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Habitat Use by Bluegills Pomoxis annularis and Oregon Chub Oregonichthys crameri in an Off-channel Habitat in the Willamette Valley

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## Habitat Use by Bluegills Pomoxis annularis and Oregon Chub Oregonichthys crameri in an Off-channel Habitat in the Willamette Valley

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Abstract-Nonnative fishes have been implicated in the decline of Oregon Chub Oregonichthys crameri. Bluegills Lepomis macrochirus are the most common nonnative fish in Willamette Valley floodplain habitats that are occupied by Oregon Chub. Recent floodplain studies suggest that these two species are able to coexist under some conditions with limited impact to Oregon Chub; however, mechanisms that allow coexistence are unknown. We describe habitat use by Bluegills and Oregon Chub in an off-channel habitat in the North Santiam River subbasin. To meet our objective we: (1) tagged Bluegills with passive integrated transponder (PIT) tags, (2) installed fixed PITtag antennas to quantify Bluegill habitat use, (3) marked Oregon Chub with visual implant elastomer marks, (4) examined minnow trap catch to describe Oregon Chub habitat use, (5) mapped site bathymetry and temperature, (6) monitored changes in depth and temperature, and (7) assessed Bluegill occurrence probability in relation to water temperature and depth using a modified, spatial capture-recapture model. Results indicate that Bluegills do not use all habitats equally, there was a significant interaction between depth and temperature (Bluegills selected shallower habitats as temperatures warmed), Bluegill occurrence probability differed between crepuscular and non-crepuscular time periods, there was no apparent temporal change in Bluegill habitat use during the study period, and Oregon Chub used a broader range of habitats than Bluegills.

## INTRODUCTION

Oregon Chub are endemic to the Willamette River basin in western Oregon, where they occupy off-channel habitats, such as sloughs, side channels, oxbows,
forested wetlands, and beaver ponds, and low gradient tributaries. Oregon Chub were listed as endangered under the Endangered Species Act in 1993 (Federal Register 1993), but were removed from the threatened and endangered species list in 2015 (Federal Register 2015). Predation and competition from nonnative fishes and habitat loss were implicated in the species' decline. Oregon Chub abundance has typically been found to be lower in habitats containing nonnative fishes than in habitats where nonnatives are absent (Scheerer 2002). Bluegills are the most common nonnative fish in off-channel floodplain habitats that are occupied by Oregon Chub (Bangs et al. 2015). Recent evidence suggests that the two species are able to coexist in some off-channel habitats under unknown conditions with limited impact to Oregon Chub (Bangs et al. 2015). We hypothesize that Oregon Chub are able to minimize the negative impacts of competition by using different microhabitats within off-channel habitats.

Current research is providing data on habitat conditions for Oregon Chub in the Willamette River basin (Bangs et al. 2015); however, data on interactions between Oregon Chub and nonnative fish such as Bluegills are scarce. Additionally, the U.S. Army Corps of Engineers has been drawing down Fall Creek Reservoir, in the Middle Fork Willamette River, below the typical minimum winter reservoir elevation to facilitate downstream passage of listed salmonids and to reduce the populations of nonnative fishes in the reservoir. Similar drawdowns of this and other Willamette Valley reservoirs are proposed for future years. These drawdowns have the potential to flush nonnative fishes downstream, thereby increasing the distribution and abundance of nonnative fishes in off-channel habitats used by Oregon Chub downstream from the reservoirs. The objective of this study was to describe Bluegill and Oregon Chub habitat use and
overlap in relation to water depth and temperature in an off-channel floodplain habitat. This study was developed to complement information currently being collected at 39 floodplain study sites in the Willamette River basin (Bangs et al. 2015). Results from this study will assist in identifying the circumstances under which Oregon Chub can coexist with nonnative Bluegills in floodplain habitats that are subject to main stem flow and temperature management.

## METHODS

Study area. - We conducted this study on Geren Island in the North Santiam River subbasin, Oregon from July 14 - October 1, 2014, a summer low stream flow period with the maximum range of water temperatures in the study area. The study was conducted in the North Intake Channel, which is a closed, currently unused water delivery channel that is fed by seepage through a screened, gated culvert and hyporheic flow from the North Santiam River. The channel is about 500 m long and 10 - 15 m wide. The downstream end has a water control structure to maintain water levels. Water temperature is warmest in the western (downstream) end of the channel and coolest in the eastern (upstream) end of the channel. Temperatures are also cooler near the substrate, likely due to hyporheic input from the adjacent North Santiam River. The channel varies in depth from $0.1-1.9 \mathrm{~m}$ and has an abundance of aquatic vegetation. The site is inhabited primarily by Bluegills and Oregon Chub, with smaller numbers of native Redside Shiners Richardsonius balteatus, Speckled Dace Rhinichthys osculus, Northern Pikeminnows Ptychocheilus oregonensis, Largescale Suckers Catostomus macrocheilus, and Prickly Sculpins Cottus asper. We estimated

1,370 adult Oregon Chub (95\% CI: 1,217-1,542) in the channel in April 2014 (Bangs et al. 2014).

Habitat characterization and monitoring.- We installed $20 \mathrm{Hobo}^{\circledR}$ temperature data loggers in the channel to measure temperatures during the study period. We placed them in the middle of the water column at each of the 20 passive integrated transponder (PIT) tag antenna locations (see "Bluegill habitat use" section) (Figure 1). Temperature data loggers were programmed to record at half-hour intervals on the hour and half-hour. We measured the water depth at each antenna location when the antenna was initially installed and adjusted the depth for changes in the water level in the channel during the study period. We made these adjustments based on data recorded from a water level logger that has been present in the study area since 2009. We compiled the adjusted water depth at half-hour intervals on the hour and half-hour for each antenna. These data were used to describe the water depth of habitats used by Bluegills and Oregon Chub at or near each antenna, respectively.

We created a bathymetric map of the study site by measuring site depth along equally spaced transects. Transects were oriented perpendicular to the flow in the channel and were spaced at 5-m intervals. Water depth was measured at 2-m intervals along each transect. We used a rotating laser level, laser sensor, and a telescoping survey rod to record channel depth (+/-0.05 m). We recorded Universal Transverse Mercator (UTM) coordinates in the North American Datum 1927 coordinate system using a handheld Global Positioning System (GPS) at each location where depth was measured. We used ArcGIS ${ }^{\circledR}$ (version 10.1) to generate Triangulated Irregular Network


FIGURE 1. Map of the study area at Geren Island on the North Santiam River showing the locations of the PIT-tag antennas (green dots), and water temperatures at the surface (upper panel) and substrate (lower panel).
(TIN) files from the surveyed geographic coordinates and measured depths. We created TIN files though linear interpolation of elevation between pairs of nearestneighbor survey points. We used these files to describe the bathymetric surface and to quantify wetted surface area and volume using $\operatorname{ArcGIS}^{\circledR}$. We used the laser level to
reference the initial depths measured in the channel with those on the water level logger and adjusted the channel depths from the bathymetric map with water level logger readings. These data were used to quantify the habitat available at different water depths in the channel at half-hour intervals during the study period.

We mapped the water temperatures along transects spaced 20-m apart (every fourth transect from the bathymetry mapping) on August 18. We collected water temperatures at five equidistant points spaced horizontally across each transect and vertically every $0.5-\mathrm{m}$ starting at the substrate of the channel. We generated a threedimensional temperature map (Figure 1) using the ArcGIS $^{\circledR}$ procedure described above for the bathymetric map. From this map we calculated the proportional volume of available habitat in $1^{\circ} \mathrm{C}$ temperature bins. We visually examined plots of temperature as a function of time for the 20 temperature data loggers and noted that patterns of temporal variation in temperature were generally consistent among temperature logger locations (Appendix Figure A.1.). Therefore, we used the temperature map created from the August data, adjusted these temperature data with changes in temperature from the temperature data loggers (average of 20 devices), and estimated the quantity of habitat available in each $1^{\circ} \mathrm{C}$ temperature bin at half-hour intervals over the duration of the study. These data were used to quantify the amount of available habitat in the channel at different water temperatures at half-hour intervals for the duration of the study.

Bluegill habitat use.-We collected Bluegills using three hoop nets set overnight on July 3. The hoop nets had six 0.92-m diameter panels with dual $7.6-\mathrm{m}$ long $\times 0.92-\mathrm{m}$
tall wings and 13-mm mesh. We placed the captured Bluegills in aerated buckets and released all other fishes. We anesthetized the Bluegills using Tricaine methanesulfonate (MS-222; $20 \mathrm{~g} / \mathrm{L}$ ) buffered with sodium bicarbonate ( $20 \mathrm{~g} / \mathrm{L}$ ) and measured total length (TL) to the nearest 1 mm . We marked 523 Bluegills (57-153 mm TL) with $10-\mathrm{mm}$ half-duplex PIT tags. We made a small incision into the abdominal cavity behind the pectoral fins and slightly off-center of the mid-line of the fish with the tip of a hypodermic needle and implanted the PIT-tag into the abdominal cavity. After processing and recovery in aerated buckets, we released the Bluegills back into the western end of the channel where most were captured.

We distributed 18 stationary PIT antennas, measuring 1-m wide $\times 1$-m tall (Figure 1; Appendix Table A.1.), at selected locations within the channel to describe Bluegill habitat use during the summer low flow period. Each antenna was composed of 1 m of horizontal wire on the channel substrate plus 1 m of vertical wire connected to rebar extending upwards from both the left and right hand sides of the horizontal wire and 1 m of horizontal wire across the top. The total volume of water sampled by an antenna (V) with a detection-range radius of $r$ is a cube measuring $1 \times 2 r \times 1 \mathrm{~m}$, plus half a cylinder attached to the left and right sides of the cube ( $V=1^{*} 2 r^{*} 1+1^{*} \pi^{*} r^{2}$; Figure 2 ). We installed the antennas along the thermal gradient of the habitat at depths varying from 0.2 - 0.9 m. All antenna locations had silt/organic substrate and dense aquatic vegetation nearby. We extended two antennas across the channel ( $\sim 16 \mathrm{~m}$ wide $\times 1.2 \mathrm{~m}$ tall) and located them at one-third and two-thirds of the length of channel, separating the channel into three reaches (reaches 1-3: upstream $\rightarrow$ downstream). At each


FIGURE 2. Top view showing the detection-range radius (r) and detection-range volume (shaded) of a PIT-tag antenna (dashed line).
antenna, we recorded the water depth (m) at the time of installation and referenced this to the depth at the water level logger. We recorded the UTM coordinates for each antenna in the NAD27 coordinate system using a handheld GPS. We downloaded the PIT-tag antenna multiplexors one or two times per week and re-tuned the antennas as needed. We recorded the antenna detection ranges and any periods when the antennas were not functioning. Because we had difficulty maintaining the crosschannel antennas without detection gaps, we removed these antennas on September 2 and replaced them with 1-m x 1-m antennas, placed at the same approximate longitudinal channel location as the cross-channel antennas they replaced.

We examined the relationship between Bluegill occurrence probability and habitat conditions (water temperature and water depth) during the summer low flow period, a period when off-channel habitats are typically more isolated from main stem river sections. For this analysis, we tallied the Bluegill detections as the number of unique fish detected per half-hour interval. In a database, we linked the water temperature, water depth, and Bluegill detections for each antenna, by half-hour interval. We used a new class of mark-recapture techniques that provides a statistical
framework for jointly modelling habitat (space) use, resource selection, and population density by integrating spatial capture-recapture (SCR) data with resource selection data from telemetered individuals (Royle et al. 2013). The model output estimates occurrence probabilities to describe habitat selection, defined as habitat use in greater proportion than habitat availability. Because the method developed by Royle et al. (2013) does not accommodate temporal variability or differences among individuals, we modified their R statistical program code to allow inclusion of a variable that changed through time (temperature) in addition to a spatially heterogeneous variable (depth). Additionally, we examined the effects of spatial (depth) and temporal (temperature) factors in relation to diurnal cycles and the size of individual fish.

Royle et al. (2013) describes an encounter matrix, $y$, with rows corresponding to individuals ( $i$ ) and columns corresponding to traps/antennas ( $j$ ). The numerical entries in the encounter matrix $y_{i j}$ are counts of detections of a given individual at a given trap or antenna, taken over $K$ observational periods. The number of rows in $y$ is equal to the total number of detected individuals, and the number of columns in $y$ is equal to the total number of antennas. If a given individual was never detected at a given antenna, then $y_{i j}=0$. The entries in $y$ were regarded as a binomial random variable, where the probability of a given count is:

$$
\begin{equation*}
f\left(y_{i j} \mid K, p_{i j}\right)=\binom{K}{y_{i j}} p_{i j} y_{i j}\left(1-p_{i j}\right)^{K-y_{i j}} . \tag{eq. 1}
\end{equation*}
$$

The parameter $K$ was known from the experimental design and the probability of detection, $p_{i j}$, was estimated by choosing a value that maximized equation 1 . This was the maximum likelihood estimate of $p_{i j}$.

We expanded the binomial model in equation 1 to address spatial habitat use. We created a raster map of the Geren Island North Intake Channel from bathymetric data. Pixel size was chosen to match the maximum detection-range radius measured at any antenna during the study period. Since the PIT antenna were elongated 1 m and could detect tags at a maximum of 0.61 m , we calculated the pixel diameter at $1+2^{*} 0.61=2.22 \mathrm{~m}$, for a total of 837 pixels within the channel. We use the notation $z(x)$ to note that depth, $z$, depends on the location of the pixel, $x$. Because, a biological model of the effects of $z(x)$ on the presence of Bluegills should include the possibility that they are not capable of using all the habitats (space) within the channel, our assessment of Bluegill occurrence probability accounts for potential limits to habitat availability (Manly et al. 2002). We accomplished this by defining a centroid of an individual's home range as $s$ and $d(s, x)=\|x-s\|$ as the distance between pixel $x$ and the individual's activity center. Although an individual's activity center is not known, we integrated it out of the likelihood by evaluating it over all possible values for $d(s, x)$. We then developed a spatial model for the probability of use at a pixel (occurrence probability) given an activity center, by using a complementary log-log link relating $p_{i j}$ to $\log \left(\lambda_{i j}\right)$, where $\lambda_{i j} \equiv \lambda\left(x_{j} \mid s_{i}\right)$

$$
\log \left(\lambda_{i j}\right)=\alpha_{0}-\alpha_{1} d(s, x)^{2}+\alpha_{2} z(x)
$$

and

$$
p_{i j}=1-e^{-e^{\lambda_{i j}}}
$$

where $\alpha_{0}$ is an intercept, $\alpha_{1}=\frac{1}{2 \sigma^{2}}$ is the rate at which the occurrence probability declines with distance from the activity center, $d(s, x)$, and $\alpha_{2}$ is the effect size of the
spatial covariate $z(x)$, which is a parameter of primary interest. Note that if $\alpha_{1}=0$, then all of the pixels in the channel are equally available, and that the size of the home range declines as $\alpha_{1}$ increases.

To incorporate distance from the activity center $d(s, x)$ into our model, we assigned $d(s, x)$ as a matrix with 20 rows and 837 columns, corresponding to the number of antennas and pixels in the channel, respectively. The entries for $d(s, x)$ were the Euclidian distances between each antenna and every pixel in the channel. We considered a vector of counts for the first individual summarized over all antenna locations, $y_{i=1, j=1: 20}$ and computed the likelihood of data $y_{i=1, j=1: 20}$ with equations 1 and 2. We calculated the likelihood of the 20 numbers in $y_{i=1, j=1: 20}$ (most were zeros) separately for all 837 columns of $d(s, x)$. We then multiplied together the likelihood values to integrate out the unknown activity center of individual $i=1$. We repeated this procedure for all individuals, and then multiplied together the likelihoods associated with each individual (assuming independence among individuals) to obtain the conditional likelihood of the entire data set $y$, given parameters $\alpha_{0}, \alpha_{1}$, and $\alpha_{2}$. We used a numerical optimizer to find values of $\alpha_{0}, \alpha_{1}$, and $\alpha_{2}$ that maximized the joint likelihood.

Next, we expanded upon the basic model of resource selection to include temporal and individual-level covariates. Our data $y$ were counts of PIT-tag detections tallied at 30-min intervals within a day. If a Bluegill was detected multiple times at a single antenna within a 30-min period, then it was recorded as a single observation at that antenna. But if a Bluegill was detected in four different 30-min periods within a day, then $y_{i j}=4$. Thus, within a single day there were 48 time periods (30-min periods), and the value for $K$ in equation 1 was 48 . There were a small number of Bluegills that
were detected at multiple antennas within a 30-min period (99 of 13,214 detections; $0.7 \%$ ) and a small number of half-hour intervals with multiple detections of an individual Bluegill at multiple antennas (99 of 3,118 intervals; 3.2\%). These detections of an individual Bluegill at multiple antennas within a half-hour interval were retained in the data set that we analyzed, because we thought it was more important to show additional, differential habitat use by Bluegills than it was to be concerned with the low level of bias this might have added to our analysis.

To incorporate temporal variability in water temperature, we summarized counts $y_{i j}$ for each of the 88 d of the study. Thus, our data were now $y_{i j t}$ and equation 2 a was extended to

$$
\log \left(\lambda_{i j t}\right)=\alpha_{0}-\alpha_{1} d(s, x)^{2}+\alpha_{2} z(x)+\alpha_{3} \gamma_{t}+\alpha_{4} z(x) \gamma_{t},
$$

where $\gamma$ is the water temperature on day $t$, which is the same number for all individuals and all locations, but changed through time. The parameter $\alpha_{4}$ is the effect of an interaction between depth and temperature, which allows the effect of depth on Bluegill occurrence probability to change as temperature changes.

Because each antenna had a different detection-range radius and the detectionrange radius of each antenna often varied over time, we incorporated this into the model by simply assuming a linear link between detection-range volume, V , of the $f^{\text {th }}$ antenna on day $t$ and detection probability:

$$
p_{i j t}=1-e^{-e^{\lambda_{i j}}} \mathrm{~V}_{\mathrm{jt}} .
$$

We set $\mathrm{V}_{\mathrm{jt}}=1$ for the antenna with the longest detection-range radius ( r ) ever measured. The value $\mathrm{V}_{\mathrm{jt}}$ for all other antennas and days were expressed as a fraction of the volume sampled by the antenna with the largest detection-range radius. Note that V
increases "geometrically" over equal intervals of detection-range radius, and that we assumed a linear decline in detection probability with decreasing antenna detectionrange volume.

We multiplied all 88 likelihoods together (88 d of monitoring), which corresponds to $y_{i j t}=1: 88$. Thus, the entire dataset described by Royle et al. (2013) was equivalent to a single day in our analysis. Stated another way, Royle et al. (2013) would obtain our data if they repeated their study 88 times over a period when each replicate dataset was collected under a unique level of a temporally fluctuating variable.

We examined the effects of depth and temperature on Bluegill habitat selection during crepuscular and non-crepuscular times of the day. We defined crepuscular times as 2 h before and after sunrise plus 2 h before and after sunset ( 8 h of the day). Because our study lasted 88 d , the time of day when sunrise and sunset occurred changed. We used a custom R script that computed the time of day of sunrise and sunset at the longitude and latitude of the channel for all 88 d of this study. We then binned the detections into crepuscular and non-crepuscular times of day. This created
 $\{8,16\}$. For both subsets, we forced the values of $\alpha_{0}$ and $\alpha_{1}$ to be identical, but allowed $\alpha_{2}, \alpha_{3}$, and $\alpha_{4}$ to take on unique values during the crepuscular and non-crepuscular time periods.

To examine the effect of Bluegill size on Bluegill habitat selection, we conducted an analysis where Bluegills were classified as either large ( $>70 \mathrm{~mm}$ ) or small ( $\leq 70 \mathrm{~mm}$ ). Similar to the previous analysis, we forced the values of $\alpha_{0}$ and $\alpha_{1}$ to be identical for both groups of data, but allowed $\alpha_{2}, \alpha_{3}$, and $\alpha_{4}$ to take on unique values for large and
small Bluegills. Ideally, we would have combined the crepuscular-effects analysis with the size-effects analysis into a single statistical model. However, this posed challenges that we could not resolve and so we conducted two separate analyses for crepuscular-non-crepuscular times of day and Bluegill size effects on depth and temperature use.

We calculated confidence intervals for the point estimates from a Hessian matrix, which was obtained from R's "optim" function used to maximize the likelihood function. The Hessian matrix contains second-order partial derivatives of the parameters evaluated at their maximum likelihood estimates. Since "optim" minimizes functions, the log likelihood is maximized by multiplying the likelihood by -1 . With a Hessian computed for a negative log likelihood, the observed Fisher information $(F(\theta))$ is equivalent to the Hessian, $H(\theta)$, and inverting the Fisher information matrix yields an estimator of the asymptotic covariance matrix. Standard errors were thus obtained by taking the square roots of the diagonal elements of the covariance matrix (inverted Hessian). Since the standard errors are asymptotic estimates, we multiplied them by $+/-$ 1.96 and then added the point estimate to obtain $95 \%$ confidence intervals. In summary, if $L(\theta)$ is the negative log likelihood, then:

$$
(\theta)=H(\theta)=\frac{\partial^{2}}{\partial \theta_{i} \partial \theta_{j}} L(\theta) \cdot \operatorname{Var}\left(\hat{\theta}_{M L E}\right)=\left[F\left(\hat{\theta}_{M L E}\right)\right]^{-1} \text { and so } S E\left(\hat{\theta}_{M L E}\right)=\frac{1}{\sqrt{F\left(\hat{\theta}_{M L E}\right)}}
$$

Using R, we calculated confidence intervals with:
fisher_info<-solve(mod\$hessian)\#invert Hessian of -log(L) prop_sigma<-sqrt(diag(fisher_info))
upper<-mod\$par+1.96*prop_sigma lower<-mod\$par-1.96*prop_sigma

Oregon Chub habitat use.-We used minnow trap catch to describe Oregon Chub habitat use because Oregon Chub were too small to PIT tag using 10-mm PIT tags, the smallest PIT tags that provided sufficient detection range given equipment limitations Minnow traps measured $23 \mathrm{~cm} \times 46 \mathrm{~cm}$ with 3.2-mm mesh. Minnow traps were first set on July 3, 2014 (initial capture event) and were then set weekly from July 15 through August 19, 2014. Each minnow trap was baited with one-third slice of wheat bread. Minnow traps were distributed throughout the channel and allowed to soak overnight. We set minnow traps surrounding each of the antennas, but not within the antenna detection range to avoid recording continuous tag detections from PIT-tagged Bluegills also captured in the minnow traps. We acknowledge that PIT-tagged Bluegills that we captured in minnow traps were temporarily unavailable for detection at the PITtag antennas. However, we believe that this had negligible impact on our Bluegill habitat use assessment, because minnow traps were only set for a total of $60 \mathrm{~h}(2.8 \%$ of the study period) and only 41 PIT-tagged Bluegills were captured in the minnow traps ( $<6$ fish/week of trapping; $0.3 \%$ of all Bluegill detections). During the first four weeks of the study, we set minnow traps at all of the antennas in one reach (six traps per antenna; six antennas per reach) on one day, all of the antennas for the next reach on the following day, and all of the antennas from the last reach on the following day. During the last two weeks, we set traps at all of the antennas on a single day (two traps per antenna; 18 antennas), to reduce handling stress on individual Oregon Chub that might be captured (resampled) on successive days.

We placed captured Oregon Chub in aerated buckets and released all other fishes. We anesthetized Oregon Chub using MS-222, using the same procedure
described above for Bluegills, and measured TL to the nearest 1 mm . During the initial capture event, we marked 521 Oregon Chub (37-81 mm TL) with blue visual implant elastomer (VIE) under the surface of the skin near the base of the anal fin on the right side of the fish following the methods of Olsen and Vøllestad (2001) during the initial capture event (July 3). After processing and recovery, Oregon Chub that were captured during the initial capture event were released near the longitudinal midpoint of the channel. During subsequent capture events (July 15 through August 19) we either 1) did not mark Oregon Chub if they did not already have a blue VIE mark or 2) marked Oregon Chub with an additional VIE mark if they had been previously marked. To provide information on movement patterns from the initial capture event release location, previously captured Oregon Chub where marked with either a black VIE (fish recaptured in the upstream reach) or purple VIE (fish recaptured in the downstream reach). After processing and recovery, Oregon Chub that were captured from July 15 through August 19 were released near their capture location.

We examined the distribution of recaptured individuals to describe the direction and extent of Oregon Chub movement during the study period. We recorded the total Oregon Chub catch, fish total length, and presence of VIE marks and tallied catch and recaptures by reach and antenna. We stopped trapping Oregon Chub on August 19 due to increasing water temperatures and concerns related to handling stress. We compared Oregon Chub and Bluegill habitat use at or near all of the PIT-tag antennas during the time periods when Oregon Chub and Bluegill sampling overlapped.

## RESULTS

Habitat characterization and monitoring.- Water depth in the Geren Island North Intake Channel was shallower in the eastern (upstream) end of the channel and along the channel margins and was deeper in the western (downstream) end of the channel. Water depth, measured at the water level logger, only varied by 0.17 m during the study period. Water temperature was warmest in the western (downstream) end of the channel and coolest in the eastern (upstream) end of the channel (Figure 1). Temperatures were also cooler near the substrate, likely due to hyporheic input from the adjacent North Santiam River (Figure 1). Despite this spatial variation, temporal changes in temperature during the study period were similar among antenna locations. Daily temperature fluctuation was generally highest at the eastern antennas (cooler end of channel) and lowest at antennas $9-13$ located in the middle portion of the channel, an area of suspected hyporheic input (Appendix Figure A.1.).

Bluegill habitat use. - We recorded a total of 13,214 unique detections (by half hour interval; $n=3,118$ intervals) of tagged Bluegills at the PIT antennas. The majority ( $76 \%$ ) of these detections were at three antennas near the downstream end of the channel ( $n=6,889$ ) and two antennas near the upstream end of the channel $(n=3,135)$ (Figure 3). We detected a total of 244 individual Bluegills. The average number of detections (by half hour interval) of individual tagged Bluegills was 54 (range 1-622) and the median was 26 detections. We observed no apparent temporal changes in spatial distribution of PIT-tagged Bluegills during the study (Figure 4).


FIGURE 3. Distribution of Bluegill detections at PIT-tag antennas in the Geren Island North Intake Channel.

We observed substantial variability in habitat use by individual Bluegill in relation to temperature and depth. On any given day of the study, there were broad ranges of depths and temperatures (Figure 5) used by individual Bluegill. Additionally, some Bluegills used habitats that were consistently deeper or shallower than the average for all habitats and some Bluegills used habitats that were consistently warmer or cooler than the average for all habitats.

There was a significant interaction between temperature and habitat depth on Bluegill occurrence probability (Table 1). Overall, occurrence probability was greater where water depths were shallow. However, occurrence probability was similar among temperatures at the greatest habitat depths, but at shallower habitat depths occurrence probability increased with increasing temperature (Figure 6).


FIGURE 4. Bluegill detections at PIT-tag antennas for four time periods during the study. Cross channel antennas 7 and 14 , which we had difficulties maintaining without detection gaps, are not included in these figures.


FIGURE 5. (A.) Mean water depth (red line) and the range of depths (gray hatched area) for all Bluegill detected on each day of the study. (B.) Mean water temperature (red line) and range of temperatures (gray hatched area) for all Bluegill detected on each day of the study.

TABLE 1. Model parameters describing Bluegill occurrence probability in relation to depth and temperature. Parameters were statistically significant $(p \leq 0.05)$ when the confidence intervals do not include zero.

|  |  | $95 \%$ Confidence limits |  |
| :--- | :---: | :---: | :---: |
| Parameter | Point estimate | upper | lower |
| Intercept | 3.61 | 3.85 | 3.37 |
| Log (distance) | 15.00 | 418.06 | -388.06 |
| Depth | -3.05 | -3.14 | -2.97 |
| Temperature | 0.58 | 0.83 | 0.31 |
| Depth x temperature | -0.17 | -0.27 | -0.08 |



FIGURE 6. Plot of Bluegill occurrence probabilities in relation to water temperature ( ${ }^{\circ} \mathrm{C}$ ) and depth (m).

The distance from activity center was not identifiable, i.e. we were unable to determine if there was a center of activity at the scale of this study, because the distance parameter was not significant and had no effect on the estimates of occurrence probability.

There was a statistically significant interaction between depth and temperature on Bluegill occurrence probability during crepuscular time periods (i.e., as temperature increased, Bluegill occupancy increased at shallower depths), but not during noncrepuscular time periods (Table 2; Figure 7). The effect of temperature was not significant during non-crepuscular times. At the extremes of depth and temperature in our study, occurrence probabilities were highest at the shallowest depth and maximum temperature during crepuscular (0.017) and non-crepuscular time periods (0.010) and were substantially higher (5-10 times) than at the deepest depths (0.0009-0.0019) (Table 3). Distance from activity center was not identifiable and had no effect on the estimates of occurrence probability.

The effect of depth on occurrence probabilities of both small and large Bluegills was statistically significant (Bluegill occurrence probability increased as depth decreased) (Table 4). The effects of temperature and the depth-temperature interactions were not statistically significant. Note however, that there were few large Bluegills PIT tagged during this study - only $22 \%$ of the fish were in the large size group and only 5\% were larger than 100 mm TL. Distance from activity center was not identifiable and had no effect on the estimates of occurrence probability.

TABLE 2. Model parameters describing Bluegill occurrence probability in relation to depth and temperature, during crepuscular and non-crepuscular time periods.
Parameters were statistically significant ( $\mathrm{p} \leq 0.05$ ) when the confidence intervals do not include zero.

|  |  | 95\% Confidence limits |  |
| :--- | :---: | :---: | :---: |
| Parameter | Point estimate | upper | lower |
| Intercept | 4.08 | 4.32 | 3.84 |
| Log (distance) | 14.03 | 179.44 | -151.37 |
| Depth, non-crepuscular | -3.15 | -3.06 | -3.24 |
| Depth, crepuscular | -2.97 | -2.88 | -3.05 |
| Temperature, non-crepuscular | 0.22 | 0.59 | -0.14 |
| Temperature, crepuscular | 0.85 | 1.22 | 0.48 |
| Depth x temperature, non-crepuscular | -0.06 | 0.07 | -0.19 |
| Depth $x$ temperature, crepuscular | -0.29 | -0.15 | -0.42 |



FIGURE 7. Plots of occurrence probabilities in relation to water temperature ( ${ }^{\circ} \mathrm{C}$ ) and depth (m) for crepuscular and non-crepuscular time periods and for small and large Bluegills.

TABLE 3. Bluegill occurrence probabilities, at 0.5 hour intervals, for crepuscular and non-crepuscular time periods. These probabilities were modelled using the mean detection range for all antennas and represent the extremes for both depth and temperature recorded during the study.

| Parameters | Occurrence probability |
| :--- | :---: |
| Shallowest depth and maximum temperature, during crepusular times | 0.0170 |
| Shallowest depth and maximum temperature, during non-crepusular times | 0.0103 |
| Deepest depth and maximum temperature, during non-crepusular times | 0.0009 |
| Deepest depth and minimum temperature, during crepusular times | 0.0019 |
| Deepest depth and minimum temperature, during non-crepusular times | 0.0008 |

TABLE 4. Model parameters describing Bluegill occurrence probability in relation to depth and temperature, for large ( $>70 \mathrm{~mm} \mathrm{TL}$ ) and small Bluegills ( $\leq 70 \mathrm{~mm} \mathrm{TL}$ ).
Parameters were statistically significant ( $\mathrm{p} \leq 0.05$ ) when the confidence intervals do not include zero.

|  |  | 95\% Confidence limits |  |
| :--- | :---: | :---: | :---: |
| Parameter | Point estimate | upper | lower |
| Intercept | 4.78 | 5.14 | 4.42 |
| Log (distance) | 15.00 | 608.29 | -578.29 |
| Depth, large fish | -3.47 | -3.34 | -3.60 |
| Temperature, large fish | 0.24 | 1.07 | -0.60 |
| Depth $x$ temperature, large | -0.10 | 0.20 | -0.40 |
| Depth, small fish | -3.46 | -3.33 | -3.59 |
| Temperature, small fish | -0.25 | 0.20 | -0.70 |
| Depth $x$ temperature, small fish | 0.12 | 0.28 | -0.04 |

Oregon Chub Habitat Use.- Oregon Chub used habitats throughout the channel (Figure 8). Recaptures of VIE marked Oregon Chub indicated that most moved from the middle reach, where they were originally captured and marked, into one or both of


FIGURE 8. Proportion of VIE marked Oregon Chub captured in minnow traps, by week and by reach, in the Geren Island North Channel, summer 2014. Also included are the mean weekly water temperatures and range of temperatures (in parentheses).
the adjacent reaches. By week 7, nearly 97\% of the VIE marked Oregon Chub that we recaptured had more than one color of VIE mark (i.e., they did not stay in the middle reach where they were marked and released). Over half (53\%) were captured in all three reaches and 44\% were captured in two reaches (Table 5). Of the Oregon Chub captured in only two reaches, $75 \%$ had marks from the middle and upper (cooler) reach and $25 \%$ percent had marks from the middle and lower (warmer) reach.

Oregon Chub habitat use varied spatially during the period of study, with an apparent reduction in use of cooler habitats (reach 1) during weeks 6 and 7 (Figure 8). Oregon Chub were more commonly captured in reach 2 (near antennas 8-13) than Bluegills, which were rarely detected at the antennas in reach 2. Oregon Chub also used some of the same areas that Bluegills used (e.g. - antennas 3, 19, and 20) (Figure $9)$.

TABLE 5. Proportion of the Oregon Chub catch with VIE marks from different reaches, by week. All marked Oregon Chub were released in the middle reach (reach 2). Only VIE marked Oregon Chub that were recaptured were given subsequent marks. Reach 1 is the upstream (cooler) reach and reach 3 is the downstream (warmer) reach.

| Week | Reach 2 | Reaches $2 / 1$ | Reaches 2/3 | Reaches $1 / 2 / 3$ |
| :---: | :---: | :---: | :---: | :---: |
| 2 | 0.83 | 0.17 | 0.00 | 0.00 |
| 3 | 0.28 | 0.09 | 0.40 | 0.24 |
| 4 | 0.17 | 0.16 | 0.33 | 0.34 |
| 5 | 0.10 | 0.05 | 0.26 | 0.60 |
| 6 | 0.17 | 0.06 | 0.31 | 0.46 |
| 7 | 0.03 | 0.11 | 0.33 | 0.53 |



FIGURE 9. Habitat use by Oregon Chub and Bluegills, expressed as the proportion of the minnow trap catch and PIT-tag detections, respectively, during weeks 4-6 of the study. Also shown is the average water temperature (dotted line) for the $\sim 16 \mathrm{~h}$ period when the minnow traps were set.

## DISCUSSION

Occurrence probability of Bluegill was greater in shallow habitats in the Geren Island floodplain channel, and this pattern was consistent during crepuscular and noncrepuscular time periods and for large and small Bluegills. Additionally, occurrence probability of Bluegills increased in shallow-water habitats as temperature increased during crepuscular time periods. The maximum temperature recorded in the Geren Island floodplain channel during our study $\left(28.2^{\circ} \mathrm{C}\right)$ was considerable less than the preferred temperature reported for Bluegills $\left(31.0^{\circ} \mathrm{C}\right.$; Beitinger and Magnuson 1975), which may have influenced our observations.

Bluegill feeding and movements occur primarily during crepuscular time periods (Spotte 2007). During crepuscular time periods, there was a positive relationship between Bluegill occurrence probability and water temperature, and the effect of temperature on occurrence probability strongly depended on water depth. However, during non-crepuscular periods, there was no relationship between Bluegill occurrence probability and temperature and the temperature-depth interaction was not significant.

Some fish species segregate along temperature gradients and show intraspecific differences in thermal distribution of size classes (Brandt et al. 1980). Intraspecific competition for thermal resources may allow socially dominant individuals to exploit the preferred range of the resource and exclude subordinate conspecifics (Magnuson et al. 1979). Bluegills are highly aggressive and social dominance, as expressed by frequency of aggression, is directly related to fish size. Bluegill size had no effect on their occurrence probability in our study, i.e. the effects of temperature and the depthtemperature interactions were similar and were not significantly different between size
groups. Note that most of the Bluegills PIT-tagged in our study were small-sized, putative juvenile fish ( $78 \%$ were in the small size group and $95 \%$ were $<100 \mathrm{~mm} \mathrm{TL}$ ); Bluegills mature from about 75-160 mm TL (Keast et al. 1978; Beitinger 1974; Beitinger and Magnuson 1975; Belk 1995).

In a laboratory study, juvenile Bluegills (95-110 mm TL), in the absence of adult Bluegills, selected their preferred temperature $\left(31.0^{\circ} \mathrm{C}\right)>75 \%$ of the time, when given a choice (Beitinger and Magnuson 1975). However in the same study, when an adult Bluegill was present, juvenile Bluegills chose non-preferred temperatures $\left(27^{\circ} \mathrm{C}\right.$ or $\left.34^{\circ} \mathrm{C}\right)$ $99 \%$ of the time and spent more time in their preferred temperature during the night than day. The presence of a few large, presumably adult, Bluegill may have had a similar effect on Bluegill (mostly juvenile sized) selection of shallower habitats in the Geren Island channel. Additionally, Bluegills exhibit marked intraspecific size-class differences in vertical distribution. Adult Bluegills were found predominantly in the deeper littoral zone of Midwestern lakes and the majority of juvenile Bluegills were confined to the shallow 0.5-1.0 m stratum near or just above aquatic vegetation (Werner et al. 1977; Werner and Hall 1988; Mittelbach 1984). This is consistent with results from our study where Bluegill occurrence probability increased with decreasing water depth.

Habitat partitioning and partitioning of food resources are common among fish assemblages (Werner et al 1977; Brandt et al. 1980; Heggenes et al. 2002). Spatial habitat segregation of fish species often occurs along gradients of depth, temperature, distance from shore, vertical height in the water column, and vegetational structure (Werner et al. 1977; Brandt et al. 1980; Crowder and Cooper 1982; Jackson et al. 2001, Grossman et al. 1998). Behavioral thermoregulation, where different species within a
system inhabit and forage in different thermal zones has the potential to minimize competitive interactions (Beitinger 1974; Beitinger and Magnuson 1975; Brandt et al. 1980; Urban and Brandt 1993; Snucins and Gunn 1995; Matern et al. 2000; Baird and Krueger 2003). In the Geren Island floodplain channel, Bluegill and Oregon Chub habitat use overlapped, but Oregon Chub habitat use was broader. Despite our inability to use PIT-tags for marking Oregon Chub, trapping results suggest that Oregon Chub are habitat generalists, which may reduce competitive interactions with Bluegills when they occur in sympatry in floodplain habitats in the Willamette Valley.

Spatial capture-recapture models are relatively new methods for using capturerecapture data and auxiliary information about individual capture locations for gaining inference about habitat selectivity. These models relate the capture process with the way individuals use habitat (space) and allow investigators to model how the landscape and habitat influence movement and occurrence probability by individuals within their home range. In our study, use of a SCR model allowed us to examine relationships between Bluegill occurrence probability and availability. To our knowledge, this was the first application of the Royle et al. (2013) SCR model to a dataset with both spatial and temporal variability.

In summary, Bluegills in the Geren Island floodplain channel selected some habitats and rarely used others, and this habitat selection was consistent during the study period, i.e. they displayed no temporal shifts in spatial distribution. Oregon Chub, which also feed primarily in the water column and on a planktivorous diet (Pearsons 1989), used some of the same habitats as Bluegills, but also used habitats that Bluegills rarely used. For example, Oregon Chub used habitats in the middle and the upstream
(cooler) reaches more than Bluegills did. Additionally, and in contrast to Bluegills, Oregon Chub showed temporal shifts in spatial distribution during the study period. This suggests that Oregon Chub may be able to minimize the effects of competition with Bluegills by using different habitats and the predominant outcome resulting from competitive interactions with Bluegills may be niche segregation (see also Jackson et al. 2001).

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APPENDIX TABLE A.1. Details describing the habitat and locations of the PIT-tag antennas installed at Geren Island. Note, antennas 21 and 22 replaced antennas 7 and 14, respectively, on September 2, 2014.

| Start Date | End Date | Reach | Antenna | Easting | Northing | Depth $(\mathrm{m})$ | Size $\left(\mathrm{m}^{2}\right)$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 1 | 519627 | 4960023 | 0.3048 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 2 | 519604 | 4960032 | 0.2540 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 3 | 519599 | 4960048 | 0.4953 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 4 | 519567 | 4960043 | 0.3175 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 5 | 519545 | 4960060 | 0.5207 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 1 | 6 | 519535 | 4960065 | 0.5588 | 1.0 |
| $07 / 14 / 14$ | $09 / 01 / 14$ |  | 7 | 519507 | 4960077 | 0.7366 | 52.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 8 | 519487 | 4960080 | 0.4572 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 9 | 519468 | 4960089 | 0.7493 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 10 | 519455 | 4960080 | 0.3302 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 11 | 519440 | 4960088 | 0.7874 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 12 | 519442 | 4960085 | 0.4572 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 2 | 13 | 519412 | 4960092 | 0.7620 | 1.0 |
| $07 / 14 / 14$ | $09 / 01 / 14$ |  | 14 | 519400 | 4960093 | 0.8890 | 61.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 15 | 519406 | 4960095 | 0.3048 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 16 | 519382 | 4960097 | 0.9144 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 17 | 519362 | 4960102 | 0.2286 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 18 | 519339 | 4960105 | 0.2032 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 19 | 519314 | 4960094 | 0.4318 | 1.0 |
| $07 / 14 / 14$ | $10 / 01 / 14$ | 3 | 20 | 519294 | 4960103 | 0.8636 | 1.0 |
| $09 / 02 / 14$ | $10 / 01 / 14$ | 1 | 21 | 518748 | 4959578 | 0.3680 | 1.0 |
| $09 / 02 / 14$ | $10 / 01 / 14$ | 2 | 22 | 519724 | 4959995 | 0.5842 | 1.0 |


















APPENDIX FIGURE A1. Temporal variability in water temperatures measured at each PIT antenna from 14 July through 1 October 2014.


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