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RESEARCH ARTICLE

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Expansion of smallmouth bass distribution and habitat overlap with juvenile Chinook salmon in the Willamette River, Oregon

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Abstract

Smallmouth bass populations have expanded far beyond their native range and these predatory fish present a pervasive threat to native aquatic species throughout North America. In the western United States, smallmouth bass are now present in river and reservoir habitats where Pacific salmon are found and are considered a potential threat to salmon recovery in many locations. We conducted a study to determine if smallmouth bass are expanding their range in the mainstem Willamette River, Oregon, and developed a model to assess habitat overlap between smallmouth bass and juvenile Chinook salmon. Sampling during 2011–2022 revealed that the distribution of smallmouth bass had expanded throughout that timeframe to encompass the entire mainstem Willamette River, including important rearing habitats for juvenile Chinook salmon. The model predicted that smallmouth bass and juvenile Chinook salmon habitat overlap was substantial, highlighting the need for additional research to evaluate for potential negative impacts to salmon recovery in the basin. The model was also used to evaluate the efficacy of using flow management to reduce interactions between these two species, but the scenarios we examined suggested that this was not a viable option. These results highlight the need for continued research to assess interactions between smallmouth bass and juvenile salmon, and other native species of concern, in the Willamette River Basin. The development of the model is useful for resource managers to understand interactions between these species to prioritize locations for sampling in the future.

KEYWORDS
distribution expansion, habitat modeling, habitat overlap, juvenile Chinook salmon, *Micropterus dolomieu*, smallmouth bass, Willamette River

1 | INTRODUCTION

Smallmouth bass *Micropterus dolomieu* is a nonnative fish that is widely distributed in rivers, reservoirs, and lakes throughout North America. These fish are widespread in habitats of juvenile Pacific salmon *Oncorhynchus* spp. throughout the Pacific Northwest, United States (Carey et al., 2011; Hughes & Herlihy, 2012; Rubenson & Olden, 2019; Tiffan et al., 2016) and have been shown to be a significant predation threat (Fritts & Pearsons, 2004; Tabor et al., 1993; Tiffan et al., 2020). Interactions between smallmouth bass and juvenile salmon increase during spring and summer as water temperature warms. During this period, smallmouth bass become increasingly active (behaviorally and metabolically) as spawning begins and they expand their range to include habitat that was thermally unsuitable during fall and winter (Fritts & Pearsons, 2004; Rubenson & Olden, 2016; Rubenson & Olden, 2017). This has led to concerns about population-level effects of smallmouth bass predation on Pacific salmon and other native fishes (Carey et al., 2011; Hughes et al., 2005; ISAB, 2019; Rubenson et al., 2020). These concerns are compounded by predictions that smallmouth bass will expand their range by two-thirds in the Columbia River Basin under future climate change scenarios (Rubenson & Olden, 2019). Thus, monitoring to describe how smallmouth bass distributions change over time will be important, especially in rivers where salmon recovery efforts are a priority.

Habitat overlap between juvenile Chinook salmon *O. tshawytscha* and smallmouth bass is of concern in the Willamette River Basin where spring-run Chinook salmon are listed as "threatened" under the U.S. Endangered Species Act (ESA) (NOAA, 2021). Several studies have shown that juvenile Chinook salmon spend a substantial amount of time (weeks to months) rearing in the mainstem Willamette River and in its tributaries (Friesen et al., 2007; Schroeder et al., 2016; Whitman et al., 2017). For example, Whitman et al. (2017) reported that 87% of the juvenile Chinook salmon (from a total of 1443 fish) that were recaptured after PIT-tagging were located at or near the original collection site. In that study, Whitman et al. (2017) found that residence time in the mainstem Willamette River (and tributaries) averaged 120–151 days. These extended residence times could lead to increased susceptibility to chronic predation if smallmouth bass are present in reaches where rearing occurs. Several studies have demonstrated that smallmouth bass is the most encountered non-native fish species in the lower Willamette River, but existing information suggests that they are primarily distributed downstream of the Willamette River/Santiam River confluence (rkm 173.8; Hughes & Gammon, 1987; Friesen, 2005; Hughes et al., 2005; LaVigne et al., 2008). Conversely, important rearing areas for juvenile Chinook salmon are primarily located in lower reaches of Santiam and McKenzie rivers and in the mainstem Willamette River upstream of rkm 173.8 (Whitman et al., 2017). Thus, predation by smallmouth bass has not been deemed a significant mortality threat for juvenile Chinook salmon in the Willamette River (Friesen et al., 2007; Summers & Daily, 2001), but this risk increases substantially if smallmouth bass expand their range to include reaches upstream of rkm 173.8. Based on this concern and the current status of spring-run Chinook salmon in the Willamette River, there is a need to further evaluate how smallmouth bass are distributed in the basin and to develop methods to assess habitat overlap between these two species.

Streamflow on the Willamette River is regulated by more than 20 major dams, including the Willamette Valley Project which is operated by the U.S. Army Corps of Engineers. The Willamette Valley Project is a series of 13 dams and reservoirs that provide anthropogenic benefits such as flood control protection and hydropower. However, operation of these dams has severely altered the natural hydrograph (Wallick et al., 2013), and recent efforts have focused on developing environmental flow options aimed at protecting listed Chinook salmon and steelhead *O. mykiss* (DeWeber & Peterson, 2020; Peterson et al., 2022). To support these efforts, the U.S. Geological Survey (USGS) developed high-resolution (3-m^2) hydraulic models to evaluate aquatic habitats within approximately 200 river kilometers (rkm) of the mainstem Willamette River (Peterson et al., 2022; White et al., 2022; White & Wallick, 2022). These models provided insights into the potential for flow management to improve habitat availability for juvenile and adult Chinook salmon and steelhead. Based on these existing models, and the need to evaluate for potential interactions between juvenile Chinook salmon and smallmouth bass, we conducted a study to: (1) determine if there is evidence of an expanding distribution of smallmouth bass in the mainstem Willamette River based on fish sampling data from 2011 to 2022; (2) develop a model to predict habitat availability for smallmouth bass in the mainstem Willamette River; (3) quantify habitat overlap between smallmouth bass and juvenile Chinook salmon; and (4) assess flow management options to minimize habitat overlap between these species.

2 | METHODS

2.1 | Study area

The Willamette River, in western Oregon, is a major tributary to the lower Columbia River and the 13th largest river (based on total discharge) in the continental United States (Kammerer, 1987). Our study was conducted on the mainstem Willamette River between the city of Newberg, Oregon (rkm 80) and the Willamette River/McKenzie River confluence (rkm 282; Figure 1). In this river segment, the Willamette River exists in two distinct geomorphic regions which are commonly referred to as the "Upper Willamette" and "Middle Willamette" (Wallick et al., 2013; White & Wallick, 2022). The Upper Willamette (rkm 210–300, which includes 20 rkm upstream of our study area) is a relatively dynamic reach with a multi-thread channel that is often bounded by low-elevation, bare gravel bars. The Middle Willamette (rkm 80–210) is primarily a single thread channel bound by both natural and human-built constrictions, with far fewer bare gravel bars (Wallick et al., 2013). Geomorphic differences between these reaches result in notably different hydraulic conditions across the range of streamflows that occur (White & Wallick, 2022). At low streamflow, the Upper Willamette generally has shallow depths, elevated velocities, and side-channels and alcoves that provide slow-water habitat. At higher streamflow, the Upper Willamette quickly inundates adjacent low-lying gravel bars, floodplains, and side channels, creating expansive areas of low velocity shallow water. Due to a natural lack of channel complexity as well as channel armoring, the Middle Willamette typically accommodates streamflow increases by increasing velocity within the reach, and inundated gravel bars and floodplains at high flow are scarcer than in the Upper Willamette (Wallick et al., 2013; White & Wallick, 2022).

Historically, Pacific salmon were restricted from accessing most of the Willamette River Basin by Willamette Falls, a 12-m-high natural waterfall located at rkm 43, except during late winter and early spring when high flows provided conditions that allowed for passage by winter steelhead and spring-run Chinook salmon (Myers et al., 2006). This

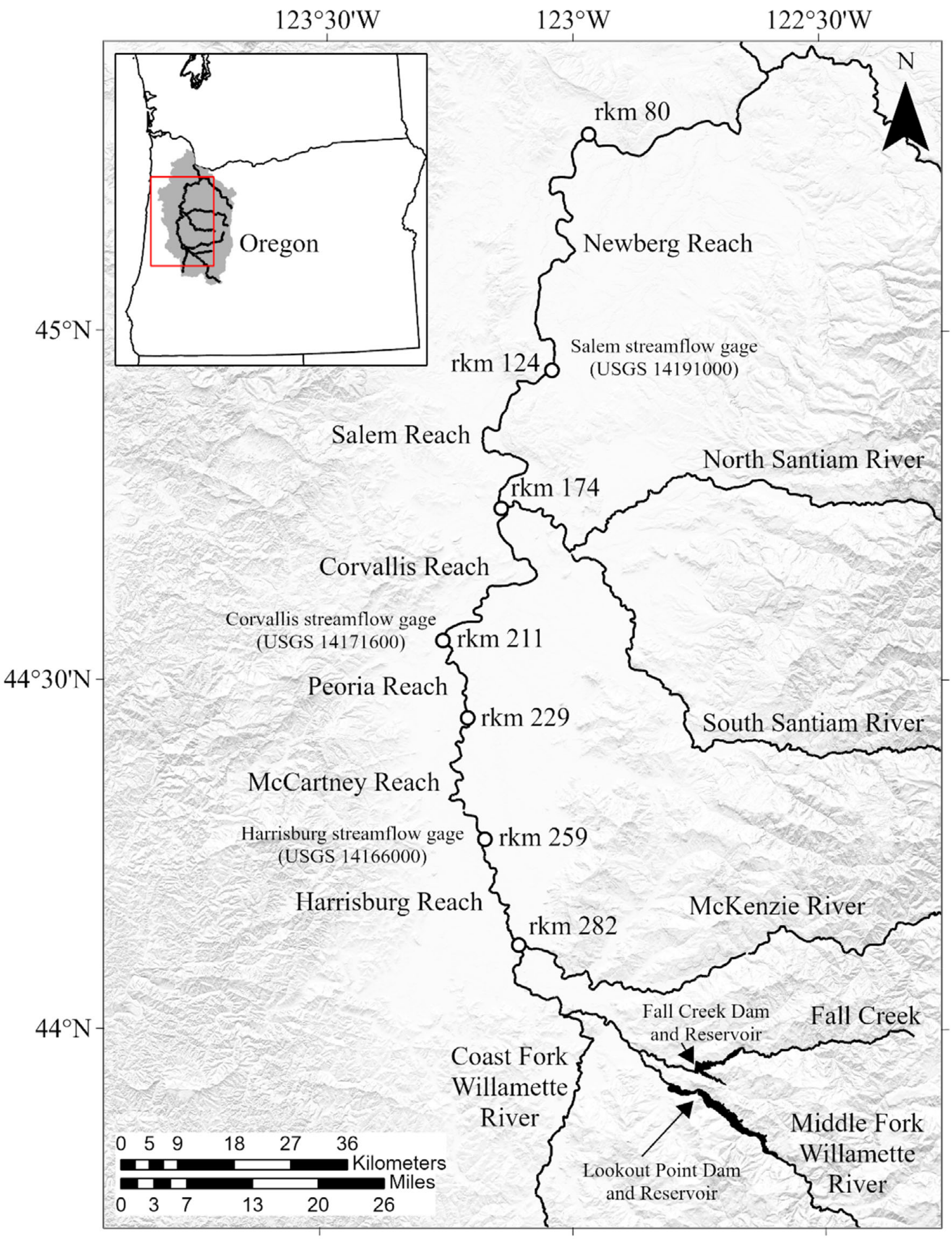

FIGURE 1 Map of the Willamette River Basin in western Oregon showing the mainstem river, primary tributaries, and study reaches. [Color figure can be viewed at wileyonlinelibrary.com]

passage barrier was eventually addressed by human interventions including fish ladder construction (in 1885) and subsequent passage improvements (Frazier, 1988; Kostow, 1995). These actions improved passage conditions such that spring-run Chinook salmon, fall-run Chinook salmon, coho salmon *O. kisutch*, winter-run steelhead, and summer-run steelhead now successfully access river reaches upstream of Willamette Falls. For this study, we focused on spring-run Chinook salmon because they are native to the upper Willamette River Basin and are a species-of-concern due to their perilous population status. Willamette River spring-run Chinook salmon have been extensively studied, and much is known about their diverse life histories (Schroeder et al., 2016; Whitman et al., 2017). Most returning adults move upstream past Willamette Falls during May–July each year and spawn during September and October. Juveniles which are produced from these spawning adults rear in the major spawning tributaries (McKenzie River, North Santiam River, South Santiam River) and the mainstem Willamette River (Whitman et al., 2017) for various durations and outmigrate both as subyearlings and as yearlings. Schroeder et al. (2016) reported that primary outmigration periods occur during June–July (as subyearling smolts), March–May (as yearling smolts), and November–December (as yearling "autumn smolts").

Smallmouth bass were first brought to the West Coast by Livingston Stone in 1874 and were initially introduced in Oregon (in the Willamette River) during 1923–1924 (Lampman, 1946). The Willamette River introductions were focused in two locations: in Oswego Lake (near Portland) where fish could access the mainstem Willamette River; and "in suitable reaches of the upper Willamette River" (Lampman, 1946). Fish sampling from 1944 to 51 yielded smallmouth bass in the mainstem Willamette River between rkm 283 and 301 (Dimick & Merryfield, 1945). However, sampling during 1982–2008 indicated that smallmouth bass were only present in the lower Willamette River between rkm 0 and rkm 184 (LaVigne et al., 2008). Harvey and Kareiva (2005) hypothesized that summer water temperatures were likely limiting the upstream distribution of smallmouth bass in the Willamette River relative to other large Oregon rivers such as the Umpqua and John Day Rivers. While smallmouth bass are the focal non-native species in this study, they are one of 19 non-native fish species known to occupy the Willamette River, including know piscivorous predators such as walleye *Sander vitreus*, largemouth bass *Micropterus salmoides*, and green sunfish *Lepomis cyanellus* (Williams, 2014).

2.2 | Fish sampling

Smallmouth bass were collected as part of two fish community assessments in the mainstem Willamette River during 2011–2013 and 2021–2022 following protocols described in Gregory et al. (2002) and Williams (2014). Sampling occurred at sentinel and random sites across a consistent spatial framework (Hulse & Gregory, 2004) from rkm 80 to rkm 282 during the seasonal low flow period of May–September each year when water temperatures were <18°C. This thermal limit was based on federal and state permitting requirements to avoid stressing ESA-listed fish (and other species-of-concern). At every sampling location, boat and backpack electrofishing was used to collect fish. The crew consisted of three people; one person operated the electrofishing unit and two people netted fish. Each boat electrofishing survey was 200-m in length, and the boat sampled in a downstream direction to facilitate fish observation and netting. For each boat survey, the vessel was located approximately 4–10 m from shore in water depths of 1–4 m (where possible). Backpack electrofishing surveys targeted microhabitats that represented the variety of shallow water habitat and associated structure (e.g., wood, vegetation, riprap, bed material) within each slice of the spatial framework. Backpack electrofishing was conducted initially along the long axis of the microhabitat, and then repeated in the opposite direction. At the end of every survey, all fishes ≥30 mm were identified (by species), and individual fork lengths were recorded. In all years, mainstem sampling consisted of four boat electrofishing surveys per slice, and alcove (active channel feature that maintains a connection at the downstream end to the low-flow mainstem channel) sampling consisted of three electrofishing surveys per slice because alcoves were generally too small to accommodate systematic sampling of more than three 200-m boat electrofishing runs. Lateral microhabitat samples for both mainstem and alcoves included four backpack electrofishing surveys per slice. The sampling protocol produced data that indirectly measured species abundance between sites and years based on catch per unit effort. Thus, capture of a given species provided evidence of that species occurrence at a site. However, lack of capture of a species at a given location did not provide proof of the absence of a species (i.e., fish could be present at a site but not captured).

2.3 | Model description

We used a hydraulic model (resolution ~3-m^2) that was previously developed and used in other studies in the Willamette River Basin (detailed model descriptions in Peterson et al., 2022; White & Wallick, 2022; White et al., 2022) to estimate habitat availability and to predict habitat overlap between smallmouth bass and juvenile Chinook salmon. For our study, the hydraulic model was applied to the mainstem Willamette River from rkm 80 to rkm 282 and we modified it in several ways to address our objectives. We divided the study area into six separate reaches, which ranged in length from 16 to 53 km, based largely on hydraulic model reaches and external fish-sampling efforts (Peterson et al., 2022) (Figure 1). These included the Harrisburg reach, McCartney reach, Peoria reach, Corvallis reach, Salem reach, and Newberg reach (Table 1). The Harrisburg, McCartney, and Peoria reaches are in the Upper Willamette and the Corvallis, Salem, and Newberg reaches are in the Middle Willamette. Streamflow data from USGS gages were used as a primary modeling input; data from the Harrisburg gage (14166000; USGS 2023) was used for the Harrisburg, McCartney, and Peoria reaches, data from the Corvallis gage (14171600; USGS 2023) was used for the Corvallis reach, and data from the Salem gage (14191000; USGS 2023) was used for the Newberg reach. For this study, we included streamflows typically observed during spring, summer, and early fall (≤70th percentile of daily average) because these flow conditions represent those that occur when juvenile salmon are rearing and when smallmouth bass are most active. Streamflow percentiles were used to compare results between reaches as a way to normalize streamflow between reaches, and percentiles were calculated from the mean daily streamflow at the respective gage in each reach between 1970 and 2022.

We used three parameters to model smallmouth bass habitat: water depth, water velocity, and revetment presence. Parameter values for water depth and water velocity were developed from a literature review focused on studies conducted on riverine populations of smallmouth bass (Table 2). Based on the literature review, we selected water depths that exceeded 0.50 m and water velocities that

TABLE 1 River reaches, reach boundaries, and streamflow gages (U.S. Geological Survey, 2023) used to in modeling to estimate habitat availability for adult smallmouth bass *Micropterus dolomieu* and habitat overlap for adult smallmouth bass and juvenile Chinook salmon *Oncorhynchus tshawytscha*.

Reach	Reach name	Rkm start	Rkm end	Streamflow gage used	Section
McKenzie River to Harrisburg	Harrisburg	282	259	Harrisburg (14166000)	Upper Willamette
Harrisburg to Peoria	McCartney	259	229	Harrisburg (14166000)	Upper Willamette
Peoria to Corvallis	Peoria	229	211	Harrisburg (14166000)	Upper Willamette
Corvallis to Santiam River	Corvallis	211	174	Corvallis (14171600)	Middle Willamette
Santiam River to Salem	Salem	174	124	Salem (14191000)	Middle Willamette
Salem to Newberg	Newberg	124	80	Salem (14191000)	Middle Willamette

TABLE 2 Parameter values used to estimate habitat availability for adult smallmouth bass in the Willamette River, Oregon. Values were obtained by a literature review from sources identified in the table with a focus on riverine populations of smallmouth bass.

Parameter	Input value	Data source
Water depth	>0.50 m	Rankin (1986) Todd and Rabeni (1989) Orth and Newcombe (2002) Fore et al. (2007)
Water velocity	<0.50 m/s	Edwards et al. (1983) Rankin (1986) Probst et al. (1984) Sechnick et al. (1986) Groshens and Orth (1993)
Revetments	All cells within 10 m	Friesen et al. (2007)

were less than or equal to 0.50 m/s as suitable habitat for smallmouth bass (Table 2). Previous studies in the Willamette River Basin reported that smallmouth bass were commonly observed near revetments (Friesen, 2005; Williams, 2014), so the model identified all habitat cells located within 10 m of these structures as suitable habitat for smallmouth bass regardless of water depth or water velocity. The predictive accuracy of the model for smallmouth bass was evaluated by calculating the percent of locations where smallmouth bass were observed during fish sampling that were correctly assigned as smallmouth bass habitat by the model.

Habitat attributes for juvenile Chinook salmon were more refined than for smallmouth bass because previous research (Hansen et al., 2023, Appendix S1) evaluated habitat use by juvenile Chinook salmon in the Willamette River and produced resource selection functions that predicted presence probability in habitat cells based on water depth and water velocity for two life stages: Chinook salmon fry (≤60 mm fork length; and Chinook salmon parr (>60 mm fork length). These resource selection functions were used to classify habitat cells as suitable or non-suitable for juvenile Chinook salmon based on streamflow scenarios we examined. Because these resource selection functions were developed from data collected in the Willamette River Basin, we did not further evaluate the predictive accuracy of the model for juvenile Chinook salmon.

To evaluate how habitat predictions and overlap varied across a range of streamflow scenarios, we used flow data from April to October for 3 years (2011, 2015, and 2016). These years were selected because they had distinct flow and temperature characteristics in relation to long-term "average" conditions in the Willamette River Basin: 2011 was unusually cool and wet; 2015 was unusually hot and dry; and 2016 was warmer than average, with typical streamflow (Figure 2) (Stratton Garvin et al., 2022). This range of conditions was selected to characterize the bounds of annual variation and to assess if habitat overlap was sensitive to changes in streamflow. Results from this analysis provide context to the extent to which potential changes in streamflow management could limit habitat overlap between juvenile Chinook salmon and smallmouth bass.

3 | RESULTS

3.1 | Smallmouth bass distribution

Data collected during fish sampling surveys from 5 years between 2011 and 2022 showed a sequence of upstream changes in smallmouth bass distribution in the mainstem Willamette River (Figure 3). In 2011, four smallmouth bass were collected at three sites upstream of the Santiam River confluence (rkm 173.8) and the farthest upstream location where smallmouth bass was observed was rkm 198. In 2012, eight smallmouth bass were collected at five sites upstream of the Santiam River confluence and the farthest upstream fish was collected at rkm 229. In 2013, 13 smallmouth bass were collected at eight sites upstream of the Santiam River confluence and the upstream extent of collection was at rkm 256. Sampling did not occur during 2014–2020. In 2021, a total of 83 smallmouth bass were collected upstream of the Santiam River confluence in a total of 21 sites and the upstream most collection occurred at rkm 262. In the final year of sampling (2022), 57 smallmouth bass were collected upstream of the Santiam River confluence and bass were observed at sites up to rkm 270. Overall, the most upstream location where smallmouth bass wasobserved increased by 72 rkm between 2011 and 2022 (Figure 3).

Smallmouth bass collection efforts provided data useful for assessing the predictive accuracy of the model. Overall, a total of 436 smallmouth bass were collected at 103 locations within the modeling

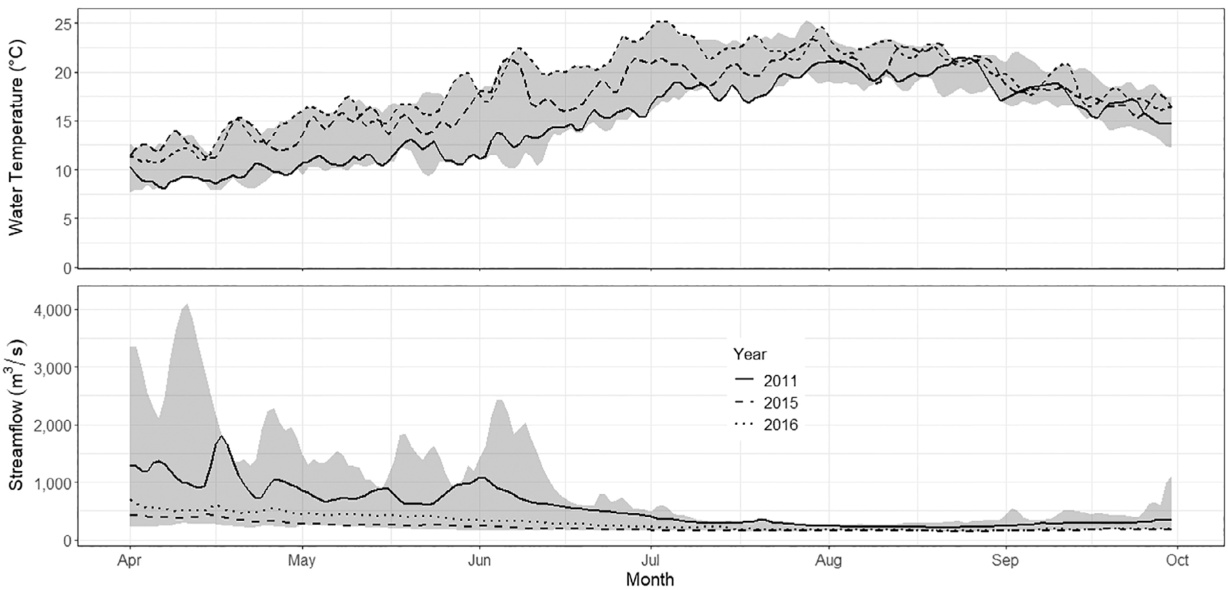

FIGURE 2 Streamflow and water temperature ranges (shaded grey area) in the Willamette River at Salem (USGS gage 14191000; USGS, 2023) during April–October 1970–2022. Highlighted years include 2011 (solid line), 2015 (long, dashed line), and 2016 (short, dashed line) which were used in model simulations.

domain in the Willamette River during our study. The model classified habitat at locations where 350 (80%) of the smallmouth bass were collected. Smallmouth bass that were collected at locations that were not identified correctly as habitat were present in locations where water velocities exceeded (0.50–2.06 m/s) the habitat parameter value (<0.50 m/s). Additional details on model validation can be found in Appendix S1.

3.2 | Reach-specific habitat availability

Smallmouth bass habitat availability varied substantially with increasing streamflow, and the Upper Willamette and Middle Willamette responded differently to streamflow changes. The smallmouth bass model estimated that increasing streamflow from 100 m^3/s (about the 5th percentile flow) to 250 m^3/s (about the 65th percentile flow) resulted in substantial increases in smallmouth bass habitat availability in the Harrisburg (20% increase), McCartney (17% increase), and Peoria reaches (22% increase) (Figure 4). Conversely, smallmouth bass habitat availability decreased in Middle Willamette reaches across the same relative flow range (67% decrease in the Corvallis reach; 64% decrease in the Salem reach; 44% decrease in the Newberg reach) (Figure 4).

3.3 | Habitat overlap between smallmouth bass and juvenile Chinook salmon

Modeled results showed that habitats for smallmouth bass and juvenile Chinook salmon are primarily located near shorelines in the mainstem Willamette River. Substantial habitat overlap was predicted between these two species, and when habitats do not overlap, the species are predicted to occur in proximity to one another (Figure 5). We found that smallmouth bass habitat overlapped with a substantial percent (approximately 50%–60%) of Chinook salmon fry habitat, whereas overlap with Chinook salmon parr habitat was lower (approximately 10%–20%; Figure 6). Habitat overlap between smallmouth bass and Chinook salmon fry was relatively constant across the range of streamflows we examined, except for the Harrisburg and Peoria reaches where overlap increased slightly as streamflow increased (Figure 6). We also observed that predicted smallmouth bass and juvenile Chinook salmon habitats occur in close proximity to locations where they do not overlap directly. In the Salem reach, 95% of Chinook salmon fry habitat was within 50 m of smallmouth bass habitat. Similarly, 74% of Chinook salmon parr habitat was predicted to occur within 50 m of smallmouth bass habitat. In the Harrisburg reach, 99% and 85% of Chinook salmon fry and parr habitat, respectively, overlapped with smallmouth bass habitat. Overall, 84%–99% of Chinook salmon fry habitat was within 50 m of smallmouth bass habitat throughout all reaches, compared to 57%–85% of Chinook salmon parr habitat. The Newberg reach had the least amount of overlap for both life stages, where 84% of Chinook salmon fry and 57% of Chinook salmon parr habitat was within 50 m of smallmouth bass habitat. The Harrisburg reach had the greatest amount of Chinook salmon habitat in close proximity to smallmouth bass habitat, with 99% of fry and 85% of parr habitat meeting the criteria.

3.4 | Effectiveness of flow management to minimize habitat overlap

Predicted habitat overlap between smallmouth bass and juvenile Chinook salmon fluctuated minimally under the streamflow scenarios we

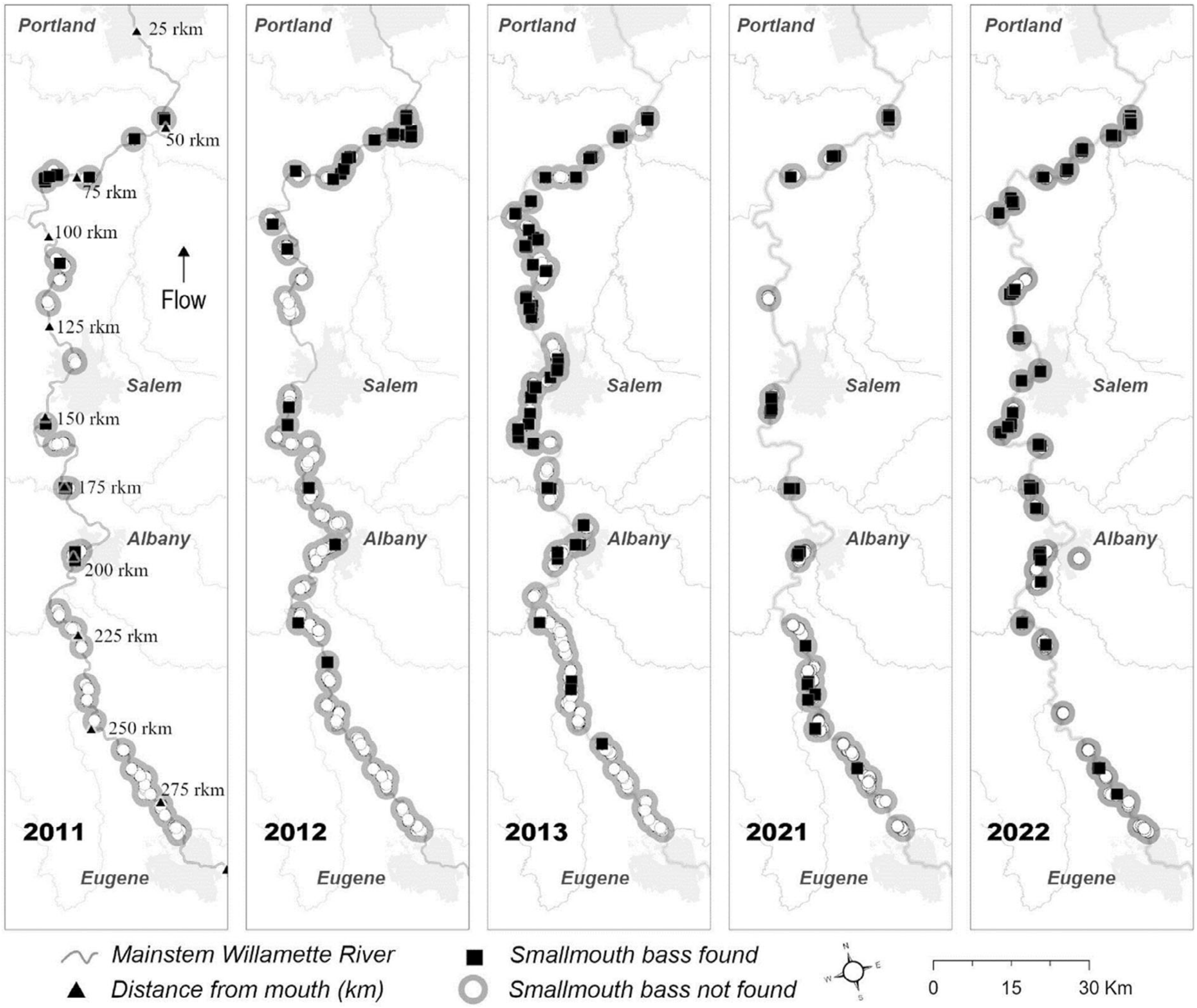

FIGURE 3 Schematic of locations where smallmouth bass were observed (filled squares) and not observed (open circles) during annual sampling conducted during 5 years (2011–2013, 2021–2022) on the Willamette River, Oregon.

examined, suggesting that flow management is an unlikely option for reducing overlap. For example, in the Harrisburg reach, overlap between smallmouth bass and Chinook salmon fry and parr was estimated to be approximately 62% and 3%, respectively, with minimal variation across streamflows ranging from the 1st to the 60th daily flow percentile (Figure 6). These relationships were generally similar across reaches (Figure 7, additional reaches in Appendix S1). This consistent response of the relative amount of habitat overlap is evident in the comparisons between different flow years, where although the total amount of habitat overlap between smallmouth bass and Chinook salmon varied on the order of 100% at times between years, the relative amount of habitat overlap is consistent in the three modeled years (Figure 7). For example, results show that the dry summer of 2015 had <5% difference in fry habitat overlap compared to the wet summer of 2011. There is even less difference in parr habitat overlap between modeled years, with typically only 1%–2% differences. Differences on the order of 10%–40% in habitat overlap occur for both fry and parr between the years in May and June, which is attributable to the large natural variation of streamflow during this period.

4 | DISCUSSION

Results from this study suggest that smallmouth bass have significantly expanded their distribution throughout the mainstem Willamette River during recent years. Smallmouth bass was collected progressively farther upstream throughout our sampling period as the maximum location where smallmouth bass was observed increased from rkm 198 in 2011 to rkm 270 in 2022. This trend was also numerically evident as we collected a total of four smallmouth bass upstream of the Santiam River mouth in 2011 compared to 83 smallmouth bass upstream of that location in 2021. These findings are noteworthy because they indicate that smallmouth bass are now present in critical rearing reaches for juvenile Chinook salmon, at least during summer months when our sampling occurred.

The mechanism for population expansion by smallmouth bass in the Willamette River Basin is currently unclear, but several possibilities exist. Smallmouth bass become increasingly active during spring as water temperature warms and spawning commences, and in many rivers throughout the Pacific Northwest seasonal migration (upstream

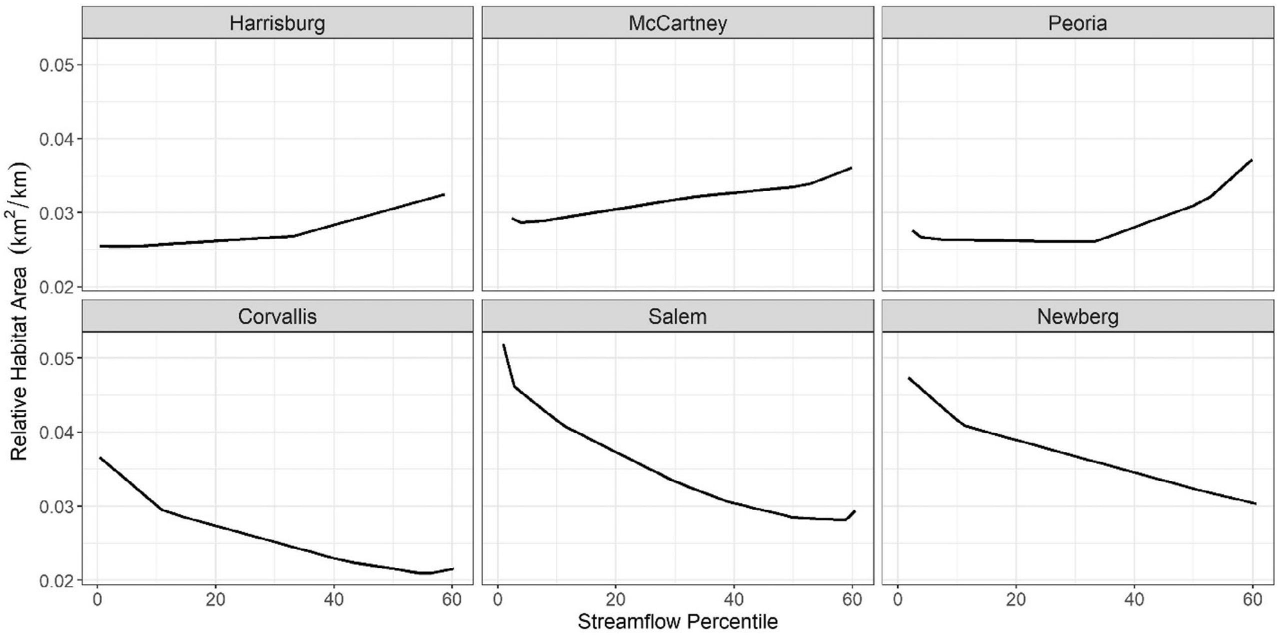

FIGURE 4 Total predicted habitat for smallmouth bass in the Willamette River, Oregon, across the range of streamflow that typically occur during spring and summer months.

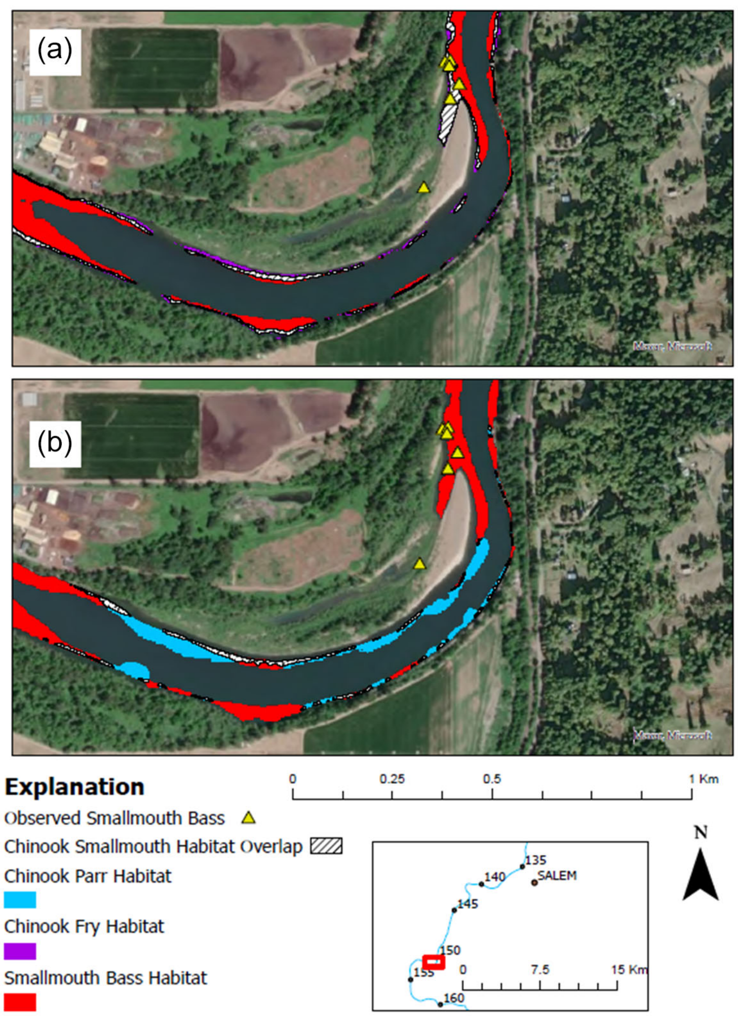

FIGURE 5 Examples of predicted smallmouth bass habitat, including overlap with Chinook salmon fry habitat (a) and Chinook salmon parr habitat (b), in the Willamette River, Oregon. Smallmouth bass observations from fish sampling at comparable streamflow are also shown (yellow triangles). [Color figure can be viewed at wileyonlinelibrary.com]

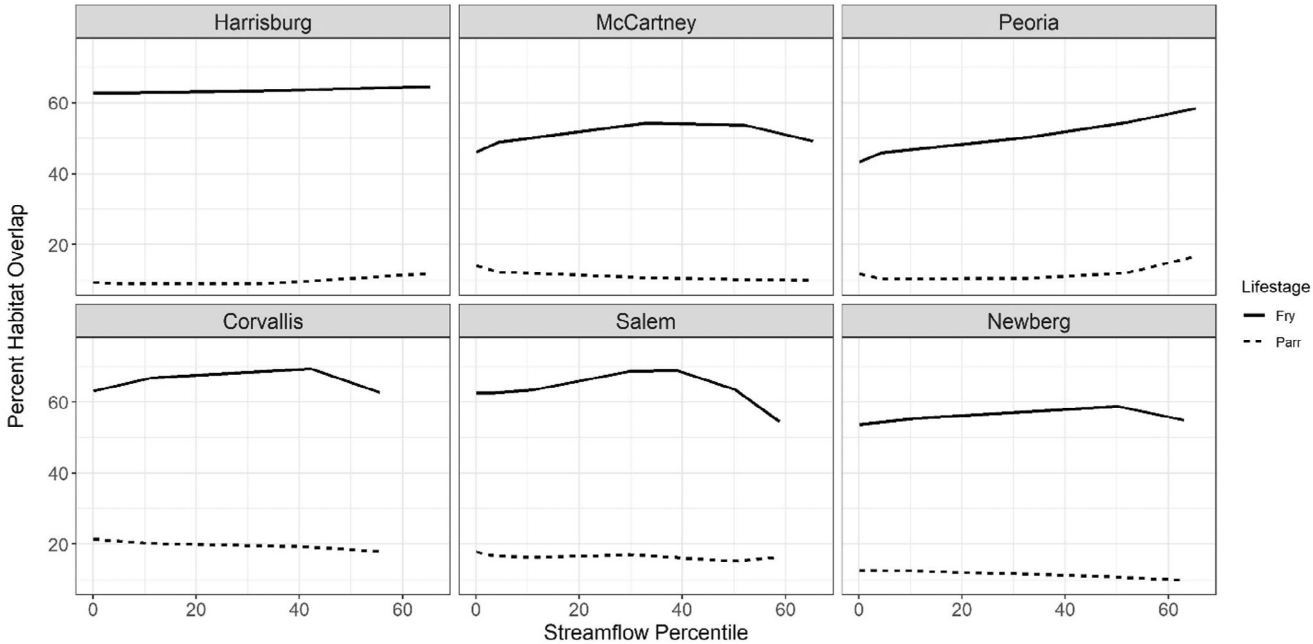

FIGURE 6 Relative predicted habitat overlap between smallmouth bass and two life stages of Chinook salmon (fry and parr) across a range of streamflows in six river reaches of the Willamette River, Oregon.

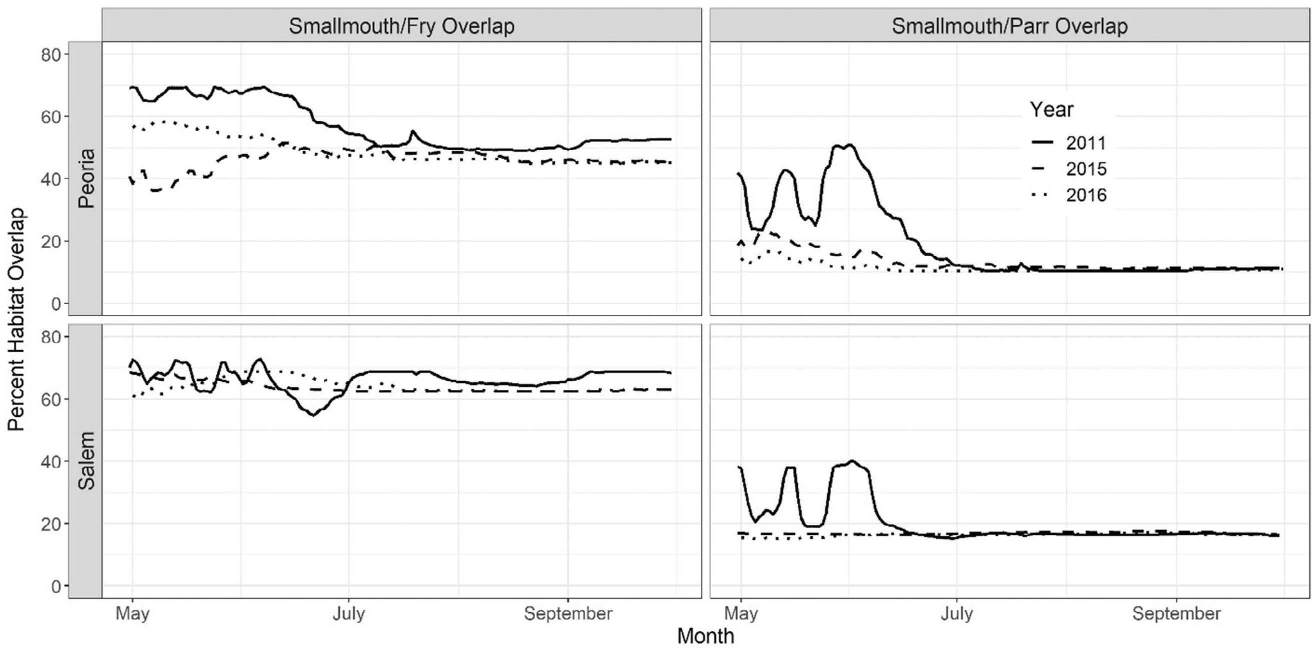

FIGURE 7 Relative predicted habitat overlap between smallmouth bass and two life stages of Chinook Salmon (fry and parr) during three hydrologically distinct summers (2011, 2015, 2016) in the Willamette River, Oregon. The Peoria and Salem reaches are shown as representative reaches assessed during this study.

and downstream) into novel habitat occurs (Fritts & Pearsons, 2004; Kock & Hansen, 2023; Rubenson & Olden, 2016, 2017). Because fish sampling occurred during spring and summer in our study, we could have collected fish that moved upstream seasonally, although that would not explain why smallmouth bass was collected progressively farther upstream throughout the study period. Another potential explanation is that environmental conditions are changing in the Willamette River such that upstream reaches are becoming increasingly hospitable for smallmouth bass. This supports predictions of an expanding population distribution in the basin made by Rubenson et al. (2020). Our data suggest that the realized expansion could substantially exceed their estimates of approximately 4% (Rubenson & Olden, 2019). It is also possible that smallmouth bass moved downstream from tributaries and reservoirs upstream of high head dams in the Willamette Valley Project. The U.S. Army Corps of Engineers conducted deep winter drawdowns in Fall Creek Reservoir (Figure 1) during 1969–1979, 1987, and 2011–present to facilitate downstream passage of juvenile Chinook salmon. Fall Creek Reservoir supports abundant populations of nonnative fish species which are also passed downstream during these drawdowns. Murphy et al. (2019) documented largemouth bass, bluegill *Lepomis machrochirus*, black crappie *Pomoxis nigromaculatus*, and white crappie *Pomoxis annularis* in screw traps located downstream of Fall Creek Reservoir during 2006–2017 and concluded that the deep drawdown was successful in "decreasing the abundance of invasive fish species in the reservoir." While this result may be positive for juvenile Chinook salmon residing in habitat upstream of Fall Creek Dam, the management action could lead to increased downstream populations of nonnative fish species (including smallmouth bass) if those fish survive and reside in the Willamette River Basin. While the factors responsible for an increased smallmouth bass distribution remain unclear, this finding highlights the need for future evaluations that comprehensively assess smallmouth bass effects on juvenile salmon (and other native fish) populations.

Our model predicted that smallmouth bass habitat is extensively present throughout the mainstem Willamette River, but we found that geomorphic differences among reaches affected habitat availability across the range of streamflows we examined. Modeled smallmouth bass habitat area varied substantially with streamflow and ranged from 0.75 to 3.0 km^2 in the various reaches of the study area. In Upper Willamette reaches, increasing streamflow resulted in increased habitat availability as multi-thread channels, gravel bars, and off-channel features became increasingly inundated, thereby supporting habitat attributes preferred by smallmouth bass. Conversely, in the channelized Middle Willamette, streamflow increases failed to inundate off-channel features, such as side channels and alcoves, resulting in increased water velocities in the main channel and, in turn, reductions in smallmouth bass habitat. While our results show that habitat is plentiful for smallmouth bass across a range of streamflows throughout the mainstem Willamette River, habitat availability is predicted to increase with increasing streamflow in the Peoria, McCartney, and Harrisburg reaches which are known critical areas for rearing juvenile Chinook salmon. Although previous fish sampling studies have indicated that smallmouth bass was not present in these critical rearing reaches (Friesen, 2005; Hughes et al., 2005; Hughes & Gammon, 1987; LaVigne et al., 2008), our data suggest that smallmouth bass have recently expanded their distribution to include the majority of the mainstem Willamette River.

Smallmouth bass habitat and juvenile Chinook salmon habitat overlapped directly, or occurred in close proximity, throughout the mainstem Willamette River, and predicted habitat overlap was largely unaffected by streamflow alterations. Modeled smallmouth bass habitat overlapped with greater than 50% of predicted Chinook salmon fry habitat in our study reaches and approximately 5%–40% of predicted Chinook salmon parr habitat. A recent study by Hansen et al. (2023) showed that juvenile Chinook salmon moved farther offshore into areas with increased water velocity with increasing body size, which likely explains why Chinook salmon parr habitat overlap was lower than for Chinook salmon fry. However, we found that smallmouth bass habitat occurred within 50 m of most (>75% or more) juvenile Chinook salmon habitat, regardless of life stage, highlighting the potential for these two species to experience substantial interactions. One of the main objectives of this study was to assess the efficacy of using flow management to minimize potential interactions between smallmouth bass and juvenile Chinook salmon, but we found that habitat overlap was largely unaffected by streamflow alterations. This is important because streamflow is one of the factors that can be directly manipulated by resource managers.

While our model predictions suggest that flow management is not a viable option for reducing habitat overlap between juvenile Chinook salmon and smallmouth bass, there are additional factors that should be considered. For example, our approach did not account for fish behavior and other biological considerations that could affect how species distribute when present in similar locations. Peterson and Rabeni (2001) found that prey-sized fish in their study altered their habit use in response to predation risk from larger aquatic predators. Thus, behavioral responses by juvenile Chinook salmon to smallmouth bass presence could reduce overlap between these species. Additionally, in numerous studies, streamflow has been shown to influence smallmouth bass in various ways including altering spawn timing and nesting success (Lukas & Orth, 1995), altering growth rates and survival of juveniles (Paragamian & Wiley, 1987; Smith et al., 2005), and affecting adult density and fishing yield (Peterson & Kwak, 1999). In the Upper Colorado River Basin, Bestgen and Hill (2016) evaluated how managed streamflows affected spawning and growth of juvenile smallmouth bass and concluded that management of flow and water temperature using controlled releases at dams in the system was a viable strategy for reducing negative effects of nonnative fish species and enhancing growth and survival of native species. Based on these observations, there is substantial evidence to support continued assessment of flow management options for reducing effects of smallmouth bass on imperiled native fish species in the Willamette River Basin and elsewhere.

Collectively, our results highlight the need for additional research focused on evaluating the expanding distribution of smallmouth bass in the Willamette River Basin, assessing for predation effects on juvenile Chinook salmon and other native fish species, and collecting data that can be used to improve the predictive capability of our model. Data collected during fish sampling for this study provide compelling evidence of an expanding population of smallmouth bass, but future studies that evaluate seasonal movement patterns and describe the year-around population distribution will provide insights useful for understanding potential impacts to rearing juvenile Chinook salmon. In that regard, studies that explicitly evaluate seasonal diet composition of smallmouth bass will likely be needed to assess for predation effects on juvenile Chinook salmon and other species of concern such as winter steelhead and Oregon chub *Oregonichthys crameri* (Hughes et al., 2019). Several studies have raised concerns about the implications of smallmouth bass presence and predation (Carey et al., 2011; Kuehne et al., 2012; Rubenson & Olden, 2019), or documented significant consequences in other rivers (Erhardt et al., 2018; Hughes & Herlihy, 2012). To that end, our model was developed to take advantage of existing hydraulic models and fish sampling data, and its predictive accuracy appears to be reasonable for predicting smallmouth bass presence, habitat overlap with juvenile Chinook salmon, and assessing for potential flow-management options to reduce overlap. However, a more comprehensive effort to collect fine-scale habitat information at precise locations where smallmouth bass are collected (e.g., Remshardt & Fisher, 2009), and include other important variables such as water temperature (Shuter et al., 1980; Todd & Rabeni, 1989) would enhance the usefulness of the model for resource managers. These steps may be necessary to enhance ongoing salmon recovery efforts in the Willamette River Basin.

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DATA AVAILABILITY STATEMENT

Willamette monitoring data described in this report are available by request from Brooke Penaluna. Hydraulic models used to develop the smallmouth bass models are available online at https://www.usgs.gov/data/two-dimensional-hec-ras-models-and-topo-bathymetric-datasets-willamette-river-oregon.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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