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Lauren M. Kuehne & Julian D. Olden

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ARTICLE

Environmental Drivers of Occupancy and Detection of Olympic Mudminnow

Lauren M. Kuehne* and Julian D. Olden

School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195, USA

Abstract

The Olympic Mudminnow *Novumbra hubbsi* is a highly endemic freshwater fish found only in Washington State, where their distribution is limited to low-elevation wetland habitats. The distributional extent of the Olympic Mudminnow is well established, but local and watershed environmental features associated with their presence or absence within the range are poorly understood, making it difficult to determine habitat needs versus availability. We surveyed 22 sites in 2 years along the Chehalis River with the objective of modeling environmental characteristics associated with occupancy by Olympic Mudminnows, while also accounting for incomplete detection. Occupancy and detection probabilities were highly similar between years, and occupancy that incorporated detection probabilities was 47% higher than naive estimates in a given year. Modeling with environmental covariates supported the importance of low temperatures for predicting the occurrence of Olympic Mudminnows at sites, and detection within sites was associated most strongly with shallow depths and low dissolved oxygen. These results are consistent with prior research indicating the preferential use of groundwater springs by Olympic Mudminnows, particularly in warmer summer months. Our research expands the existing knowledge of Olympic Mudminnow distributions by documenting main-stem-oriented populations at varying levels of abundance and suggesting habitat features that may increase occupancy and detection probabilities. The sampling and modeling approach we describe also informs development of standardized survey protocols for Olympic Mudminnows, helping to optimize resources for monitoring occupancy and abundance across their limited range.

The Olympic Mudminnow *Novumbra hubbsi* is Washington State's only endemic fish species, distributed in low-elevation, slow-water habitats in the southwestern and northern coastal areas of the state. The limited distributional range of the Olympic Mudminnow—the smallest range of any species of mudminnow (family Esocidae) (Kuehne and Olden 2014)—and their close association with areas of glacial refuge during the Pleistocene era have been well established by extensive geographic sampling (Harris 1974). On the basis of their limited distribution as well as on some evidence of population decline in recent decades, the Washington Department of Fish and Wildlife assigned the Olympic Mudminnow to the category of “Sensitive” in 1999, indicating their vulnerability or risk for decline without management or the removal of

threats (Mongillo and Hallock 1999). Recent genetic analysis across the entire range found that even populations in close geographic proximity are often genetically distinct (DeHaan et al. 2014), underscoring concerns that the Olympic Mudminnow may become vulnerable in future years if individual populations succumb to threats.

Like other mudminnow species, Olympic Mudminnows are small-bodied (<90 mm fork length) habitat specialists, favoring marshy, shallow-water habitats (Kuehne and Olden 2014). These include isolated wetlands and marshes, as well as partially connected off-channel areas such as oxbow lakes, beaver-dammed tributaries, and seasonally flooded wetlands (Meldrim 1968; Harris 1974; Beecher and Fernau 1983; Henning et al. 2007). The microhabitat preferences of

*Corresponding author: lkuehne@uw.edu

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Olympic Mudminnows for shallow water, shaded areas, and mud or silt substrate is well established (Meldrim 1968), but landscape factors that might explain presence, absence, and abundance at larger scales have not been well or conclusively studied (Mongillo and Hallock 1999). Without an understanding of the factors that determine habitat availability and occupancy, it is very difficult to establish whether crucial habitats are being compromised and if additional conservation concern is warranted.

We sought to fill this knowledge gap by identifying large- and small-scale factors associated with Olympic Mudminnow presence through a longitudinal survey along the main-stem Chehalis River, Washington, an area that constitutes the southeastern part of the range. This survey offered an opportunity to simultaneously examine the role of incomplete detection in surveying or monitoring Olympic Mudminnows. Incomplete detection—or the probability that a species is present even when undetected by sampling—is a particular problem in monitoring for species that are rare, elusive, or difficult to sample (MacKenzie et al. 2006). Furthermore, surveys which do not incorporate detection probability into occupancy estimates can result in an underestimation of the proportion of sites occupied, confounding the interpretation of assessments for threatened or sensitive species. The marshy slow-water habitats favored by Olympic Mudminnows are extremely challenging to sample, and available research funding remains very limited. Monitoring and research studies for Olympic Mudminnows are often opportunistic or small in scale (Kuehne and Olden 2014), elevating the importance of understanding occupancy and detection probabilities in order to guide monitoring strategies and optimize sampling resources.

The current paucity of data related to occupancy, habitat needs, and population sizes is particularly concerning given a large-scale dam project proposed for the Chehalis River (Scott et al. 2013). Dams and other forms of water regulation are strongly implicated in historical declines of European Mudminnow *Umbra krameri* (Povž 1995a; Wanzenböck 1995). This may be due to the loss of connectivity with temporary wetland areas, which are utilized by several species of mudminnow during periods of flooding and which may play an important role in providing spawning habitat (Kováč 1997; Henning et al. 2007; Kuehne and Olden 2014). Recent genetic analysis by the U.S. Fish and Wildlife Service has also identified a small and historically isolated subpopulation of Olympic Mudminnows along the north coast of Washington as a high priority for conservation research (DeHaan et al. 2014), spurring a need for research to inform monitoring and conservation efforts across the range.

In addition to detecting new populations of Olympic Mudminnows in the study region, the objectives of our study were (1) to estimate the detection probability of a commonly used sampling method and account for incomplete detection in estimating the proportion of sites occupied and (2) to identify local habitat and landscape environmental characteristics determining Olympic Mudminnow presence. Our study

informs the development of survey and sampling guidelines for Olympic Mudminnows, in addition to guiding the optimal allocation of resources for monitoring occupancy and abundance over time.

METHODS

Study Area and Site Selection

Our survey was conducted along approximately 40 km of the Chehalis River, which drains a 2,700-km² watershed and flows 200 km through southwestern Washington. The river is a low-gradient, rain-dominated system (Reidy Liermann et al. 2012) typified by many semi- and partially connected habitats (oxbow lakes, seasonal wetlands) and is home to commercially and recreationally important fish species (e.g., three species of salmonids) as well as the Olympic Mudminnow. The basin exhibits mixed geological foundations of sedimentary and volcanic rocks, Pleistocene glacial drift, and alluvium, which supports significant groundwater resources (Gendaszek 2011). Land cover is predominantly (74%) forested, with smaller percentages (5–8% each) of developed, wetland, and agricultural areas (Gendaszek 2011).

We surveyed 22 sites along the main stem and in adjacent habitats of the Chehalis River in 2013 and 2014 (Figure 1), sampling once in each year between late July and mid-August. The region of river sampled represented an area of moderate Olympic Mudminnow occupancy based on historical occurrence data (WDFW 2014). Although our initial goal was to sample sites along a continuous reach between Centralia and Elma (65 km of river), limited access restricted sampling to approximately 5 km upstream and downstream of boat launches, resulting in a survey of suitable sites over 40 km of river (Figure 1). Sites were selected based on known habitat preferences of Olympic Mudminnows for vegetated areas with little to no streamflow (Meldrim 1968; Harris 1974) and included backwater areas, sloughs, and incoming (dammed) creeks. There is extensive beaver activity in this region, and many sites were formed by either seasonal or semipermanent beaver dams. The majority of sites were separated by more than 0.5 km along the main stem (Figure 1), with the exception of two creeks, where we sampled both above and below beaver dams. In each of these cases, two or more beaver dams separated the upstream (i.e., off-channel) site from the downstream (i.e., main-stem-oriented) site; subsequent analysis showed significant differences in fish communities between these areas, supporting their treatment as independent sites (results not shown). Incoming groundwater springs were evident at many backwater sites.

Between sampling seasons, a subset of our sites ($n = 7$) were treated to reduce infestations of the nonnative aquatic plant parrotfeather *Myriophyllum aquaticum*. Parrotfeather plants in these sites were treated with an application of imazapyr in late summer of 2013; the single chemical treatment did not noticeably reduce

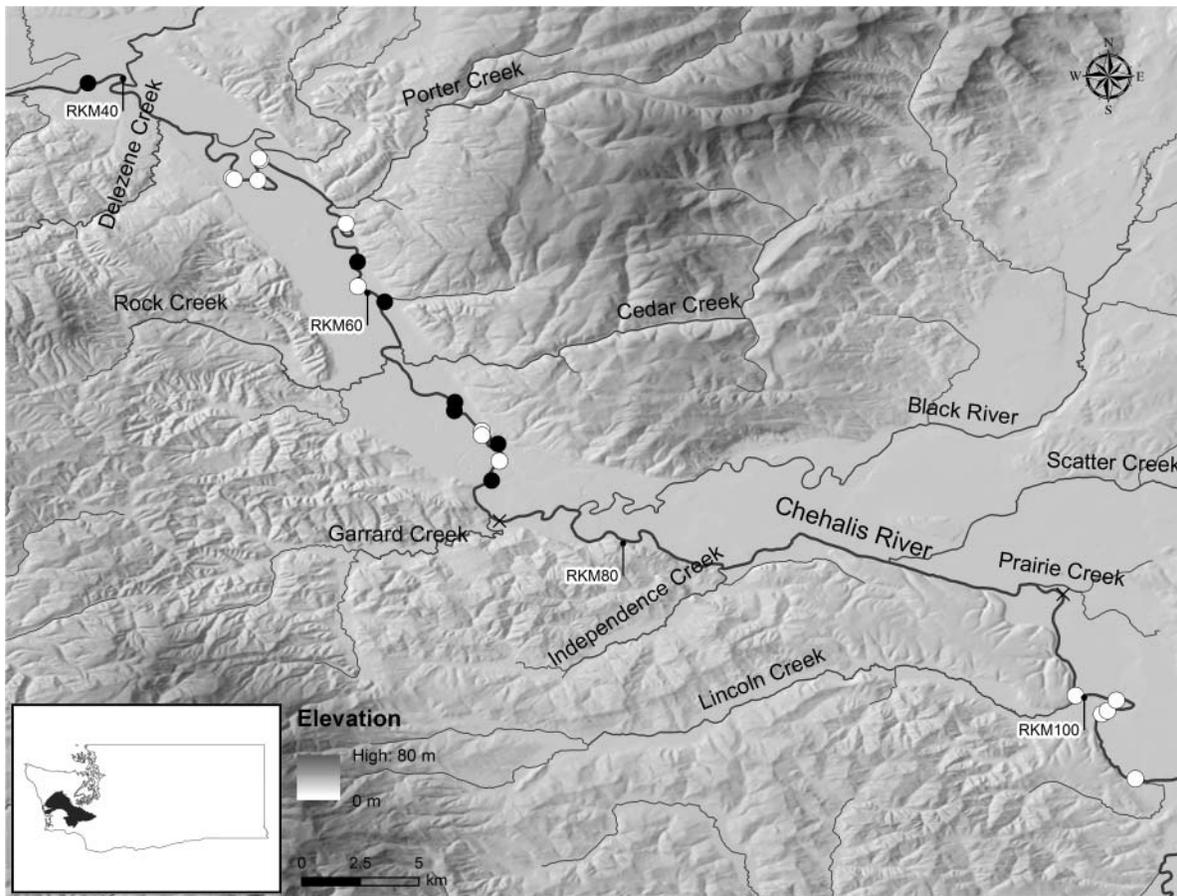


FIGURE 1. Area of study with 22 sampling sites along the main-stem Chehalis River and incoming tributaries (stream order > 1 depicted). The sites are designated as Olympic Mudminnow detected (black circles) and not detected (white circles). The inset shows the location of the Chehalis River watershed within Washington State. Restricted river access resulted in the exclusion of river kilometer (RKM; measured from the mouth of the Chehalis River) RKM 95 to 72 (between the × symbols) from survey and sampling.

native or nonnative vegetation, which were both substantially more abundant in 2014 due to warm temperatures and low streamflows in that year (L. M. Kuehne, unpublished data).

Data Collection

Sites were sampled using Gee minnow traps (23 × 44 cm, 2.5-cm opening, 0.6-cm mesh) deployed in lines perpendicular to shore 5 m apart and with 3 m between individual traps. Traps were baited with approximately 100 g of dry dog food supplemented with a small cube (50 g) of chicken liver (based on preliminary sampling that tested a variety of bait types). The minimum length of fish captured using this method was 36 mm (mean ± SD = 55 ± 11 mm). We experienced some mortality of fish in the first year of sampling in a small number of traps set in shallow vegetation, where the trap was just submerged; presumably oxygen became depleted by plant respiration at night. This issue was largely resolved in the second year by setting those traps slightly shallower (allowing exchange with atmospheric oxygen). There was no evidence that traps were disturbed by larger predators (e.g., raccoons *Procyon*

lotor or birds), although this can be of concern when trapping in shallow areas.

Sites were selected based on the criteria of having little to no flow and some areas with shallow vegetation. These conditions resulted from varying combinations of habitat type (backwater, side channel, or incoming tributaries) and the presence of beaver dams, and sites varied considerably in total area (range = 120–12,500 m²). To account for differences in area, we scaled the number of traps according to site size, with a minimum of 10 traps deployed in the smallest sites and a maximum of 30 traps per site. Five sites were too large (>2,500 m²) to be surveyed by 30 traps (without spacing traps too far apart), and a representative portion of these sites were sampled instead.

Traps were set in the afternoon and retrieved the following morning; set times ranged from 17 to 25 h (mean ± SD = 20.8 ± 2.3 h). All fish species in the traps were identified and counts recorded. In both years, we recorded depth, distance from shore, and percent vegetative cover (visually estimated for the surrounding 1 m²) for each trap. In 2014, we also recorded temperature, conductivity, and dissolved oxygen

measurements at each trap using a handheld YSI meter (Model Pro2030). Collection of this comprehensive trap-level covariate data added substantial sampling time but allowed us to better characterize both between-site and within-site variability and microhabitat selection by Olympic Mudminnows.

Detection probabilities can be influenced by differences in the abundance of individuals between areas (Royle 2006). To explore this possibility and quantify any related detection heterogeneity, in 2014 we conducted additional trapping at three sites that varied in the abundance of Olympic Mudminnows based on the prior year's sampling. At each site the number of traps was doubled from the previous year (total $n = 40$ at each site), with the added traps spaced so as to not interfere with the sampling pattern replicated from the previous year.

Statistical Analyses

Occupancy and detection.—The first objective of our study was to estimate occupancy (Ψ) and detection probability (P) for Olympic Mudminnows across the study area, based on site selection and trapping protocols. We applied a likelihood-based approach based on replicate surveys to estimate occupancy rates for species with detection probabilities < 1 (MacKenzie et al. 2002); this method has been widely used and extended over time to include parameterizations for exploring occupancy and detection across seasons, population abundances, and species co-occurrence (MacKenzie et al. 2006). Applying this framework to our data, detection probability is the probability of capture within a single trap (hereafter “quadrat”) if Olympic Mudminnows were present at a site, and occupancy is the estimate of the proportion of occupied sites across the study area. We used the free software program PRESENCE version 8.4 (Hines and MacKenzie 2014) to analyze our data and test hypotheses using these models.

Care must be taken when using spatial units (e.g., quadrats) as replicates in occupancy and detection models, which were developed primarily for the analysis of repeated temporal surveys. Lack of independence between sampling units (i.e., unequal probability of encounter) can lead to large and unpredictable bias in the occupancy estimate (Kendall and White 2009). This bias is avoided if units have a constant probability of occupancy that is independent from other units (Guillera-Arroita 2011). Our sites represented areas of potentially suitable habitat for Olympic Mudminnows; traps were also placed in regularly spaced intervals (i.e., grid formation with lines perpendicular to shore) to assess areas independently of other traps. In this situation, the likelihood of encountering Olympic Mudminnows was equal (and independent) across spatial replicates and should result in unbiased estimates of occupancy.

We used the multiseason approach described in MacKenzie et al. (2003) to estimate detection probability and occupancy from our quadrat data collected in both sampling seasons (2013 and 2014) and compared these to naive occupancy estimates. The model includes parameters for both colonization

and extinction, but with small sample sizes, we chose a simpler model that estimated only the extinction (ϵ) parameter between years. Candidate models included those for which occupancy and detection were constrained to be constant or estimated separately by year. In our models we assumed that detection probability was constant across all quadrats, a realistic assumption based on site selection and sampling protocols. Models were fit to the 2 years of data and ranked using Akaike information criterion corrected for small sample size (AIC_c ; using the number of sites as the basis for adjustment for small sample sizes) based on the maximum likelihood estimates generated in PRESENCE. Under AIC_c , top-ranked models ($\Delta AIC_c \leq 2.0$) are considered the best descriptors of the data from the candidate set and model weights (w) indicate the relative support for each model (Burnham and Anderson 2002). Model-averaged estimates of the parameters were calculated using all models in the candidate set.

We used these model results to also evaluate the effectiveness of our sampling protocols for Olympic Mudminnows as a function of the number of quadrats (N) sampled within sites. We extracted estimates of P across all sites for every N and used the equation $(1 - P)^N$ to calculate a cumulative detection probability; this was compared with the range and average number of quadrats sampled.

The influence of abundance on detection probability was investigated by fitting finite-mixture models to the data from the three sites designated as low, medium, and high abundance. Finite-mixture models introduce parameters that estimate the probability of sites belonging to (unknown) groups with differing detection probabilities (MacKenzie et al. 2006: pages 137–139); we specified models with one, two, and three groups and compared models using AIC_c to determine support for abundance-induced heterogeneity in P . We also modeled and extracted quadrat-level estimates of P from these three sites to calculate and compare cumulative detection probabilities across sites of varying abundance.

Site-level and microhabitat characteristics.—The second objective of our survey was to identify the environmental characteristics associated with Olympic Mudminnow presence both within and across sites. Based on literature review we expected that Olympic Mudminnows would be associated with shallow and densely vegetated areas (Kuehne and Olden 2014). Temperature has also been suggested as a potentially important habitat feature in previous research studies but with highly uncertain relationships to occupancy and abundance (Meldrim 1968). We applied multivariate and modeling approaches to our 2014 sampling data (when a comprehensive suite of covariates was measured in each quadrat) to explore Olympic Mudminnow abundance, occupancy, and detection in relation to these environmental variables.

A principal component analysis (PCA) was used to summarize and visualize patterns of presence and abundance in relation to the quadrat-level environmental variables in sites where Olympic Mudminnows were present. The

log-transformed matrix of variables included the following: depth, distance to shore, temperature, conductivity, dissolved oxygen, and percent vegetative cover. The PCA was conducted using the *vegan* library in the R statistical programming environment (Oksanen et al. 2015).

A key advantage in the modeling approaches outlined by MacKenzie et al. (2002) is the ability to model both occupancy and detection as a function of covariates, helping to identify environmental associations at the site versus quadrat level (e.g., Albanese et al. 2007; Schloesser et al. 2012). We modeled occupancy as a function of percent vegetative cover (mean) and variation in depth (coefficient of variation [CV] = $100 \cdot \text{SD} / \text{mean}$); based on the PCA results we also included the minimum water temperature measured on the day of sampling within each site. Due to initial difficulties with model convergence, occupancy variables were screened for autocorrelation, but variance inflation factors were consistently low. We next examined the distribution of detection data across the range of each variable and identified a lack of sufficient spread in detections across the range of values for the CV of depth (i.e., the majority of Olympic Mudminnow detections were in sites with a high CV), which is problematic for regression modeling. To address problems of model convergence with the continuous depth variable as an occupancy covariate, we used a binary depth variable that distinguished sites with the highest variability in depth (upper quartile of CV) from other sites.

All quadrat-level environmental variables were included in the detection model (as sample or detection covariates), with the exception of distance to shore, which was strongly correlated with depth. Olympic Mudminnows preference for shallow depth and dense vegetation is well established (Meldrim 1968; Harris 1974), as is the tolerance of all mudminnow species for areas of low dissolved oxygen (Kuehne and Olden 2014). Temperature and conductivity were included in detection models due to their importance as indicators of groundwater input as well as their support in the PCA. All combinations of occupancy and detection variables were combined into 256 models and compared using AIC_c . Model-averaged estimates of parameters and errors were calculated using all models in the candidate set; relative variable importance was calculated by summing weights across all models containing the parameter (Symonds and Moussalli 2011).

RESULTS

Occupancy and Detection Modeling

Olympic Mudminnows were detected at 7 of our 22 sites (32%); two of these sites were substantially impacted by a beaver dam and the remaining five were backwater sloughs (Table S.1 in the online supplement). We sampled 421 quadrats in each year (mean = 19/site), with similar numbers of detections in 2013 (10 quadrats) and 2014 (11 quadrats). Sites with detections were consistently shallow, with a maximum recorded depth of 1.5 m (mean \pm SD = 0.6 ± 0.3 m). The

connectivity of sites with the main-stem river was reflected in overall high mean temperature (mean \pm SD = $20.6 \pm 2.0^\circ\text{C}$) and dissolved oxygen (5.7 ± 2.5 mg/L) levels, but these could be highly variable within sites (Table S.1 in the online supplement). At a site level, co-occurring species were common (minimum five species; Table S.1 in the online supplement) and were similar to suites of species captured at nondetection sites (data not shown).

We found strong evidence for consistent levels of occupancy across the two sampling years according to multiseason model selection; models with year-specific occupancy received only 7% of the AIC_c weights (Table 1). The second-ranked model—containing the parameter for local extinction—was within $\Delta AIC_c < 2$ of the most parsimonious model and had considerable weight, suggesting an overall constant level of occupancy with some extinctions and therefore similar numbers of colonizations. There was only weak support for differences in detection probability between years. Model averaging supported highly similar occupancy and detection between sampling years, and occupancy estimates were 47% higher than naive estimates (0.34 versus 0.23; Table 1). Changes in occupancy due to extinction or colonization was nonzero but with a high amount of variance.

Cumulative detection probabilities modeled as a function of the number of quadrats sampled (i.e., traps set) resulted in a low to moderate climbing detection curve (Figure 2A) but with fairly high detection probability ($>80\%$) for the average number of traps ($n = 19$) set at sites. Cumulative detection probability curves differed very little for sites with varying abundance that were sampled intensively in 2014 (Figure 2B). Model selection using AIC_c on finite-mixture models did not support more than one grouping of these sites based on detection probabilities, with the top-ranked (single group) model receiving 94% of the total weight and a ΔAIC_c of 5.72 between the first and second models.

Habitat Characteristics of Olympic Mudminnow Presence

In sites where Olympic Mudminnows were detected in 2014, quadrats with detections were clustered in relation to environmental characteristics, with 61% of the variation explained by the first two principal components (PCs; Figure 3). Olympic Mudminnow detections and abundance were associated strongly with PC1 (40% of variation explained; $P < 0.001$), which distinguished lower temperature followed by higher vegetative cover and conductivity. Relative to PC2 (21% variation explained; $P = 0.12$), Olympic Mudminnows were located in areas of shallow depth (close to shore) and with low dissolved oxygen.

The results of the PCA were supported and refined by model selection for occupancy and detection based on site- and quadrat-level variables across all sites (Table 2). The top-ranked model contained minimum temperature as predictor for occupancy, and depth and dissolved oxygen as

TABLE 1. Summary of the model selection procedure and parameter estimates (SE in parentheses) for Olympic Mudminnows in two seasons of sampling. Abbreviations are as follows: ΔAIC_c is the difference from the top-ranked AIC_c model, w is the AIC_c model weight, and K is the number of parameters. Parameters for occupancy (Ψ) and detection probability (P) were modeled as constant (.) or year specific (year); the parameter for extinction (ϵ) was modeled as constant. An asterisk indicates that the parameter was fixed and therefore known without error.

Model	ΔAIC_c	w	K	Ψ_{2013}	Ψ_{2014}	ϵ_{2013}	P_{2013}	P_{2014}
$\Psi(.)P(.)$	0.00	0.48	2	0.37 (0.118)	0.37 (0.118)	0.00 0.000*	0.06 (0.015)	0.06 (0.015)
$\Psi(.)\epsilon(.)P(.)$	1.21	0.26	3	0.30 (0.107)	0.30 (0.107)	0.28 (0.240)	0.07 (0.020)	0.07 (0.020)
$\Psi(.)P(\text{year})$	2.65	0.13	3	0.37 (0.118)	0.37 (0.118)	0.00 0.000*	0.06 (0.019)	0.06 (0.020)
$\Psi(.)\epsilon(.)P(\text{year})$	4.09	0.06	4	0.30 (0.106)	0.30 (0.106)	0.29 (0.237)	0.07 (0.024)	0.08 (0.029)
$\Psi(\text{year})\epsilon(.)P(.)$	4.23	0.06	4	0.31 (0.127)	0.30 (0.122)	0.29 (0.275)	0.07 (0.020)	0.07 (0.020)
$\Psi(\text{year})\epsilon(.)P(\text{year})$	7.41	0.01	5	0.33 (0.144)	0.28 (0.118)	0.32 (0.268)	0.07 (0.027)	0.08 (0.030)
Model-averaged estimates				0.34 (0.115)	0.34 (0.115)	0.29 (0.246)	0.07 (0.019)	0.07 (0.019)
Naive estimates				0.23	0.23			

good predictors of Olympic Mudminnow detection probability; this model was four times more likely than the second-ranked model based on model weights (0.20 and 0.05, respectively). However, a relatively large proportion of model weight ($\sim 30\%$) is represented in the subsequent

seven models, which are highly similar in structure to the top-ranked model, consistently differing by only one parameter (Table 2).

The support of multiple similar (“nested”) models is a recognized hazard in considering all model subsets (Burnham

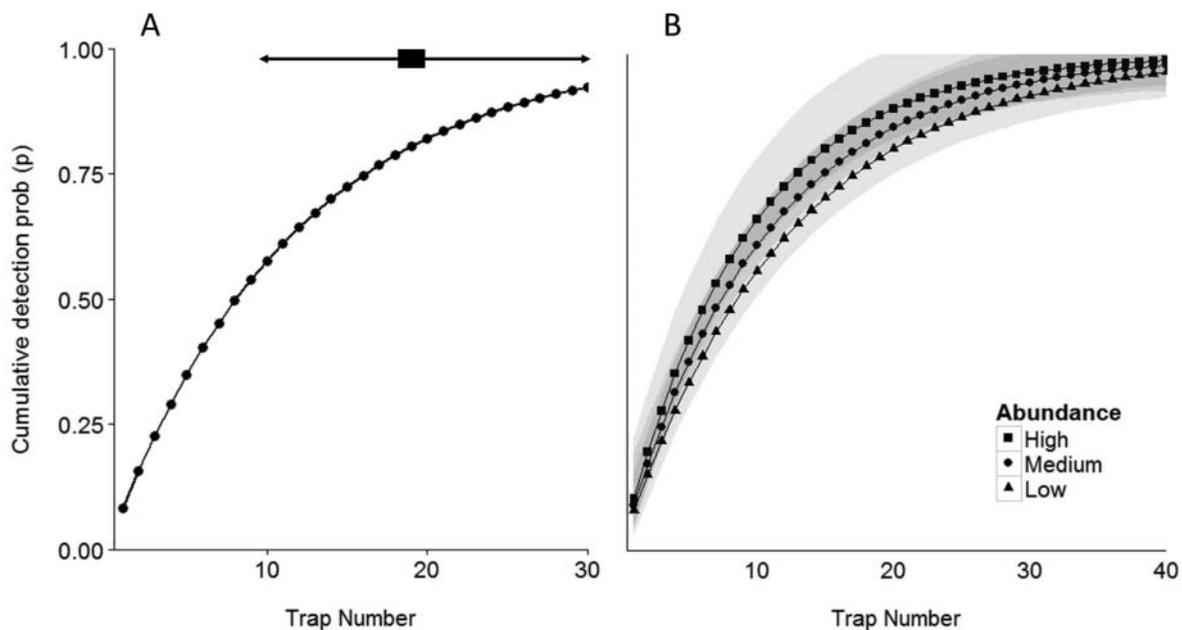


FIGURE 2. Cumulative detection probability for Olympic Mudminnows (A) as a function of the number of quadrats sampled (i.e., traps set) within a site. The horizontal bar at the top indicates the range (10–30 traps) and the filled box indicates the mean number (19) of traps set per site. Cumulative detection probability was also calculated (B) based on supplemental trapping (total $n = 40$) in 2014 in three sites known to vary in abundance of Olympic Mudminnows. The confidence intervals for the three curves are indicated in the overlapping shaded areas. The abundance was categorized based on CPUE as low (0.1), medium (0.3), and high (1.2).

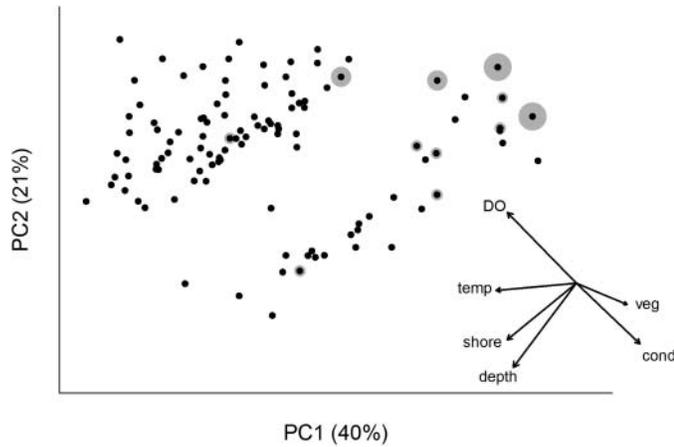


FIGURE 3. Principal component analysis of environmental data in sites where Olympic Mudminnows were detected in the second (2014) sampling season (five of seven total detection sites) when detailed trap-level environmental covariates were measured. The black circles represent all the traps, and the gray circles indicate Olympic Mudminnow abundance (\log_e abundance + 1; larger circles indicate higher abundance). The inset indicates the importance and relationship of each environmental metric to the first and second axes, which together explained 61% of the variation. Environmental vectors are coded as follows: DO = dissolved oxygen, veg = percent vegetation, cond = conductivity, shore = distance to shore, and temp = temperature ($^{\circ}$ C).

and Anderson 2002) and an appropriate case for the use of model averaging to estimate relative variable importance (Symonds and Moussalli 2011). The summed model weights for occupancy factors indicated that temperature was 2.5 times greater in importance than depth variability or percent vegetation (Table 3). Dissolved oxygen and depth were of similar importance in detection, followed by temperature and (to a much lesser degree) vegetation and conductivity.

TABLE 2. Summary of occupancy (Ψ) and detection probability (P) model selection procedure for the 2014 sampling season. The 10 highest-ranked models are shown; the null model $\Psi(\cdot)$, $P(\cdot)$ was minimally ranked relative to the covariate models ($\Delta\text{AIC}_c = 24.37$) and is not shown. Model selection procedures were based on all combinations of site-level occupancy covariates (MINTEMP = minimum temperature recorded, CV = coefficient of variation for depth > 75% of values, and VEG = mean percent vegetation) and quadrat-level detection covariates (Depth, Temp = temperature, DO = dissolved oxygen, Cond = conductivity, and Veg = percent vegetative cover).

Model	ΔAIC_c	w	K
$\Psi(\text{MINTEMP}), P(\text{Depth}, \text{DO})$	0.00	0.200	5
$\Psi(\text{MINTEMP}), P(\text{Depth}, \text{Temp}, \text{DO})$	2.73	0.051	6
$\Psi(\text{MINTEMP}, \text{VEG}), P(\text{Depth}, \text{DO})$	2.97	0.045	6
$\Psi(\text{CV}), P(\text{Depth}, \text{DO})$	3.07	0.043	5
$\Psi(\text{MINTEMP}, \text{CV}), P(\text{Depth}, \text{DO})$	3.07	0.043	6
$\Psi(\text{MINTEMP}), P(\text{Depth}, \text{DO}, \text{Cond})$	3.14	0.042	6
$\Psi(\text{MINTEMP}), P(\text{Depth}, \text{Veg}, \text{DO})$	3.15	0.041	6
$\Psi(\text{MINTEMP}), P(\text{Temp}, \text{DO})$	3.20	0.040	5
$\Psi(\cdot), P(\text{Depth}, \text{DO})$	4.63	0.020	4
$\Psi(\text{MINTEMP}), P(\text{DO})$	4.76	0.019	4

TABLE 3. Model-averaged parameter estimates, standard errors, and sums of model weights (w) for site-level and quadrat-level factors modeled as predictors of Olympic Mudminnow occupancy (Ψ) and detection probability (P). Model averaging was done using the entire candidate set. Parameter abbreviations are defined in Table 2.

Parameter	Estimate	SE	w (%)
Ψ_{CV}	-0.49	1.36	23
Ψ_{MINTEMP}	-0.91	0.39	62
Ψ_{VEG}	0.11	0.44	15
P_{Cond}	0.44	1.42	7
P_{Depth}	-3.54	1.79	30
P_{DO}	-0.54	0.21	37
P_{Temp}	-0.27	0.18	17
P_{Veg}	0.06	0.12	8

The model-averaged estimates for parameters support the increased probability of occupancy in sites with areas of low temperature (Table 3). Averaged estimates also indicated higher occupancy in sites with increased vegetation and more uniform depths, but large standard errors warrant caution in interpreting these relationships. Detection was positively associated with quadrats that were shallow, had low dissolved oxygen, and had lower temperatures. Detection was also positively associated with increased conductivity and vegetation, but large variances and low variable importance (Table 3) for these parameters suggest that they are not particularly good predictors of microhabitat selection by Olympic Mudminnows.

DISCUSSION

Occupancy and detection modeling for Olympic Mudminnows resulted in an occupancy rate that was 47% larger than naive estimates in any single year, demonstrating the utility of incorporating detection probabilities into monitoring programs for this species. Variances in our results were fairly large, which is likely to be an artifact of the sampling design. We surveyed a relatively low number of sites with large numbers of quadrats sampled; the number of quadrats was also scaled to site area, resulting in apparent missing observations in smaller sites. All of these factors can reduce precision in these modeling approaches (MacKenzie et al. 2002). Sampling a larger number of sites is recommended for future surveys but must be weighed against the need to carefully and comprehensively survey areas. Our results show (and are confirmed by experience in the field) that rather than being dispersed within sites, Olympic Mudminnows were often detected in proximity to a particular microhabitat (emergent springs). Moreover, detection was largely independent of abundance; both of these factors underscore the need for the comprehensive sampling of sites to increase the likelihood of detection.

Occupancy and detection were highly similar between sampling years, suggesting consistency in the ability of our

protocols to detect Olympic Mudminnows as well as the potential for site fidelity of individuals from year to year. Although site fidelity is assumed for this species in more discrete waterbodies (e.g., off-channel wetlands, oxbows) due to extremely poor dispersal ability (Meldrim 1968; DeHaan et al. 2014), much less is known about populations living in main-stem river environments. One hypothesis is that main-stem populations are simply sinks for permanent populations in nearby off-channel habitats; our results suggest instead that habitat specialization—whether in off-channel or main-stem areas—may be a greater determinant of Olympic Mudminnow presence in landscapes.

Occupancy and detection modeling based on environmental covariates identified the primary importance of lower temperature as a predictor of Olympic Mudminnow presence across sites. Within sites, dissolved oxygen and depth were of almost equal importance in predicting Olympic Mudminnow presence. Associations with shallow, shaded habitats have long been recognized for all mudminnow species, along with the ability to tolerate low dissolved oxygen (Kuehne and Olden 2014). However, our results suggest that in addition to shallow vegetation, Olympic Mudminnows may be seeking out regions with low dissolved oxygen, very low temperatures, and high conductivity, all of which are strong indicators of groundwater influence (Hendricks and White 1991). Field observations confirmed that Olympic Mudminnow detections tended to be aggregated in areas with very cold (e.g., 13–15°C as opposed to main-stem temperatures of ~20°C) springs nearby, particularly in 2014 when extremely low streamflows revealed emergent springs.

An association with groundwater is only partly surprising in the context of earlier research for Olympic Mudminnows as well as more current investigations for European Mudminnows. Meldrim (1968) conducted comprehensive year-round surveys of six sites across the range of Olympic Mudminnows and assessed movements in response to seasonal environmental characteristics over a 4-year period. His dissertation research documented temperature-dependent movements in both laboratory experiments and field surveys, with substantially greater effects observed during summer months. Although Meldrim's field sites were not selected randomly, he tellingly notes that studied sites had "numerous underground springs" (Meldrim 1968:16) and qualitatively noted aggregations of Olympic Mudminnows near springs in summer as we did. Thermoregulatory movements during peak summer months has also been suggested for European Mudminnow in oxbow lakes (Povž 1995b). Lastly, a study which modeled critical environmental factors for a remnant population of European Mudminnow in Austria concluded that restoration and sustainability of groundwater levels was the primary factor in persistence for that population (Wanzenböck 2004).

Areas of groundwater input can offer substantial advantages to fish, particularly for species like Olympic Mudminnows with low dispersal ability. Groundwater tends to be consistent between years over long time scales, buffering

against potential site desiccation in extremely dry years. It also offers a stable temperature regime year-round that is cooler than ambient temperature in the summer and warmer in winter (Power et al. 1999). Tolerance for low dissolved oxygen and temperature has been documented for all species of mudminnow and is largely assumed to facilitate habitation of shallow and densely vegetated areas, which are subject to environmental extremes (Martin-Bergmann and Gee 1985; Tonn 1985). The affinity for groundwater-influenced areas offers an added potential explanatory context for some of the biological attributes and environmental tolerances of not only Olympic Mudminnows but other species of mudminnow (Kuehne and Olden 2014).

Our results should be considered in light of the sampling restrictions and data limitations present in our study. Sites were not selected in a truly random fashion but represented areas of zero or extremely low flow along the river margin; sites were (by default) often shallow and densely vegetated. In this way we potentially influenced the occupancy and detection modeling by flattening the signal of some variables (e.g., depth and vegetation), which might be important in a randomized or systematic sampling or monitoring program. However, given the strong degree of habitat specialization documented for all species of mudminnow, we believe this heuristic level of initial site selection is appropriate.

Our occupancy and detection models were at times hampered by data limitations (i.e., a small number of sites) and sparse detections, both of which can be common in fisheries research—perhaps particularly when surveying rare, elusive, or cryptic species. Model convergence was initially problematic when we included a continuous variable (CV of depth) with too little spread of detections across the variable values, requiring categorization and subsequent loss of information in a potentially useful descriptor. We recommend that this factor—an indicator of both habitat heterogeneity and the presence of beaver dams—be further explored.

Even given these limitations, our results advance the science for the conservation and management of Olympic Mudminnows. A fundamental study objective was to detect new populations along the Chehalis River. The section of river we surveyed complements the extensive, rangewide investigations for Olympic Mudminnows by Harris (1974), who conducted very limited sampling east of the Satsop River (the downstream extent of our survey). Harris suspected that Olympic Mudminnow occurrence was infrequent and patchy east of the Satsop watershed (page 7), a conclusion consistent with our results. Beecher and Fernau (1983) sampled eight sites in the same area as our study, but like Harris and other historical sampling efforts, emphasized off-channel habitats (WDFW 2014). To our knowledge, the seven locations where we found Olympic Mudminnows are some of the very few detections in main-stem-oriented sites, and our results suggest that these may represent stable populations over time. Although we were able to anecdotally report on species co-occurrence at sites

with and without Olympic Mudminnows, our study was not designed to determine the role of potential competitors and predators in occupancy and detection. Prior research has indicated negative impacts or the potential exclusion of mudminnows by other fish species (Kuehne and Olden 2014); we recommend that this topic remains a priority for investigation for Olympic Mudminnows.

Detection probabilities for the average number of traps deployed were approximately 80%, giving us confidence in our ability to detect Olympic Mudminnows using these sampling protocols. Paired trapping and dipnetting efforts in the field showed that dipnetting was effective only at the highest levels of abundance recorded in our survey and is unlikely to detect Olympic Mudminnows at moderate to low levels of abundance (Kuehne, unpublished data). Electrofishing has also been used for this species in the past and offers a rapid survey technique but is confounded by dense vegetation, marshy substrates, and water clarity unless abundances are very high (Harris 1974). If the detection of populations at low to moderate abundance is desired, minnow traps likely represent the optimal sampling strategy, also offering a greater ability to estimate and compare abundances between sites and over time.

We detected a range of abundances in our sampling, including multiple sites where only a single fish was captured. Rather than a distribution consisting of the occupancy of limited, specialized habitats with locally abundant but highly discrete populations, our results suggest the potential for a patchy population that includes varying abundances and a greater diversity of suitable habitat. This is potentially good news for the conservation of Olympic Mudminnows in the Chehalis River basin, but it deserves greater attention through monitoring, including the estimation of changes in abundance as well as occupancy over time, particularly in response to potential future dam construction.

Importantly, our results indicate that riverine Olympic Mudminnow populations may rely on areas with groundwater springs during at least a portion of the year; these results are supported by similar findings by Meldrim (1968), who sampled largely in off-channel habitats. The affinity of Olympic Mudminnows for emergent springs could be for purposes of thermoregulation, for reducing predation or competition pressure by inhabiting areas with low dissolved oxygen (Tonn and Paszkowski 1986; Rahel and Nutzman 1994), or for other unknown reasons ripe for investigation. Groundwater resources can be compromised to the point of negatively impacting native fish (Deacon et al. 2007), particularly for highly endemic species (Votteler 1998). Given the concerns about development and agricultural pressures on the existing groundwater supplies in the Chehalis basin (Gendaszek 2011) and the potential for changes in groundwater dynamics through altered hydrologic regimes (Wanzenböck 2004), we believe our results point to a need to investigate the mechanisms and importance of this groundwater relationship for

Olympic Mudminnow occurrence and persistence on the landscape.

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Supplement: Characteristics of Sites where Olympic Mudminnows were Detected

Supplementary Table S.1. Environmental characteristics and catch rates for sites where Olympic Mudminnows were detected in 2013 and 2014. The mean and range of environmental covariates are reported for 2014, when the comprehensive suite of covariates were measured at the quadrat level. The CPUE is reported separately for the two sampling seasons as the rate across all traps, with the maximum number of fish (max) captured in a single trap in parentheses. Abbreviations are as follows: RKM = river kilometer, DO = dissolved oxygen, temp = temperature, and nd = no Olympic Mudminnows were detected in that year at that site.

Site location (latitude, longitude)	RKM	Area sampled (m ²)	Habitat type	Mean depth in meters (range)	Mean DO in mg/L (range)	Mean temp in °C (range)	Number of traps	Co-occurring species	CPUE 2013 (max)	CPUE 2014 (max)
46.83262, -123.2527	70.5	1,230	Backwater slough	0.44 (0.15–1.05)	6.7 (1.2–9.6)	20.1 (13.5–23.1)	20	Rock Bass <i>Ambloplites rupestris</i> , <i>Cottus</i> spp., Threespine Stickleback <i>Gasterosteus aculeatus</i> , Pumpkinseed <i>Lepomis gibbosus</i> , Northern Pikeminnow <i>Ptychocheilus oregonensis</i> Largescale Sucker <i>Catostomus macrocheilus</i> , <i>Cottus</i> spp., Pacific Lamprey <i>Entosphenus tridentatus</i> , Threespine Stickleback, Pumpkinseed, Coho Salmon <i>Oncorhynchus kisutch</i> , Northern Pikeminnow, Redside Shiner <i>Richardsonius balteatus</i> , Speckled Dace	nd	0.05 (1)
46.84675, -123.2503	69.0	1,840	Backwater slough	0.37 (0.20–0.80)	5.1 (2.3–9.2)	20.0 (18.3–22.9)	26	<i>Rhinichthys osculus</i>	0.04 (1)	nd
46.85946, -123.2671	66.5	1,600	Dammed slough	0.73 (0.10–1.40)	2.0 (1.1–4.6)	20.6 (19.7–25.1)	20	Rock Bass, Common Carp <i>Cyprinus carpio</i> , Threespine Stickleback, Pumpkinseed, Northern Pikeminnow	nd	0.20 (1)
46.86275, -123.2669	65.0	1,400	Dammed slough	0.80 (0.15–1.30)	5.3 (4.6–6.6)	20.2 (20.0–21.2)	20	Rock Bass, <i>Cottus</i> spp., Largescale Sucker, Threespine Stickleback, Pumpkinseed, Northern Pikeminnow, Speckled Dace	0.05 (1)	nd

Site location (latitude, longitude)	RKM	Area sampled (m ²)	Habitat type	Mean depth in meters (range)	Mean DO in mg/L (range)	Mean temp in °C (range)	Number of traps	Co-occurring species	CPUE 2013 (max)	CPUE 2014 (max)
46.90141, -123.2939	60.5	1,400	Backwater slough	0.71 (0.10–1.50)	7.1 (1.5–11.2)	21.4 (13.2–23.2)	20	Rock Bass, <i>Cottus</i> spp., Threespine Stickleback, Pumpkinseed, Northern Pikeminnow	0.90 (17)	1.55 (16)
46.91685, -123.3043	58.0	2,700	Backwater slough	0.56 (0.20–1.50)	6.4 (2.6–10.6)	21.4 (18.1–23.0)	30	Brown Bullhead <i>Ameiurus nebulosus</i> , Rock Bass, <i>Cottus</i> spp., Threespine Stickleback, Pumpkinseed, Warmouth <i>Lepomis gulosus</i> , Black Crappie <i>Pomoxis nigromaculatus</i> , Northern Pikeminnow	0.03 (1)	0.03 (1)
46.98561, -123.408	38.5	2,250	Backwater slough	0.44 (0.10–1.30)	7.0 (3.1–9.9)	20.0 (14.2–21.6)	20	Brown Bullhead, Rock Bass, <i>Cottus</i> spp., Threespine Stickleback, Pumpkinseed, Northern Pikeminnow, Redside Shiner	0.80 (6)	0.45 (4)