

Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales

CHRISTIAN E. TORGERSEN* AND DAVID A. CLOSE†

*Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, U.S.A.

†Tribal Fisheries Program, Department of Natural Resources, Confederated Tribes of the Umatilla Indian Reservation, Pendleton, OR, U.S.A.

SUMMARY

1. Spatial patterns in channel morphology and substratum composition at small (1–10 metres) and large scales (1–10 kilometres) were analysed to determine the influence of habitat heterogeneity on the distribution and abundance of larval lamprey.
2. We used a nested sampling design and multiple logistic regression to evaluate spatial heterogeneity in the abundance of larval Pacific lamprey, *Lampetra tridentata*, and habitat in 30 sites (each composed of twelve 1-m² quadrat samples) distributed throughout a 55-km section of the Middle Fork John Day River, OR, U.S.A. Statistical models predicting the relative abundance of larvae both among sites (large scale) and among samples (small scale) were ranked using Akaike's Information Criterion (AIC) to identify the 'best approximating' models from a set of *a priori* candidate models determined from the literature on larval lamprey habitat associations.
3. Stream habitat variables predicted patterns in larval abundance but played different roles at different spatial scales. The abundance of larvae at large scales was positively associated with water depth and open riparian canopy, whereas patchiness in larval occurrence at small scales was associated with low water velocity, channel-unit morphology (pool habitats), and the availability of habitat suitable for burrowing.
4. Habitat variables explained variation in larval abundance at large and small scales, but locational factors, such as longitudinal position (river km) and sample location within the channel unit, explained additional variation in the logistic regression model. The results emphasise the need for spatially explicit analysis, both in examining fish habitat relationships and in developing conservation plans for declining fish populations.

Keywords: habitat structure, larval lamprey, longitudinal pattern, scale dependency, spatial heterogeneity

Introduction

Habitat heterogeneity influences the distribution and abundance of stream organisms over a range of spatial and temporal scales and plays an important

role in biological processes of freshwater ecosystems (Hildrew & Giller, 1994; Palmer & Poff, 1997). Recent studies on the spatial arrangement and composition of resource patches in streams have shown that organismal responses to environmental heterogeneity are complex and often scale dependent (Lancaster & Belyea, 1997; Palmer *et al.*, 2000; Swan & Palmer, 2000). Thus, there is a need to quantify the distribution of stream organisms and physical habitat at a resolution and extent that provides the flexibility to

Correspondence: Christian Torgersen, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, U.S.A.
E-mail: ctorgersen@usgs.gov

analyse species–habitat relationships at multiple scales (Li *et al.*, 2001; Thompson, Petty & Grossman, 2001). Although stream ecologists recognise the importance of understanding factors influencing the distribution of benthic organisms (e.g. Lancaster & Hildrew, 1993; Palmer *et al.*, 2000; Silver *et al.*, 2000; Swan & Palmer, 2000), spatially explicit investigations of benthic organisms at large spatial scales are relatively uncommon (Rice, Greenwood & Joyce, 2001; Howard & Cuffey, 2003). This is partially because of sampling difficulties, which may preclude the collection of high-resolution data (i.e. large sample size) over areas that are large enough to evaluate both small- and large-scale patterns, ranging from metres to kilometres.

Among stream-dwelling fauna, lampreys (Petromyzontidae) provide a unique opportunity to study a benthic organism that responds to habitat heterogeneity at both small and large scales, and yet is relatively easy to sample. The Pacific lamprey, *Lampetra tridentata* Gairdner, is an anadromous parasitic lamprey that completes the freshwater phase of its life cycle in streams and rivers from Baja California, Mexico along the northern Pacific Rim to Hokkaido, Japan (Moyle, 2002). A highly migratory species, the Pacific lamprey spawns in low-gradient streams, often hundreds of kilometres inland in the upper catchments of large rivers in Oregon, Washington, Idaho and British Columbia. Pacific lampreys spend more than half of their 6–10-year life span as filter-feeding larvae burrowing in the fine sediments of streams and are susceptible, like other species of larval lampreys, to habitat alteration by channelisation and flow regulation (Kirchhofer, 1995). Although most efforts in the United States and Canada have been directed at controlling invasive sea lamprey (*Petromyzon marinus* Linnaeus) populations in the Great Lakes (Smith & Tibbles, 1980), recent concerns have been raised for the conservation of lampreys in the Northern Hemisphere (Renaud, 1997), specifically in the Columbia River Basin (Pacific Northwest) and Europe where hydroelectric facilities have impeded migrations of lampreys (Ojutkangas, Aronen & Laukkanen, 1995; Almeida & Quintella, 2002; Close, Fitzpatrick & Li, 2002; Moser & Close, 2003). The construction of migration barriers has occurred concurrently with modification of larval rearing habitats in headwater streams. Thus, a need exists to evaluate the habitat requirements of larval Pacific lamprey and develop

methods for monitoring status and trends in larval abundance.

Previous studies of larval lampreys at large scales (>1 km) have been qualitative (Baxter, 1957) or have focused on trends in abundance rather than habitat relationships (Ojutkangas *et al.*, 1995). Studies of larval lampreys at the microhabitat scale are usually quantitative but are not designed to evaluate distributional patterns and habitat associations at more than one scale (Malmqvist, 1980; Potter *et al.*, 1986; Beamish & Jebbink, 1994; Beamish & Lowartz, 1996; Sugiyama & Goto, 2002). Detailed studies at small scales have shown that larval lampreys are associated with patchy fluvial features, such as backwaters, eddies, insides of bends and the downstream end of sand bars, in which fine sediments (sand and silt) tend to accumulate. However, the probability of larvae occurring within these 'preferred' habitats is typically low (<50%) (Sugiyama & Goto, 2002). The high degree of spatial heterogeneity in larval abundance, even in optimal habitats, suggests that larval habitat relationships may be highly dependent on the spatial context and scale of observation (*sensu* Inoue & Nunokawa, 2002).

Small-scale studies of larval lamprey habitat have been useful for developing a general understanding of the biology of lampreys. However, the conservation and management of lamprey populations requires the ability to evaluate and predict spatial patterns in larval abundance at several scales. With the increased interest in issues of scale and the development of spatial analysis techniques, statistical models are now being used to predict the distribution of stream fishes at multiple spatial scales (Knapp & Preisler, 1999; Torgersen *et al.*, 1999; Thompson *et al.*, 2001). Similar approaches can be used for lampreys to evaluate the suitability and effectiveness of restoration programmes and to increase the precision of efforts to control lampreys where they are invasive species. However, spatially explicit larval habitat models require extensive field data of sufficient resolution to define the scales at which habitat variables influence patterns of larval abundance. Because stream fishes often exhibit discontinuous spatial distributions, new approaches to sampling and analysis are required to elucidate the effects of habitat structure on fish populations (Angermeier & Smogor, 1995; Angermeier, Krueger & Dolloff, 2002).

Our goal was to evaluate spatial patterns and habitat relationships of larval Pacific lamprey at two different spatial scales. We hypothesised that (i) habitat heterogeneity at both small and large scales influences the distribution of larval lamprey abundance, and (ii) stream habitat variables predict patterns in larval abundance but play different roles at different spatial scales. Specifically, we were interested in identifying the role of locational factors, such as longitudinal position in a stream segment (reach scale) and sample location within a channel unit (subunit scale), in a spatially explicit model of larval lamprey abundance. In addition to elucidating the factors that influence the spatial distribution of larval Pacific lamprey, we also assess the effectiveness of a nested sampling design for evaluating spatial patterns and habitat relationships of benthic organisms in heterogeneous stream environments (Armitage & Cannan, 1998).

Methods

Study area and site selection

Larval Pacific lamprey were collected in the upper 55 km of the Middle Fork John Day River, a fourth- to fifth-order stream in north-eastern Oregon, U.S.A. (Fig. 1). The upper Middle Fork John Day River ranges in altitude from 1000 to 1300 m and flows through semi-arid rangelands in alluvial valleys and alluviated canyons vegetated on the upslopes with mixed conifer forest (*Pinus ponderosa* Lawson and

Abies grandis Lindley). The basin has been influenced by a number of land-use practices, including mining, logging, channelisation and grazing, which have nearly eliminated deciduous riparian vegetation (*Populus balsamifera trichocarpa* Brayshaw, *Crataegus douglasii* Lindley, and *Alnus rubra* Bongard) in unconstrained alluvial valley reaches.

Detailed maps of stream habitat (channel unit type and dimensions) and channel gradient provided a high-resolution, spatially continuous context for selecting larval sampling sites in our 55-km study section (Fig. 2). Longitudinal profiles of water depth and channel gradient derived from extensive habitat surveys (conducted by state and federal agencies for salmonid research) and 10-m digital elevation models (DEM) were rectified to 1 : 5000-scale hydrography and compared with respect to river km (rkm), defined as the distance upstream from the lower boundary of the survey section (rkm 0). Thirty sites were distributed along the survey section and stratified based on longitudinal patterns in water depth and channel gradient (Fig. 2). Sampling sites were located in the field with a hand-held global positioning system (GPS) to ± 50 m.

Larval lamprey sampling

We used a nested sampling design to evaluate heterogeneity in larval abundance and habitat at two different spatial scales – both within- and among-sites. The nested approach was employed because it provided information on habitat and biological response at

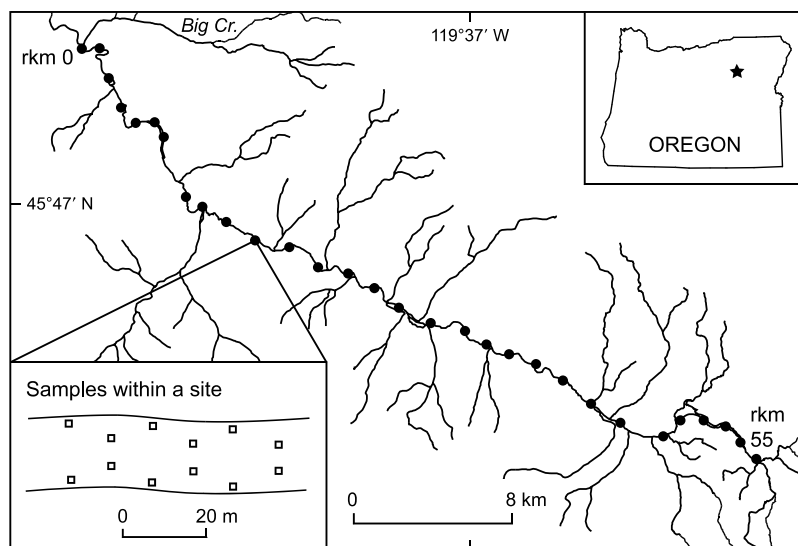
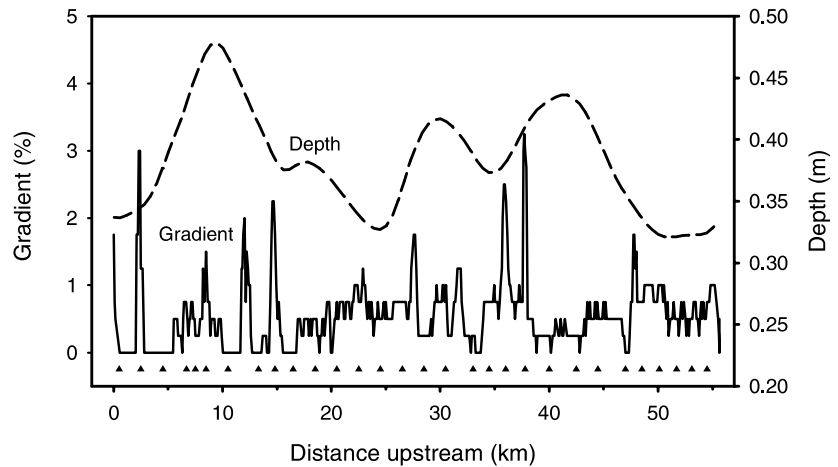


Fig. 1 Study area and sampling design for the survey of larval Pacific lamprey in the upper 55 km of the Middle Fork John Day River, Oregon, U.S.A. Solid circles indicate the locations of larval sampling sites. The direction of river flow is from right to left.

Fig. 2 Spatially continuous longitudinal profiles of channel gradient and water depth and the stratification of sample sites throughout the upper 55 km of the Middle Fork John Day River. The longitudinal profile of channel gradient was generated from a 10-m digital elevation model (DEM) with a 500-m moving window for slope calculations. Locally weighted scatterplot smoothing (LOWESS) was used to evaluate spatial patterns in water depth. Solid triangles above the horizontal axis indicate the locations of larval sampling sites along the longitudinal profile.



multiple scales (Armitage & Cannan, 1998). Sampling locations (1×1 m quadrats, $n = 12$) within a site were distributed in the mid channel and along stream margins in six transects spaced every 10 m (Fig. 1). The 1-m^2 quadrat sampling approach has been applied effectively to collect benthic fishes and was appropriate for a capturing sedentary species such as larval lamprey (Peterson & Rabeni, 2001). Sampling was completed in 1 month (at base flow in August 2000) to obtain synoptic data during a time when larval movement was limited. Larvae were collected at each sampling location in two 90-s passes with a backpack model AbP-2 larval lamprey electrofishing unit (Engineering Technical Services, University of Wisconsin, Madison, WI, U.S.A.). The electrofishing unit delivered 3 pulses s^{-1} (125 volts DC) at a 25% duty cycle, with a 3 : 1 burst pulse train (three pulses on, one pulse off) to draw larvae from the substratum (Weisser & Klar, 1990). Once in the water column, larvae were stunned with 30 pulses s^{-1} to facilitate capture. After collection, larvae were anaesthetised in buffered MS-222 (tricaine methanesulphonate at 250 mg L^{-1}), identified on the basis of caudal pigmentation patterns (Richards, Beamish & Beamish, 1982), and total length measured (± 1 mm) before they were returned to the stream.

Depletion estimates for two-pass removal were calculated with the Capture software program and converted to larval density per sample (no. m^{-2}) (Zippin, 1958; White *et al.*, 1982). Larval abundance was defined as the sum of larval densities per site. We did not evaluate the capture efficiency of electrofishing because of restrictions on other sampling methods (e.g. dredging) to protect threatened and endangered

resident salmonids. However, capture efficiency with similar backpack electrofishing gear for larval sea lamprey (*P. marinus*) has been estimated at 48% (Steeves *et al.*, 2003).

Habitat description

The assessment of larval habitat was conducted at the sample or site level depending upon the nature of stream habitat variables (Table 1). Measurements of water velocity at 60% depth (Model 201D flowmeter, Marsh-McBirney, Inc., Frederick, MD, U.S.A.) and total water depth were taken once per sample, and dominant substratum and larval habitat type were estimated visually within each $1 \times 1\text{-m}$ sampling quadrat. The following definitions were used to classify visually larval habitat types: (i) a mixture of soft sediment particles including silt, clay, fine organic matter and some sand, (ii) similar to type I habitat but with a large component of sand and (iii) bedrock, hard clay, cobble, or coarse gravel substrata.

At the site level, habitat characteristics were expressed either as a proportion of samples within each habitat category (channel unit, substratum, and larval habitat types) or as site means (channel dimensions and water velocity) (Table 1). Channel unit type (pool/riffle) was classified based on channel morphology and surface water velocity (Bisson *et al.*, 1982). Measurements of channel gradient (Model RL-HB rotating laser, Topcon Corp., Paramus, NJ, U.S.A.), pH, and conductivity (pH/Con 10, Oakton Instruments, Vernon Hills, IL, U.S.A.) were collected once per site. Percent canopy closure was assessed with a concave spherical densiometer at three equally

Table 1 Explanatory variables evaluated for associations with the relative abundance of larval Pacific lamprey

Variable	Units/ category	Data type	Description
Water depth	m	Continuous	
Organic depth	cm	Continuous	Depth of organic debris overlying substratum
Velocity*	m s ⁻¹	Categorical	Design variable based on percentiles
0–0.11			First to 33rd percentile
0.12–0.23			33rd to 66th percentile
0.24–1.00			66th to 100th percentile
Channel unit type		Binary	Channel unit type (Bisson <i>et al.</i> , 1982)
Pool	1		
Riffle	0		
Substratum		Categorical	Dominant substratum type in sample area
Organics	1		Organic debris
Silt	2		<0.1 mm
Sand	3		0.1–2 mm
Small gravel	4		3–10 mm
Large gravel	5		11–100 mm
Cobble	6		101–300 mm
Boulder	7		>300 mm
Bedrock	8		
Habitat type		Categorical	Larval burrowing habitat classification
Type I	1		Silt, clay, fine organic matter, and sand
Type II	2		Mostly sand
Type III	3		Bedrock, hard clay, cobble, or coarse gravel
Position		Binary	Location of sample in stream channel
Margin	1		Stream margin (within 20 cm of bank)
Mid-channel	0		Middle of channel
Wetted width [†]	m	Continuous	Measured at three equally spaced transects
Canopy closure	Percent	Continuous	Measured at three equally spaced transects
pH		Continuous	Measured once in the middle of each site
Conductivity [†]	µmho cm ⁻¹	Continuous	Measurement taken with pH
Gradient	Percent	Continuous	Channel slope calculated for 50-m site
Temperature	°C	Continuous	Measured with remote sensing
River km	km	Continuous	Distance upstream from lower boundary of survey section (rkm 0)

Notes: All variables were measured at the sample level except for wetted width and canopy closure (transect level) and pH, conductivity, gradient, temperature, and river km (site level).

*Velocity was measured as a continuous variable but exhibited a non-linear relationship with the logit and was therefore modelled as a categorical design variable.

[†]Wetted width and conductivity exhibited a significant ($P \leq 0.05$) linear relationship with river km and were detrended with linear regression.

spaced transects along the length of the site (Platts *et al.*, 1987). Spatially continuous profiles of channel gradient and water depth were generated in a GIS and analysed longitudinally with a 400-m moving window for gradient calculations and with locally weighted scatterplot smoothing (LOWESS) to identify trends in depth (Trexler & Travis, 1993; SPSS, 2001).

Statistical analysis

We used logistic regression to describe the relationship between larval abundance and habitat variables

within and among sites. Logistic regression has been applied to predict fish–habitat relationships at a variety of scales (Dunham & Rieman, 1999; Knapp & Preisler, 1999; Torgersen *et al.*, 1999) and was appropriate for modelling larval response to habitat heterogeneity because it requires limited assumptions regarding normality or homoscedasticity (Hosmer & Lemeshow, 1989; Trexler & Travis, 1993). The patchy distribution of organisms rarely meets these assumptions and, therefore, may require the logistic modelling approach (Hirzel & Guisan, 2002). The logistic model uses maximum likelihood estimation and the

logit transformation of a binary response variable to predict the probability of occurrence in relation to binary, categorical or continuous explanatory variables. To evaluate larval habitat relationships within sites (i.e. among samples), we modelled larval occurrence (binary response) with respect to continuous and categorical habitat variables measured at the sample and transect levels (Table 1). To assess larval habitat relationships among sites, we compared the spatial correspondence of peaks and troughs in larval abundance with longitudinal profiles of stream habitat. We created a binary response variable (i.e. a peak or trough in larval abundance) by standardising larval abundance with respect to the median. Site-level explanatory variables were also analysed as binary variables standardised with respect to the median or to the residuals from linear regression if variables exhibited a significant ($P \leq 0.05$) linear relationship with river km (e.g. wetted width and conductivity).

Logistic regression is sensitive to multicollinearity among predictor variables and to non-linear relationships between continuous explanatory variables and the linear predictor (i.e. the logit transform of the fitted response) (Tabachnick & Fidell, 2001). Therefore, we assessed all pairwise correlations between explanatory variables for multicollinearity and evaluated graphically relationships between continuous explanatory variables and the linear predictor. Only one continuous variable, velocity (sample-level), exhibited a non-linear relationship with the linear predictor and was converted to a categorical design variable based on percentiles. Logistic regression also requires that observations of the response variable be independent. Therefore, the degree of spatial autocorrelation must be evaluated quantitatively and if necessary accounted for by incorporating spatial structure into the statistical model (Legendre, 1993).

We used correlograms with the autocorrelation coefficient Moran's I to test for statistically significant spatial autocorrelation in the response variable (Legendre & Fortin, 1989). Longitudinal profiles of larval lamprey abundance in sites and samples were first assessed for stationarity (i.e. the presence of large-scale trends) (Rossi *et al.*, 1992). There was a statistically significant linear relationship ($P \leq 0.05$) between larval abundance and river km at both site- and sample-level spatial scales. Therefore, the resi-

duals from linear regression were used to construct correlograms. A test for spatial autocorrelation was then performed by determining whether the correlogram contained at least one value that was significant ($P \leq 0.05$) according to the Bonferroni method of correcting for multiple tests (Legendre & Fortin, 1989). The residuals of larval lamprey abundance exhibited no significant spatial autocorrelation at the site or sample level, so it was not necessary to apply more sophisticated techniques to incorporate spatial structure in the statistical models. However, to account for the linear trend in larval lamprey abundance among sites and the spatial arrangement of samples within sites, we included locational predictors (i.e. river km and sample position in the stream channel) in both site- and sample-level models.

Model selection was conducted with Akaike's Information Criterion (AIC) to identify the 'best approximating' models from a set of *a priori* candidate models determined from the literature on larval lamprey habitat associations (Burnham & Anderson, 2002). Using the approach of Harig & Fausch (2002), we evaluated two sets of statistical models for each spatial scale of analysis: one set with single-variable models [number of models (R) = 22 at the site level, and R = 14 at the sample level], and a second set with combinations of the 'best' models from the first set (R = 11 at the site level, and R = 15 at the sample level). These models were ranked by AIC (lower values indicate a better fit) and evaluated with respect to Δ AIC (i.e. the difference in AIC between a given model and the highest ranked model) and Akaike weight (w_i), which is a measure of the weight of evidence for a model given the data (Buckland, Burnham & Augustin, 1997). To minimise the potential for overfitting, the number of explanatory variables in the combination model set was limited to only those models that ranked higher than the locational variables (i.e. river km and position). Akaike's Information Criterion was corrected for small-sample bias (all site-level models) and overdispersion (sample-level combination models) as recommended by Burnham & Anderson (2002). Leave-one-out cross-validation was used with a probability cutoff of 0.50 to evaluate model predictions within models (Dunham, Rieman & Chandler, 2003). All statistical analyses were performed in the SAS software package (SAS, 1996).

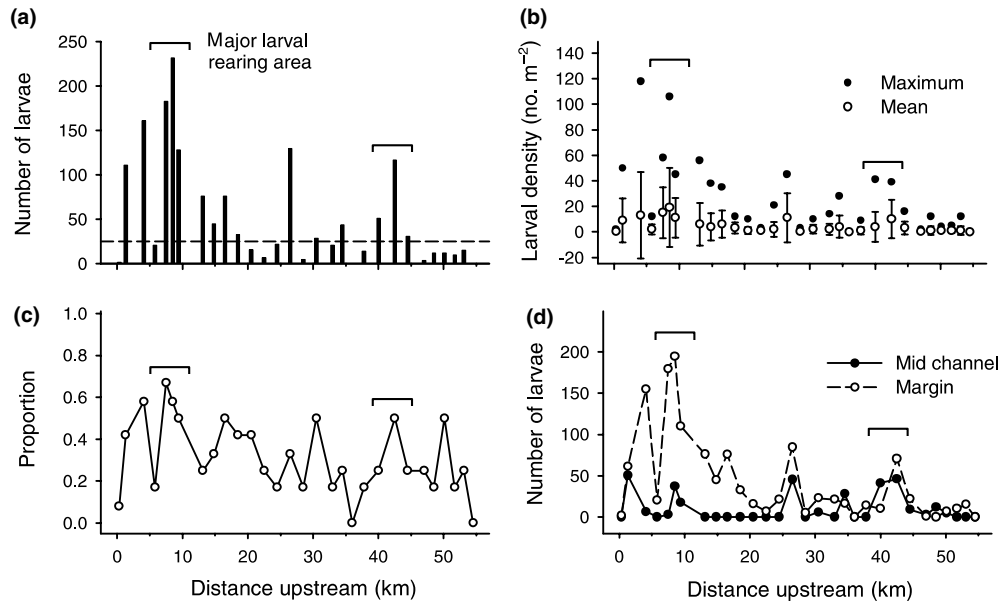


Fig. 3 Longitudinal variation in larval abundance within and among sites. Brackets indicate the locations of major larval rearing areas. Various measures of larval lamprey abundance are plotted versus river km, the distance upstream from the lower boundary of the survey section: (a) larval abundance (dashed horizontal line indicates the median), (b) variation in mean (\pm SD) and maximum larval density within sites, (c) the proportion of samples containing larvae within individual sites, and (d) the distribution of larvae in mid-channel versus stream margin sampling locations.

Results

Spatial distribution of larval lamprey

Larval lampreys occurred throughout the 55-km survey section of the Middle Fork John Day River and 1609 individuals were estimated in the sampled area (360 m²). Identification of larvae at the time of capture indicated that the Pacific lamprey (*L. tridentata*) was the only species of lamprey present in the study area. Variation in larval occurrence was low among sites and high within sites, with larvae present in 28 of the 30 sites but in only 111 of the 356 samples. The maximum larval density (no. m⁻²) in a 1-m² sample ($n = 118$) was approximately 50% of the maximum number of larvae found in an entire 12-m² site ($n = 232$).

Larval distribution was patchy throughout the survey section and peaked at rkm 9, 26 and 43 (Fig. 3a). Although larvae were present throughout the survey section, they were most abundant in the lower 27 km of the stream. Peaks in larval abundance among sites corresponded with longitudinal patterns of maximum larval density within sites (Fig. 3a & b). The proportion of samples containing larvae within individual sites was low throughout the survey

section, even in sites in which larvae were abundant (Fig. 3c). Larval density was correlated with the proportion of samples containing larvae and explained 55% of the variation in larval occurrence among samples (positive relationship, $P < 0.01$).

Larval abundance was heterogeneous laterally across the stream channel. Over 80% of the larvae

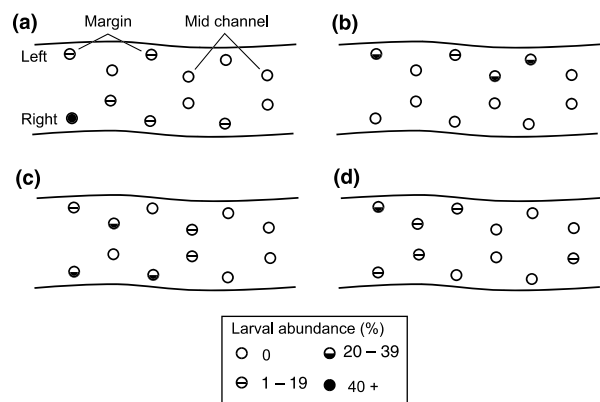


Fig. 4 Spatial distribution and percent abundance of larval lamprey in mid-channel and stream margin sampling locations within sites. Sites represent high- and low-density reaches in the longitudinal distribution of larval lamprey: (a) rkm 8.5, $n = 232$; (b) rkm 26.5, $n = 130$; (c) rkm 42.5, $n = 117$; and (d) rkm 50.1, $n = 12$.

occurred along stream margins, and the difference in larval abundance between stream-margins and mid-channel habitats was most pronounced at rkm 0–10 (Fig. 3d). Peaks in mid-channel larval abundance at rkm 2, 8, 27 and 40–43 corresponded with peaks in larval abundance in stream margins. Within high-density sites, larval abundance was greatest in channel margins and was generally skewed towards the left or right stream margin (Fig. 4a–c). In both high- and low-density sites, more than 40% of the larvae in each site were concentrated in one or two neighbouring samples (see Fig. 4 for representative sites).

Habitat heterogeneity at multiple scales

Spatially continuous longitudinal patterns in channel gradient and water depth revealed the complex

geomorphic structure of the Middle Fork John Day River survey section (Fig. 2). Peaks in LOWESS-smoothed water depth at rkm 10, 30 and 42 indicated the presence of reaches with a high frequency of deepwater habitats (e.g. pools and glides). Reaches with a high channel gradient (2–3%) and low water depth (0.3–0.4 m) (i.e. riffle reaches) occurred at rkm 2, 15 and 36. A canyon reach characterised by a gradient of >3% and a water depth of 0.4 m was located at rkm 38. The longest contiguous low-gradient reaches of the survey section coincided with the highest peaks in water depth at rkm 5–12 and 40–43 (Fig. 2). Wetted width and conductivity were the only two habitat variables that exhibited linear longitudinal trends (Fig. 5a & b). Average distance between peaks in longitudinal habitat profiles provided a rough indicator of the varying scales at which habitat heterogeneity was expressed.

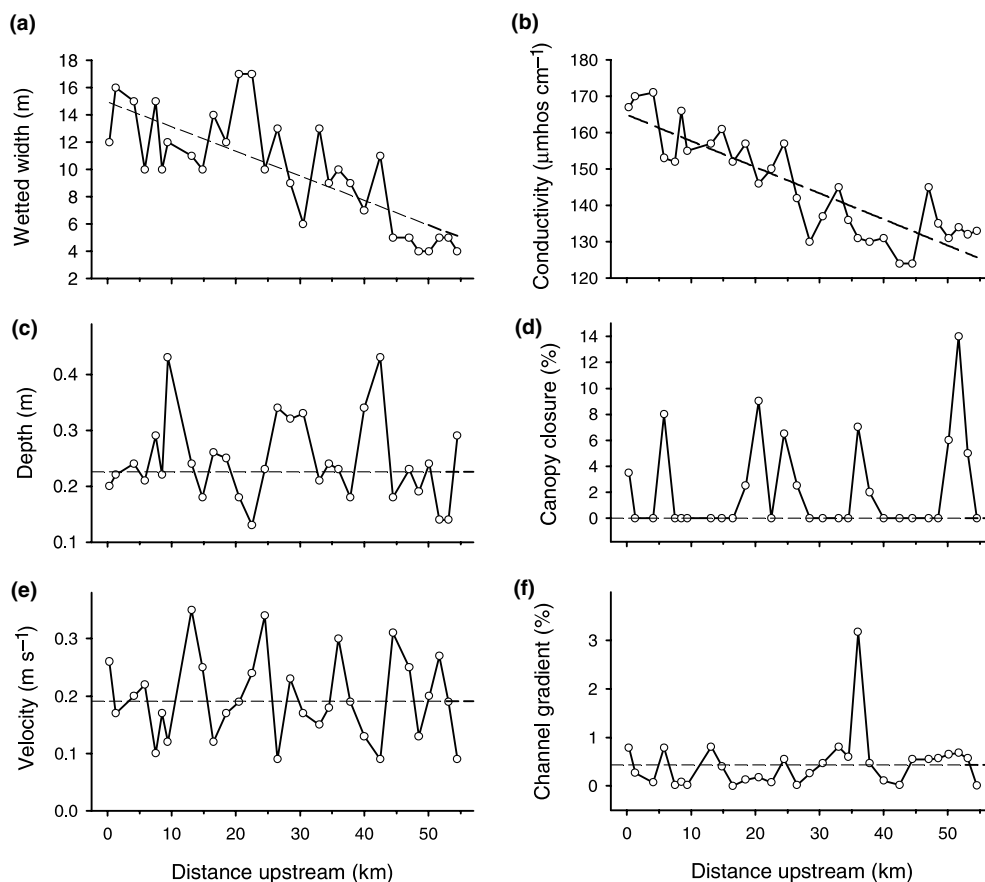


Fig. 5 Longitudinal variation in channel morphology and stream habitat among sites. Longitudinal habitat patterns are plotted versus river km, the distance upstream from the lower boundary of the survey section: (a) wetted width, (b) conductivity, (c) water depth, (d) canopy closure, (e) water velocity, and (f) channel gradient. Dashed lines indicate either the median (horizontal line), or the trend (diagonal line) from linear regression.

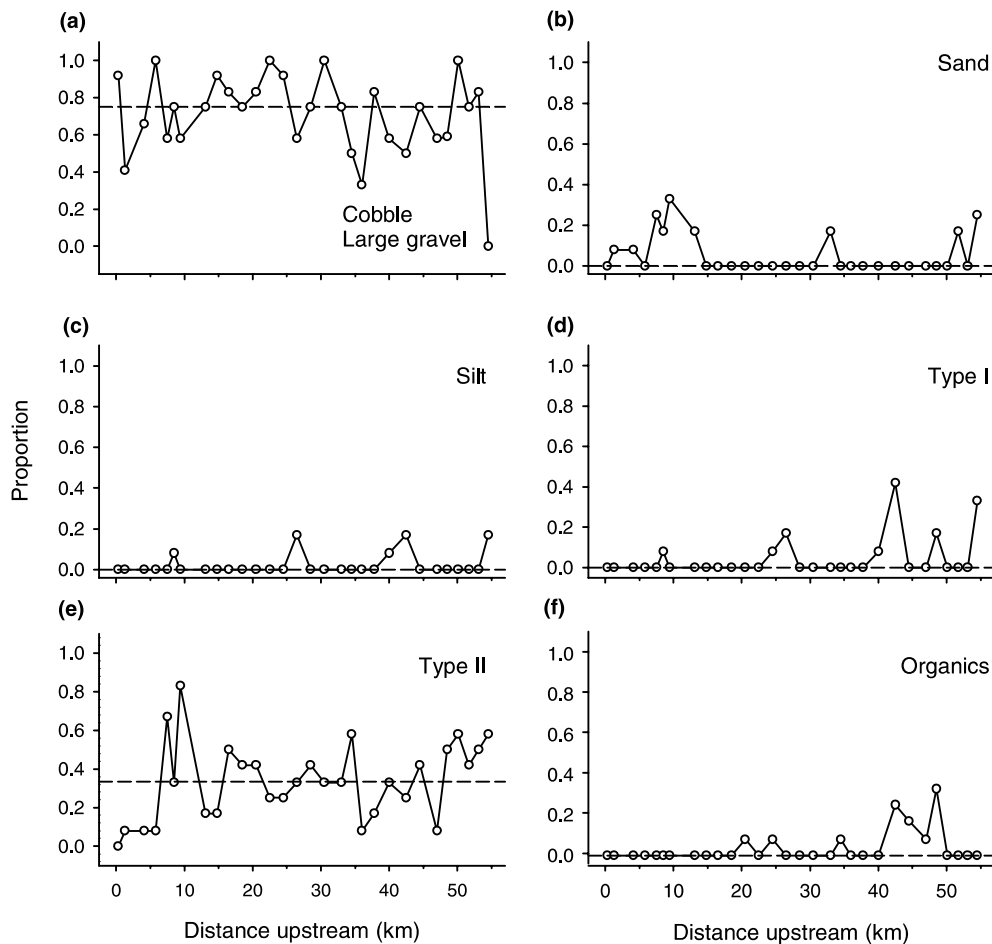


Fig. 6 Longitudinal variation in substratum composition among sites. Substratum composition is expressed as the proportion of samples within each substratum category by site. Longitudinal patterns are plotted versus river km, the distance upstream from the lower boundary of the survey section: (a) cobble and large gravel, (b) sand, (c) silt, (d) type I burrowing habitat, (e) type II burrowing habitat, and (f) organic debris. Dashed lines indicate either the median (horizontal line), or the trend (diagonal line) from linear regression.

Longitudinal profiles of canopy closure and channel gradient reflected geomorphic processes occurring over large spatial scales (10–15 km) (Fig. 5d & f), whereas wetted width, conductivity, water depth and velocity varied over smaller scales (<10 km) (Fig. 5a–c & e). Patterns of substratum composition also reflected the influences of fluvial and depositional processes occurring over larger (e.g. sand, silt, type I burrowing habitat) and small scales (e.g. cobble/large gravel, type II burrowing habitat and organics) (Fig. 6).

Spatial heterogeneity in larval habitat was particularly apparent at small spatial scales within and among channel units (<50 m). Cobble and large gravel substratum types dominated the survey sites and typically composed >60% of the sampled area per site

(Fig. 6a). Sand, silt and organic debris made up smaller proportions (<0.40) of the sampled area (Fig. 6b, c & f). The proportion of suitable burrowing habitat (type II) within a given site was <0.60, and only seven sites contained substratum optimal for burrowing (type I) (Fig. 6d & e). Mean within-site variability (coefficient of variation) in wetted width was low (0.14) compared with water depth (0.51) and water velocity (0.78). Differences in wetted width, water depth and water velocity within sites ranged from 0.4–7.8, 0.2–0.8, and 0.2–1.0 m s⁻¹, respectively.

Statistical models of larval lamprey habitat associations

Water depth, canopy closure, gradient and river km were the highest ranked variables in the first set of

Table 2 Logistic regression models of single variables predicting the relative abundance of larval lampreys from habitat and locational data collected at site- and sample-level spatial scales. Akaike's Information Criterion (AIC), AIC difference between a given model and the highest ranked model (Δ AIC), and Akaike weights (w_i) indicate the relative plausibility of models given the data. Models with the lowest AIC and the highest w_i are those that best fit the data

Model	AIC	Δ AIC	w_i
Site-level variables			
Water depth	36.99	0.00	0.42
Canopy closure	38.57	1.58	0.19
Gradient	39.24	2.25	0.13
River km	40.96	3.97	0.06
Sample-level variables			
Velocity	366.82	0.00	0.99
Habitat type	376.18	9.36	0.01
Position	391.46	24.64	<0.01
Channel unit type	429.46	62.64	<0.01
River km	438.14	71.32	<0.01

Notes: Akaike's Information Criterion was corrected for small-sample bias in the site-level models. Only those models that ranked higher than the locational variables (i.e. river km and position) are presented.

models predicting the relative abundance of larval lamprey among sites (Table 2). At the sample level, the highest ranked models predicting larval occurrence among samples included velocity, burrowing habitat type, position in the channel, channel unit type and river km (Table 2). The weight of evidence for water depth as the single 'best' predictor of the relative abundance of larvae among sites was substantially less (2 : 1) than that of velocity in predicting larval occurrence among samples (10 : 1). In the combination set of the 'best' single-variable models predicting larval abundance among sites, the model containing water depth, canopy closure and river km was four times as likely (4 : 1) as the next best model (Table 3). For the site-level combination models, AIC differences between the highest ranked model and subsequent models indicated that there was substantial support for the top three models but considerably less for the remaining six. Although the locational variable, river km, was less likely than gradient as a single variable predicting larval abundance (Table 2), it added considerably to the predictive capability of the models when it was combined with water depth, and to a lesser degree canopy closure (Table 3). In the models predicting the occurrence of larval lampreys among samples, there was strong evidence (10 : 1) that

Table 3 Logistic regression models predicting the relative abundance of larval lampreys from habitat and locational data collected at two spatial scales. Site- and sample-level models are a combination of the 'best' single-variable models

Model	AIC	Δ AIC	w_i
Site-level variables			
Water depth, canopy closure, river km	30.20	0.00	0.51
Water depth, river km	32.95	2.75	0.13
Water depth, canopy closure, gradient, river km*	33.10	2.90	0.12
Water depth, canopy closure	34.63	4.43	0.06
Water depth, gradient, river km	34.73	4.53	0.05
Water depth, canopy closure, gradient	35.59	5.39	0.03
Canopy closure, river km	35.65	5.45	0.03
Water depth, gradient	36.48	6.28	0.02
Canopy closure, gradient, river km	36.57	6.37	0.02
Sample-level variables			
Velocity, habitat type, channel unit type, position, river km*	239.04	0.00	0.90
Velocity, habitat type, position, river km	244.74	5.70	0.05
Habitat type, channel unit type, position, river km	245.19	6.15	0.04

Notes: Modified versions of AIC were used to correct for small sample size (AIC_c) and overdispersion (QAIC) in site- and sample-level models, respectively (Burnham & Anderson, 2002). Only models with Δ AIC < 7 are presented as supportive of the data. The global model containing all explanatory variables is indicated with an asterisk.

the global model containing velocity, burrowing habitat type, channel unit type, position in the channel and river km was more plausible than the other two models given the data (Table 3). Akaike weights and AIC differences supported the hypothesis that strong predictors of larval abundance at one scale are weak predictors at the other (e.g. water depth, velocity, burrowing habitat type), with the exception of river km, which was an important predictor at both spatial scales.

The 'best approximating' models from the combination model sets indicated that peaks in the relative abundance of larval Pacific lamprey in the Middle Fork John Day River were positively associated with water depth and negatively associated with canopy closure and distance upstream (river km) at the site level (Table 4). At the sample level, the occurrence of larval lamprey was positively associated with channel unit type (pools), burrowing habitat types I and II, and positions near the channel margin. The two variables with which larval lampreys were negatively associated in the sample-level model were water velocity and distance upstream (Table 4). Overall

Table 4 Logistic regression parameter estimates, SE, and confidence intervals for the 'best approximating' models predicting the relative abundance of larval lamprey from habitat and locational data collected at site- and sample-level spatial scales

Parameter	Estimate	SE	95% confidence interval	
			Lower bound	Upper bound
Site-level model				
Intercept	2.00	1.30	–	–
Water depth	3.15	1.33	0.54	5.76
Canopy closure	–2.67	1.31	–0.11	4.19
River km	–0.09	0.04	–0.01	4.66
Sample-level model				
Intercept	–2.91	0.50	–	–
Velocity				
0–0.11 m s ^{–1}	1.56	0.45	0.67	2.44
0.12–0.23 m s ^{–1}	0.81	0.46	–0.09	1.71
Channel unit type				
Pool	1.10	0.36	0.40	1.80
Habitat type				
Type I	1.60	0.69	0.24	2.96
Type II	1.61	0.33	0.95	2.26
Position				
Margin	1.18	0.33	0.53	1.83
River km	–0.04	0.01	–0.06	–0.02

Notes: Regression statistics for the site-level model ($n = 30$) were deviance = 42 (intercept only) and 21 (intercept and covariates); and for the sample-level model ($n = 356$) deviance = 442 (intercept only) and 294 (intercept and covariates).

accuracy for the cross-validations within models were similar, with 83% of the observations correctly classified in the site-level model and 81% in the sample-level model. However, site- and sample-level models performed differently in predicting the direction of binary response (i.e. one or zero). For example, the site-level model performed equally well in predicting both peaks (87%) and troughs (80%) in larval abundance, whereas the sample-level model was considerably better at predicting the absence of larval lamprey (88%) than it was at predicting their presence (63%).

Discussion

Patterns in larval Pacific lamprey abundance were closely linked to variation in habitat structure. Physical gradients in channel morphology established the geomorphic template for larval distribution among reaches and set the context for larval habitat associations at finer scales. Environmental heterogeneity in streams can be described as patches within patches at

sequentially smaller spatial scales (Townsend, 1989; Kotliar & Wiens, 1990; Dunham, Rieman & Peterson, 2002). Fish may respond to habitat heterogeneity differently at each respective scale, but patterns of distribution and abundance are products of the collective spatial structure of the riverine environment (Montgomery *et al.*, 1999; Baxter & Hauer, 2000).

Quantitative analysis of habitat relationships across scales requires sampling approaches that are specifically designed to identify discontinuities in distribution and characterise patch structure (Petty & Grossman, 1996; Angermeier *et al.*, 2002). We were able to separate the relative influences of habitat heterogeneity on patterns in larval abundance at two spatial scales by using a nested sampling design and a high sampling density (Armitage & Cannan, 1998). Increasing the number of samples may require a reduction in sampling efficiency because of time constraints (e.g. using backpack electrofishing instead of a more labour-intensive method such as dredging). However, in studies of relative abundance, a decrease in sampling efficiency is not problematic as long as the potential bias is consistent among habitat types, otherwise it is necessary to account for habitat-induced sampling bias in models of habitat association (Peterson & Rabeni, 2001). We did not evaluate the capture efficiency of larval lampreys with respect to the different habitat variables, but we suspect that this had a limited effect on our results because the biases reported for a similar species of lamprey with similar sampling gear were in the opposite direction of the habitat relationships we detected (Steeves *et al.*, 2003). For example, the capture efficiency of larval sea lampreys (*P. marinus*) with backpack electrofishing gear in tributaries of the Great Lakes (U.S.A.) was greater in shallow water, whereas we found larval Pacific lampreys to be positively associated with water depth at the site level and not at all associated with larval occurrence at the sample level. More specific information is needed on the effectiveness of backpack electrofishing gear for sampling larval Pacific lampreys and other lamprey species that are potentially at risk.

Habitat heterogeneity both within and among sites influenced patterns of larval Pacific lamprey abundance and habitat use. The spatial distribution of larval lampreys at the site level indicated that nearly the entire 55-km survey section was suitable for larval rearing. However, analysis of larval occurrence at the

sample level revealed that suitable habitats for burrowing were much more limited. Thus, the perception that suitable rearing habitat was either common or uncommon was largely dependent on the scale of observation. This phenomenon of differences in spatial variance structure at small versus large scales suggests a hierarchical structure in larval abundance patterns and a high degree of heterogeneity in habitat suitability at the channel-unit level. Highly structured larval distribution patterns at small scales were most probably generated both passively with respect to physical gradients and actively through larval movement. Larvae may emerge from their burrows and disperse actively to more suitable living and feeding conditions (Potter, Hill & Gentleman, 1970; Potter, 1980). Feeding primarily on suspended material (e.g. diatoms and desmids), the larvae of some species of lamprey have specific flow requirements (Moore & Mallatt, 1980). Water velocity for larval Pacific lampreys presumably must be fast enough to provide a steady influx of food and yet slow enough to promote the deposition of soft sediments needed for burrowing ($0.05\text{--}0.15\text{ m s}^{-1}$). Thus, in streams with sufficient flow for filter feeding, suitable burrowing habitats for larval Pacific lamprey may be more limited than is immediately apparent from large-scale habitat patterns.

Spatial scale and larval habitat relationships

The problem of scale and its influence on the nature and relative strengths of environmental variables in determining animal distribution is of great interest in ecology (Wiens, 1989; Levin, 1992). The evaluation of ecological patterns and processes at multiple scales may reveal causal factors that are important at one scale, but are less important or have an opposite effect at other scales. In aquatic ecology, scaling effects have been demonstrated most notably in marine systems (Menge & Olson, 1990; Schneider, 2001), but there is considerable interest in unifying marine and freshwater ecology through their common interest in scale (Giller, Hildrew & Raffaelli, 1994). In designing studies that address ecological patterns and processes at multiple scales, stream ecologists have made significant advances in understanding physical and biological processes in lotic systems (Poizat & Pont, 1996; Lancaster & Belyea, 1997; Dent, Grimm & Fisher, 2001). Further research

on spatial scaling is needed in the study of stream fishes where there seems to be a mismatch between the scale at which research is conducted and the scale that is relevant for biological conservation and management (Fausch *et al.*, 2002).

Investigations of lamprey ecology in streams and rivers have addressed the interplay of macro- and microenvironmental factors and their influence on larval distribution (Baxter, 1957; Hardisty & Potter, 1971). Broad-scale distribution patterns of larval lampreys have been attributed to variation in channel gradient within and among streams (Baxter, 1957; Young, Kelso & Weise, 1990). We also observed that patterns in larval lamprey abundance follow longitudinal patterns in channel gradient. However, the relative importance of these relationships is very likely to depend on the scale at which gradient is measured. In our study of larval distribution in a fourth- to fifth-order stream, channel gradient corresponded with large-scale larval abundance patterns but was not an important predictor of larval abundance after accounting for water depth and canopy closure. Based on our observations of larval distribution, we suspect that the relative influence of channel gradient as a predictor of larval abundance increases at larger spatial scales because of changes in bedform morphology at the stream segment or network scale (Wooldridge & Hickin, 2002).

Larval associations with low water velocity, fine-particulate burrowing substratum and pools, described for other species of lamprey (Malmqvist, 1980; Potter *et al.*, 1986; Beamish & Jebbink, 1994; Beamish & Lowartz, 1996), confirm our observations of habitat selection by larval Pacific lampreys. However, our findings indicate that these habitat variables were only significant at small spatial scales. Moreover, variables we identified as positively associated with larval abundance at large scales (e.g. water depth and an open riparian canopy) have been considered as negative correlates of larval abundance in the literature (Potter *et al.*, 1986). Water depth was not a significant predictor of larval occurrence among samples (small scale) but was highly significant among sites (large scale). At small spatial scales, larvae selected pools over riffles because the morphology of pool margins was more conducive to sediment deposition than riffle margins. The interactions between depth, water velocity and channel morphology provide a potential explanation for the differential

responses of larvae to depth among and within streams and in different seasons (Potter *et al.*, 1986; Kelly & King, 2001). For example, sediments suitable for burrowing are deposited along stream margins at high flow, leaving deeper thalweg habitats scoured of sediments during summer low flow. Water depth at large spatial scales, however, was positively associated with larval abundance because reaches containing large numbers of deep pools were structurally complex and therefore likely to protect larval lamprey from flow-induced stresses (Howard & Cuffey, 2003).

The relationship between the relative abundance of larval Pacific lamprey and riparian vegetation may be related more to spatial context and geomorphic factors than to larval behaviour, as has been suggested in the literature. Potter *et al.* (1986) found that shade from riparian vegetation was positively related to larval density at small scales and attributed the association to photophobic behaviour by larvae. We could not directly test the association between larval occurrence and riparian canopy at small scales because we did not measure canopy closure or shade at the appropriate scale (i.e. canopy closure was measured at the transect level). However, as sample positions near channel margins tend to be more shaded than samples in the mid channel, there may be a strong interaction between shade and sample position in predicting larval density at small spatial scales. At the site level, we observed exceptionally high larval density (>100 larvae m²) in the most exposed sites and found that an open canopy was an important predictor of larval abundance at large scales. No other quantitative studies of larval lamprey have analysed large-scale associations with riparian cover, but qualitative observations of larval Pacific lamprey in Oregon coastal streams confirm a negative association with riparian canopy closure and may indicate differences in habitat selection related to primary productivity and the availability of larval food sources (Kan, 1975). Other potential factors, such as tributary junctions and valley segment type (canyon versus alluvial valley), may influence large-scale larval distribution patterns, as has been shown for benthic invertebrates (Rice *et al.*, 2001). However, the small size of the tributaries relative to the mainstem and the large valley segments in the study area suggest that the 55-km survey section would need to be extended downstream to detect these large-scale geomorphic effects.

Larval abundance is directly linked to environmental variables, but the spatial context of biological factors, such as the spawning distribution of adults, also plays an important role in larval distribution. Larvae were more abundant in downstream versus upstream portions of the study stream, although upstream habitats had a greater proportion of habitat suitable for burrowing (Fig. 6d & f). The disproportionate distribution of larvae in downstream reaches may be attributable to adult spawning patterns. Thus, it is important to consider the effects of spatial context in distribution studies because standard statistical analyses (e.g. multiple linear regression, principle components analysis and analysis of variance) are sensitive to non-normally distributed data (Ramsey & Schafer, 1997). Statistical analyses can be designed to account for spatial context by standardising the response variable with respect to the median, thereby creating a binary response variable that places upstream and downstream peaks in larval abundance on equal footing (Torgersen *et al.*, 1999). Further incorporation of spatial structure in statistical analysis can be achieved by including locational variables, such as river km and sample position in the stream channel, in the regression model (Knapp & Preisler, 1999). Direct inclusion of locational variables may explain additional variation in the regression model because habitat characteristics alone may be ineffective in predicting the distribution of stream fishes (Fausch *et al.*, 2002).

Lamprey conservation and management

The measurement of spatial patterns in larval abundance and the detection of larval habitat relationships are important components of lamprey conservation programmes. Larval habitat assessment methods in small streams can benefit from spatially explicit as opposed to random sampling approaches. Although a stratified random sampling design may be effective for obtaining larval population estimates in homogeneous deepwater habitats (Bergstedt & Genovese, 1994; Pajos & Weise, 1994), extrapolation of larval abundance from a limited number of samples should be based on spatially continuous habitat surveys, particularly in heterogeneous stream environments (Hankin & Reeves, 1988). A Hankin-Reeves survey approach has yet to be applied to larval lamprey, but the information provided in this study on spatial

variation in larval abundance will be useful in designing future studies with the objective of obtaining larval population estimates in small streams.

The size, number and arrangement of sample plots have effects on the detection of patterns in larval distribution and habitat relationships. Collecting multiple samples within sites increases precision in distinguishing between suitable and unsuitable habitats and achieves a higher level of reproducibility than taking fewer large samples (Southwood & Henderson, 2000). This concept has been tested quantitatively in habitat suitability modelling with computer simulations, demonstrating that improvements in sampling design can be made by: (i) increasing sample size (i.e. number of samples), (ii) using systematic as opposed to random sampling, and (iii) including environmental information in the design (Hirzel & Guisan, 2002). Given the high degree of heterogeneity in larval abundance patterns at small scales, we concluded that twelve 1-m² samples distributed over 50 m of stream were more effective at capturing variability in larval abundance than a single 12-m² sample. Other empirical studies have concluded that the sampling area for a given electrofishing quadrat be small (approximately 1 m²) and that large numbers of samples be collected because of the high degree of environmental heterogeneity likely to occur in large samples (Potter *et al.*, 1986; Peterson & Rabeni, 2001). In our review of the literature on larval habitat, we found that such an approach for sampling larval lampreys is uncommon and could be applied more frequently in studies of this type, particularly when there has been no *a priori* assessment of habitat heterogeneity in the environments to be surveyed. In choosing the appropriate distribution and number of sites, a systematic design with a large number of samples is superior for detecting spatial pattern but is also more labour-intensive. However, spatially continuous stream habitat data and 10-m DEM are often available through natural resource agencies and can be used to stratify site locations more economically based on longitudinal habitat patterns. Once an initial assessment of larval distribution patterns has been completed, follow-up monitoring of temporal trends in larval abundance can be conducted in a selection of representative sites to aid in conservation and management.

Simplification of stream habitats through channelisation has been identified as a significant cause for

the decline of lampreys in Europe (Bohl, 1995; Kirchhofer, 1995) because larval lampreys in headwaters and low-order streams depend on complex channel structures (e.g. meanders, bars, alcoves, backwaters and large wood) to create environments suitable for burrowing and filter feeding. Suitable larval habitats may occur throughout an entire stream section but be relatively limited at smaller spatial scales. Lamprey conservation and restoration efforts in rivers and streams need to focus on the importance of habitat heterogeneity at multiple scales to promote complexity in channel morphology and sediment composition. Increased understanding of habitat heterogeneity and larval abundance also has implications for management. For example, managing for habitat heterogeneity is likely to improve habitat conditions for declining lamprey populations in fast-flowing streams. Furthermore, the relative ease of sampling larval lampreys compared with other benthic organisms provides an opportunity to study the ecological effects of habitat heterogeneity, which is an important component in the biology of freshwater organisms and warrants further descriptive and experimental study.

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