

# Integrating models to predict distribution of the invertebrate host of myxosporean parasites

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**Abstract:** *Manayunkia speciosa*, a freshwater polychaete, is the invertebrate host of myxosporean parasites that negatively affect salmonid populations in the Pacific Northwest of the USA. Factors that drive the distribution of *M. speciosa* are not well understood, which constrains our understanding of disease dynamics and the development of management solutions. We described the distribution of *M. speciosa* at 3 sites on the Klamath River, California, based on 2-dimensional hydraulic models (2DHMs) and a generalized linear mixed model (GLMM). 2DHMs were built to explain hydraulic variation at each site and used to stratify biological sampling effort along depth–velocity gradients and by substrate class. We assessed the presence/absence of *M. speciosa* at 362 georeferenced locations in July 2012 and built GLMMs to describe relationships between hydraulic and substrate variables and the distribution of *M. speciosa*. The best-fitting GLMMs demonstrated that *M. speciosa* distributions were associated with depth–velocity conditions and substrate size during base discharge (area under the receiver operating characteristic curve [AUC] = 0.88) and at peak discharge (AUC = 0.86). We evaluated the GLMMs with an independent data set collected in July 2013 ( $n = 280$ ) and found that the top models predicted the distribution of *M. speciosa* with a high degree of accuracy (AUC = 0.90). These results support the conclusion that the summer distribution of *M. speciosa* is related to observed hydraulic and substrate conditions during base discharge (summer) and modeled hydraulic and substrate conditions during peak discharge (late winter to early spring). These results may have implications for the use of flow manipulation as a disease management tool. These results also illustrate the importance of examining species distribution data in the context of temporally disconnected environmental factors and demonstrate how models can fulfill this need.

**Key words:** *Manayunkia speciosa*, salmonid disease, enteronecrosis, *Ceratonova shasta*, *Parvicapsula minibicornis*, two-dimensional hydraulic model, niche

Flow modification is one the most conspicuous negative anthropogenic effects on riverine hydrology (Bunn and Arthington 2002, Carpenter et al. 2011). Flow modification can affect the dynamics of infectious and parasitic diseases (Patz et al. 2000, Marcogliese 2001, 2008, Carpenter et al. 2011) because it affects many aspects of ecosystem function (Karr 1991, Poff et al. 1997, 2007). Changes in flow regime can create or expand habitat for invertebrate hosts, which can in turn exacerbate disease risk. For example, the construction of large dams is correlated with increased risk of schistosomiasis (bilharzia) and malaria because dams create or expand habitat for aquatic invertebrate hosts (Jobin 1999, Seto et al. 2008). Methods for predicting how disease dynamics may respond under future conditions will be in demand as anthropogenic disturbance and global climate

change intensify. However, studies describing relationships between altered environmental conditions and invertebrate host-species distributions are uncommon. These data are necessary for understanding how rapidly changing environmental conditions may alter the distribution of hosts and, in turn, the dynamics and risk of freshwater diseases.

The freshwater polychaete, *Manayunkia speciosa*, is the obligate invertebrate host of 2 myxosporean parasites, *Ceratonova* (syn *Ceratomyxa*) *shasta* (Bartholomew et al. 1997) and *Parvicapsula minibicornis* (Bartholomew et al. 2006) that infect salmonids in the USA Pacific Northwest. *Ceratonova shasta* causes necrosis of intestinal tissue that can be accompanied by a severe inflammatory reaction (enteronecrosis) and subsequent death of the salmonid host (Bartholomew et al. 1989). *Parvicapsula minibicornis* causes ne-

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DOI: 10.1086/688342. Received 3 November 2015; Accepted 11 May 2016; Published online 22 July 2016.  
Freshwater Science. 2016. 35(4):1263–1275. © 2016 by The Society for Freshwater Science.

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crisis of kidney tissue (glomerulonephritis) (Kent et al. 1997, Raverty et al. 2000) that has been implicated as a causal factor in elevated salmonid prespaw mortality (St-Hilaire et al. 2002). Both parasites alternate between 2 waterborne spore stages, myxospores and actinospores (Bartholomew et al. 1997, 2006). Myxospores infect *M. speciosa* (Meaders and Hendrickson 2009). After infection, parasites develop into actinospores and are released into the water column where they may encounter and infect salmonids (Bartholomew et al. 1997, 2006, Meaders and Hendrickson 2009). After salmonid infection, parasites develop into myxospores and are released either as they mature (*P. minibicornis*, shed along with urine; Kent et al. 1997) or upon death of infected fish (*C. shasta*; Bartholomew et al. 1997, Bjork and Bartholomew 2009). Both *C. shasta* and *P. minibicornis* infect salmonids in the Klamath River, California (Hendrickson et al. 1989, Stocking et al. 2006, Bartholomew et al. 2007, True et al. 2013).

Interest in understanding and managing *C. shasta* in the Klamath River ecosystem is considerable because infection has been linked to population declines in juvenile and adult fall-run Chinook Salmon (Fujiwara et al. 2011, True et al. 2013). Reducing polychaete populations is one potential management action that warrants consideration because prophylaxes do not exist for fish and reducing waterborne parasite stages would be difficult and expensive (e.g., Lukins et al. 2007). Salmonid whirling disease, caused by the myxosporean parasite *Myxobolus cerebralis*, has been managed successfully in hatcheries by reducing obligate invertebrate host habitat (Wagner 2002, Kerans and Zale 2002). Reducing *M. speciosa* habitat in the Klamath River may be effective for managing *C. shasta* in Klamath River salmon. However, the ecological requirements of *M. speciosa* are not well understood and must be described before the development of solutions to reduce polychaete host habitat for fish disease management.

Flow manipulation has been proposed as a method for reducing polychaete host habitat but the degree of manipulation required to alter the suitability of habitat for *M. speciosa* is unknown. The importance of velocity and substrate has been demonstrated for benthic invertebrates (Resh et al. 1988, Townsend et al. 1997, Jowett 2003). *Manayunkia speciosa* (Leidy 1883) is a tiny (3–5 mm; Holmquist 1967) benthic suspension feeder that constructs and inhabits flexible tubes composed of mucus and fine sediment particles (Poe and Stefan 1974, Fauchald and Jumars 1979). In the Klamath River, *M. speciosa* (Hazel 1966) has been collected from habitats with velocities from 0 to 0.31 m/s and depths up to 3 m (Stocking and Bartholomew 2007, Jordan 2012) but high densities (>100,000 individuals [ind]/m<sup>2</sup>) have been observed only in slowly flowing (≤0.05 m/s) areas 1 to 2 m deep (Stocking and Bartholomew 2007, Jordan 2012). These observations suggest that these conditions may be optimal. However, *M. speciosa* distribution has not been described along the entire depth–velocity continuum in this system,

and whether specific combinations of depth–velocity may preclude colonization or establishment is not known.

The distribution of *M. speciosa* is also influenced by substrate in the Klamath River (Stocking and Bartholomew 2007, Malakauskas and Wilzbach 2012). Polychaetes have been detected on substrates ranging in grain size from <1 to >256 mm (silt–bedrock), but high densities (>100,000 *M. speciosa*/m<sup>2</sup>) have been observed only on silt, sand, boulder, and bedrock substrates (Stocking and Bartholomew 2007, Jordan 2012, Alexander et al. 2014), which suggests these substrates are optimal. However, interannual variation in polychaete densities among substrates suggests suitability is not static. For example, high densities of *M. speciosa* were observed on silt/sand and boulder/bedrock substrates in summer following a low peak discharge (49.8 m<sup>3</sup>/s), whereas high densities were observed on only boulder/bedrock substrates in summer following a higher (161.3 m<sup>3</sup>/s) peak discharge (Jordan 2012) and were associated with periphyton (*Cladophora* sp.) in velocities >0.15 m/s (Stocking and Bartholomew 2007). One explanation for the difference is that high velocities during peak discharge caused dislodgement of *M. speciosa* and limited recolonization. Malakauskas et al. (2013) demonstrated that substrate type and shear velocities >3 cm/s influenced dislodgement probability of *M. speciosa* in a controlled laboratory flume study. Dislodgement risk in natural systems probably differs among substrate types (e.g., flow refugia; Lancaster and Hildrew 1993) and flow conditions. Thus, interactions between hydraulics and substrate type could explain much of the variation in the distribution of *M. speciosa* in the Klamath River.

If habitat selection is based on both hydraulic and substrate suitability, the spatial distribution of *M. speciosa* should correspond to the spatial pattern of physical conditions in a river reach. The ability to relate the distribution of *M. speciosa* to the physical environment is critical for our understanding of this host's ecological requirements and may facilitate the development or evaluation of disease management solutions. Our approach was to use a study design that stratified sampling effort to represent best the range of hydraulic and substrate conditions and to test the association of *M. speciosa* presence with the range of hydraulic and substrate variables. We integrated 2-dimensional hydraulic models (2DHMs) and generalized linear mixed models (GLMMs) to examine the spatial distribution of *M. speciosa* in relation to microhabitat-scale hydraulic and substrate conditions. The objectives of our study were to formally test the association of polychaete presence with physical environmental variables based on variables that were measured in situ or predicted with 2DHMs and to build a model to predict distribution of *M. speciosa* within selected study sites. We collected polychaete (presence/absence) and environmental (hydraulic and substrate) data during summer months when sampling was possible because of low-flow conditions. We used the 2DHMs primarily to predict hydraulic (depth, velocity, shear stress) data during times of the year when conditions pre-

cluded sampling, in particular during peak-discharge events, so we could evaluate relationships between seasonal peaks in polychaete distribution (summer) and the physical environmental conditions that occur during peak discharge (late winter to early spring). The purpose of the GLMM was to predict the spatial distribution of *M. speciosa* based on substrate and hydraulic conditions during base (summer; observed and modeled conditions) and peak (late winter to early spring; modeled conditions only) discharge. Our specific objectives were to: 1) test for significant variation in habitat variables (e.g., depth, velocity, and substrate size) related to the distribution of *M. speciosa*, 2) develop a model for predicting probability of *M. speciosa* presence, and 3) evaluate the predictive performance of the GLMM with an independent data set.

## METHODS

### Study sites

We conducted our study in the Klamath River, California, where salmonid population declines have been attributed to *C. shasta* (Fujiwara et al. 2011, True et al. 2013). The Klamath River watershed encompasses ~26,000 km<sup>2</sup> in California and 14,000 km<sup>2</sup> in Oregon and flows into the Pacific Ocean near Klamath, California (Fig. 1). A series of irrigation and hydropower dams divide the river into upper and lower basins, and Iron Gate Dam, the most-downstream

dam at river kilometer (rkm) 310 is a barrier for anadromous salmonids. Anadromous salmonids in the lower basin include spring- and autumn-run Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*Oncorhynchus kisutch*), Steelhead (*Oncorhynchus mykiss*), and Cutthroat Trout (*Oncorhynchus clarkii*).

We sampled polychaetes in July 2012 and 2013 at 3 study sites on the mainstem river downstream from Iron Gate Dam. The study sites included one near the Tree of Heaven Campground (site A, rkm 281; 350 m in length), one upstream of the confluence with Beaver Creek (site B, rkm 264; 550 m), and one downstream from the confluence with Beaver Creek at the Klamath Community Center (site C, rkm 259; 850 m) (Fig. 1).

### Hydraulic model development

We built 2DHMs for each study site to provide fine-scale predictions of depth, mean column velocity, and shear stress values over a range of discharges using the US Geological Survey's (USGS) Multi-Dimensional Surface-Water Modeling System (McDonald et al. 2005, 2006). The 2DHMs required input data including site topography, a stage-discharge relationship describing the boundary conditions, water surface elevations for calibration and validation, and spatially delineated bed roughness height in terms of substrate grain size and vegetation type. The methods and data

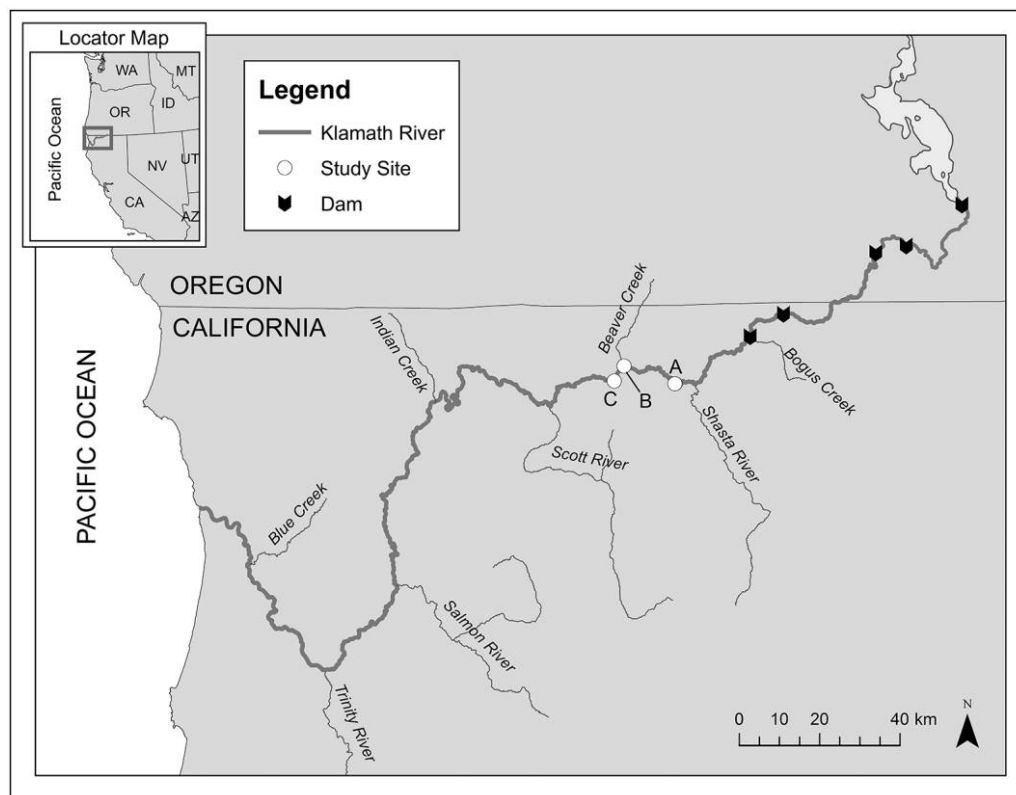


Figure 1. Map of the study area on the Klamath River, California, showing the 3 study sites for which 2-dimensional hydraulic models were developed and used to stratify sampling effort for *Manayunkia speciosa* in 2012 and 2013.

used in the development and validation of the 2DHMs were described by Wright et al. (2014). Water surface elevations for calibration and validation were surveyed over a range of measured discharges (33.33–149.99 m<sup>3</sup>/s) that occurred 10 February–17 August 2011. We generated hydraulic predictions at a mesh element resolution of 0.25 m<sup>2</sup> (sites A and B) or 0.56 m<sup>2</sup> (site C).

### Sampling methods

We assessed the presence or absence of polychaetes at a total of 362 (99–136/site) georeferenced sampling points from 5–26 July 2012. We adopted a model-based sampling strategy based on D-optimality (Kiefer 1958). Under D-optimality, a sampling design is most efficient at detecting effects when samples are allocated to regions of the explanatory variables' multivariate space with the greatest leverage. Under this strategy, we first allocated samples to the extremes of the combinations of (model-predicted) depth and velocity variables separately for each substrate classification. We generated substrate maps for each site by classifying the surveyed reach-wide median substrate grain size ( $D_{50}$ ) with a modified Wentworth scale (silt/sand: <2 mm, gravel: 2–64 mm, cobble: 65–256 mm, boulder: >256 mm, bedrock; Wentworth 1922) (Wright et al. 2014). We added samples at intermediate combinations of depth and velocity to allow estimation and assessment of interaction effects between, and quadratic effects within, depth and velocity. We spatially stratified samples falling within the same general depth, velocity, and substrate groups along the longitudinal gradient of each study site.

We selected sampling locations based on hydraulic conditions (i.e., depth, velocity) predicted from the 2DHM for the peak discharge of the water year based on a priori hypotheses that *M. speciosa* distribution was related to hydraulic conditions that occurred during peak discharge. We estimated water-year peak discharge for each study reach by summing the maximum mean daily discharge measured at USGS gaging station 11516530 downstream of Iron Gate Dam with estimated tributary accretions based on tributary watershed size (Reclamation 2011). In 2012, the maximum daily discharge occurred on 8 April and estimated site discharges were 122.10 (site A), 126.69 (site B), and 135.95 m<sup>3</sup>/s (site C). We predicted depth and velocity that occurred at peak discharge (hereafter denoted by a PD subscript) for each 2DHM mesh element and preselected sampling points for all combinations of low, medium, and high depth ( $D_{PD}$ ) and velocity ( $V_{PD}$ ) for each substrate class. All substrate types were sampled in both years, but boulder substrates composed the largest proportion of sampling points (Table 1).

### Field sampling

We located and georeferenced sampling points with a differential global positioning system (GPS; ProXH with

Table 1. Presence/absence samples shown by site, substrate category, and study year.

Site	Substrate	2012		2013	
		Absent	Present	Absent	Present
A	Cobble	28	3	14	0
	Gravel	16	14	17	0
	Silt/sand	26	11	19	0
	Boulder/bedrock	5	24	20	11
B	Cobble	23	1	24	2
	Gravel	19	2	19	0
	Silt/sand	15	0	15	1
	Boulder/bedrock	23	16	31	13
C	Cobble	29	3	26	1
	Gravel	21	4	14	1
	Silt/sand	27	1	16	0
	Boulder/bedrock	22	29	17	18

Zephyr antenna; Trimble, Sunnyvale, California). GPS positions were corrected using the wide-area augmentation system. Observations (hereafter denoted by a OBS subscript) were collected at each sampling point by divers using snorkel ( $\leq 1.5$ -m depth) or SCUBA ( $> 1.5$ -m depth) equipment. To collect a polychaete observation, the divers positioned a 50-cm<sup>2</sup> grid over the sampling point and noted the presence or absence of tubes inhabited by *M. speciosa*. Many aquatic invertebrates construct tubes attached to substrate, but those constructed and inhabited by *M. speciosa* have a characteristic morphology that is conducive to field identification by trained observers. We have not previously observed empty or uninhabited tubes, but we collected benthic samples at a subset of observation points to confirm the association of *M. speciosa* with the presence of tubes.

We collected environmental data including in situ depth ( $D_{OBS}$ ), mean column velocity ( $V_{OBS}$ ), and  $D_{50}$  at each sampling point. We measured  $D_{OBS}$  to the nearest 0.02 m with a wading rod. We measured  $V_{OBS}$  with a portable flow meter (FH950; Hach Instruments, Loveland, Colorado) at  $0.6 \times$  depth to estimate mean column velocity. To measure substrate size, divers selected a rock characterizing the  $D_{50}$  of the sampling point and measured its secondary axis to the nearest 0.001 m. We used the modified Wentworth scale to classify this  $D_{50}$  within substrate size classes. We used these substrate data as GLMM inputs. We also recorded the presence of other invertebrates, periphyton, organic matter, macrophytes, and woody debris at each sampling point. We recorded anoxia when velocity was 0 m/s, gas bubbles were released upon sediment disturbance, and the odor of S was detected.

At the time of 2012 data collection, river discharge was estimated as 33.90, 32.96, and 32.36 m<sup>3</sup>/s at sites A, B, and C, respectively, based upon stage–discharge rating curves

developed by Wright et al. (2014). We used these values to model base (low) discharge conditions (the model equivalents for  $V_{\text{OBS}}$  and  $D_{\text{OBS}}$ ). They are denoted with subscript BD (e.g.,  $D_{\text{BD}}$  to denote modeled depth values at base discharge).

In 2013, we collected an independent data set to evaluate the prediction performance of the GLMM (constructed using the 2012 data). We used the same 3 sites because 2DHMs were not available for other sites. We used the same methods to select the new sampling locations. Sampling occurred 8–24 July 2013, and a total of 279 samples were collected from new sampling points at the 3 sites (81–105/site).

### Predictive model development

We used a GLMM to estimate the association of polychaete presence with physical variables. In this model, we used a logit link and a random effect to account for the correlation of samples collected at each of the 3 sites. Our model is:

$$Y(\mathbf{s}) = \begin{cases} 1 & \text{if polychaetes present at } \mathbf{s} \\ 0 & \text{if no polychaetes present at } \mathbf{s} \end{cases} \quad (\text{Eq.1})$$

with

$$\begin{aligned} Y(\mathbf{s}) &\sim \text{Ber}(p(\mathbf{s})), \\ \text{logit}(p(\mathbf{s})) &= x(\mathbf{s})\beta + w(\mathbf{k}), \\ w(\mathbf{k}) &\sim N(0, \sigma^2 R(\varphi)) \end{aligned} \quad (\text{Eq.2})$$

where  $Y$  denotes the presence or absence of polychaetes,  $\mathbf{k}$  indicates site, and  $\mathbf{s}$  indicates spatial location within site; and  $x(\mathbf{s})$  are spatially referenced explanatory variables,  $\beta$  is a vector of coefficients,  $\text{Ber}$  represents the Bernoulli distribution (i.e., a binomial distribution with index parameter = 1), and  $w(\mathbf{k})$  is a random effect allowing correlation among samples collected within the same site ( $R(\varphi)$ ). We obtained maximum likelihood parameter estimates with adaptive Gauss–Hermite quadrature via the GLIMMIX procedure in SAS (version 9.2; SAS Institute, Cary, North Carolina).

Candidate models included either  $D_{\text{OBS}}$  and  $V_{\text{OBS}}$  or their counterparts predicted by the 2DHM during peak discharge ( $D_{\text{PD}}$  and  $V_{\text{PD}}$ ) or base discharge ( $D_{\text{BD}}$  and  $V_{\text{BD}}$ ). We considered quadratic effects of these variables, their interactions, and a categorical variable for observed substrate size class. We considered univariate models for shear stress at peak discharge and base discharge ( $SS_{\text{PD}}$  and  $SS_{\text{BD}}$ ), but excluded other variables because of multicollinearity concerns. We considered other biologically sensible models including presence of biota (e.g., periphyton), univariate models (e.g., substrate, distance to boulder/bedrock), and simpler multivariate models (e.g., depth and velocity). We ranked individual models based on Akaike's Information Criteria (AIC). We opted a priori to select the most parsimonious model

as that which had the fewest parameters within 2 points of the minimum AIC score (Burnham and Anderson 2002).

### Predictive model assessment

AIC ranks the model fit among a set of candidate models, but does not assess the adequacy of model performance. To assess the predictive accuracy of our selected model, we calculated the area under the receiver operating characteristic (ROC) curve (AUC) for the predicted values based on our chosen model. AUC is a widely used measure of predictive performance for continuous outputs (e.g., predicted probabilities of presence that range from 0–1) (Fawcett 2006, Wang et al. 2011) and has been used to assess the predictions of aquatic organisms generated from GLMMs (Wenger et al. 2013). Graphically, AUC plots the true positive rate (sensitivity) against the false positive or true negative (specificity) rate across the range of threshold values. AUC values range from 0 to 1, where 1 indicates perfect classification and 0 indicates perfect misclassification. A common reference AUC value is 0.5, which indicates performance is no better than random classification. We evaluated our AUC values according to Swets (1988), where 0.5–0.7 indicates low accuracy, 0.7–0.9 indicates good accuracy, and 0.9–1.0 indicates high accuracy. We used the R package *pROC* (Robin et al. 2011) to calculate AUC values and create the figures, which included 95% confidence intervals (CIs) generated with 2000 bootstrap resamples (Carpenter and Bithell 2000).

We calculated AUC values comparing the predicted and observed values from the selected model for the 2012 data (used to fit the model and estimate parameters) and also for the independent data set collected in 2013. We incorporated the random effects of our model into our predictions in 2 ways. For mixed effects models (those containing both fixed and random effects), prediction can be cast as either marginal or conditional. Predictions that contain the estimated site-specific random effects values are called conditional, whereas marginal predictions arise when the site-specific information is not included (Welham et al. 2004). Because marginal predictions do not incorporate site-specific information, they are prone to larger prediction errors (Meng et al. 2009). For the 2012 data, we computed conditional predictions. For the 2013 data, we computed marginal predictions. We adopted this approach to be conservative in our assessment of the predictive capabilities of our GLMM because this approach mimics the scenario of making predictions at other river locations where site-specific random effects are not known.

## RESULTS

### Observation data

Samples were collected from depths of 0.05 to 5.6 ( $D_{\text{OBS}}$ ), 0.04 to 5.79 ( $D_{\text{BD}}$ ), and 0.31 to 6.46 m ( $D_{\text{PD}}$ ) and velocities of 0 to 1.73 ( $V_{\text{OBS}}$ ), 0 to 1.4 ( $V_{\text{BD}}$ ), and 0.01 to 2.85 m/s

( $V_{PD}$ ). Samples were collected from all substrate types and from areas of shear stress modeled from 0 to 51.38 ( $SS_{BD}$ ) and 0.003 to 138.72 ( $SS_{PD}$ ).

### Candidate predictive models

The top-ranked model by AIC included  $D_{OBS}$ ,  $V_{OBS}$ ,  $D_{OBS}^2$ , and the categorical substrate variable and was >10 AIC units better than the next-best-fitting model (Tables 2, 3). The 2<sup>nd</sup> and 3<sup>rd</sup> best-fitting predictive models included the same variables as the top-ranked model with the addition of an interaction term for depth and velocity, but with variables predicted based on the 2DHMs at peak and base flow discharge respectively rather than those measured in situ (Table 2).

In general, the probability of polychaete presence was highest at intermediate depths and decreased with increasing velocity (Fig. 2A–D, Table 3). Substrate also had a strong estimated effect (Table 3), with the highest predicted probabilities (>0.875) of polychaete presence occurring only on the boulder and bedrock substrates (Fig. 2A), intermediate probabilities (<0.625) occurring on gravel (Fig. 2C), and low probabilities (<0.375), occurring on the remaining substrate types, cobble, and sand/silt (Fig. 2B, D).

### Predictive model assessment

We used the AUC to evaluate predictive model performance. When we evaluated the ability of model 1 to predict the data used to estimate its parameters, the AUC value was 0.88 (95% CI: 0.84–0.91; Fig. 3A) with values spanning from good to excellent accuracy (Swets 1988). The model's predictive capabilities were nearly identical when we evaluated the predictions for the independent 2013 data, with AUC = 0.88 (95% CI: 0.83–0.93; Fig. 3B). The AUC

value for the best-fitting model using peak-discharge covariates (model 2) was 0.86 (95% CI: 0.82–0.90; Fig. 3C), again with similar results regarding predictive performance with the independent 2013 data (AUC = 0.90; 95% CI: 0.85–0.94; Fig. 3D) (Table 3).

## DISCUSSION

We used a novel approach for modeling the spatial distribution of *M. speciosa* (obligate host for salmon parasites) by integrating outputs from 2DHMs with field observations to develop a predictive model. We used the 2DHMs to stratify our sampling effort to capture covariation in depth, velocity, and substrate, which allowed us to test hypotheses that specific physical environmental variables drive the distribution of *M. speciosa*. The 2DHMs also provided a method for predicting hydraulic conditions at peak discharge that enabled us to examine relationships between environmental variables when they could not be sampled (peak discharge occurs in winter to late spring) and the summer distribution of *M. speciosa* (peak abundance season; Jordan 2012). Quantifying the relationship between *M. speciosa* and hydraulic conditions during peak discharge is important for the Klamath River system because managers are interested in using flow manipulation to reduce polychaete host abundance as a method to mitigate salmonid disease risk.

We constructed GLMMs using environmental data that were measured either in situ or were output from the 2DHMs and *M. speciosa* presence/absence data collected in 2012. We presented results for 2 of the top-ranked models, including 1 derived from inputs of observed data (Model 1) and 1 derived from inputs of 2D modeled data

Table 2. Summary of the top 10 Akaike's Information Criterion (AIC)-ranked candidate models considered for predicting the probability of *Manayunkia speciosa*. D = water depth, V = mean column velocity,  $OBS$  = measured in situ at base discharge,  $BD$  = predicted using 2-dimensional hydraulic models (2DHMs) at base discharge (33.90, 32.96, and 32.36  $m^3/s$  at sites A, B, and C, respectively, based upon stage–discharge rating curves developed by Wright et al. 2014),  $PD$  = predicted using 2DHMs at peak discharge (122.10, 126.69, and 135.95  $m^3/s$  at sites A, B, and C, respectively). SE = standard error,  $\Delta AIC$  = difference in AIC between the model and the top model,  $D|V = D + V + (D \times V)$ .

Model	Model variables	Site effect (SE)	AIC score	$\Delta AIC$
1	$D_{OBS}$ , $V_{OBS}$ , $D_{OBS}^2$ , substrate	0.89 (0.80)	314.08	–
2	$D_{PD} V_{PD}$ , $D_{PD}^2$ , substrate	0.73 (0.67)	326.70	12.62
3	$D_{BD} V_{BD}$ , $D_{BD}^2$ , substrate	0.69 (0.60)	327.32	13.24
4	$D_{PD} V_{PD}$ , substrate	0.58 (0.54)	339.49	25.41
5	$D_{OBS} V_{OBS}$ , substrate	0.60 (0.56)	341.89	27.81
6	$D_{BD} V_{BD}$ , substrate	0.59 (0.55)	343.79	29.71
7	Substrate	0.63 (0.58)	353.26	39.18
8	$D_{OBS} V_{OBS}$	0.15 (0.16)	426.24	112.16
9	ShearStress $_{BD}$	0.14 (0.15)	434.93	120.85
10	ShearStress $_{PD}$	0.13 (0.14)	436.84	122.76

Table 3. Effects table for model 1:  $D_{OBS}$ ,  $V_{OBS}$ ,  $D_{OBS}^2$ , substrate (AIC = 314.08); and model 2,  $D_{PD}|V_{PD}$ ,  $D_{PD}^2$  substrate (AIC = 326). See Table 2 for explanation of variables.

Effect	Substrate	Estimate	SE	df	<i>t</i>	<i>p</i>
Model 1						
Intercept		-0.5469	0.7569	2	-0.72	0.5450
$D_{OBS}$		2.3366	0.5128	353	4.56	<0.0001
$V_{OBS}$		-3.2823	0.7298	353	-4.50	<0.0001
$D_{OBS}^2$		-0.4768	0.1072	353	-4.45	<0.0001
Substrate	Cobble	-3.1934	0.5110	353	-6.25	<0.0001
	Gravel	-2.2350	0.4182	353	-5.34	<0.0001
	Silt/sand	-3.2021	0.4857	353	-6.59	<0.0001
	Boulder/bedrock	0	-	-	-	-
Model 2						
Intercept		0.2421	1.093	2	0.22	0.8453
$D_{PD}$		1.6374	0.6745	352	2.43	0.0157
$V_{PD}$		-2.2079	0.6483	352	-3.41	0.0007
$D_{PD} \times V_{PD}$		0.5019	0.2136	352	2.35	0.0194
$D_{PD}^2$		-0.3775	0.119	352	-3.17	0.0016
Substrate	Cobble	-3.2756	0.5057	352	-6.48	<0.0001
	Gravel	-2.1311	0.4115	352	-5.18	<0.0001
	Silt/sand	-3.5425	0.4888	352	-7.25	<0.0001
	Boulder/bedrock	0	-	-	-	-

(Model 2), despite a difference in AIC score of 12.62 points between models (Table 2). Usually, such a difference in AIC from the top-ranked model would warrant no consideration of any remaining candidate models. However, model performance (AUC metrics) demonstrated that model performances were comparable, and supported evaluating the peak-flow model (Model 2). Moreover, the 2DHM equivalent of the observed model (Model 3) was ranked below the peak-discharge model (Model 2) by 0.62 AIC points, which suggests that the lower performance may be attributable to differences between data measured in situ (e.g., depth) and 2DHM prediction errors rather than lower predictive power of environmental variables at peak-discharge conditions.

2DHMs are good predictors of spatial velocity and depth patterns, but they do not perfectly predict fine-scale variations observed in depth and velocity, and they are prone to prediction errors (Pasternack et al. 2006). The prediction performance of our 2DHMs was independently peer reviewed, and although we acknowledge some inherent error, they performed well (Wright et al. 2014). These small errors have little consequence for a sampling design aimed at the extremes of depth and velocity combinations, but could explain the poorer model fit (the lower AIC) we observed. Had we been able to measure hydraulic variables during peak-discharge conditions, a better AIC-ranked observed peak-discharge model may have resulted.

Our goal was to relate the distribution of *M. speciosa* to discrete environmental variables statistically so we could

better understand the ecological requirements of this host and, ultimately, facilitate the development and evaluation of proposed management strategies. We tested for variation in habitat variables (depth, velocity, substrate, shear stress, and biota), developed a model for predicting *M. speciosa* presence, and evaluated the performance of the model with independent data. Our approach is novel because we used the 2DHMs to guide sampling for *M. speciosa*. Others have used outputs from hydraulic models as input data for habitat-preference models as a method to assess the amount of habitat available at a specific discharge (Gore et al. 2001). Using the 2DHMs to guide sampling in addition to generating input data ensured that our sampling effort was stratified along the range of depths, velocities, and substrates present at each study site, maximizing our power to detect a hypothesized effect.

Predictive models have been used extensively to simulate the spatial distribution of plant and animal species (Franklin 1995, Guisan and Zimmermann 2000, Scott et al. 2002) and have been useful for filling knowledge gaps in species' ecology because models theoretically can approximate the set of physical variables constituting the fundamental niche (Hutchinson 1957). Our modeling results demonstrate that the distribution of *M. speciosa* (and, thus, the fundamental niche) is influenced by depth, velocity, and substrate, supporting the hypotheses that habitat selection is based on hydraulic and substrate suitability. *Manayunkia speciosa* construct and inhabit flexible tubes attached to a

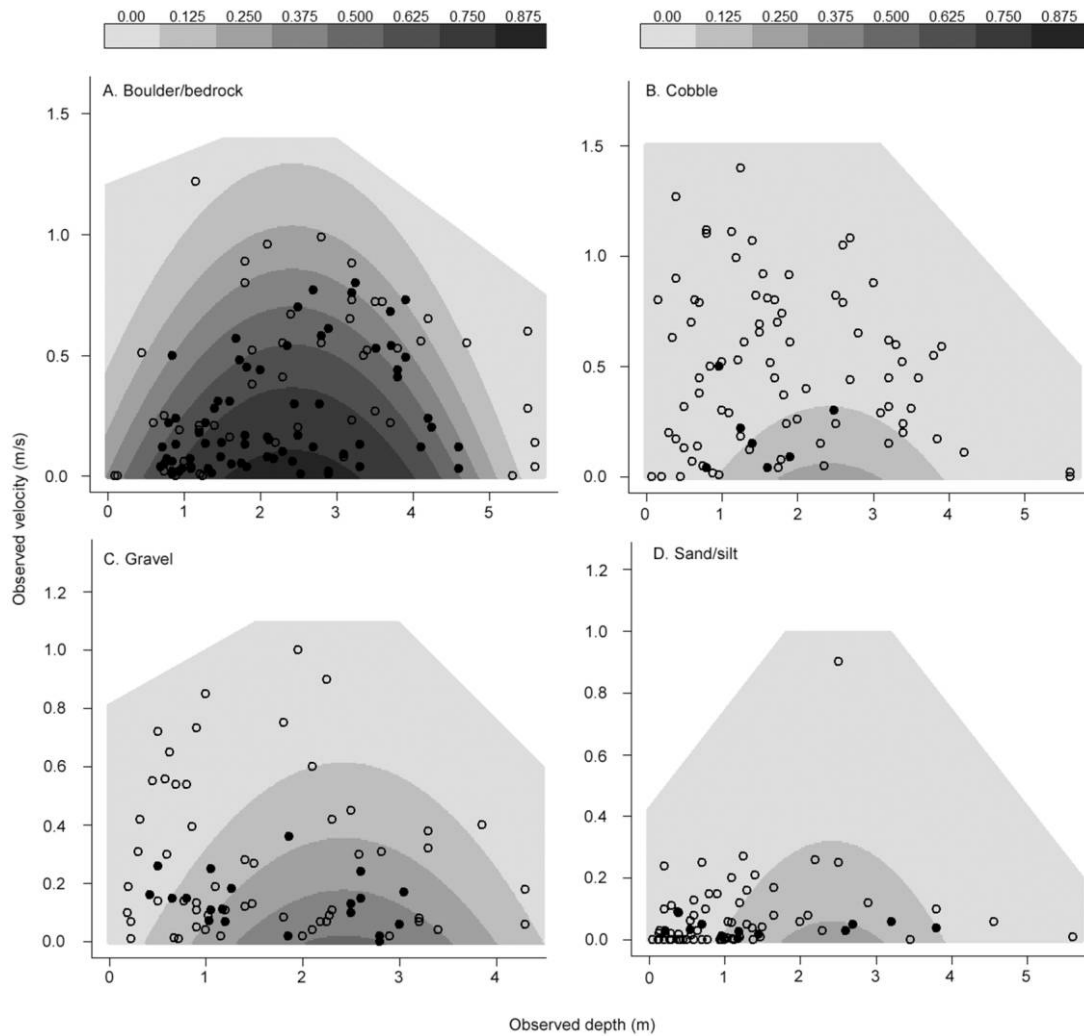


Figure 2. Observed data plotted with the estimated effects of depth ( $D_{OBS}$ ), velocity ( $V_{OBS}$ ), and the quadratic effects of depth ( $D_{OBS}^2$ ) in bedrock/boulder (A), cobble (B), gravel (C), and silt/sand (D) substrates overlaid on the probability of *Manayunkia speciosa* presence predicted from our selected model. Open circles represent observations where polychaetes were not detected and filled circles represent observations where polychaetes were detected. Grayscale shading represents binned probability values in 0.125 increments, and the legend labels correspond to the lower limit of each bin. Estimated probabilities were computed by applying the anti-logit function to the linear predictor from our model containing maximum likelihood parameter estimates.

variety of substrates, an adaptation that may be advantageous for life in moderately deep, slowly flowing areas with stable (large) substrates. Depth may influence the distribution of *M. speciosa* through upper and lower thresholds. Low depths may be stressful at base flow because of seasonal changes in water surface elevation and because of diel temperature fluctuations or desiccation. Stocking and Bartholomew (2007) also observed that *M. speciosa* densities decreased rapidly in reservoirs as distance from the inflow (and, thus, depth) increased. Depths >3 m could be less optimal for *M. speciosa* because periphyton (e.g., *Cladophora* spp.) and diatom abundance may be lower in these areas (Whitton 1970). Assemblages of *M. speciosa* frequently are associated with *Cladophora*, which may facilitate *M. speciosa* attachment (Stocking and Bartholomew

2007) and persistence during elevated flow conditions (Malakauskas et al. 2013).

Velocity may influence polychaete distribution by several means. High velocities may dislodge polychaetes, mobilize the substrate, thereby causing displacement or mortality, or make the environment too turbulent for feeding. Dislodgement or displacement are likely explanations for restriction of polychaetes to lower velocities (e.g. <0.05 m/s; Jordan 2012). Malakauskas et al. (2013) measured shear stress associated with flow velocities and substrate and observed low dislodgement at shear velocities <3 cm/s equivalent to mean column velocity <0.55 m/s. Above this level of shear, probability of dislodgement was strongly affected by substrate type and velocity, and they suggested that velocity restricts *M. speciosa* to substrates whose surfaces



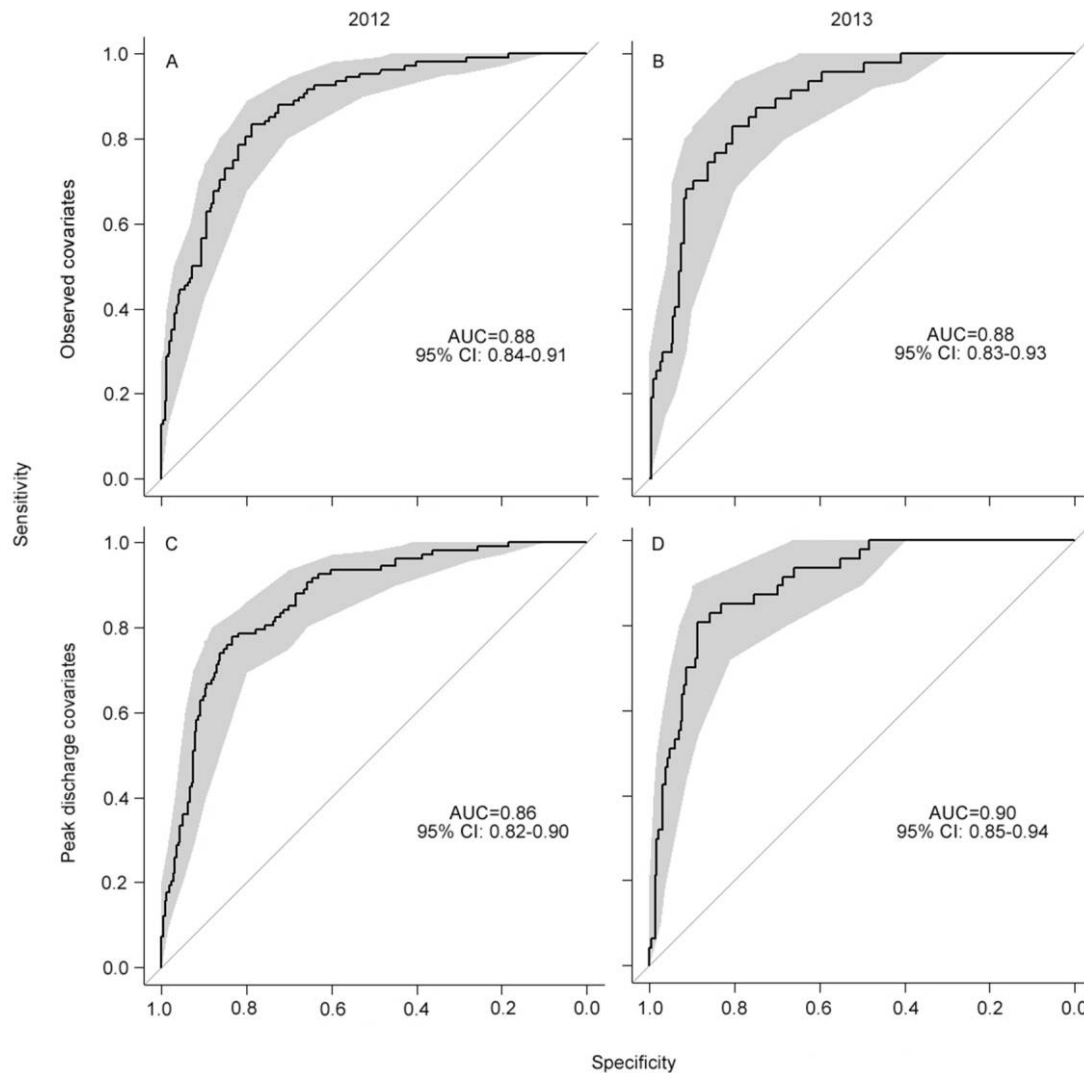


Figure 3. Area under the receiver operating characteristic (ROC) curves (AUC) assessing the performance of top-fitting model predictions of data from 2012, the data that also were used to fit the model and estimate parameters (A, B) and for an independent validation data set collected in 2013 (C, D) based on field-observed measurements of covariates (A, C) and the statistical model based on 2-dimensional hydraulic model-generated estimates of peak-discharge covariate values (B, D).

are subjected to flows  $<0.55$  m/s. The mechanism was not described, but the specialized chaete (hooks) on the polychaetes' abdominal segments that enable attachment to their tubes probably are overwhelmed at higher velocities. In addition, they observed a variety of behaviors for avoiding increases in flow, including abandoning tubes, extrusion of mucus, burrowing into sediments, and movement to nearby lower-velocity microhabitats, which suggests displacement as a mechanism. Higher velocities also may affect distribution indirectly by making the environment too turbulent for foraging. *Manayunkia speciosa* are passive suspension feeders that rely on ambient currents to deliver food to them (e.g., Hentschel and Larson 2005), and Malakauskas et al. (2013) noted that *M. speciosa* retreated into their tubes at an experimental high-velocity level (1.40 m/s) but exhibited behavior consistent with feeding (crown of

tentacles extended) at the low-velocity level (0.55 m/s). These relationships may further influence the distribution of infected polychaetes because myxospores, which are negatively buoyant, may settle out in areas that are deeper and slowly flowing and may be more likely to infect polychaetes when velocities are low (Bjork and Bartholomew 2009).

The best-fitting model results show that the highest predicted probabilities of polychaetes were associated with large (boulder and bedrock) substrate situated in suitable depth and velocity ranges. Correlations between substrate type and *M. speciosa* have been reported in previous studies (Stocking and Bartholomew 2007, Jordan 2012, Malakauskas and Wilzbach 2012, Alexander et al. 2014). However, *M. speciosa* appears to exhibit some plasticity in substrate use that our model does not capture. Jordan (2012) ob-

served densities of *M. speciosa* >100,000 ind/m<sup>2</sup> on fine (silt and sand) and coarse (boulder and bedrock) substrates in summer 2010, a water year characterized by a peak discharge of 36 m<sup>3</sup>/s (below average), but observed high densities of *M. speciosa* only on coarse substrates the following summer, when the water year was characterized by peak discharge of 159 m<sup>3</sup>/s (~2-y magnitude flood). Thus, substrate suitability for *M. speciosa* may be context specific. Our 2-y study enabled us to test the effect of yearly variation in peak discharge, but future studies will benefit from incorporating data from a wider variety of water-year types, particularly if habitat suitability changes during drought or flood years (e.g., colonization of fines during drought years; Jordan 2012). A clear understanding of the relationship between polychaete distribution and substrate suitability is especially important for fine substrates because these particles will be most easily mobilized and managed during flow manipulation and discharge events.

Shear stress is a major driver of benthic invertebrate distribution (Poff and Ward 1992, Gore et al. 2001, Hoover and Ackerman 2011), and changes in stream discharge translate into changes in near-bed hydraulic conditions. Given the importance of substrate, depth, and velocity, we were surprised that shear stress was such a low-performing univariate model. One potential explanation for this result is that shear stress calculated with the 2DHMs may not reflect accurately the near-bed shear stress where we measured polychaetes. Alternatively, our use of presence/absence as a response variable might explain why we did not detect a significant shear stress effect. One of the primary limitations associated with the use of presence/absence data is that it does not provide any information on density, which can be more tightly correlated with variables that are reflected only as changes in distribution over longer time scales. This limitation also might explain why models including biotic predictor variables performed poorly compared to those including only physical predictor variables. We plan to include density metrics and re-examine these results in future work.

A number of factors can drive the distribution and abundance of freshwater invertebrates. Flow regime, including flow history, controls or influences many facets of the physical aquatic environment and the timing of reproduction and migration of many organisms (Hemphill 1991, Power et al. 1996, Poff et al. 1997, Milner et al. 2001). Rather than trying to generate a comprehensive model capturing many of these factors, we focused on physical variables directly associated with discharge because these variables can be affected directly and are quantifiable. In-stream flow incremental methodology (IFIM) has been used to quantify negative environmental effects associated with in-stream flow levels on fish to guide flow-level regulation and management (Bovee 1986).

Our approach was similar to that of riverine habitat simulation within the IFIM framework, which allows in-

vestigators to model flows that are not actually observed. However, our approach allowed us to model habitat conditions when we physically could not get in the river and measure polychaetes. Our objective differs from IFIM and most species distribution models underpinned by conservation goals with the intent to change things to generate more habitat. Our objective was to describe the relationship between habitat and *M. speciosa* quantitatively so that managers could take steps to reduce habitat and, in turn, reduce the distribution of hosts. This simple and practical approach is logical because dams and water storage in the upper basin of the Klamath River provide an opportunity to use flow manipulation as a tool to mitigate the effects of disease on salmon by reducing polychaete host abundance in the Klamath River. However, like many freshwater systems in the western USA, water is a limited and very contentious resource in the Klamath River basin. Thus, evaluating the efficacy of actions that would alter water availability is both warranted and necessary. Our study results provide a tool (a model) that allows us to evaluate how polychaete distribution might respond to flow modification at the study sites and evaluate whether flow management is likely to decrease polychaete habitat and reduce disease risk to salmonids.

Our approach was applied at 3 sites in the Klamath River where salmonid population declines have been attributed to  $\geq 1$  of the parasites (Fujiwara et al. 2011, True et al. 2013) that require *M. speciosa* (obligate host) and *C. shasta* levels are high (Hallett et al. 2012). The conservation of Klamath River salmon is a high priority. *Manayunkia speciosa* plays a key role in the dynamics of these myxosporeans because they produce the actinospore stage that infects salmonid hosts. Therefore, management agencies charged with maintaining healthy salmonid populations are interested in a probabilistic description of *M. speciosa* distribution. Our study is the first to provide such data, which represent an important first step to being able to evaluate the potential efficacy of flow manipulation as a method for reducing the distribution of *M. speciosa* populations.

Changes in the dynamics of infectious and parasitic diseases have been associated with alteration of the natural flow regime in other systems (Jobin 1999). Consequently, quantifying the potential negative effects of flows before flow manipulation can be considered is important. The high degree of model accuracy for predicting the 2013 data set demonstrates that *M. speciosa* distribution is influenced by hydraulic and substrate suitability. Velocity and substrate type can drive dislodgement of *M. speciosa* directly in laboratory experiments (Malakauskas et al. 2013). Our results lead us to conclude that investigating the potential utility of flow modification to reduce Klamath River *M. speciosa* populations has significant merit.

Knowledge of species distributions is important for understanding interactions between environmental change and parasitic diseases. Our approach falls somewhere along the

spectrum of traditional habitat-suitability modeling to inform in-stream flow incremental methods (e.g., Bovee 1986) and species distribution modeling (e.g., Guisan and Zimmermann 2000). We demonstrate how model measurements (2DHMs) and field measurements can be used to predict benthic macroinvertebrate spatial distribution. In our case, the biologically relevant hydraulic information made available through this effort provides insight into physical conditions underlying host spatial distribution, which is an important first step for providing managers with a rationale for allocating water resources to this issue. More broadly, our results speak to the importance of untangling drivers of systems, and reducing uncertainty for species distributions is important to provide reliable predictions that are useful for conservation endeavors. This statement is particularly true for species whose habitat is negatively affected by climate or landuse changes that enhance the uncertainty in future species distributions.

#### ACKNOWLEDGEMENTS

We thank the following persons for hydraulic model development: D. H. Goodman, T. B. Hardy; field assistance: M. Jordan, M. Jakaitis, R. Craig, E. Nebergall, R. Ray, M. Magnuson, L. Knutson, S. Rizza, J. Green, N. Van Vleet, E. Chen, P. Colombano, A. Goodman, S. Gough, S. Burstein, K. Smith; laboratory assistance: M. Jordan, C. Fisher, J. Graen, T. Wilson. We thank the editors and 2 anonymous referees for their time and constructive comments, which helped us to improve the manuscript. Funding was provided by the Bureau of Reclamation through cooperative agreement R15PG00065, National Fish and Wildlife Foundation 8006.2013.041149/2010-0501-005. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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