

OCCUPANCY PATTERNS OF MAMMALS AND LENTIC AMPHIBIANS IN THE ELWHA RIVER RIPARIAN ZONE BEFORE DAM REMOVAL

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ABSTRACT

The downstream transport of sediments and organics and upstream migration of anadromous fishes are key ecological processes in unregulated riverine ecosystems of the North Pacific coast, but their influence on wildlife habitats and populations is poorly documented. Removal of two large hydroelectric dams in Washington's Elwha Valley provides an unprecedented opportunity to study long-term responses of wildlife populations to dam removal and restoration of these key ecological processes. We compared pre-dam removal patterns in the relative abundance and occupancy of mesocarnivores, small mammals and lentic amphibians of the Elwha River riparian zone above, between and below the dams. Occupancy of riparian habitats by three mesocarnivore species diminished upriver but did not appear to be closely linked with the absence of salmon in the upper river. Although the importance of salmon in the lower river cannot be discounted, other gradients in food resources also likely contributed to observed distribution patterns of mesocarnivores. Abundance and occupancy patterns within congeneric pairs of new world mice (*Peromyscus* spp.) and shrews (*Sorex* spp.) indicated that closely related species were negatively associated with each other and responded to habitat gradients in the riparian zone. The availability of lentic habitats of amphibians was highly variable, and occupancy was low as a result of rapidly changing flows during the larval development period. We speculate that long-term changes in habitat conditions and salmon availability following dam removal will elicit long-term changes in distribution of mesocarnivores, small mammals and amphibians. Long-term monitoring will enhance understanding of the role of fish and restored ecosystem processes on wildlife communities along salmon-bearing rivers in the region. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: relative abundance; occupancy; species richness; salmon restoration; dam removal; mesocarnivore; small mammal; amphibian

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INTRODUCTION

High-head hydroelectric dams disrupt key ecological processes of riverine ecosystems, including both the downstream flow of sediments and organics and the upriver movement of anadromous fishes and associated nutrients (Hart *et al.*, 2002). The disruption of sediment transport and deposition alters fluvial dynamics and channel morphologies downstream of dams (Collier *et al.*, 1996), with attendant effects on riparian vegetation dynamics and associated habitat conditions for both salmon and terrestrial wildlife (Shaffroth *et al.*, 2002). The effects of sediment deprivation often include armouring of the river channels with coarse substrate materials and reduced lateral movement and increased incision of river channels (Collier *et al.*, 1996). Consequently, dams may reduce the rate of dynamic change in floodplains

downriver and increase the prevalence of older land surfaces and associated vegetation communities (Kloehn *et al.*, 2008).

In the absence of fish passage facilities, dams are also impenetrable barriers to the upstream movement of anadromous fishes that import marine nutrients to freshwater ecosystems. Nutrients delivered in the form of gametes, excretion and carcasses of spawning salmon contribute to the productivity and food web diversity in oligotrophic (nutrient poor) inland waters of the Pacific Northwest (Cederholm *et al.*, 1999; Gende *et al.*, 2002; Schindler *et al.*, 2003). Increased production of aquatic systems attributed to salmon has been reported in phytoplankton and periphyton blooms (Richey *et al.*, 1975), invertebrate diversity, density and growth rates (Piorkowski, 1995; Wipfli *et al.*, 1998; Chaloner and Wipfli, 2002) and fish growth (Bilby *et al.*, 1996). Studies of marine isotope concentrations in tissues of such diverse taxa as bears, mustelids, sciurids and rodents indicate the extent that salmon-borne nutrients may permeate food webs of terrestrial wildlife along salmon-bearing rivers and streams, either by direct consumption of salmon by wildlife or indirectly by wildlife consuming vegetation or other organisms that

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have been enriched by salmon (Hilderbrand *et al.*, 1996; Ben-David *et al.*, 1997, 1998, 2004). Although the influences of dams on the distribution and abundance of wildlife populations remain poorly understood, seasonal and spatial variations in salmon abundance may influence the productivity, life-history traits or diversity of populations and communities of mammals and birds (Ben-David, 1997; Hilderbrand *et al.*, 1999; Gende and Willson, 2001).

In 2011, the US Department of the Interior began dismantling two high-head hydroelectric dams in the Elwha Valley on Washington's Olympic Peninsula, thereby initiating the largest dam decommissioning and one of the most significant river restoration programmes ever (Duda *et al.*, 2008). The Elwha Dam, a 32-m tall earthen-fill dam completed in 1913, and the Glines Canyon Dam, a 64-m tall concrete arc dam completed in 1927, have disrupted the longitudinal movements of sediments and nutrients in the Elwha River system for over a century. Neither dam provided measures for fish passage, so historical runs of up to 500 000 salmon have been reduced to an average return of about 5500 salmon annually restricted to <8 km below the lower dam, a small fraction of the habitat used by 10 stocks of native anadromous salmon and trout historically (Pess *et al.*, 2008). Dam removal will reconnect anadromous fishes to over 180 km of mainstem, tributary and side-channel habitats above the downstream dam (Pess *et al.*, 2008), most of which is protected as wilderness within Olympic National Park. Moreover, dam removal will also restore natural fluvial processes downstream of the dams, including the transport of coarse woods and sediments that will transform the riverine landscape and enhance habitat qualities for salmon and other wildlife (Kloehn *et al.*, 2008).

Dam removal in the Elwha Valley provides an unprecedented opportunity to investigate wildlife community responses to restoration of key ecosystem processes in rivers of the North Pacific coast. Because so little is known of wildlife responses to dam removal and salmon restoration, our objectives were to describe patterns of relative abundance, occupancy and species richness for key wildlife groups that we expect will respond to different changes in ecosystem processes following dam removal. From 2006 to 2008, we conducted systematic surveys of selected species of mesocarnivores, small mammals and lentic (pond-breeding) amphibians along a longitudinal gradient extending from the river's mouth upriver well above both dams. Earlier studies indicated that two species of generalist carnivores, the raccoon (*Procyon lotor*) and spotted skunk (*Spilogale gracilis*), were commonly observed consuming carcasses of spawned salmon in rivers of the Olympic Peninsula (Cederholm *et al.*, 1989). We hypothesized that occupancy patterns of generalist mesocarnivores may reflect the absence of salmon above the lower dam. Similarly, previous studies revealed that two common species of mice

(*Peromyscus* spp.) were associated with gradients of forest age on the Olympic Peninsula (Songer *et al.*, 1997). Hence, we speculated that mice will be useful indicators of vegetation change associated with changes in sediment, channel and vegetation dynamics following dam removal. We hypothesized that the Keen's mouse (*Peromyscus keeni*) and deer mouse (*Peromyscus maniculatus*) would segregate longitudinally in response to vegetative gradients of the Elwha River riparian zone. Lastly, because lentic ponds are critically linked to dynamic fluvial processes on riverine floodplains, we also examined patterns in the presence of ponds along the riverine gradient in the Elwha Valley and their occupancy by pond-breeding amphibian species.

STUDY AREA

The Elwha River originates in the mountainous interior of Washington's Olympic Peninsula (Figure 1). The watershed comprises 833 km², 83% of which is preserved within Olympic National Park, an International Biosphere Reserve and World Heritage site. Lands outside the park are a mosaic of private, tribal, state and federal land ownerships. The lower Elwha Reservation comprises 405 ha that largely

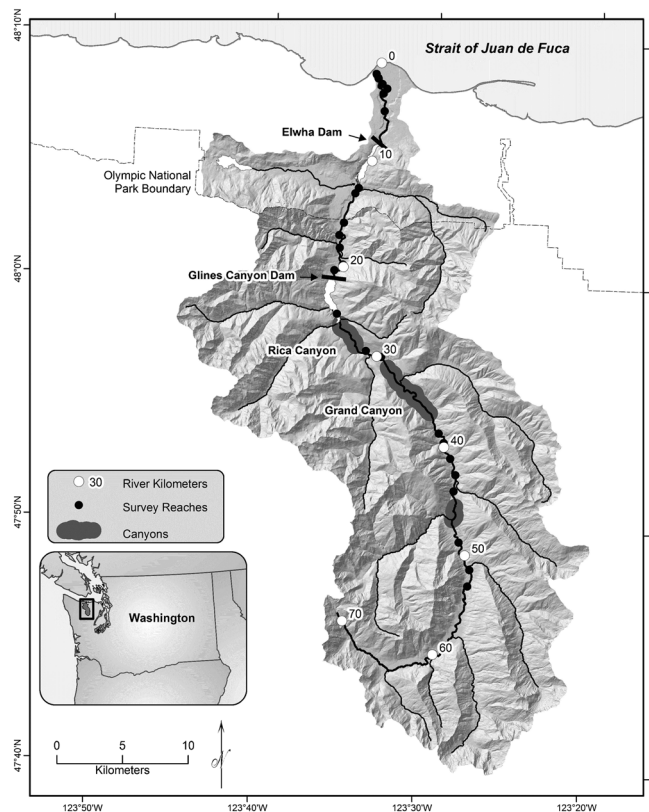


Figure 1. The Elwha River, showing locations of 500-m sampling reaches, dams and major river canyons

encompasses the mouth of the Elwha River where it meets salt water.

The Elwha Dam and Glines Canyon Dam partition the river continuum into three sections: (i) the upper river, where fluvial processes are not affected by the dams, but salmon are absent; (ii) the middle river, where fluvial processes are affected by the upriver dam, and salmon are absent; and (iii) the lower river, where fluvial processes are affected by the dams, but native anadromous fish are present. Floodplains of the Elwha River are imbedded in a matrix of principally old-growth Douglas fir-western hemlock (*Pseudotsuga menziesii*-*Tsuga heterophylla*) forests in the upper river in Olympic National Park, whereas surrounding upland forests in the middle river are predominately second-growth Douglas fir and bigleaf maple (*Acer macrophyllum*) stands regenerating from selective harvests of large trees prior to park establishment. The lower river is a mosaic of gallery deciduous forests and upland terraces of second-growth Douglas fir, and semi-rural agricultural and residential development.

The Elwha River is an anabranching gravel-bed river over most of its length (Draut *et al.*, 2011). Topography is a series of alternating canyons and alluvial floodplains that form on glacial outwash gravels (Figure 1). Mean gradient of the river ranges from 1.3% in the upper river to 0.4% on floodplains of the lower river (Brenkman *et al.*, 2012). Floodplains are dominated by willow (*Salix* spp.), red alder (*Alnus rubra*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) communities on younger alluvial terraces (predominately <75 years old), and Douglas fir, Grand fir (*Abies grandis*) and bigleaf maple on older terraces (Kloehn *et al.*, 2008). Upstream of the dams, natural fluvial processes result in greater sinuosity of the river channels and a greater diversity of river bed particle sizes than below the dams (Kloehn *et al.*, 2008; Draut *et al.*, 2011). River beds are armoured by large particle sizes immediately below the dams because of the disruption of sediment delivery (Pohl, 2004; Draut *et al.*, 2011). The middle river contains the most stable floodplains because of channel armouring. This causes the middle river to have the greatest proportion of mature floodplain forests >75 years old and the oldest mean age of alluvial surfaces (Kloehn *et al.*, 2008). More detailed descriptions of the study area have been published previously (Duda *et al.*, 2008; Kloehn *et al.*, 2008; Draut *et al.*, 2011).

METHODS

Field sampling

We sampled mesocarnivore, small mammal and lentic amphibian assemblages systematically from the river's mouth upriver to include upper, middle and lower river sections. The sampling frame consisted of sequential 500-m

reaches of the river and associated floodplains, excluding the primary canyons and reservoirs (Figure 1). We included every third river reach in the sample, beginning with the second reach upriver of the mouth, which we selected at random. Infrequently, we substituted an adjacent reach when we could not obtain access permission on private lands or when a selected reach was heavily used as a backcountry camping area. Additionally, we added three reaches to the lower river to increase sample size. Our sampling extended upriver to river kilometre (RK) 54 for mesocarnivores and lentic amphibians and RK 44 for small mammals. In each reach, we sampled on one side of the river only as a safety measure. All procedures involving animals were reviewed and approved by the Animal Care and Use Committee at Oregon State University (ACUP permit number 3405).

Mesocarnivores. We detected presence of mesocarnivores using a linear array of baited track-plate stations and motion-triggered cameras in each sampling reach. During 2006, we used three track-plate boxes distributed 100 m apart along the vegetated bank of the mainstem of the Elwha River in the centre of each reach. During 2007–2008, we used four track-plate boxes and one motion-triggered camera distributed approximately 50 m apart. Individual stations were positioned 1–50 m from the river bank in forested habitat. The camera station, always the central station of the array, consisted of a 35-mm film camera coupled with a passive-infrared event recorder (TM35-1 camera and TM550 event recorder, Trailmaster, Lenexa, KS, USA). Track-plate stations consisted of a 20×76-cm aluminium plate (1 mm thick) housed in a 26×26×82-cm box constructed of lightweight corrugated plastic sheeting and blocked at one end with 1.27-cm mesh hardware cloth. We covered about 60% of the track plate with photocopy toner to serve as the tracking medium (Belant, 2003) and placed a sheet of white contact paper, sticky side up, on the remaining section of the plate to record tracks. Boxes with plates were placed beside trees, logs or other woody debris, anchored for stability, and camouflaged with vegetation.

Field crews revisited detection devices at 3–5-day intervals, depending on logistical considerations, for 4–6 sampling sessions in 2006, 6–16 sessions in 2007 and 10–11 sessions in 2008. The variable sample duration in 2007 helped us determine an optimum number of sampling intervals while providing sufficient revisits at all sites to estimate occupancy (Mackenzie *et al.*, 2006). Both track-plate and camera stations were baited with an 85-g can of cat food, placed within track-plate boxes or affixed to a tree or log for camera stations. We also suspended a punctured film can containing a commercial scent lure as a long-distance attractant. We replaced bait every 1–2 visits, replaced camera batteries as needed prior to depletion and replaced

commercial scent lures every visit (alternating between Gusto, long-distance weasel lure and shellfish oil [Minnesota Trapline Products, Pennock, MN, USA]) to maintain novelty of attractants. Sampling occurred between 11 July and 6 September each year.

We identified tracks on the basis of species-specific characteristics (Taylor and Raphael, 1988) and an online reference collection of verified tracks (<http://www.fs.fed.us/psw/topics/wildlife/mammal/tracks.shtml>. Accessed 8/28/2012). Because tracks of ermine and long-tailed weasels are not reliably distinguished, we refer to weasels collectively as *Mustela* spp.

Small mammals. We sampled abundance of small mammals using Sherman live traps (Sherman Co., Tallahassee, FL, USA) distributed along transects in the riparian zone of each sample reach. We were unable to sample all the 500-m reaches that comprised the systematic sample. Rather, we subsampled four randomly selected reaches in each of the upper, middle and lower river sections. We also sampled a fifth reach in the lower river in 2006 to provide additional data in the estuarine environment near the river's mouth. We sampled small mammals between late July to mid-September in 2006 and 2007.

We established small mammal-trapping transects along the vegetated edge of an active river channel in the centre of each sample reach. Transects ran parallel to the main channel and consisted of 25 trapping stations spaced 10–15 m apart and 1–15 m from the vegetated edge of the active channel. We placed two Sherman traps, one large (7.6 × 8.9 × 22.9 cm) and one small (5.1 × 6.4 × 16.5 cm), within 2 m of each other in suitable cover, generally beside downed wood. We assessed general habitat conditions associated with small mammal-trapping sites by recording the type of vegetation at each trap site (early seral vegetation [i.e. pioneering willow and red alder communities], mature hardwood, mature conifer, mature hardwood/conifer mix, other), measuring hardwood and conifer basal area using a five-factor basal area prism, and by ocularly estimating per cent ground cover of herbaceous and deciduous shrub vegetation within a 1-m radius of each trap site.

We checked traps for three consecutive mornings for a total of 150 trap nights per transect. We baited traps with a mixture of peanut butter, rolled oats and molasses, and placed polyester batting in each trap for bedding and thermal protection. Prior to release, we marked each *Peromyscus* by taking a 1-mm punch from the right (2006) or left (2007) ear, which allowed us to recognize previously captured individuals. We distinguished between adults of the deer mouse and Keen's mouse on the basis of tail length (Keen's mouse with tail ≥ 96 mm; classification accuracy = 95%; Allard *et al.*, 1987). Because juveniles cannot be identified to species on the basis of tail length, we recorded juveniles

(<15 g) as *Peromyscus* spp. We collected shrews for species identification at the Burke Museum at the University of Washington.

Lentic amphibians. We completely searched floodplains within each sampled reach for lentic pools (hereafter, we refer to these as pools). To delineate the floodplain objectively, we searched areas <500 m from the mainstem channel or <5 m in elevation above the river as determined using a digital elevation model, whichever value was less. We defined pools as standing water with depth >10 cm, surface area >1 m² and no surface inflow or outflow. We searched all the sampled reaches for pools in 2006. To understand temporal variability in pools, we resurveyed pools in 2007 and 2008 within a subset of four reaches within river sections where pools were found in 2006. Personnel searched for pools by walking straight transects 25 m apart, and recorded length, width and maximum depth of each pool. Suitable topography (i.e. depressions, older river channels and braids) was then examined more closely. Surveys were conducted between 1 June and 18 August each year.

We determined presence of amphibian breeding (larvae, embryos or eggs) on the basis of visual encounter surveys of all pools found within the sampled reaches. Two observers walked the perimeter of each pool while scanning for amphibians, searching beneath moveable submerged rocks and logs and sweeping through submerged vegetation using a dip net. Additional passes were made wading through larger pools as required to obtain complete coverage. During 2006, we searched all pools within the sampled reaches. In 2007 and 2008, we searched pools found during pool resurveys conducted those years or pools found in 2006 for reaches not resurveyed.

We used unbaited collapsible mesh funnel traps (2.5-cm gape diameter) at a subsample of reaches to obtain information on species presence independent of the visual encounter surveys, thus providing the information necessary to estimate detection probabilities. In reaches where there were large numbers of pools, we randomly selected a subsample of 1–15 pools for funnel trapping, with the probability of selection proportional to the surface area of the pool. We set traps in shallow water such that the trap openings were below the water surface, yet air was available in the upper part of the trap. We set traps at a density of 1–2 traps per square metre of suitable water depth preferentially among submerged litter, woody structures or vegetation where larvae may hide. Traps remained in place for one night.

Data analyses

Abundance indices. We computed species-specific detection rates (detections per unit of effort) as indices of abundance. For mesocarnivores, we computed the number

of detections per 3- to 5-day sampling period (pooled among 2006–2008). Here, we treated multiple detections of the same species at a single device within a 3- to 5-day sampling session as a single detection (i.e. multiple photographs or multiple tracks obtained within a 3- to 5-day checking period). For small mammals, we computed the number of uniquely marked and captured individuals per 100 trapping nights (pooled among 2006 and 2007) as an index of abundance. We adjusted the number of trapping nights to account for sprung but empty traps (Nelson and Clark, 1973).

Habitat gradients and small mammal associations. We characterized two primary gradients in habitat characteristics of the small mammal transects on the basis of principal components analysis (PROC Princomp; SAS Institute, 1990). Principal components analysis reduced correlated habitat variables into orthogonal combinations of the original standardized variables. We ordinated each of the small mammal-trapping transects in two-dimensional space defined by the first two principal component axes (PC1 and PC2) to describe gradients in habitat structure associated with small mammalian indices. Further, we examined correlations between relative abundance indices of small mammals and principal component scores along the two primary habitat gradients to identify species-habitat associations.

Occupancy analyses. We used Bayesian occupancy models to describe the distributions of several mammalian and amphibian taxa while accounting for sources of variation in the probability of detection (p) conditional on presence (Mordecai *et al.*, 2011). Specifically, we cast the multi-scale model of Nichols *et al.* (2008) as a simple latent variable Bayesian model programmed in WinBUGS 1.4 (Gilks *et al.*, 1994). The multi-scale framework was used to estimate the probability of large-scale occupancy (ψ) of the 500-m reaches and the probability of small-scale occupancy (θ) of subunits conditional on reach occupancy. We used temporal subunits (i.e. sampling sessions) for mesocarnivore analyses as opposed to the spatial subunits used in the small mammal and lentic amphibian analyses. This was necessary to accommodate the required assumption of closure within subunits for the highly mobile mesocarnivores. We felt that for mesocarnivores, it was more likely that the area of an array of traps (three to five traps) collectively would be closed to changes in occupancy over a 3- to 5-day sampling session than it was likely the area of a single trap would be closed to changes in occupancy over a protracted sampling season of many weeks. By contrast, lentic-breeding amphibians were confined to their spatial subunits (isolated pools) during the brief interval sampled, ensuring closure, and small mammal movements were thought to be small relative to the brief duration of their sampling and the size of spatial

subunits. Application of temporal versus spatial subunits is discussed by Nichols *et al.* (2008).

We defined Y as a latent vector of true reach-level occupancy data (i.e. a vector of binary data [1s and 0s] that are unobserved), Z as a matrix of subreach level (spatial or temporal) occupancy data that are also latent and X as an array of completely observed detection/non-detection data. $X_{r,i,j}$ was 1 if species i was detected at reach r at occasion j , or 0 otherwise. We used conditioning with the latent Y , Z and observed X to represent the probability model in Nichols *et al.* (2008) as follows:

$$\begin{aligned} Y_r &\sim \text{dbern}(\psi) \\ Z_{r,i} &\sim \text{dbern}(Y_r * \theta_r) \\ X_{r,i,j} &\sim \text{dbern}(Z_{r,i} * p_{r,i}) \end{aligned}$$

where $\sim \text{dbern}(\eta)$ represents the likelihood for a Bernoulli (i.e. single coin flip) outcome with parameter η . As described in the succeeding text, we linked explanatory variables and random effects to ψ using the logit link function as standard in logistic regression. The latent Y and Z were estimated as parameters in the Bayesian model. This conditional framework was then adapted to handle complications such as repeated measures, associations among species and among sites in detection probability, spatial autocorrelation, and for the small mammal analysis, a multinomial rather than binary response in X .

Mesocarnivores. We modelled the probability of reach occupancy (ψ) over the annual sampling interval (11 July to 6 September) and the probability of reach occupancy during each sampling session (θ) conditional on annual occupancy. We modelled annual occupancy probability as a function of RK standardized to one standard deviation about the mean and used random effects of reach to account for repeated sampling of the same reaches over the 3 years

$$\text{logit}(\psi_r) = \beta_0 + \beta_1 RK_r + f_r \quad (1)$$

We modelled the normal random reach effects (f_r) as spatially autocorrelated because movement of individual animals between nearby reaches seemed probable for this mobile group. The spatial random effects were modelled using the spatial disc function of WinBUGS 1.4. We modelled variation in θ between reaches with a beta distribution to allow for unexplained variation. Similarly, we modelled variation in p between reaches for track-plate boxes and variation in p between reaches for remote cameras, each with beta distributions.

Small mammals. For small mammals, the capture of any one species in a trap prohibited the capture of other

species over the same 24-hour interval between trap checks. We accounted for the lack of independence this caused between species by changing the binomial captured versus not captured response of typical occupancy models, to be a multinomial response (i.e. no species captured, or species 1 captured, or species 2 captured, ..., up to species 16). With the multinomial response, the parameter ψ still describes annual occupancy probability by a species at the reach scale over the period of sampling within the year. The parameter θ describes occupancy probability by the species at the scale of the trap station (composed of two traps), conditional on reach occupancy. Capture probability for any one species however is dependent on the presence/absence of all of the other species as follows: let π_s be the probability of capturing species s in a trap given it is present in the vicinity of a trapping station, and the trap is not closed by any other species. Now, if K is the total number of species that could be present, the probability $\xi_{m,0}$ that no detections are made in a single trap at trapping station m is

$$\xi_{m,0} = \prod_{h=1}^K (1 - Z_{m,h}\pi_h)$$

The probability $\xi_{m,s}$ that species s is captured by a single trap at m can be written

$$\xi_{m,s} = \left(1 - \prod_{h=1}^K (1 - Z_{m,h}\pi_h)\right) Z_{m,s}\pi_s / \left(\prod_{k=1}^K (1 - Z_{m,k}) + \sum_{l=1}^K Z_{m,l}\pi_l\right)$$

The vector ξ_m with length $K+1$ is the probability vector for the multinomial response.

For each small mammal species, we used the same linear combination to model reach-level occupancy that was used for the mesocarnivores (Equation 1). Separate intercepts, coefficients and random effects were estimated for each species. The random effect standard deviation was common to all species. Again, for each species, we used beta distributions to model unexplained variation in station-level occupancy probability within reaches, and for variation in p between species for small and large traps separately.

Lentic amphibians. For lentic amphibians, ψ represents the probability of reach occupancy over the period of sampling each year and θ represents the probability of occupancy of individual isolated pools within the reach. Just as in the mesocarnivore analyses, we related reach-level occupancy to standardized RK and included random reach effects (Equation 1). Separate intercepts, coefficients and random effects were estimated for the six lentic-breeding species, and the random effect standard deviation for the random reach effects was common to all species.

We modelled θ with a fixed effect of species and random effects of reach and pool within reach. We modelled variation in p between species and between visual encounter occasions using a beta distribution. Similarly, for funnel trapping occasions, we modelled variation between species and occasions with a beta distribution.

Species richness. We estimated mean species richness of breeding amphibians within sampled pools in the three river sections using methods for finite sample estimation (Royle and Kéry, 2007). We used the posterior distribution of the latent occupancy data ($\mathbf{Y}$ and $\mathbf{Z}$), computing the posterior mean of the latent number of species present per pool within each river section and year. Similarly, for the small mammals, we computed the finite sample average species richness as the posterior mean of the average number of species present per reach in the sampled reaches using the posterior distribution of $\mathbf{Y}$.

We used non-informative prior distributions for model intercepts, coefficients and Beta parameters, and weakly informative prior distributions for random effect standard deviations. For intercepts and coefficients, we use normal (0, var=100) prior distributions. For the parameters of beta distributions, we used normal distributions normal (0, var=10 000) that were constrained to be positive using the $I(\cdot)$ function of WinBUGS 1.4. We used normal (0, var=1) distributions constrained to be positive for random effect standard deviations to impart our prior belief that these parameters were likely to be near zero. We determined model convergence using the Brooks–Gelman–Rubin criterion (Gelman and Rubin, 1992; Brooks and Gelman, 1998). Posterior distributions were 5000 samples taken every 50th iteration of the Markov chains after an initial burn-in period.

RESULTS

Mesocarnivores

We detected seven species of carnivores in the Elwha River riparian zone (Supporting Information) but examined detection frequencies and occupancy patterns only for abundant species: spotted skunks, raccoons and weasels. Raccoons were detected primarily in the lower and middle river sections but were never detected upriver from RK 24 (Figure 2). Spotted skunks were detected with greatest frequency in the lower river section and with the least frequency in the upper section, never upriver from RK 32 (Figure 2). Weasels were detected with greatest frequency in the middle section and as far upriver as RK 42 (Figure 2).

All three species occupied the Elwha River riparian zone with decreasing probability from the lower to the upper river (Figure 3). Weasels occupied individual reaches of the lower

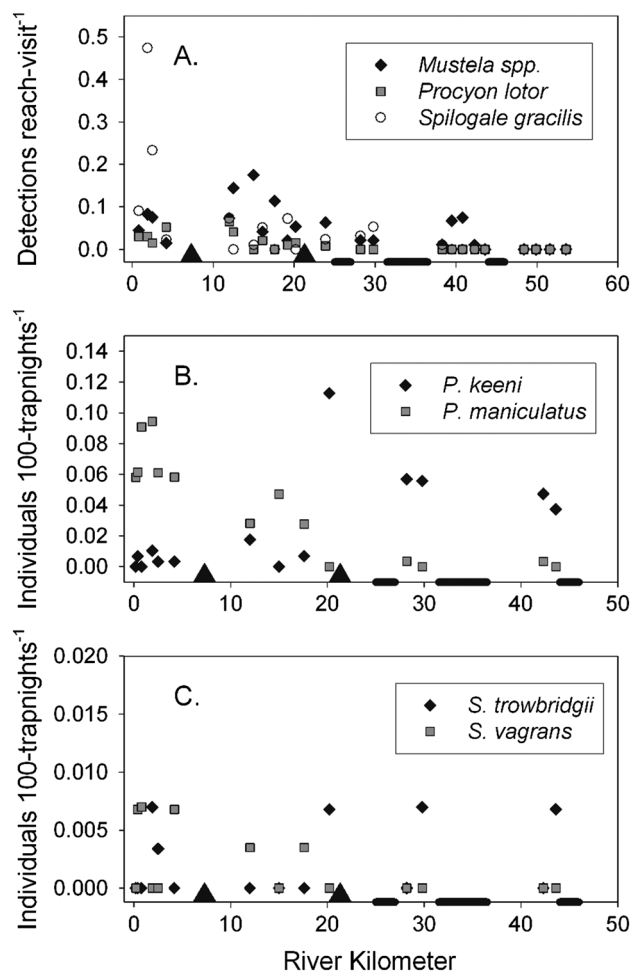


Figure 2. Abundance indices for (A) mesocarnivores, (B) deer mice and Keen's mouse and (C) shrews within 500-m reaches of the Elwha River riparian zone, 2006–2008. Mesocarnivore indices are the number of detections per device during 3- to 5-day sampling sessions (multiple photographs or tracks of a species at a sampling station were considered a single detection). Small mammal indices are the number of individuals captured per 100 trap nights of sampling effort. Black triangles on the abscissa represent locations of the Elwha and Glines Canyon Dams and associated reservoirs, whereas thick lines represent locations of major canyons

and middle river sections with near perfect certainty, but probability of occupancy by weasels decreased abruptly in the upper river section. Raccoons occupied the lower river section with nearly perfect certainty. Occupancy rates by raccoons decreased in the middle river and were negligible in the upper river, particularly above the Grand Canyon (RK 32–36). Variable detection rates of spotted skunks among the 3 years of this study contributed to high variability in the annual occupancy estimates; however, spotted skunks also occupied the lower and middle sections most frequently and rarely occupied the upper river above the Grand Canyon (Figure 3).

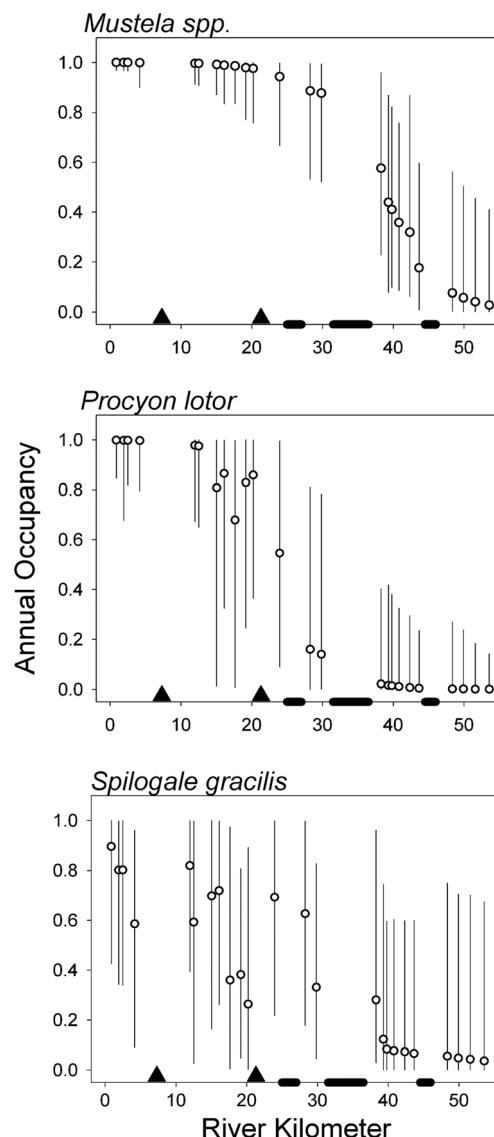


Figure 3. Mean annual occupancy of 500-m reaches of the Elwha River riparian zone by mesocarnivore species, 2006–2008. Annual occupancy is defined as the probability of a species using a 500-m reach during an annual summer sampling period. Intervals are 95% credibility intervals based on the 2.5th and 97.5th percentiles of posterior distributions. Black triangles on the abscissa represent locations of the Elwha and Glines Canyon Dams and associated reservoirs, whereas thick lines represent locations of major canyons

Small mammals

Principal components analysis revealed two primary habitat gradients associated with the small mammal transects (Figure 4). The first axis (PC1) corresponded with a gradient extending from sites with high basal area of conifers to those having a high basal area of hardwood trees and ground cover of herbaceous vegetation and deciduous shrubs. An increasing score on the second axis (PC2) was highly correlated with the

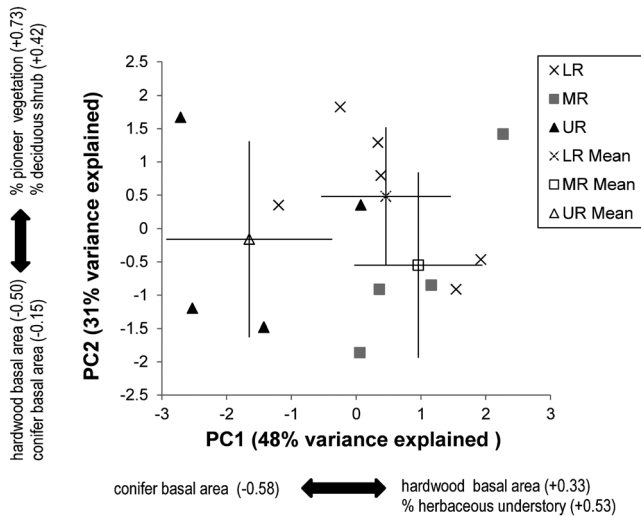


Figure 4. Principal components analysis of vegetation gradients associated with small mammal-trapping sites in the Elwha River riparian zone, 2006–2007. Vegetation characteristics of individual transects (plus means and standard deviations) in the lower (LR), middle (MR) and upper (UR) river segments are plotted in two dimensions of habitat space defined by the primary principal component axes (PC1 and PC2). The top four vegetation variables correlated with each axis (and Pearson's correlation coefficients) are displayed beside or below the axis labels

proportion of trap sites in pioneering vegetation (willow and young alder). Hence, PC1 described the prevailing vegetation on the older landforms, and PC2 corresponded with the proportion of transect in early seral rather than mature forest communities. The ordination of transects along these two gradients revealed a greater prevalence of mature conifer stands (i.e. high conifer basal area) in the upper than the middle and lower river sections. Transects were highly variable in the proportion of pioneering vegetation, but pioneering vegetation was more prevalent in the lower river than the middle river (Figure 4).

We captured 471 small mammals of 14 species in 3768 trap nights of effort (Supporting Information). We also captured 129 juvenile *Peromyscus* that were not identified to species. Abundance of Keen's mouse and the deer mouse was negatively associated with one another (Figure 2; $r = -0.75$, $p = 0.002$). Keen's mouse tended to be negatively associated with both PC1 ($r = -0.38$, $p = 0.17$) and PC2 ($r = -0.34$, $p = 0.23$), suggesting an affinity for mature conifer vegetation. In contrast, the deer mouse tended to be correlated positively with both axes (PC1: $r = 0.46$, $p = 0.10$; PC2: $r = 0.37$, $p = 0.19$), suggesting a greater affinity for mature hardwood and early seral vegetation. Similarly, relative abundance of two shrew species were negatively associated (Figure 5; $r = -0.50$, $p = 0.07$), with the Trowbridge's shrew (*Sorex trowbridgii*) most closely associated with mature conifer vegetation (PC1: $r = -0.38$,

$p = 0.17$) and the vagrant shrew (*Sorex vagrans*) more positively associated with mature hardwoods and seral vegetation (PC1: $r = 0.35$, $p = 0.21$; PC2: $r = 0.35$, $p = 0.21$).

The deer mouse and vagrant shrew occupied the lower river reaches with nearly 100% probabilities, and they less frequently occupied the upper river reaches (Figure 5). By contrast, occupancy rates of Trowbridge's shrew tended to increase upriver, whereas the Keen's mouse occupied all sections of the river gradient with relatively high probability. Differences in the observed patterns of occupancy and relative abundance of Keen's mouse between the lower and upper river sections suggest that the Keen's mouse occurred at relatively low numbers but high probability in the lower river and at greater density in the upper river section (Figures 2 and 5).

Species richness of small mammals did not vary longitudinally upriver (Figure 6). We estimated mean species richness ranging from 6 to 8 species within individual 500-m reaches (Figure 6).

Lentic amphibians

Lentic habitats of amphibians were highly variable on the Elwha floodplain (Figure 7). The number of pools found in reaches was highest in the lower and middle river sections, and lower in the upper river, particularly above the Grand Canyon (RK 32–37). Independent surveys of pools conducted in a subsample of reaches also revealed high temporal variation in pool abundance among three summers (i.e. 8–34 pools were identified in the second reach from the river's mouth, Figure 7).

Size and depth of pools did not differ among the three river sections (Figure 8; Kruskal–Wallis test: $X^2_{\text{area}} = 2.02$, 2 d.f., $p = 0.36$; $X^2_{\text{depth}} = 0.22$, 2 d.f., $p = 0.89$). The majority of pools on the floodplain were small (median size = 13.5 m²; median depth = 31 cm; Figure 8). Hence, most pools were ephemeral, and variability among counts likely reflected the timing of surveys relative to recent flows and hydroperiod.

We detected larvae of six species of lentic amphibians in 187 pools searched (Supporting Information). Both the northwestern salamander (*Ambystoma gracile*) and Pacific chorus frog (*Pseudacris regilla*) reached highest occupancy in the middle river (Figure 9). The remaining species were not sufficiently abundant to reveal spatial patterns in occupancy. Species richness tended to be highest in the middle river, reflecting the more common occurrence of the northwestern salamander and chorus frogs (Figure 10).

DISCUSSION

Distribution and occupancy patterns of mesocarnivore species were not closely associated with salmon presence in the lower river, contrary to our initial hypothesis. Detection

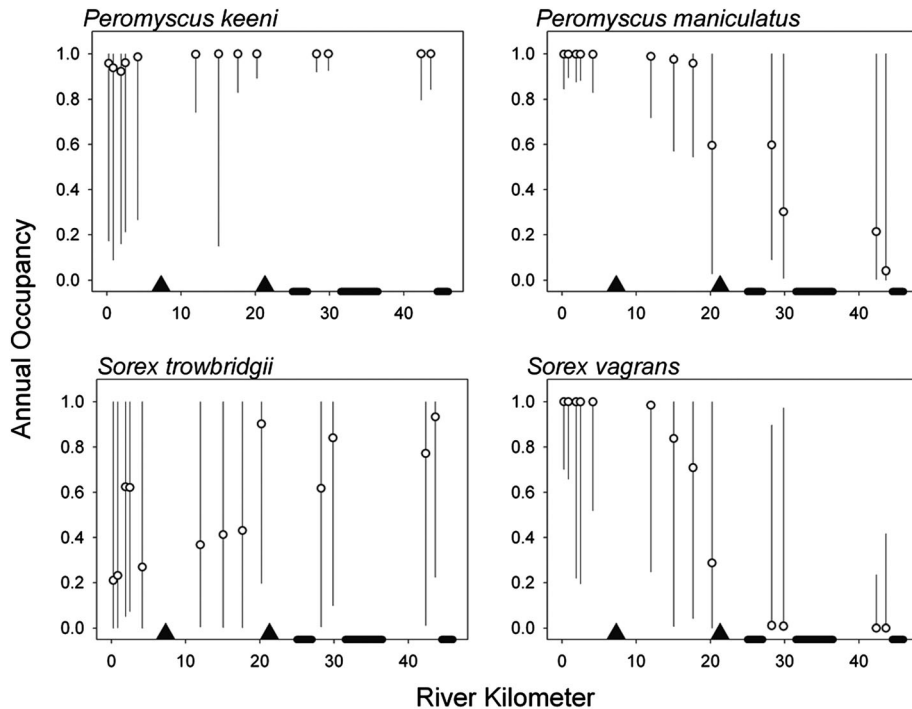


Figure 5. Annual probability of river reach occupancy by two *Peromyscus* species and two *Sorex* species in the Elwha River riparian zone, 2006–2007. Annual occupancy is defined as the probability of species presence within a 500-m reach of the riparian zone during an annual summer sampling period. Intervals are 95% credibility intervals based on the 2.5th and 97.5th percentiles of posterior distributions. Black triangles on the abscissa represent locations of the Elwha and Glines Canyon Dams and associated reservoirs, whereas thick lines represent locations of major canyons

and occupancy rates of each species were greatest in the lower river section, where salmon were most abundant, and were least in the upper river sections above both dams consistent with the hypothesis. But we did not observe any clear association between occupancy of mesocarnivores and the Elwha Dam, the lowest barrier to fish movement in the Elwha. Rather, all species were found with relatively

high probabilities in the middle river section, where salmon were absent. Moreover, spatial discontinuities in occupancy patterns were more clearly associated with canyons in the upper river than with the lower of the two dams (Figure 3).

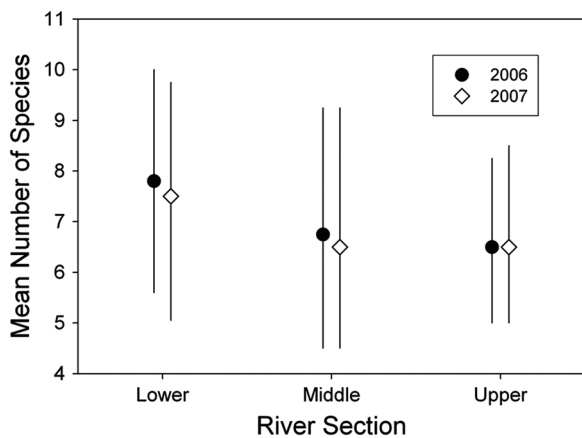


Figure 6. Mean species richness ($\pm 95\%$ confidence limits) of small mammal species within 500-m reaches of the riparian zone in lower, middle and upper sections of the Elwha River riparian zone, 2006–2007

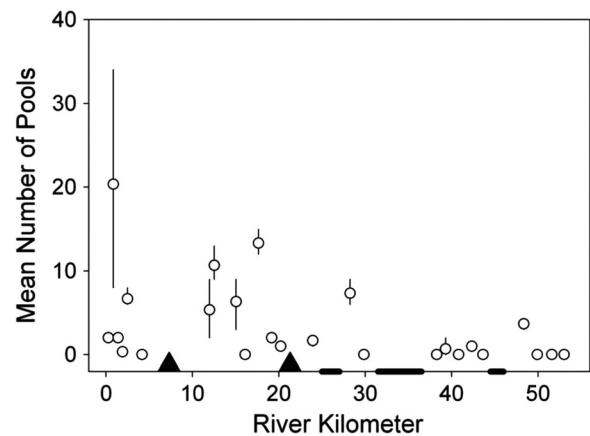


Figure 7. Mean number of pools counted in 500-m river reaches of the Elwha River floodplains, 2006–2008. For reaches in which pools were counted in three consecutive years, error bars represent minimum and maximum counts made in different years. Black triangles on the abscissa represent locations of the Elwha and Glines Canyon Dams and associated reservoirs, whereas thick lines represent locations of major canyons

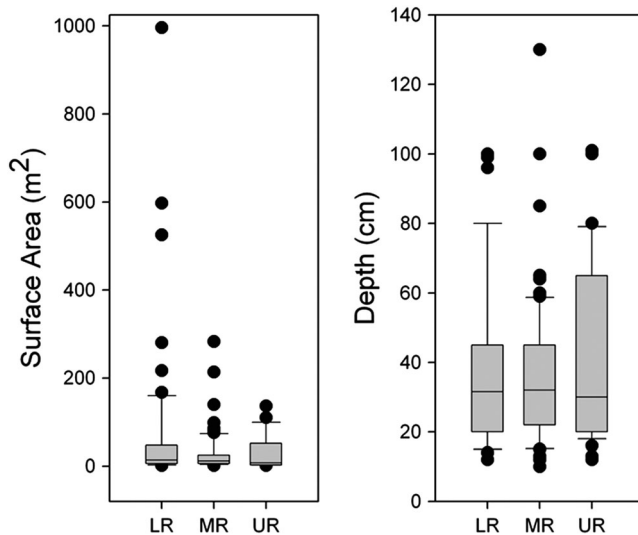


Figure 8. Pool characteristics on floodplains of the lower (LR), middle (MR) and upper (UR) river sections of the Elwha Valley, 2006–2008. Each box shows the 25th and 75th percentiles of the distribution with the median in the middle. Whiskers extend from the 10th to 90th percentile and outlying records are shown as dots

The patterns in mesocarnivore distributions likely reflected species responses to multiple gradients in food resources that decreased upriver. We did not measure availability of food resources, but mesocarnivores associated with the lower river had access to diverse assemblages of marine fishes and foods associated with the Elwha estuary and nearshore environments (Duda *et al.*, 2011a; Rubin *et al.*, 2011). In addition, anthropogenic foods associated with human habitation (i.e. refuse, pet foods, orchard fruits or garden crops), recreation (i.e. refuse, unsecured food) and fish hatcheries were most available to generalist herbivores in the lower river and least available in the upper river, particularly above Glines Canyon dam, which is primarily wilderness. We speculate that the raccoon, the most generalist of omnivores, and, to a lesser degree, the spotted skunk likely benefited from the availability of anthropogenic foods in areas of human habitation and recreation as has been reported previously (Kaufmann, 1982). The weasels, by contrast, had the most specialized diets of the species we examined, preying principally on small mammals (Maser *et al.*, 1981). We did not measure the collective abundance of all mammalian prey (e.g. mountain beaver [*Aplodontia rufa*], snowshoe hares [*Lepus americanus*], bushy-tailed woodrats [*Neotoma cinerea*]), but small mammals were captured with the greatest frequency downriver and least upriver (Supporting Information). Increasingly deep snows and lower temperatures associated with the elevation gradient and topographic effects of a narrower canyon upriver may also have affected availability of food resources and nutrients available to mesocarnivores in the upper watershed.

Small mammal abundance and occurrence patterns reflected habitat gradients on the floodplain as we initially predicted. The deer mouse and vagrant shrew were more abundant and occupied primarily deciduous forests with developed herbaceous and shrub-dominated understories, which were prevalent in the lower river (Shaffroth *et al.*, 2011). By contrast, Trowbridge's shrew and Keen's mouse were more abundant in conifer-dominated floodplains, which were more prevalent in the middle and upper watershed. Habitat affinities we observed among congeneric mice and shrew species is similar to that reported previously in Pacific coastal forests. For example, the Keen's mouse reaches peak abundance in mature conifer forests on the Olympic Peninsula, whereas the deer mouse is most abundant in younger managed forest landscapes (Songer *et al.*, 1997). The vagrant shrew is usually most abundant in moist grassy areas with shrubs and deciduous cover, whereas Trowbridge's shrew is more consistently a Douglas fir coniferous forest specialist throughout western Oregon and Washington (Maser *et al.*, 1981; Terry, 1981; Verts and Carraway, 1998).

We cannot be sure to what extent preferences for conifer versus deciduous forest communities reflect the fundamental niches of these species and to what extent interspecific competition may influence their realized niches. Songer *et al.* (1997) reported that relative abundance of the two species of deer mice varied inversely on the Olympic Peninsula, even among similar habitats, suggesting a competitive influence on species distributions. Furthermore, early observations of shrew distributions in Oregon indicated that Trowbridge's shrew was rarely found where the vagrant shrew was abundant (Dalquest, 1941). Interspecific differences in abundance patterns of shrews may be related to intrinsic interspecific differences in soil and moisture (Terry, 1981), but Dalquest (1941) also reported that Trowbridge's shrew were less aggressive than the vagrant shrew, suggesting a potential influence of interspecific competition.

We found the greatest proportion of pools occupied by amphibians, greatest species richness and highest density of pools in the middle section of the Elwha River. We speculate that both the abundance of pools suitable for breeding and their occupancy by breeding amphibians in the Elwha are strongly related to seasonal variations in discharge. The hydrograph of the Elwha River indicates that peak discharges occur in late May and June (Duda *et al.*, 2008). Consequently, many isolated pools found on the floodplain from June to mid-August survey periods were inundated and scoured during the period of egg and larval development (Nussbaum *et al.*, 1983). The prevalence of small, shallow pools on the floodplain and high variability among years in counts of pools also suggests a highly ephemeral breeding environment in many floodplains throughout the system. Because the dams were operated as run of the river, the dams did not appear to affect lentic habitats by altering

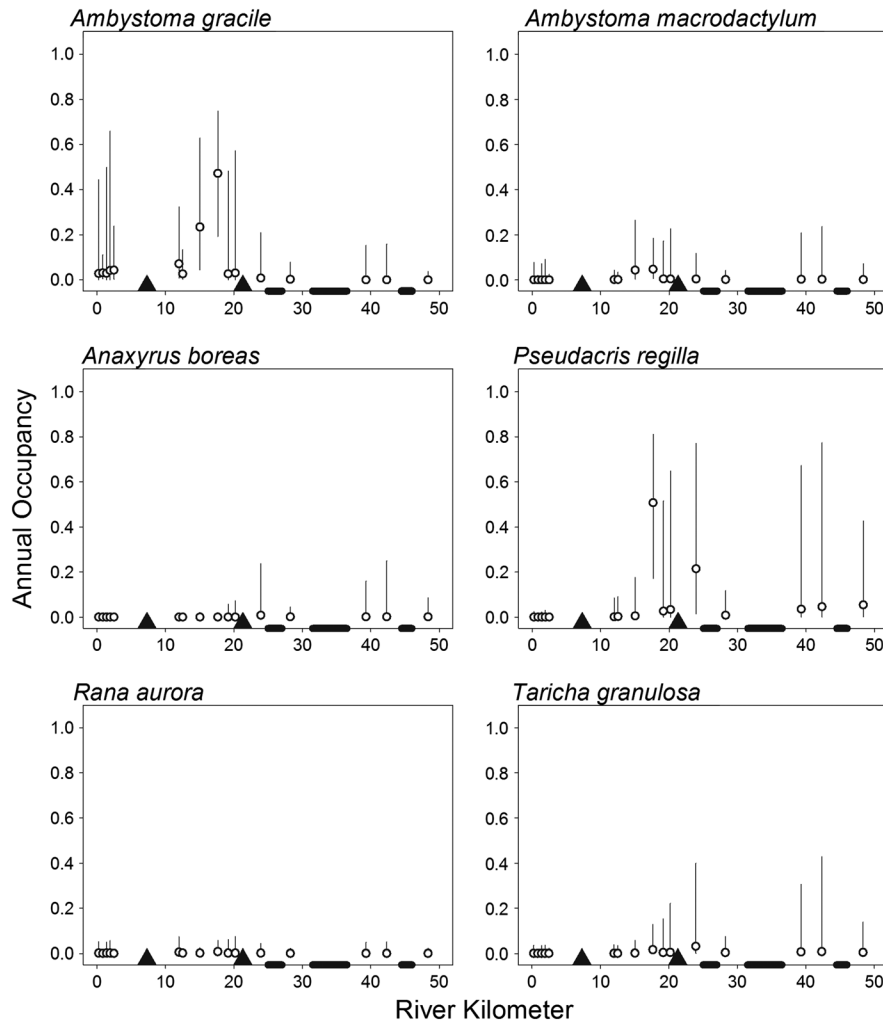


Figure 9. Mean annual occupancy of pools by amphibian species in 500-m reaches of the Elwha River riparian zone, 2006–2008. Pool occupancy is defined as the probability of species presence in pools. Intervals are 95% credibility intervals based on the 2.5th and 97.5th percentiles of posterior distributions. Black triangles on the abscissa represent locations of the Elwha and Glines Canyon Dams and associated reservoirs, whereas thick lines represent locations of major canyons

seasonal discharge. Rather pool availability may have been affected more by disruption of sediment supply. Amphibians tended to be found most frequently in pools that were disconnected from the active channel and of a later successional stage than pools in the active channels, a condition that was most prevalent during our surveys in the middle river reach where the floodplain was less active because of armouring by large cobbles and boulders (Kloehn *et al.*, 2008).

Dam removal, which began in 2011 and is to be completed in 2014, was the first step towards restoring natural ecosystem processes in the Elwha Valley. Dam removal has exposed almost 325 ha of land previously inundated by the former reservoirs, which is now managed in an effort to accelerate primary succession through the planting of

native vegetation (Chenoweth *et al.*, 2011). Furthermore, up to 7–8 million m³ of sediments that have accumulated in the reservoir deltas are expected to be transported and delivered downriver (Czuba *et al.*, 2011). Over a period of several years, sediment delivery is expected to aggrade river beds below the dams by as much as one to several metres, primarily in the lower river section (Czuba *et al.*, 2011). Aggrading river beds are likely to increase channel migration rates as well as avulsion of new river channels, resulting in increased braiding and sinuosity in the lower and middle river (Draut *et al.*, 2011). Channel migration in response to bed aggradation may increase recruitment of downed wood into the river channel, which could also affect fluvial dynamics of floodplain communities. After several decades, increased sedimentation and channel migration is expected

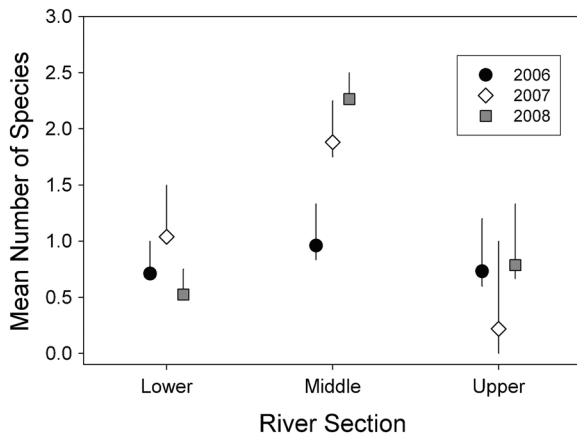


Figure 10. Mean species richness ($\pm 95\%$ confidence limits) of larval amphibians within 500-m reaches of the Elwha River riparian zone in lower, middle and upper sections, 2006–2008

to reduce the proportion of mature forest communities in the middle and lower river sections and increase the proportion of young floodplain surfaces (Kloehn *et al.*, 2008).

Dam removal will also reconnect anadromous fishes with hundreds of kilometres of relatively pristine spawning and rearing habitats upstream of the former dams. Predictions of the timing and spatial distribution of salmon and trout recolonization following dam removal depend upon the complex interactions among many species-specific characteristics of salmon and trout (migration timing, swimming abilities), barriers to migration, the proximity and abundance of source populations, as well as short-term impacts of sediments on spawning beds in the lower and middle river segments, and the effects of native resident fishes in the middle and upper river sections (Brenkman *et al.*, 2008; Pess *et al.*, 2008). It is expected that tens of thousands of Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*) will return to spawn throughout mainstem and floodplain habitats in the Elwha River within 25 years. Potentially >100000 spawning chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) will return to spawn in the lower and middle river segments, although some additional time may be required before chum and pink salmon reach full restoration potential because of potential impacts of high sediment loads on spawning beds in the middle and lower river segments in the years following dam removal (Pess *et al.*, 2008; Ward *et al.*, 2008). Previous research, indicating the highly oligotrophic condition of the upper river suggests that nutrient subsidies delivered from spawning fish could substantially increase aquatic productivity, while restructuring trophic pathways and eliciting cascading effects on a variety of aquatic and terrestrial animal communities (Morley *et al.*, 2008; Woodward *et al.*, 2008; Duda *et al.*, 2011b).

Habitat and nutrient changes in the Elwha riverine ecosystem, expressed over a period of decades, suggest that a long-term perspective will be required to evaluate the effects of dam removal on wildlife communities and distributions. The occupancy framework we adopted in the Elwha Valley has proven useful previously in examining trends in species distribution patterns in response to long-term environmental changes (Moritz *et al.*, 2008; Tingley and Beissinger, 2009). The fact that much of the middle river segment and the entire upper river are protected within Olympic National Park should allow researchers to discern future changes in distribution of mammals and amphibians with minimal confounding effects. We expect that over the long term (e.g. 1–3 decades), generalist mesocarnivores will benefit from increased nutrient subsidies from restored salmon populations, particularly in the middle river segment where there is likely to be the greatest influx of spawning salmon, but throughout the upper watershed as well. We hypothesize that generalist mesocarnivores will increase their range upriver in response to changing primary productivity and food availability following full restoration. Furthermore, we speculate that populations of the deer mouse and vagrant shrew will be favoured over the Keen's mouse and Trowbridge's shrew as primary succession ensues on the exposed lake beds and as young hardwood communities increase in extent in the middle river section. We expect the restructuring of river channel dynamics and morphology will influence both the availability of lentic habitats and the occupancy patterns of amphibians in the middle and lower river sections. The removal of dams provides an unprecedented opportunity to evaluate these and other wildlife population and community responses to restructuring of floodplains and nutrient budgets in the Elwha River in the upcoming decades.

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