodified reference location ('reference').

Lengths were measured parallel to stream flow and widths perpendicular to length (Fig. 2). Reference habitats for each nest were selected by randomly choosing an angle (θ) between 0° and 180° (in 15° increments) upstream from the centre of the pit at a distance of 1.0 m (centre to centre; Fig. 2). Two reference locations per nest were sampled in 2010 but showed little variation, and therefore, results were averaged prior to statistical analysis. A single reference location was sampled in 2011 for each nest. Pit, mound and reference treatments were demarked by individual sampling hoops constructed of 8-mm coated wire cables measuring 1.5 m in circumference, 0.48 m in diameter and *c.* 1800 cm^2 in area. Sampling hoops mimicked those used by the State of Maine Department of Marine Resources (DMR) for the sampling of Atlantic salmon redds (E. Atkinson, Maine DMR, Jonesboro, ME, personal communication). All of the nesting habitats measured had surface areas larger than our sampling hoops.

Fine-sediment coverage

Fine sediment was defined as <2 mm (a particle size considered detrimental to developing salmonine embryos; Kondolf, 2000). A 15 × 15 grid (squares measuring 2.5 × 2.5 cm) was placed over the sampling hoop
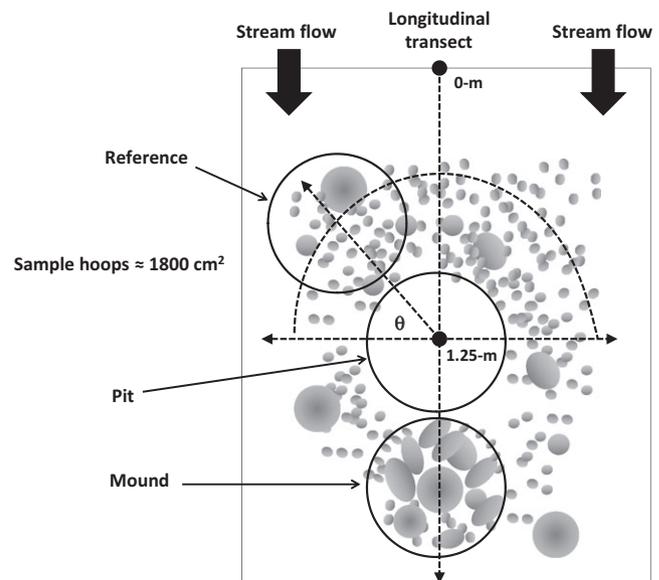

Fig. 2 Idealised sea lamprey nest illustrating hoop placement for the sampling of physical characteristics and Surber Sampler placement for the sampling of benthic invertebrates. Hoops and Surber Samplers were laid flat on the stream bed over mounds, pits and randomly selected reference locations (see Methods). The diagram provides an example of a reference hoop placement corresponding with a random draw of θ = 45°. A longitudinal transect in which a depth profile was constructed is indicated.

and viewed with an underwater viewing scope. The proportion of grid squares with 50% or more fine-sediment coverage was determined.

Embeddedness

A modified quantitative embeddedness method (Burns & Edwards, 1985; Sennatt *et al.*, 2006) was used. Thirty particles >40 mm in diameter were selected, removing free matrix particles first and then removing embedded particles by grasping the particle at the plane of embeddedness. For each particle, total depth (D_t) and embedded depth (D_e) were measured relative to *in situ* orientation (D_e is zero for free matrix particles). Length of the longest primary axis (D_m) of the particle was also measured.

A variety of computational methods have been developed for application to the original Burns method and have been cited in various publications (Burton & Harvey, 1990; Sylte & Fischenich, 2002; Sennatt *et al.*, 2006) as the Burns, Skille & King (BSK) method as derived from an unpublished technical report (Skille & King, 1989). The BSK method treats particle measurements within a hoop as a single sample (Burton & Harvey, 1990) but excludes free matrix particles from the calculation (Sennatt *et al.*, 2006). We modified the per cent embeddedness equation to include free matrix particles as follows:

$$E_{BSK} = 100 \times \left(\sum D_e \Big/ \sum D_t \right) \qquad (1)$$

where E_{BSK} is per cent embeddedness. Because per cent embeddedness is underestimated when fine sediments dominate a sample (Torquemada & Platts, 1988), we used a weighted embeddedness for all further analyses (Macdonald, Smart & Wissmar, 1991):

$$E_W = (100 \times F) + [(1 - F) \times E_{BSK}] \qquad (2)$$

where E_w is per cent weighted embeddedness, and F is the proportion of the hoop area containing 50% surface fine sediments 2 mm or less.

Interstitial spaces

We characterised the availability of interstitial spaces suitable for young-of-the-year Atlantic salmon using a modification of a method developed by Finstad *et al.* (2007). We used a cylindrical polyvinyl chloride probing device with colour-contrasting ends measuring 13 mm in diameter and 24 mm in length (typical size of a stocked Atlantic salmon fry) to identify interstitial spaces large enough to provide shelter for an emergent young-of-the-year fish. We viewed potential shelters contained within sampling hoops with a viewing scope. An interstitial space was counted if the coloured end of the probe could not be seen from any angle.

Intragravel permeability

In 2010, we used the method of Terhune (1958), as modified by Barnard & McBain (1994), to measure intragravel permeability. We drove the conical tip of a permeameter standpipe 20 cm below the surface of the stream bed. A pump was then used to evacuate the water contained within the standpipe, and the rate of recharge was measured in units of mL per second. The inflow recharge rate (mL s^{-1}) was converted to permeability (K, in cm h^{-1}) using a calibration curve and standardised with a 10° C temperature viscosity correction factor (Terhune, 1958). The average of two 10-s interval inflow recharge rates was used to calculate K if the rates were within 10% agreement. A third 10-s interval recharge rate was used to calculate the average if the agreement criterion was not reached with the first two draws. No more than three inflow rates were measured from an individual sampling hoop because Mackey (2005) reported skewed results from samples in which more than three draws were made.

Depth and current velocity

Depth and water velocity were measured at three arbitrarily selected points within each sample area using a velocity metre (Swoffer, Model 2100 Seattle, Washington, USA). Velocity was measured near the surface, at 60% of water depth and as near to the stream bed as the propeller-driven velocity metre would allow. 'Differential water velocity' was calculated as the difference between surface and stream-bed velocities. To characterise the construction of each nest, a longitudinal transect of water depth measurements was made from 1 m upstream to 1 m downstream at 0.25-m intervals through the centre of the nest (Fig. 2). Transect depths for each nest were standardised relative to the mean of all depth measurements for that nest. These data were grouped for all nests within each season and year.

Benthic invertebrate density and diversity

Benthic invertebrate sampling was carried out in 2011 at 25 unique nesting sites (different from the nests sampled for physical variables and selected randomly as described above) each during the summer and autumn using a Surber Sampler (500 μm mesh, 0.097 m^2; see Fig. 2).

Sampling entailed laying the quadrat of the sampler on the stream bed and manually disturbing the substratum for 30 s. Samples were preserved in 70% ethanol solution, and organisms were separated from detritus via a flotation technique using a 300 g L^{-1} sucrose solution (Anderson, 1959). Benthic insects were identified to family (Merritt, Berg & Cummins, 2009) and other invertebrates to class or order (Voshell & Wright, 2002; Merritt *et al.*, 2009). After processing, samples were dried at 68° C for 36 h, and the mass of dried animals was measured (±0.1 mg). Family-level diversity of aquatic insects was measured with the Shannon Diversity Index (H'). We also measured the percentage of Ephemeroptera, Plecoptera and Trichoptera (% EPT) for each sample.

Statistical analyses

Physical and benthic invertebrate data were analysed with hierarchical three-factor ANOVA models using spawning 'treatment'(mound, pit, reference) as the main effect nested within 'season' (summer, autumn) effects, which in turn were nested within 'reach' effects (HR1, HR2, HR3). To control for variability arising from differences among individual sea lamprey nests, due to pre-existing physical conditions and the number of attending adults, we used each individual nest as a blocking variable and adjusted the error terms accordingly (see Table 1). Because we were unable to detect consistent trends among variables at the effect level of reach, only statistically significant treatment effects for each year-specific ANOVA model were assessed within both seasons using Bonferroni-corrected multiple comparison tests. We report least squares means ± two standard errors (2SE) and used SAS version 9.2 (SAS Institute, 2010) at the significance level of α = 0.05 for all models. Depth and velocity data were distributed normally and did not require transformation. Per cent weighted embeddedness data were arcsine-transformed, while per cent fine sediment, interstitial space count, benthic invertebrate biomass, family richness and H' data were rank-transformed to meet assumptions of normality. All benthic invertebrate density data were square root-transformed with the exceptions of the densities of Ephemerellidae and Philopotamidae, which were rank-transformed.

Results

Nest dimensions

Pit and mound structures of sea lamprey nests were typically <1 m in both length and width (Table 2). However, for pits, we recorded a maximum length of 2.13 m and a maximum width of 2.08 m, while, for mounds, we recorded a maximum length of 1.52 m and a maximum width of 2.78 m. Although the typical total nest area was <1 m^2 with a mean value of 0.85 m^2 (Table 2), we recorded a maximum total nest area of 5.19 m^2 from a communal nest constructed during the 2011 spawning run.

Fine-sediment coverage

ANOVA indicated that the percentage cover of fine particles was influenced by treatment effect ($P < 0.001$, both years), season ($P = 0.031$, 2010; $P = 0.011$, 2011) and reach ($P = 0.005$, 2010). There were no significant interactions among factors. In both years, immediately after spawning, per cent cover by fines on the mound was less than half of that in the pit ($P < 0.001$, both years) and reference habitats ($P < 0.001$ and $P = 0.003$ for 2010 and 2011, respectively). Pits and reference habitats did not differ in either year (Fig. 3). These trends persisted into the autumn. Per cent cover of fines in mounds remained less than half of that in the pits ($P < 0.001$ for both years), but the difference between the mound and reference sites had declined by autumn to only 56%

Source	d.f.	Denom	Type III SS	MS	F value	P
1 Season	1	8	0.00067	0.00067	4.2	**0.0464**
2 Tx	2	9	0.00414	0.00207	22.55	**<0.0001**
3 Reach	2	8	0.00006	0.00003	0.18	0.8336
4 Season*Tx	2	9	0.00017	0.00008	0.92	0.4038
5 Reach*Tx	4	9	0.00044	0.00011	1.2	0.3146
6 Season*Reach	2	8	0.00006	0.00003	0.2	0.8175
7 Season*Reach*Tx	4	9	0.00024	0.00006	0.65	0.6278
8 Nest (Season*Reach)	44					
9 Nest*Tx (Season*Reach)	88					

Table 1 Example ANOVA table. Analysis of changes in per cent embeddedness for sea lamprey nests sampled in Sedgeunkedunk Stream, Maine during 2010. Sources of variation include treatment (Tx: Mound, Pit, Reference), Season (Summer, Autumn), Reach (HR1, HR2, HR3) and Nest (50 unique sample locations). Sources of variation are numbered, and the denominators used as error terms to test each effect are indicated. Significant effects (α = 0.05) are bolded

Table 2 Mean (±2SE) length, width and surface area of sea lamprey nests sampled from Sedgeunkedunk Stream. Archived data from 2008 (Gardner *et al.*, 2012) are included for annual comparisons and increased overall sample size

Year (*n*)	Pit length (m)	Pit width (m)	Pit area (m^2)	Mound length (m)	Mound width (m)	Mound area (m^2)	Total nest area (m^2)
2008 (21)	0.77 ± 0.12	0.57 ± 0.09	0.47 ± 0.13	0.59 ± 0.11	0.57 ± 0.09	0.38 ± 0.12	0.85 ± 0.24
2010 (50)	0.52 ± 0.05	0.57 ± 0.09	0.33 ± 0.08	0.49 ± 0.06	0.67 ± 0.12	0.39 ± 0.13	0.72 ± 0.21
2011 (50)	0.70 ± 0.09	0.64 ± 0.07	0.51 ± 0.12	0.59 ± 0.07	0.70 ± 0.09	0.48 ± 0.12	0.99 ± 0.24
Pooled (121)	0.64 ± 0.05	0.60 ± 0.05	0.43 ± 0.07	0.55 ± 0.04	0.66 ± 0.06	0.42 ± 0.08	0.85 ± 0.14

lower in 2010 ($P = 0.018$) and no difference in 2011 (Fig. 3).

Embeddedness

Embeddedness was influenced by treatment in both years (ANOVA; $P < 0.001$) but by season only in 2010 ($P = 0.046$) and by reach only in 2011 ($P = 0.027$) when there was also an interaction between treatment and reach ($P = 0.015$). In both years, immediately after spawning, embeddedness was reduced in mounds to about half of the value in pits ($P < 0.001$ and $P = 0.027$ for 2010 and 2011, respectively). Embeddedness in mounds was also about half that of reference locations in 2010 ($P < 0.001$) but was not different in 2011. Embeddedness of pits and reference habitats did not differ from one another in either year (Fig. 3). This trend persisted into the autumn of both years, with the mounds being 33% ($P = 0.021$) and 62% ($P = 0.019$) less embedded than pits in 2010 and 2011, respectively. In 2010, mounds were 30% less embedded than references ($P = 0.024$), but there was no difference in 2011. As in the summer, pit and reference locations did not differ from one another in autumn (Fig. 3).

Interstitial spaces

There was an influence of treatment on interstitial spaces (ANOVA; $P = 0.004$) in 2010, with no other significant factors or interactions, while in 2011, only an interaction between season and reach was revealed ($P = 0.043$). In summer 2010, the number of interstitial spaces in mounds was nearly two times greater than in pits ($P = 0.033$) and reference ($P = 0.030$) locations. Pits and reference locations did not differ (Fig. 3). No difference was detected in autumn.

Intragravel permeability

There was an effect of reach only on intragravel permeability (ANOVA on data from 2010 only, $P = 0.003$) and no finer-scale treatment effects. Intragravel permeability con-
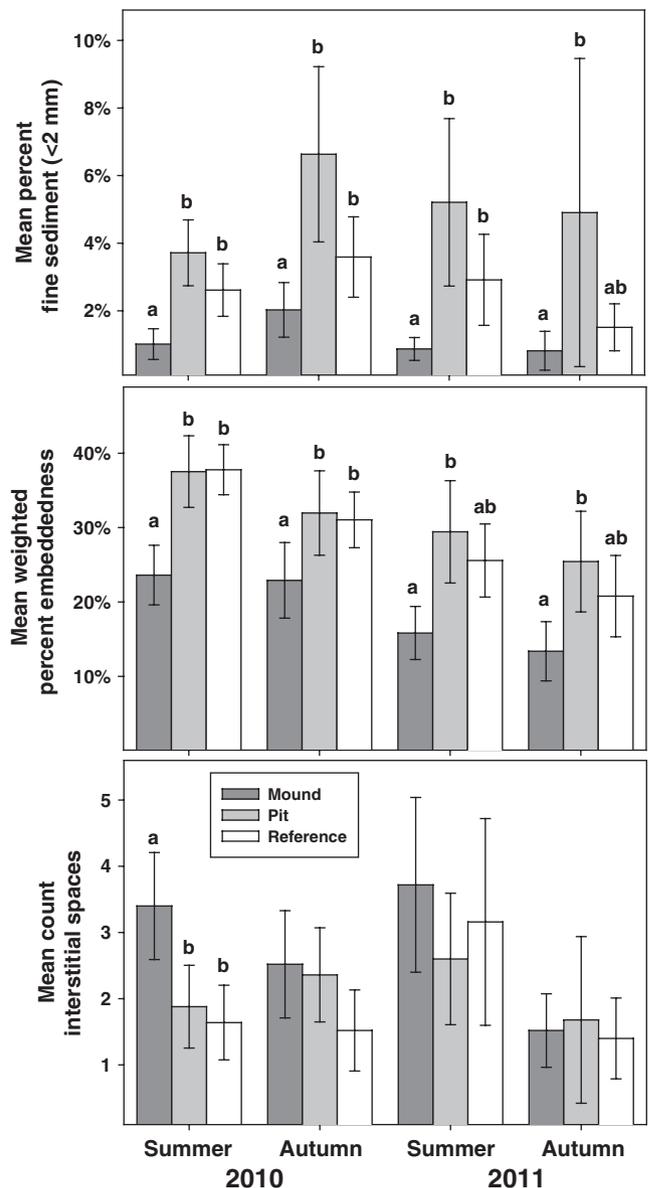

Fig. 3 Mean (±2SE) percentage cover with fine sediment <2 mm (upper panel), weighted per cent embeddedness (middle panel) and count of interstitial spaces (lower panel) as measured from sea lamprey nests (mound, pit and reference) in summer and autumn 2010 and 2011. Twenty-five different sea lamprey nests were sampled in each season. Shared letters above bars within each season indicate no statistical difference.

sistently declined from downstream to upstream (HR1: 980 ± 160 > HR2: 812 ± 190 > HR3: 575 ± 161 cm h^{-1}) with HR1 and HR3 differing ($P = 0.002$).

Mid-column velocity

There was an effect of treatment on mid-column velocity in both 2010 and 2011 (ANOVA; $P < 0.001$ for both years), while season ($P = 0.001$) and reach ($P = 0.002$) were implicated only in 2011. In both years, there was an interaction between treatment and season ($P = 0.038$ and $P = 0.036$ for 2010 and 2011, respectively). In mound habitats, mid-column velocity was 1.5 to two times greater than that in the deeper pit habitats ($P < 0.001$ for both years) and was 35–47% greater than reference habitats ($P < 0.001$ for both years) in the summer. Pits and reference habitats did not differ from one another in either year (Fig. 4). This trend persisted into the autumn, with mid-column velocity in mounds 44–45% greater than in pits ($P < 0.001$ both years) and 15–35% greater than in reference habitats ($P = 0.002$ and $P = 0.034$ for 2010 and 2011, respectively). Pit and reference locations did not differ from one another in 2010, but in 2011, mid-column velocity in reference habitats was *c.* 30% greater than in pits ($P < 0.001$; Fig. 4).

Differential velocity

The differential velocity metric differed between treatment (ANOVA; $P < 0.001$ both years) and reach ($P = 0.011$, $P = 0.006$ in 2010 and 2011, respectively) with no seasonal effects. An interaction between season and treatment was detected in both years ($P = 0.034$ and $P = 0.036$) and between season and reach in 2010 ($P = 0.017$). Differential velocity in pits was 65–68% greater than in mounds ($P < 0.001$ in both years) and 35–62% greater than reference habitats ($P < 0.001$ and $P < 0.002$ for 2010 and 2011). Differential velocity in mounds was 32% greater than in references in 2011 ($P = 0.013$) but did not differ in 2010 (Fig. 4). Differences in differential velocity did not persist into autumn 2010 but did in 2011, when the mean value in pits remained 58% greater than that in mounds ($P < 0.001$) and 35% greater than in reference locations ($P < 0.001$; Fig. 4).

Water depth

There was an effect of treatment on depth in both years (ANOVA; $P < 0.001$) with no interactions. In summer, pits were 70–78% deeper than mounds ($P < 0.001$ for
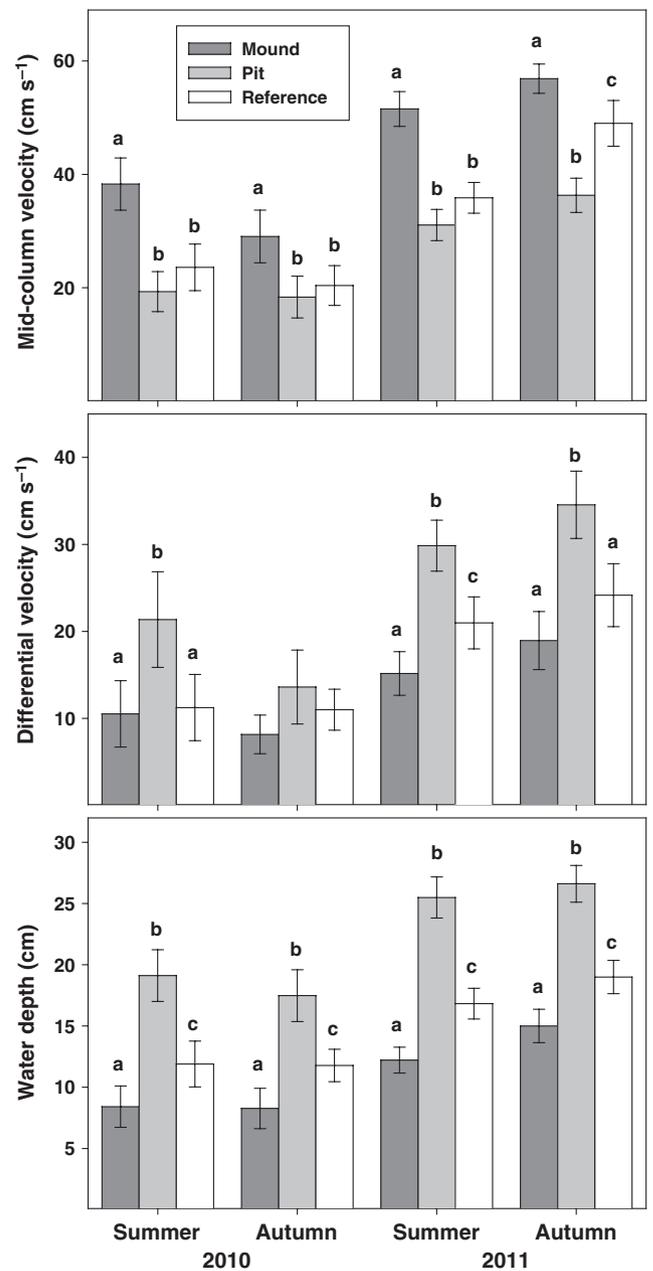

Fig. 4 Mean ($\pm$2SE) mid-column (60% depth) water velocity (upper panel), differential water velocity (middle panel) and water depth (lower panel) measured from sea lamprey nests (mound, pit and reference) in summer and autumn 2010 and 2011. Twenty-five different nests were sampled in each season. Shared letters above bars within each season indicate no statistical difference.

both years) and 41–47% deeper than reference locations ($P < 0.001$, both years). Reference locations were 32–34% deeper than mounds in summer ($P < 0.001$, both years). These structural differences persisted into the autumn for both years, with pits remaining 56–72% deeper than mounds ($P < 0.001$, both years) and 33–39% deeper than reference locations ($P < 0.001$, both years). Reference locations were 24–35% deeper than mounds in autumn

($P < 0.001$ and $P = 0.003$ for 2010 and 2011, respectively; Fig. 4).

Longitudinal depth transects

Standardised transect depths indicate a pattern of consistent depth and length of nests between seasons and years (Fig. 5). The pits were conspicuous depressions 5–10 cm deeper, while mounds were conspicuously raised such that water was *c.* 5 cm shallower than downstream. These structures persisted into the autumn of both years (Fig. 5).

Benthic invertebrate assemblage

The total benthic invertebrate assemblage as sampled from all sea lamprey nests was dominated by Trichoptera (36%), Diptera (29%) and Ephemeroptera (18%), with these three orders comprising 83% of the total abundance (Table 3). Five insect families within these orders contributed 74% of the pooled, summer and autumn benthic invertebrate assemblage. Chironomidae (larvae and pupae) and Hydropsychidae alone accounted for 27% and 26% of the pooled, summer and autumn abundance, respectively. Heptageniidae,

Philopotamidae and Ephemerellidae were also relatively abundant, contributing 8, 7 and 6%, respectively (Table 3).

Benthic invertebrate density

There was an effect of treatment (ANOVA; $P < 0.001$) on total benthic density, with no other effects or interactions. In summer, density on mounds was more than twice that in pits ($P < 0.001$) and 77% higher than in reference locations ($P = 0.001$). Benthic invertebrate densities on pits and in reference locations did not differ (Fig. 6a). These patterns persisted into autumn. Benthic density on mounds remained nearly twice that of the density in pits ($P < 0.001$) and 58% greater than in reference locations ($P = 0.001$). As in summer, density in pits and reference locations did not differ (Fig. 6a).

Individual ANOVA models for the densities of each of the five dominant insect families revealed that there were effects of treatment ($P < 0.001$, all five families), season ($P < 0.001$, all five families except Hydropsychidae, $P = 0.008$) and reach ($P = 0.012$, Hydropsychidae; $P = 0.024$, Ephemerellidae). Interactions included season and reach for the Hydropsychidae model ($P = 0.032$), treatment and season for both the Philopotamidae model
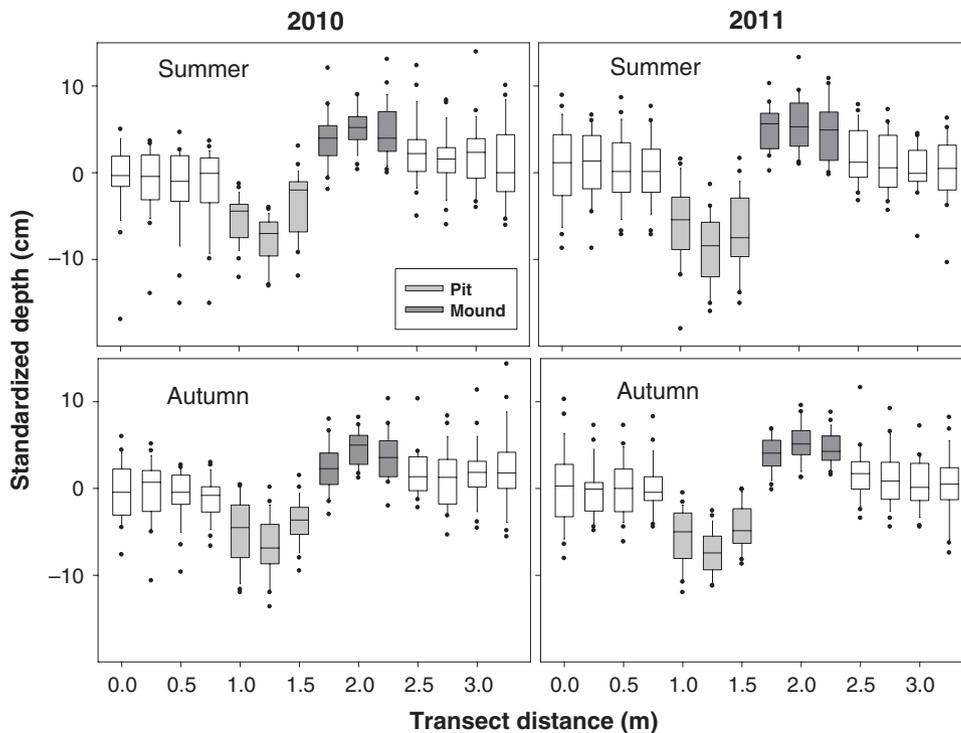

Fig. 5 Distributions of depth measurements on a longitudinal transect through sea lamprey nests (see Fig. 2). Individual depth measurements were standardised per season to changes in mean depth for each of the 25 nests. Box plots indicate 25th and 75th percentiles, and whiskers indicate 5th and 95th percentiles. Light and dark grey boxes represent pits and mounds, respectively.

Table 3 Benthic invertebrate orders and families (% of total numbers) in samples from sea lamprey nest sites during summer and autumn 2011. 'Others' represent non-insect organisms including Annelida, Bivalvia, Collembola, etc

Order (Family)	Summer (%)	Autumn (%)	Pooled (%)
Trichoptera	26.9	42.5	35.9
(Hydropsychidae)	(19.6)	(30.3)	(25.7)
(Philopotomatidae)	(4.8)	(8.3)	(6.8)
Diptera	43.2	18.0	28.6
(Chironomidae)	(42.1)	(16.5)	(27.4)
Ephemeroptera	14.5	21.0	18.2
(Heptageniidae)	(6.4)	(9.1)	(7.9)
(Ephemerellidae)	(1.3)	(9.7)	(6.1)
Coleoptera	3.1	5.1	4.3
Plecoptera	3.2	4.5	4.0
Megaloptera	4.2	3.7	3.9
Others	3.4	2.4	2.8
Odonata	1.4	2.8	2.2
Hemiptera	0.1	0.1	0.1

($P = 0.037$) and the Chironomidae model ($P < 0.001$), and two interactions for the Heptageniidae model (season and reach, $P = 0.002$; season and treatment, $P = 0.018$).

Consistent treatment trends were observed during the summer for the dominant insect families with exception of Ephemerellidae. In the summer, Hydropsychidae density on mounds was 2.5 times greater than in pits ($P < 0.001$) and 2 times greater than in reference locations ($P = 0.002$), while no differences were detected between pits and references (Fig. 6b). Summer density of Philopotamidae on mounds was nearly three times greater than in both pits ($P < 0.001$) and reference locations ($P < 0.001$), while densities were similar between pits and references (Fig. 6c). Heptageniidae density on mounds in summer was twice that in pits ($P = 0.006$), but no other differences were detected (Fig. 6e). Chironomidae density on mounds in summer was also twice that in pits ($P < 0.001$) and 1.5 times greater than in reference locations ($P = 0.001$), although no differences between pits and references were detected (Fig. 6f).

A pattern of persistent increases in densities on mounds during autumn was observed for the dominant insect families, with the exception of the Chironomidae. During autumn, Hydropsychidae density on mounds remained more than twice that of the density in pits ($P < 0.001$) and 88% greater than that of reference locations ($P < 0.001$), while pit and reference densities were similar (Fig. 6b). Philopotamidae density on mounds in
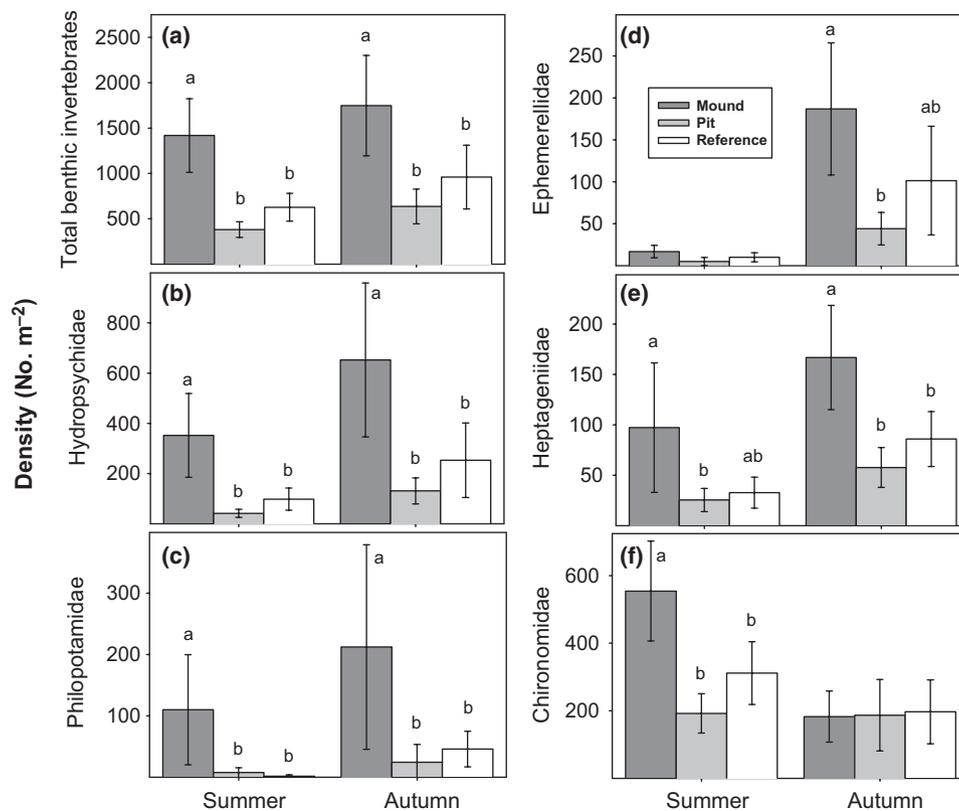

Fig. 6 Mean (±2SE) total benthic invertebrate density (a) and that of five main insects families (b-f) in Surber samplers from sea lamprey nests (mound, pit and reference) in summer and autumn 2011. Twenty-five different sea lamprey nests were sampled in each season. Shared letters above bars within each season indicate no statistical difference.

autumn was 2.5 times greater than in pits ($P < 0.001$) and more twice the density in reference locations ($P = 0.001$) (Fig. 6c). Although no differences were detected among treatments for Ephemerellidae in the summer, autumn density on mounds was more than two times greater than in pits ($P = 0.007$), but no other differences were detected (Fig. 6d). Finally, Heptageniidae density on mounds in autumn remained twice that in pits ($P < 0.001$) and was 64% greater than that of references ($P = 0.002$), while densities in pits and references remained indistinguishable (Fig. 6e).

Benthic invertebrate biomass

There were effects of treatment (ANOVA; $P < 0.001$), season ($P = 0.005$) and reach ($P = 0.008$) on benthic invertebrate biomass, but no interactions. In the summer 2011, biomass on mounds was 133% greater than in pits ($P < 0.001$), but there were no other pairwise differences (Fig. 7). This pattern persisted into autumn 2011, when biomass on mounds was twice that in pits ($P < 0.001$), but there were no other pairwise differences (Fig. 7).

Benthic invertebrate %EPT

The ANOVA for benthic invertebrate %EPT revealed effects of treatment ($P < 0.001$) and season ($P < 0.001$), but no interactions. No pairwise differences were detected among treatments in summer, although %EPT in autumn was 34% greater on mounds than in pits ($P < 0.001$) and

26% greater than in reference locations ($P < 0.001$). Pits and reference habitats did not differ (Fig. 7).

Benthic insect family richness

Insect family richness was influenced by treatment (ANOVA; $P < 0.001$), season ($P < 0.001$) and reach ($P = 0.011$) with no interactions. In summer, family richness on mounds was 40% greater than in pits ($P < 0.001$), with no other pairwise differences (Fig. 7). This pattern persisted into autumn when mounds had 24% greater richness than pits ($P = 0.022$) with no other differences detected (Fig. 7).

Benthic insect Shannon Diversity Index

There was an effect of treatment on the Shannon Diversity Index (H') (ANOVA; $P = 0.033$) and of season ($P < 0.001$), with no interactions. Pairwise comparisons of treatments within seasons revealed no differences although Bonferroni-corrected comparison tests of treatment indicated that H' values in mounds were 13% greater relative to pits overall ($P = 0.039$).

Discussion

Nest building by sea lampreys evidently produces a suite of physical effects that can persist for months after completion. With the exceptions of intragravel permeability and counts of interstitial spaces, persistent
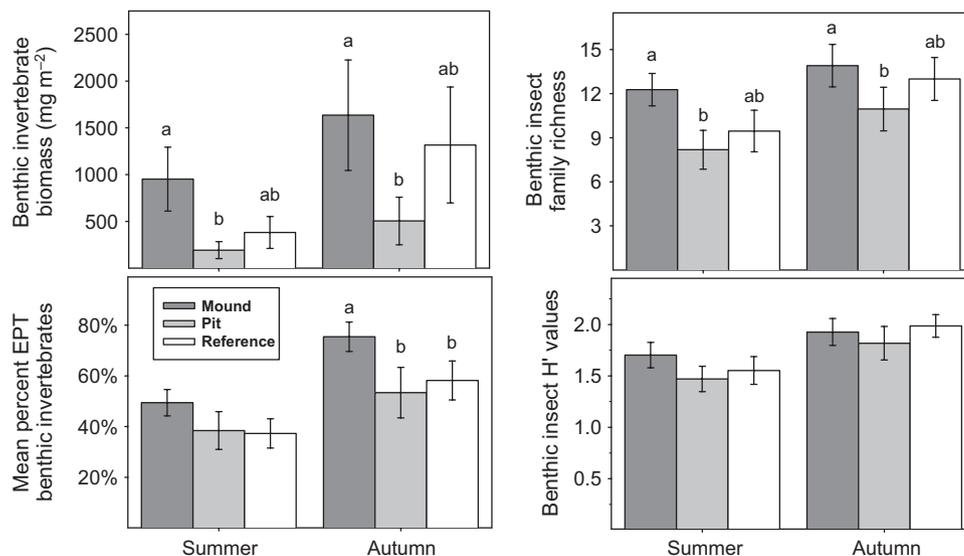

Fig. 7 Mean (±2SE) invertebrate biomass (upper left panel), percentage of EPT (lower left panel), family richness (upper right panel) and insect Shannon Diversity Index (H') (lower right panel) in Surber samplers from sea lamprey nests (mound, pit and reference) in summer and autumn 2011. Twenty-five different sea lamprey nests were sampled in each season. Shared letters above bars within each season indicate no statistical difference.

differences were detected among mound, pit and reference locations for all the physical measures. Nest building reduced both fine-sediment cover and embeddedness in the nest mound. The complexity resulting from this bioturbation changed the depth profile and increased both mid-column current velocity and differential current velocity over mound structures. Sea lamprey nests in Sedgeunkedunk Stream had a mean surface area of *c.* 1 m² with some larger communal nests in excess of 5 m². Thus, sea lamprey bioturbation may have large and ecologically relevant effects on large patches of pool tail-out to riffle habitats.

Nest construction influenced streambed topography by creating heterogeneous microhabitat patches that persisted into autumn. Pits were distinctly deeper with slower mid-column currents, whereas mounds were distinctly shallower with the fastest mid-column currents. Embeddedness in mounds was generally 10% less than in pits and reference habitats. While sea lampreys in this study selected nesting sites where surface fine-sediment accumulations were relatively low (< 10%; Fig. 3), nest building resulted in mounds that were further reduced in fine-sediment coverage by 2% and the reduction persisted into autumn (Fig. 3). These effects were a little less than the 5–6% reductions in fines reported from spawning activities of salmonines (Chambers *et al.*, 1954; Kondolf *et al.*, 1993), but are consistent with an overall pattern of substratum change.

For permeability, however, there were no differences detected among nest structures. Overall, permeability declined further up in the system, with the reach furthest upstream (HR3) having lower permeability than HR1. Inability to detect a difference may not negate a potential influence of nest building on permeability but rather probably indicates the extreme variability in this measure. McBain & Trush (2000) recommended a sample size of 17 locations to detect a difference in mean permeability by a factor of two (i.e. from 1000 cm h⁻¹ to 2000 cm h⁻¹), and our sample size exceeded this recommendation. Our sampling regime provided us with sufficient discriminatory power to detect a difference at the reach level with nominal increases in permeability along an up- to downstream gradient. Therefore, it follows that the low permeability in the upstream reaches (HR2 and HR3) may reflect a long-term absence of spawning anadromous fish due to the former Mill Dam, built more than 150 years ago. A research programme including a number of years of permeability sampling at the reach level may provide evidence that sea lamprey spawning activities have the ability to alleviate degraded permeability.

Our data demonstrate bioturbation effects that persist not only for several months but perhaps between years. Overall embeddedness gradually declined between samples from 33% in the summer of 2010 to 20% in the autumn of 2011. Within nest structures, embeddedness was markedly higher in summer 2010 (24% in mounds, 38% pit and reference) than in autumn 2011 (mounds at 14%, pits at 25% and reference habitats at 22%). While these data cannot test this hypothesis directly, they suggest that repeated sea lamprey mass spawning events may have persistent 'conditioning' effects on stream-bed topography. Sea lampreys appeared to select nesting sites in 2011 that were close to nesting sites in the previous year. A study investigating the interannual superimposition of sea lamprey nests might reveal long-term conditioning effects related to spawning similar to those detected from the repeated mass spawning events of Pacific salmon (Montgomery *et al.*, 1996).

Sea lampreys probably influence stream communities by creating structural complexity at various scales. Moore & Gregory (1988) reported that low velocity, heterogeneous substrata and structural protection from high discharge were important components of habitats selected by young-of-the-year drift-feeding salmonines. Pit habitats in our study consistently displayed similar characteristics such as comparatively lower mid-column velocities, heterogeneous substrata with remnant cobbles providing cover, and extreme contrasts between surface and bottom velocities (i.e. differential velocity). Pits were consistently deeper and therefore had the greatest differential velocity values which could potentially translate into energetically profitable foraging stations for drift-feeding fishes. The greater differential velocity values in pits result from the juxtaposition of slow, near-bed currents and fast surface currents. This extreme contrast could potentially create an environment that lessens the energetic demands of maintaining a foraging station by allowing individuals to occupy locations in slow-flowing water while maintaining access to drifting invertebrate prey delivered at a higher rate near to the surface. This logic is consistent with results from another study that found swift, shallow areas adjacent to slow, deep areas provided energetically profitable foraging habitats for juvenile Pacific salmon (Fausch & Northcote, 1992).

Sea lamprey nest excavations increased the abundance of interstitial spaces immediately after spawning in 2010, but this change did not persist into the autumn. Although the counts of interstitial spaces in mounds were similar between years, there was high variability within pits and references that reduced statistical power. Gravel and cobble substrata were packed loosely in

mounds and were less embedded, but cylindrical interstitial spaces measuring 13 by 24 mm (size of typical emergent Atlantic salmon fry) were relatively rare. Perhaps the use of smaller interstitial probing devices would better represent the size of shelters for other benthic organisms (salamanders, macroinvertebrates, etc.) and could help demonstrate the potential for community-level effects. Such considerations may be important in understanding the dynamics of benthic invertebrates in these nests. Multipatch mesocosm experiments have revealed that isolated populations of benthic invertebrates respond negatively to small-scale bioturbations, but overall community-level responses are positive when multiple heterogeneous patches are linked (Godbold, Bulling & Solan, 2011). Therefore, it follows that small-scale variations in habitat structure resulting from sea lamprey bioturbation may provide benefits that enhance the benthic community overall.

Nest pits were essentially stripped of larger pebbles, but the subsequent downstream construction of mounds provided microhabitats with reduced fine-sediment coverage, reduced embeddedness and increased interstitial spacing. Although the observed increases in benthic invertebrate density, biomass and diversity in mound habitats immediately following the spawning run may simply be explained by entrainment into the drift as lampreys dig pits and build mounds, the persistent pattern in these metrics 4 months after nest construction suggests that modification to the stream bed influenced benthic invertebrates. Previous studies have shown that, in small tributaries, benthic invertebrate abundance is correlated negatively with embeddedness (Lowe & Bolger, 2002) and that substrata with high surface heterogeneity or bed roughness have a greater propensity for macroinvertebrate colonisation than substrata with lower bed roughness (Erman & Erman, 1984). Additionally, in this study, persistent trends in density, biomass and diversity were accompanied by a rise in the proportion of EPT species, and particularly of the common net-spinning caddisflies (Hydropsychidae) that often occupy the less embedded interstitial spaces between loosely packed cobbles (Mackay & Waters, 1986). Although loose packing of cobbles may seem paradoxical for a taxon that requires stable surfaces for net-spinning, researchers have found that spawning-related bed modifications by salmonines decreased bed mobility (Montgomery *et al.*, 1996), and this phenomenon may also hold true for modifications by sea lampreys.

In summary, our data provide evidence that sea lampreys are ecosystem engineers in this and probably in other spawning streams. Recall that this study was performed where there was a modest run of sea lampreys, with access to spawning habitat only recently restored. The scale of this reported influence, therefore, is a fraction of the potential ecological impact that larger populations of sea lampreys may formerly have delivered to habitats throughout their native range.

Acknowledgements

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