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APPLIED ISSUE

Spatiotemporal patterns and habitat associations of smallmouth bass (*Micropterus dolomieu*) invading salmon-rearing habitat

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SUMMARY

1. Smallmouth bass (*Micropterus dolomieu*) have been widely introduced to fresh waters throughout the world to promote recreational fishing opportunities. In the Pacific Northwest (U.S.A.), upstream range expansions of predatory bass, especially into subyearling salmon-rearing grounds, are of increasing conservation concern, yet have received little scientific inquiry. Understanding the habitat characteristics that influence bass distribution and the timing and extent of bass and salmon overlap will facilitate the development of management strategies that mitigate potential ecological impacts of bass.

2. We employed a spatially continuous sampling design to determine the extent of bass and subyearling Chinook salmon (*Oncorhynchus tshawytscha*) sympatry in the North Fork John Day River (NFJDR), a free-flowing river system in the Columbia River Basin that contains an upstream expanding population of non-native bass. Extensive (i.e. 53 km) surveys were conducted over 2 years and during an early and late summer period of each year, because these seasons provide a strong contrast in the river's water temperature and flow condition. Classification and regression trees were applied to determine the primary habitat correlates of bass abundance at reach and channel-unit scales.

3. Our study revealed that bass seasonally occupy up to 22% of the length of the mainstem NFJDR where subyearling Chinook salmon occur, and the primary period of sympatry between these species was in the early summer and not during peak water temperatures in late summer. Where these species co-occurred, bass occupied 60–76% of channel units used by subyearling Chinook salmon in the early summer and 28–46% of the channel units they occupied in the late summer. Because these rearing salmon were well below the gape limitation of bass, this overlap could result in either direct predation or sublethal effects of bass on subyearling Chinook salmon. The upstream extent of bass increased 10–23 km (2009 and 2010, respectively) as stream temperatures seasonally warmed, but subyearling Chinook salmon were also found farther upstream during this time.

4. Our multiscale analysis suggests that bass were selecting habitat based on antecedent thermal history at a broad scale, and if satisfactory temperature conditions were met, mesoscale habitat features (i.e. channel-unit type and depth) played an additional role in determining bass abundance. The upstream extent of bass in the late summer corresponded to a high-gradient geomorphic discontinuity in the NFJDR, which probably hindered further upstream movements of bass. The habitat determinants and upstream extent of bass were largely consistent across years, despite marked differences in the magnitude and timing of spring peak flows prior to bass spawning.

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5. The overriding influence of water temperature on smallmouth bass distribution suggests that managers may be able limit future upstream range expansions of bass into salmon-rearing habitat by concentrating on restoration activities that mitigate climate- or land-use-related stream warming. These management activities could be prioritised to capitalise on survival bottlenecks in the life history of bass and spatially focused on landscape knick points such as high-gradient discontinuities to discourage further upstream movements of bass.

Keywords: Chinook salmon, habitat modelling, longitudinal pattern, non-native fish, range expansion

Introduction

Non-native piscivorous fishes have been stocked in freshwater ecosystems throughout the world to support recreational fishing opportunities (Eby *et al*., 2006). Since their initial introduction and establishment, many of these species have spread, with and without additional human assistance (Johnson, Arlinghaus & Martinez, 2009), and future range expansions of non-native fishes in response to climate change are imminent (Rahel & Olden, 2008). Although only a subset of non-native species have been shown to cause ecological harm, in some cases their impacts to recipient ecosystems are dramatic and span multiple levels of biological organisation ranging from the genome to the ecosystem (Cucherousset & Olden, 2011).

Smallmouth bass (*Micropterus dolomieu* Lacepède; hereafter referred to as bass), a cool-water fish native to central and eastern North America, provide a compelling example of the potential ecosystem consequences of introducing a novel predator. Smallmouth bass have been widely stocked in freshwater ecosystems in Africa, England, Europe, Japan and Russia (Quinn & Paukert, 2009), as well as many regions in North America (Schade & Bonar, 2005; Carey *et al*., 2011). Their introduction has resulted in reduced growth of other native predators (Vander Zanden, Casselman & Rasmussen, 1999) and induced changes in the behaviour and distribution and at times caused the local extirpation of prey fish species (MacRae & Jackson, 2001; Jackson & Mandrak, 2002; Hughes & Herlihy, 2012). The impact of smallmouth bass introductions outside of the United States has gone largely unstudied, although recent work in Japan and South Africa suggests bass are having similar effects there (Iguchi *et al*., 2004; Woodford *et al*., 2005).

In the Pacific Northwest region of the United States, bass have been purposely stocked over the past century to promote recreational fisheries in rivers, lakes and reservoirs, where their potential to overlap with salmonids residing in headwater habitats was considered to be minimal (Lampman, 1946). Many bass populations have greatly expanded from their initial introduction sites (e.g. LaVigne *et al*., 2008), and there is increasing concern that they may now seasonally occupy upstream areas where some salmonids rear. As a result, smallmouth bass have been identified as a factor contributing to the decline in wild populations of Pacific salmon (*Oncorhynchus* spp.) now listed under the U.S. Endangered Species Act (Sanderson, Barnas & Wargo Rub, 2009; Carey *et al*., 2011). Climate-induced stream temperature warming (Isaak *et al*., 2012) and land-use management practices (e.g. removal of riparian vegetation) are likely to enable range expansions of predatory bass further into salmon-rearing grounds, potentially adding more stress on an already highly threatened group of cold-water fishes (Ruckelshaus *et al*., 2002).

Prior studies examining the impact of smallmouth bass on salmonids in the Pacific Northwest have focused largely on predation of salmon smolts as they move through the hydropower corridor of the Columbia River. Bass predation on outmigrating salmon smolts is highly variable, ranging from 0% to 35% of the total wild salmon run (Sanderson *et al*., 2009). This variability is primarily associated with the abiotic conditions (e.g. temperature, water clarity, flow) that occur when these species overlap (Carey *et al*., 2011) and the size and origin of the salmon smolts available for bass consumption (Fritts & Pearsons, 2006). The largest predatory impacts of bass on salmon to date have been documented where small subyearling ocean-type Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) emigrate from their natal sites when temperatures are warm enough to allow for bass activity (>10 °C, Poe *et al*., 1991; Fritts & Pearsons, 2004). Bass predation is much lower or non-existent on larger yearling salmon smolts that outmigrate earlier in the year when river temperatures are cooler (Poe, Shively & Tabor, 1994). Little is known about the potential sympatry between bass and salmon that spend extensive periods rearing in river systems. For example, stream-type Chinook salmon spend their first year in rivers before outmigrating the following spring as yearlings. Salmonids with this type of life

history are more likely to encounter bass during their first summer rearing period. Although potential impacts are unknown to date, river conditions during this period favour bass activity, and subyearling salmon are within the size range that is vulnerable to bass predation.

Upstream range expansions of bass in Pacific Northwest rivers are probably limited by temperature, but no studies have (i) documented the seasonal use of upstream areas by bass or (ii) attempted to identify limiting factors that may prevent their further upstream expansion. High-gradient reaches characteristic of mountainous river systems may also play a role in limiting the upstream extent of bass by serving as barriers to movement, especially during high flows. Understanding the limitations to bass upstream colonisation, the habitat characteristics that determine bass distribution and the timing and extent of bass and salmon overlap is needed to develop management strategies that mitigate potential impacts of bass in salmon-rearing habitats.

Recent studies of smallmouth bass in their native range suggest that the primary habitat variables that influence their distribution depend on the scale of study, corresponding to an increasingly prominent hierarchical view of fish–habitat relationships (Brewer *et al.*, 2007; Dauwalter *et al.*, 2007). However, no prior studies have used a spatially continuous sampling methodology (i.e. sampling all channel units over a survey extent) to characterise multiscale bass–habitat relationships across a river valley segment. Spatially continuous data provide the unique opportunity to understand how discontinuities in reach-scale physical habitats (e.g. geomorphic constrictions; Poole, 2002) affect fish distribution and upstream extent, and simultaneously allow an assessment of catchment-scale environmental drivers on distributional patterns (Fausch *et al.*, 2002). Continuous surveys also allow the researcher to change the spatial scale of analysis (i.e. sample grain) to assess across-scale fish–habitat relationships.

We employed a spatially continuous sampling design to determine the extent of smallmouth bass and subyearling Chinook salmon sympatry in the North Fork John Day River (NFJDR hereafter), a river system that both supports a recreational fishery for non-native bass and contains one of the healthiest remaining stream-type Chinook salmon stocks in the Pacific Northwest (McClure *et al.*, 2003). Using these data, we determined the primary habitat variables that influence the distribution of bass in the NFJDR, and by changing the grain of our analysis, we tested whether these variables depend on the scale of study. We conducted our study over 2 years to determine whether there was year-to-year consistency in the primary habitat variables that explained bass distribution. Extensive surveys were conducted in early and late summer to determine seasonal variation in bass and Chinook salmon distribution in the NFJDR. Finally, we investigated potential factors that limit the upstream extent of bass in the NFJDR, including the influence of geomorphically defined discontinuities that disrupt more continuous longitudinal gradients in habitat. These data are essential to manage bass populations and to prevent further range expansion of non-native bass in river systems by providing information at spatial scales (e.g. 10–100 km) of management relevance.

Methods

Study area description

The free-flowing NFJDR originates in the Blue Mountains of north-eastern Oregon and is a major tributary of the John Day River, which drains into the Columbia River (Fig. 1). Chinook salmon migrate upstream to their spawning areas in the NFJDR primarily from May to June and hold in the stream until spawning occurs in September (Lindsay *et al.*, 1985). The majority of Chinook salmon fry emerge from spawning redds from March to April. These fry grow and develop in the NFJDR and its tributaries until the following February–May, when they outmigrate as yearlings. Thermally suitable habitat for Chinook salmon holding and rearing (considered <24 °C; McCullough *et al.*, 2001) is compromised in the NFJDR from a legacy of mining, livestock overgrazing and water withdrawals for irrigation.

According to Shrader & Gray (1999), smallmouth bass have been present in the Columbia River since at least the 1930s, but they were not found in the John Day River mainstem above river kilometre (RKM) 16, owing to the impassable Tumwater Falls. In the 1960s, Oregon Game Commission biologists began to consider stocking bass above Tumwater Falls, but the decision took several years because of concerns that bass may prey on migrating salmon smolts. The risk to yearling salmon smolts from predatory bass was ultimately deemed to be low, given that smolts outmigrate when water temperatures are cold (2–7 °C) and the river is high and turbid, factors that are likely to reduce the risk of bass predation. Although they were not noted in Shrader & Gray's (1999) report, the risks to subyearling Chinook salmon that rear instream during their first summer were probably considered negligible, given that bass were to be introduced far downstream of subyearling Chinook salmon-rearing grounds. Ultimately, smallmouth bass were introduced to the lower mainstem of the John Day River in 1971 (Shrader & Gray, 1999). Bass

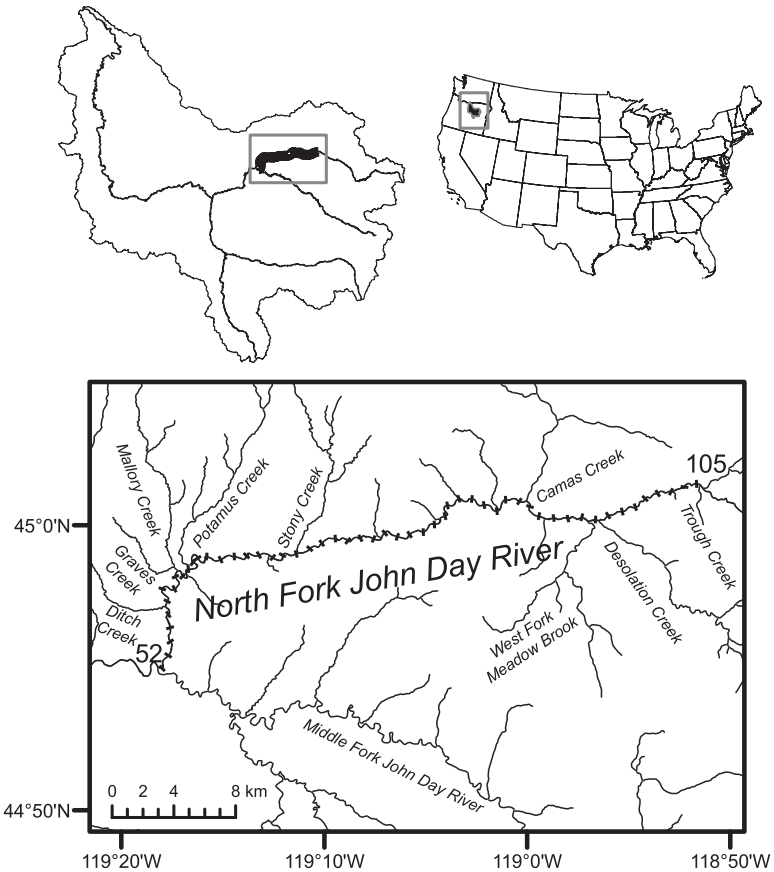

Fig. 1 Site map showing the survey extent of the North Fork John Day River (NFJDR) in north-eastern Oregon, USA. Surveys were conducted from river kilometre (RKM) 52, at the confluence with the Middle Fork John Day River, to Trough Creek at RKM 105. Hatching along the survey extent demarcates 1-km bins used in the reach-scale analysis.

were released 42 km below the confluence of the mainstem with the NFJDR, and where the NFJDR drains into the mainstem. Since that time, bass have moved progressively upstream, and recent surveys conducted by the authors reveal that bass are now seasonally sympatric with subyearling Chinook salmon in the NFJDR, 80–142 km upstream of their original release site (depending on which initial introduction site is considered their source), as well as in the upper reaches of the Middle Fork and mainstem John Day River. Although only 80 adult bass were released in the initial stocking effort (and no subsequent releases were required), the John Day River and its tributaries now host a prized recreational bass fishery, and bass are protected within the John Day River by a take limit of five individuals per day, per angler.

Other fishes observed in the NFJDR study extent included resident and anadromous rainbow trout (*Oncorhynchus mykiss* Walbaum), mountain whitefish (*Prosopium williamsoni* Girard), northern pikeminnow (*Ptychocheilus oregonensis* Richardson), largescale (*Catostomus macrocheilus* Girard) and bridgelip (*Catostomus columbianus* Eigenmann) suckers, longnose (*Rhinichthys cataractae* Valenciennes) and speckled (*Rhinichthys osculus* Girard) dace, redside shiner (*Richardsonius balteatus* Richardson), and multiple species of sculpin (*Cottus* spp.).

Temperature and discharge monitoring

Pendent temperature loggers (Onset Electronics, Onset, MA, U.S.A.) were deployed in the NFJDR to record annual water temperatures over the longitudinal extent of the survey area (RKM 52–105), with loggers positioned at RKM 52, 58, 66, 73, 86 and 105. Temperature was recorded hourly over the summer (i.e. June–August) and every other hour in the winter (September–May) in 2009 and 2010. Additional loggers (n = 13 in 2009, n = 16 in 2010) were deployed every 1–2 km immediately prior to the early summer survey and were recollected at the end of the late summer survey each year. These loggers recorded temperature at a 1-h interval.

We used degree days >10 °C (hereafter called degree days) rather than instantaneous temperatures during the

survey to describe the thermal history of the fish prior to and during the survey period and to better capture the differences in temperature dynamics between the 2009 and 2010 survey years. A 10 °C degree day threshold was chosen because bass are generally inactive and growth does not occur below this temperature (Shuter & Post, 1990). Degree days were calculated over the survey extent by summing the average daily temperature minus the 10 °C threshold from 1 May of each survey year through the last day of the survey. Because we did not install loggers until June in 2009, we used data from the U. S. Forest Service (measured hourly at RKM 99 from 1 May 2009) to determine degree days until our temperature sampling began. Temperature loggers were not deployed every RKM, so degree days were extrapolated across the survey extent based on a linear relationship between degree days and RKM in the study area (June 2009 model, $R^2 = 0.98$; August 2009 model, $R^2 = 0.97$; July 2010 model, $R^2 = 0.97$; August 2010 model, $R^2 = 0.99$).

Discharge during the survey period was determined based on a U. S. Geological Survey (USGS) long-term flow gage (station 14046000) stationed on the NFJDR at RKM 24. This station provided daily discharge data ($m^3\ s^{-1}$) from 1929 until present, allowing us to compare discharge conditions in 2009 and 2010 immediately prior to and during our surveys, as well as place our surveys in a historical context of long-term flow conditions.

Fish distribution and habitat surveys

We conducted spatially continuous fish distribution surveys of the NFJDR in the early summer (21–26 June 2009; 29 June–5 July 2010) and late summer (6–11 August 2009; 18–23 August 2010), for a total of four surveys over 2 years. Stream surveys were conducted from the NFJDR confluence with the Middle Fork John Day River (RKM 52) to Trough Creek (RKM 105), for a survey extent of 53 km. With the exception of the August 2009 survey, a 1-km reach (RKM 100–101) was not surveyed because this canyon reach contained rapids that were dangerous to snorkel. Preliminary surveys in 2008 revealed the RKM 52–105 survey extent represented the transition zone where bass seasonally utilised habitat in near proximity to, or overlapping with, rearing Chinook salmon. Chinook salmon spawning distribution in the NFJDR varies from year to year, with a downstream extent of redds at RKM 85 and an upstream extent at RKM 177 (Jeff Neal, pers. comm).

The timing of the distributional surveys was chosen to correspond to seasonally disparate flow and temperature conditions in the John Day River and to allow a comparison of bass and subyearling Chinook salmon sympatry during the early summer high-flow, cooler-temperature period and the low-flow, high-temperature, late summer condition. The timing of the early summer survey was also chosen to observe bass spawning in the NFJDR.

Fish distributional surveys were conducted utilising a modified version of a method developed by Torgersen *et al.* (1999, 2006), a spatially continuous survey technique of fish populations and their associated habitats where all channel units (i.e. riffles, glide-like riffles, glide-like pools, pools) were sampled over the study extent. Fishes were counted in each channel unit using two-person teams. Channel units were differentiated by changes in surface velocity and depth profile. Snorkelers surveyed each channel unit from downstream to upstream, first moving up one side of the stream, floating down the thalweg and then moving up the opposite bank. If the opposite bank was too shallow to snorkel, then only one bank and the thalweg were snorkelled. Snorkelers noted the species and number of each of the fishes observed. The abundance of bass adults (age 1 and older, >10 cm) and subyearling Chinook salmon is reported here. Water visibility was measured using a modified Secchi disc, a 25-cm-length and 2.5-cm-diameter PVC pipe, coloured alternately black and white. With the tube immersed in the water, the snorkeler moved slowly away from the tube until it was no longer visible, and then the distance between the snorkeler and the tube was measured. Average visibility was 6 m (standard deviation = 2 m), and visibility was lower during the high-flow early summer survey compared with the late summer period; decreases in visibility may have resulted in underestimation of counts in the early summer.

A shore-based surveyor used a global positioning unit (GPS) to georeference and delineate the channel unit. The surveyor also recorded habitat variables including the dominant and subdominant substratum (%), mean and maximum depth (m), unit length (m), average wet width (m), riparian cover along the stream bank (%) and large boulder coverage in the channel unit (%). Substrata, riparian cover and boulder cover were visually estimated; wet width and unit length were determined using a laser range finder; depth was determined by the snorkeler. Stream gradient was measured over the survey extent in a geographical information system (GIS) using 1:24 000 USGS digital raster graphics by marking points where topographic contours crossed the stream and then calculating the elevation change over the distance separating each point.

Long channel units (>100 m) were subsampled using the following rule: If the channel unit was ≤300 m, the

snorkeler surveyed 100 m of habitat, skipped 100 m and then snorkelled the remaining habitat. If the channel unit was >300 m, the snorkeler surveyed 100 m and then skipped 200 m; this subsampling procedure was repeated until the unit ended. Because riffle habitat was difficult to snorkel owing to high water velocities in the early summer and shallow conditions in the late summer, riffles were snorkelled in areas with depths typically >0.25 m; all other habitat within riffles (<0.25 m) was considered too shallow for adult bass (Orth & Newcomb, 2002; Dauwalter *et al*., 2007). This may have resulted in some underestimation of subyearling Chinook salmon numbers if they reside in very shallow sections of riffles, but previous surveys within the NFJDR (Torgersen *et al*., 2006) and other studies suggest that subyearling Chinook salmon typically occur in slower, deeper habitats (Everest & Chapman, 1972; Hillman, Griffith & Platts, 1987; Roper, Scarnecchia & La Marr, 1994).

Bass and subyearling Chinook salmon distribution was assessed across the longitudinal continuum of the NFJDR at two scales: the channel-unit scale and at a 1-km scale. The 1-km scale was chosen to describe reach-level fish–habitat relationships. Counts of each species per RKM (where RKM 0 represents the NFJDR confluence with the John Day River main stem) were determined using a custom binning script in R (version 2.13.0; R Development Core Team, Vienna, Austria). Because some long channel units were subsampled, we extrapolated counts to estimate total fish per channel unit based on a fish per unit length metric. Pools were snorkelled completely so no extrapolation was required. Riffles were treated differently because (i) we snorkelled 'useable' habitat and (ii) applying fish count estimates from 'useable' habitat to extrapolate counts to large sections of riffles that were unusable (i.e. extremely shallow) would have resulted in overestimates of fish numbers. In extremely shallow sections of riffles, we assumed that adult bass and subyearling Chinook salmon abundance was zero.

To define the upstream extent of bass reproductive activities, any bass nest encountered during the early summer surveys (i.e. late June and early July) was noted and its position was recorded using a GPS. Nest counts presented in the results represent conservative estimates because counts from sampled areas were not extrapolated to unsampled portions of channel units.

Statistical analysis

Bass-habitat relationships were analysed using a recursive partitioning algorithm widely known as classification and regression trees (CART). CART is a useful technique to model ecological data because it can handle a combination of continuous and discrete explanatory variables, it is relatively insensitive to outliers and it can accommodate both nonlinear and interactive relationships between the explanatory variables and the response variable (Olden, Lawler & Poff, 2008). The goals of the statistical analysis were to explore the primary habitat correlates of bass distribution and to determine whether the relative importance of these variables changed seasonally and at different spatial scales. Thus, the analysis was completed at two scales (i.e. channel unit and 1-km binned reach-scale data), and each of the four surveys was assessed separately (i.e. 2009 and 2010 early summer models, and 2009 and 2010 late summer models), for a total of eight models.

Reach-scale regression trees were built with bass count per kilometre as the response variable. The explanatory variables included degree days, gradient (m km^{-1}), length-weighted average maximum depth (m), channel wet width (m), percentage of riparian cover (%), percentage of large boulder cover (%) and a velocity and substratum score. The velocity metric employed in the model was semiquantitative and was calculated by (i) determining the percentage of each RKM composed of riffle, glide-like riffle, glide-like pool and pool habitat; (ii) multiplying the contribution of each of these unit types by 4,3,2 and 1, respectively (to represent fast to slow velocity units) and (iii) summing the result. Therefore, velocity scores for each RKM range between 1 and 4, depending on the overall occurrence of each unit type within that kilometre. Substratum score represents a composite score determined by multiplying the field-measured substrata data (i.e. percentage of dominant and subdominant substratum) by a score (5 = bedrock, 4 = boulder, 3 = cobble, 2 = gravel, 1 = sand), adding up that total and then applying a logarithmic transformation. This method resulted in an increasing score as substratum size increased. Trees were built using 10-fold cross-validation and pruned based on the one-standard-error rule (De'ath & Fabricius, 2000) with the *rpart* library in R.

At the channel-unit scale, the response variable for the regression trees was bass adults per km^2, measured as the channel-unit wet width multiplied by the unit length. The response variable at this scale was highly heteroscedastic, so it was log $(x + 1)$ transformed prior to analysis (Moisen, 2008). The continuous explanatory variables included in the channel-unit-scale models were degree days, channel gradient (m km^{-1}), mean unit depth (m), max unit depth (m), channel wet width (m), percentage of riparian cover (%), percentage of large boulder cover (%) and substratum score (as calculated previously). Unit type (i.e. riffle, glide-like riffle, glide-like pool and pool), a non-

Table 1 Thermal and discharge characteristics of the North Fork John Day River during the early and late summer surveys in 2009 and 2010

			Average daily temperature (°C)		Discharge (m^{-3} s^{-1})
Season	Year	Survey dates	RKM 52	RKM 105	RKM 24
Early	2009	21–26 June	13.7–20.2	10.0–16.2	21.6–30.0
summer	2010	29 June–5 July	16.0–19.9	13.2–17.0	24.1–34.6
Late	2009	6–11 August	17.4–23.9	15.1–19.3	3.5–11.9
summer	2010	18–23 August	18.5–24.1	15.4–20.8	3.1–3.7

Average daily water temperatures (°C) represent the range in mean temperatures during the survey period at river kilometre (RKM) 52 and 105, corresponding to the downstream and upstream survey extent. Stream discharge (m^{-3} s^{-1}) represents the range in discharge during the survey period. Stream discharge was measured at RKM 24, the site of a U.S. Geological Survey (USGS) long-term flow gauge.

continuous explanatory variable representing a channel unit's velocity and depth profile, was included as a factor-type variable in models at this scale. Trees were built using 10-fold cross-validation. Because we were interested in describing rather than predicting bass–habitat relationships at the channel-unit scale, the tree was allowed to grow one additional branch beyond the one-standard-error rule commonly used for pruning the tree (i.e. model simplification) during regression tree building.

Results

Stream physical characteristics during the surveys

The seasonal stream temperature profile and hydrograph of the NFJDR are typical of a snow-melt-driven Pacific Northwest river system, with peak discharge in the late spring/early summer period and maximum temperatures during the summer low-flow period (typically in early August). Average daily water temperatures during the early summer surveys were similar over the study extent between 2009 and 2010 (Table 1). Stream temperatures observed during both late summer surveys were also similar (Table 1), but they were depressed compared with temperatures recorded prior to and after each survey. For example, in late summer 2009, the peak summer temperature recorded at RKM 52 (27.6 °C) was observed 4 days prior to the survey initiation. A heavy rainstorm occurred during this survey, causing the average daily temperature recorded at RKM 52 to drop 10 °C. Degree days accumulated at both the downstream (i.e. RKM 52) and upstream areas of the survey extent (i.e. RKM 105) were higher in 2009 compared with 2010 during early and late summer, reflecting the earlier warming that year (Fig. 2a).

Discharge was also similar between early summer surveys in 2009 and 2010 (Table 1), although the timing and magnitude of peak discharge was different between years (Fig. 2b). Peak monthly mean flow in 2009 occurred in May, and although it was high relative to the 80-year historical average (152 versus 102 m^3 s^{-1}, Fig. 2b), the timing of the peak matched the long-term record. A large snow pack and a relatively cold spring delayed the peak monthly mean discharge in 2010, which occurred in June. The magnitude of the 2010 June mean monthly discharge was also high, reaching

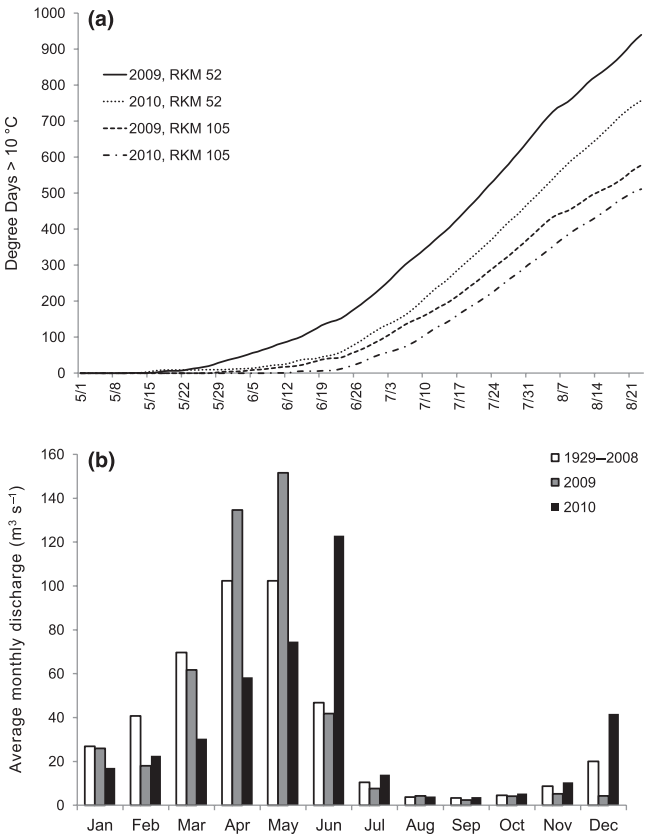

Fig. 2 Temperature and discharge conditions of the North Fork John Day River (NFJDR) during the survey period. (a) Degree days (DD) >10 °C accumulated from 1 May until 23 August for each survey year at the downstream [river kilometre (RKM) 52] and upstream extent of the survey area (RKM 105); (b) Average monthly discharge in 2009 and 2010 compared with the 59-year (1929–2008) monthly mean discharge, measured at a U.S. Geological Survey (USGS) gauge station at RKM 24.

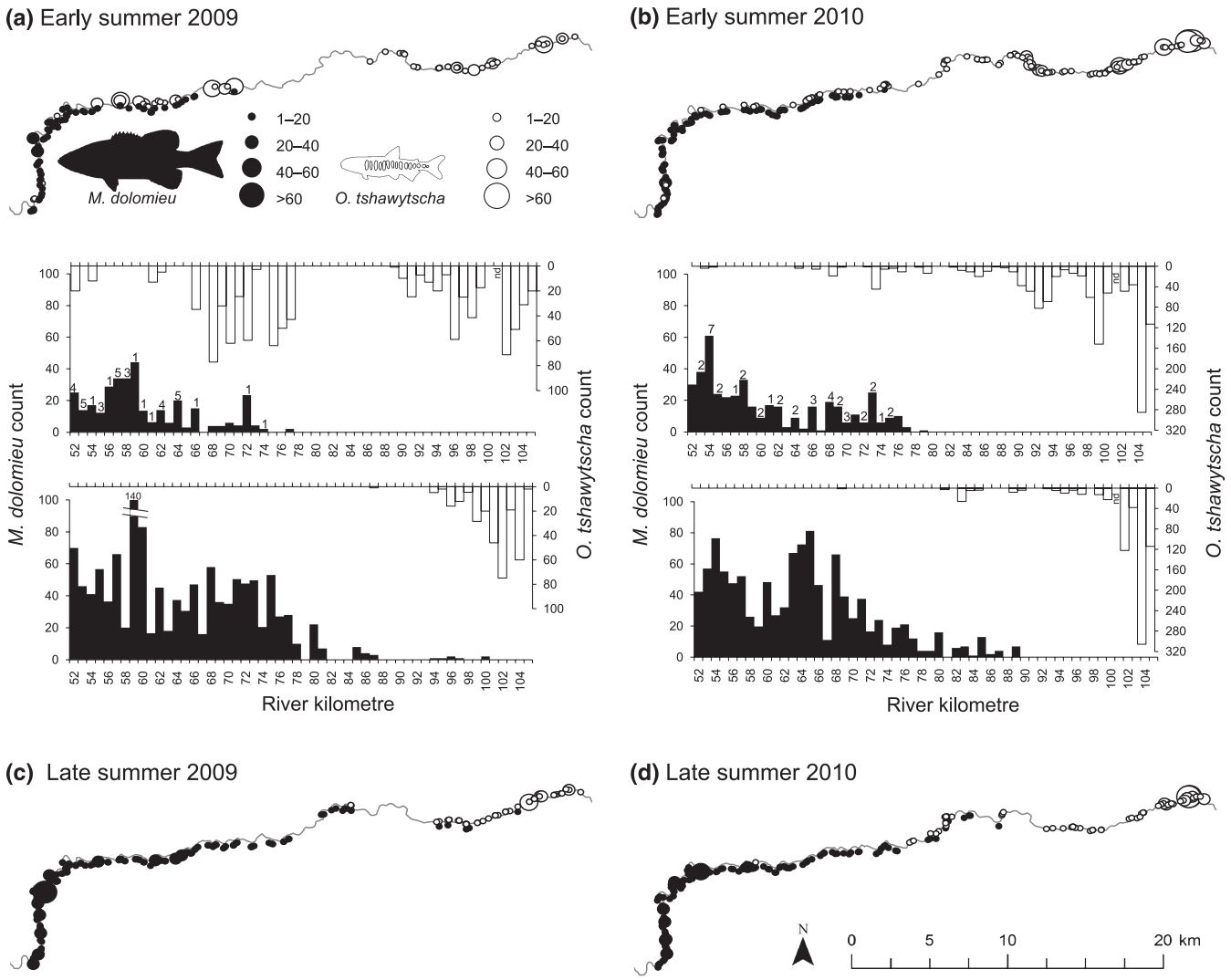

Fig. 3 Early and late summer distribution of bass and subyearling Chinook salmon in the North Fork John Day River (NFJDR) over the survey extent at channel-unit and reach (i.e. 1-km) scales. Circles displayed on the stream hydrography symbolise channel-unit counts of bass (filled symbols) and Chinook salmon (open symbols). The symbols are offset from the hydrography to allow for better visualisation of channel units in which bass and subyearling Chinook salmon co-occur. Bars represent counts of bass (filled) and subyearling Chinook salmon (open) km^{-1} at the reach scale. River kilometre (RKM) 100 was not surveyed (nd = no data) in June 2009, July 2010 and August 2010. Note that bass were found below the survey extent and subyearling Chinook salmon were found above it. (a) Early summer 2009 bass and Chinook salmon distribution at channel-unit and reach scales. Numbers above bass km^{-1} counts represent the number of bass nests observed km^{-1}. Nest counts were not extrapolated to unsampled areas (see methods); (b) Early summer 2010 bass and Chinook salmon distribution at channel-unit and reach scales. Numbers above bass km^{-1} counts represent the (unextrapolated) number of bass nests observed km^{-1}; (c) Late summer 2009 bass and Chinook salmon distribution at channel-unit and reach scales. The axis break at RKM 59 at the reach scale denotes a count of 140 bass km^{-1}; (d) Late summer 2010 bass and Chinook salmon distribution at channel-unit and reach scales.

123 m^3 s^{-1}. A heavy rain storm increased the range of discharge observed during the late summer 2009 survey and tripled the maximum discharge observed at that time compared with 2010 (Table 1).

Fish distribution and bass–Chinook salmon sympatry

Bass occurred in the lower region of our survey extent during the early summer in 2009 and 2010, with an upstream extent of RKM 77 and 79, respectively (Fig. 3). Peaks in bass counts differed spatially between years during these surveys, as revealed by the kilometre-scale distributional data. Bass were nesting during the early summer survey in both years, and the majority of nests were found in the lower survey region. The numbers of nests observed (i.e. 37 in 2009 and 40 in 2010) and the position of the most upstream nest were comparable between years (i.e. RKM 74 in 2009 and RKM 75 in 2010).

At the beginning of the survey, 7-day average daily (7DAD) minimum, mean and maximum temperatures at the upstream-most nest were 12.7, 15.0 and 17.6 °C, in 2009 and 15.1, 17.3 and 19.6 °C in 2010, respectively. The upstream extent of adult bass largely coincided with the upstream extent of bass nests in 2009 and 2010, where few adult bass were upstream of the most upstream nest.

The upstream extent and the numbers of bass observed greatly increased in the late summer survey, suggesting bass were moving up from below the lower survey extent (Fig. 3). Bass distribution was patchy during the late summer in both years, and similar to the early summer surveys, the spatial position of peak counts varied between years. The late summer upstream extent of bass was similar between years, but some bass penetrated further upstream in 2009 (i.e. up to RKM 100) compared with 2010 (i.e. up to RKM 89). Bass had completed nesting before the late summer survey, as no nests were observed. 7DAD minimum, mean and maximum temperatures where the most upstream bass were observed in late summer were 16.1, 18.8 and 22.1 °C in 2009 and 16.1, 19.9, and 24.8 °C in 2010, respectively.

Subyearling Chinook salmon co-occurred with bass at both the channel-unit (e.g. the same pool) and reach scale (i.e. within the same RKM), but the extent of overlap was higher in the early summer compared with the late summer (Fig. 3). The downstream extent of subyearling Chinook salmon in the early summer was consistent across years, with Chinook salmon found downstream to RKM 52 in 2009 and RKM 53 in 2010, although small numbers of Chinook salmon may have occurred downstream of our survey extent. In early summer, subyearling Chinook salmon numbers increased from downstream to upstream, but the pattern was more pronounced in 2010 compared with 2009. The spatially continuous nature of the survey revealed that, similar to bass, subyearling Chinook salmon distribution was patchy over the survey extent and the (reach scale) peaks in subyearling Chinook salmon distribution were not spatially similar between survey years. 7DAD minimum, mean and maximum temperatures where the downstream-most subyearling Chinook salmon were observed in early summer were 14.3, 16.7 and 19.2 °C in 2009 and 15.9, 18.2 and 20.5 °C in 2010, respectively.

Bass and Chinook salmon co-occurred from RKM 52–77 in early summer 2009 (25 km total) and RKM 53–79 in 2010 (26 km total). Within this area of overlap, bass occurred in 60% (2009) to 76% (2010) of the channel units occupied by subyearling Chinook salmon. Given that rearing Chinook salmon persist until RKM 165 (Torgersen *et al.*, 2006) and thus occur over 113 km of the NFJDR, bass occurred in 22% of the length of the mainstem NFJDR where subyearling Chinook salmon are typically present.

The overall extent of sympatry between bass and subyearling Chinook salmon declined in the late summer period in 2009 (14 km) and 2010 (21 km) (Fig. 3). Bass occupied 28% (2009) to 46% (2010) of the channel units where subyearling Chinook salmon occurred within this area of overlap. The late summer downstream extent of subyearling Chinook salmon in 2009 was RKM 87 and RKM 69 in 2010, although very few Chinook salmon were observed this far downstream during this period. 7DAD minimum, mean, and maximum temperatures at the most downstream site occupied by subyearling Chinook salmon at this time were 16.5, 19.5 and 23.1 °C in 2009 and 18.2, 21.6 and 24.9 °C in 2010. The majority of the subyearling Chinook salmon were observed above RKM 100 in August of both years.

Bass–habitat relationships

Water temperature, quantified here as degree days, was the strongest predictor of bass distribution at the reach (i.e. kilometre) scale in both seasons and both years (Fig. 4). No other habitat variable was selected through the CART analysis at this scale. Pruned regression trees built to predict bass km^{-1} had an R^2 of 0.74 [root-mean-square error (RSME = 5.4, $P < 0.0001$)] and 0.59 (RSME = 18.0, $P < 0.0001$) for early and late summer in 2009, respectively, and 0.77 (RSME = 5.9, $P < 0.0001$) and 0.70 (RSME = 13.0, $P < 0.0001$) for early and late summer in 2010, respectively. Early summer kilometre-scale trees split on 137 degree days (and subsequently on 111 degree days) in 2009 and 141 degree days (and subsequently on 113 degree days) in 2010. Late summer kilometre-scale trees split based on 628 degree days in 2009 and 674 degree days in 2010. Both late summer regression trees had only one split and two terminal nodes.

At the channel-unit scale, degree days and other habitat features, including mean and max depth, channel-unit type (e.g. riffle, pool) and wetted channel width were the primary correlates of bass density (Fig. 5). For all seasons and years, temperature and habitat variables operated in a hierarchical manner to predict the density of bass, and degree days consistently represented the first regression tree split. In the early summer 2009, slower velocity channel units (i.e. glide-like riffles, glide-like pools and pools) where accumulative degree days exceeded 107 and particularly channel units with 122 or more degree days supported the highest bass densities (model performance: $R^2 = 0.68$, RMSE = 5.77, $P < 0.0001$, Fig. 5a). Similarly, in early summer 2010, channel units with >113 degree days

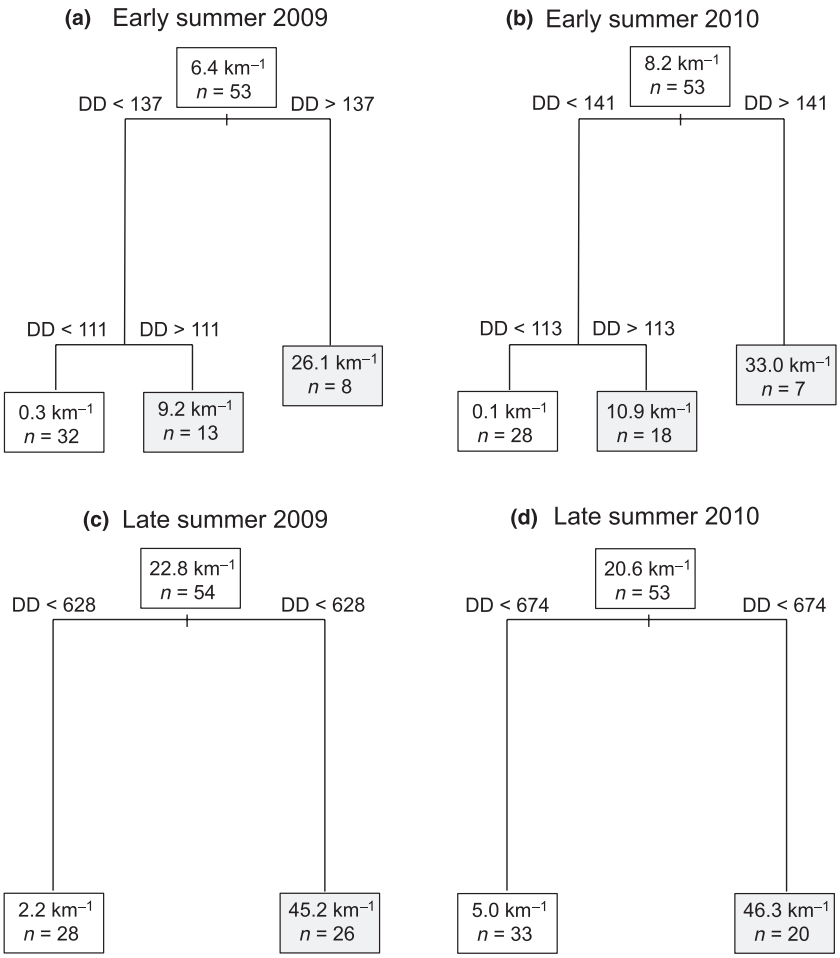

Fig. 4 Regression tree analysis of reach (i.e. kilometre)-scale bass abundance for (a) early summer 2009, (b) early summer 2010, (c) late summer 2009 and (d) late summer 2010 surveys. Parent and terminal (i.e. child) nodes of each tree are represented by a square. The number within each node denotes the mean bass count km^{-1} and the number (n) of river kilometres (i.e. sample size) in that node. DD = degree days >10 °C. Terminal nodes with grey-fill had greater bass abundance than the global average (i.e. the root node).

had the highest bass densities, particularly in glide-like riffle, glide-like pool and pool units with >140 degree days accumulated (R^2 = 0.66, RMSE = 3.85, P < 0.0001, Fig. 5b). Deeper channel units also supported higher densities of bass compared with shallow units; for example, units with 113–140 degree days with mean depths exceeding 0.55 m had nine times higher bass densities than thermally comparable, but shallower units. In late summer 2009, bass were typically present in warmer channel units with degree days exceeding 611, whereas bass were absent or rare in cooler units (Fig. 5c). In warmer channel units, bass density on average was lower in riffle habitats compared with glide-like riffles, glide-like pools and pools, and within these channel-unit types, densities were highest in units with greater maximum depth. Habitat correlates of bass density in late summer 2010 were similar to 2009. Cooler channel units (degree days <666) typically supported lower bass densities, with the exception of glide-like pool and pools units where degree days exceeded 602 (Fig. 5d). In the warmer regions of the river (degree days >666), channel-unit type was the second most important variable; riffle units had a lower density of bass compared with all other unit types. In both riffle and non-riffle habitats, units with greater maximum depth had higher bass densities. The 2009 and 2010 late summer models explained similar proportions of the overall variability in bass density at the channel-unit scale, with an R^2 of 0.71 in 2009 (RMSE = 6.52, P < 0.0001) and 0.68 (RMSE = 5.77, P < 0.0001) in 2010.

Limits to upstream movement

Continuous sampling revealed that the upstream extent of bass corresponded with a discontinuity in channel geomorphology (Fig. 6). In August 2009, bass were found

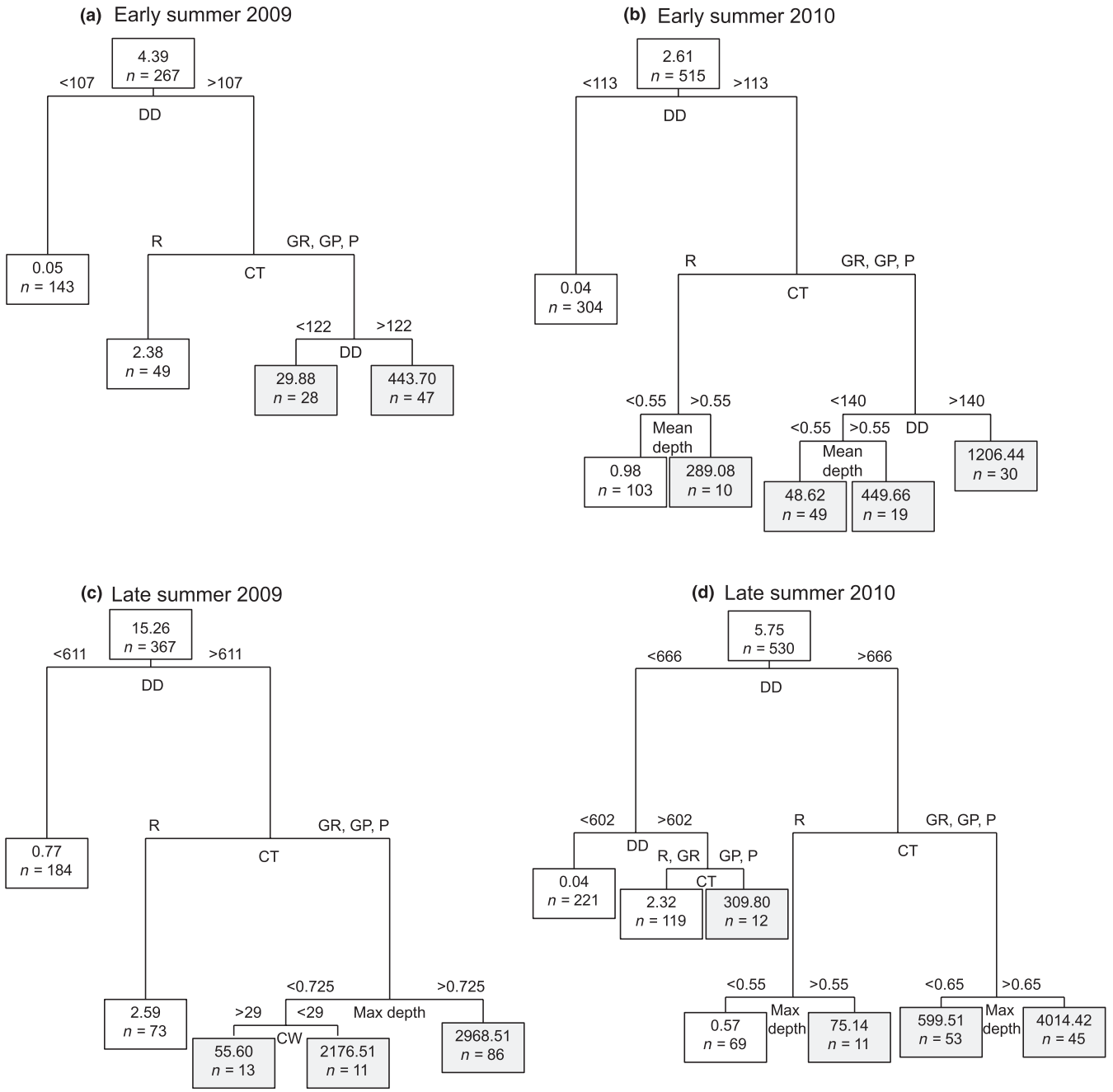

Fig. 5 Regression tree analysis of channel-unit-scale bass density (km^{-2}) for (a) early summer 2009, (b) early summer 2010, (c) late summer 2009 and (d) late summer 2010 surveys. Parent and terminal (i.e. child) nodes of each tree are represented by a square. The number within each node denotes the mean bass density (km^{-2}) and the number (n) of channel units (i.e. sample size) in that node. Degree days (DD) >10 °C; Channel-unit type (CT), where R, riffle; GR, glide-like riffle; GP, glide-like pool; P, pool; CW, channel width (m); mean and max depth (m). Terminal nodes with grey-fill had greater bass density than the global average (i.e. the root node).

just below a high-gradient river segment (8 m km^{-1}), where the NFJDR becomes highly constrained in a canyon at RKM 100. The upstream extent of bass in 2010 was RKM 89, right downstream of a segment where three tributaries (i.e. Camas, Meadowbrook and Desolation Creek) enter the NFJDR, greatly increasing its contributing basin area. This segment is also immediately downstream from a series of reaches with increasing gradient, decreasing channel width and a depression in maximum river temperatures, as measured by forward-looking infrared remote sensing (ORDEQ, 2010). Subyearling Chinook salmon distribution increased greatly upstream

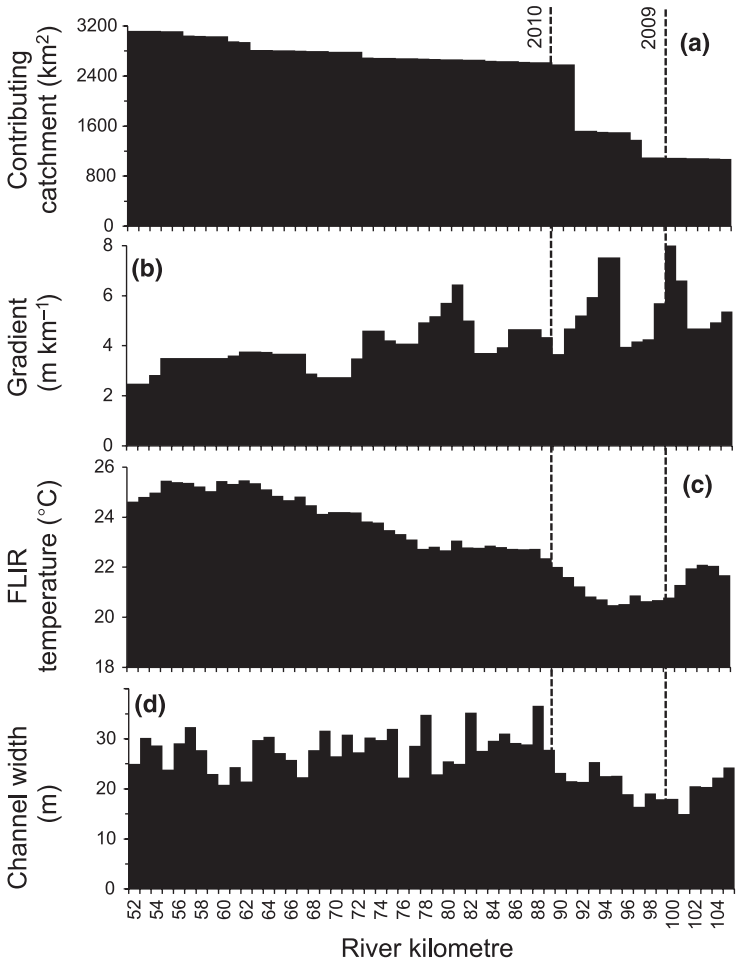

Fig. 6 Reach-scale habitat characteristics showing variability over the survey extent of the North Fork John Day River (NFJDR). (a) Contributing catchment area of the NFJDR, where large changes in area indicate tributary confluences; (b) Gradient over the survey extent; (c) Stream temperatures measured using airborne thermal remote sensing conducted at peak temperatures (i.e. early August). This stream temperature profile was formed from a composite of two helicopter flights of the NFJDR with forward-looking infrared (FLIR) remote sensing (ORDEQ, 2010); (d) Channel wet widths measured during the August 2010 survey. Dashed vertical lines denote the spatial position of the upstream-most bass in late summer 2009 and 2010, which corresponded with a relatively large change in contributing area, gradient, remote sensing–based stream temperature and channel width.

of the high-gradient discontinuity at RKM 100 (Fig. 3b,d), suggesting it might be a barrier to bass and Chinook salmon sympatry during the late summer.

Discussion

This study demonstrates that smallmouth bass have greatly expanded their upstream range from their initial introduction site, such that they now inhabit Chinook salmon-rearing habitat in the NFJDR. At the maximum extent of overlap, smallmouth bass occupied nearly a quarter of the length of the mainstem NFJDR where subyearling Chinook salmon occurred. This area represents the interface between the upstream extent of 'cool-water' bass and the downstream extent of 'cold-water' Chinook salmon. Upstream invasions by bass, although largely undocumented, are believed to be common in river systems throughout the Pacific Northwest (Carey *et al.*, 2011) and other regions (e.g. Ellender, Weyl & Swartz, 2011). Despite the ubiquity of smallmouth bass in river systems, the majority of previous studies have focused on their invasions in temperate lakes (e.g. Vander Zanden *et al.*, 2004; Sharma, Herborg & Therriault, 2009). The piscivorous nature of bass and their documented impacts on native fish communities (Jackson, 2002) make their invasions in rivers a cause for conservation concern.

Our seasonal surveys revealed that the primary period of bass and Chinook salmon sympatry in the NFJDR occurred in the early summer prior to the stream reaching peak water temperatures. Bass were nesting throughout

this zone of sympatry during the early summer period. Because male bass generally do not feed while nesting (Hanson & Cooke, 2009), spawning may reduce the potential predation of bass on subyearling Chinook salmon at this time. However, not all bass engage in spawning activities each year (Raffetto, Baylis & Serns, 1990), and females may not greatly reduce their feeding during spawning. If smallmouth bass feed prior to spawning (Tabor, Shively & Poe, 1993; Fritts & Pearsons, 2004), or if only a small fraction of the overall bass population reduces feeding activities to spawn in the NFJDR, subyearling Chinook salmon could be highly vulnerable to smallmouth bass during this period of peak overlap.

Late summer surveys revealed a decreased extent of overall sympatry between bass and subyearling Chinook salmon, although bass and Chinook salmon overlapped at the upper extent of bass distribution within the NFJDR at this time. By comparing the early and late summer surveys, it is clear that bass moved upstream and the overall numbers of bass increased in the survey extent. Upstream migrations of smallmouth bass have been observed in other river systems, and these movements may be motivated by bass seeking river segments suitable for spawning (Lyons & Kanehl, 2002) or may be the result of density-dependent processes (DeAngelis, Godbout & Shuter, 1991).

In both survey years, subyearling Chinook salmon were no longer observed in the lower NFJDR survey extent in late summer. Although the fate of these salmon is unknown, several mechanisms could account for this pattern. First, subyearling Chinook salmon could move upstream in response to downstream warming. Water temperatures in our lower survey extent regularly approach and at times exceed 24 °C, the upper thermal tolerance of juvenile Chinook salmon (McCullough *et al.*, 2001). Subyearling Chinook salmon may also move from downstream areas into adjacent cooler tributaries as stream temperatures warm. Surveys of tributaries in the John Day River system provide evidence that subyearling Chinook salmon utilise tributaries far downstream of known spawning habitat (Lindsay *et al.*, 1985); this has been documented in other river systems as well (Murray & Rosenau, 1989; Scrivener, Brown & Andersen, 1994). Predation may also account for the observed loss of subyearling Chinook salmon from the lower survey extent. Although we did not collect direct evidence of smallmouth bass predation on subyearling Chinook salmon (i.e. diet samples), prior studies have shown that smallmouth bass can have high predation rates on small subyearling Chinook salmon when water temperatures are high (Tabor *et al.*, 1993, 2007; Fritts & Pearsons, 2004). Stream-type subyearling Chinook salmon that overlapped with bass in the NFJDR during early summer were similar in size (i.e. mean 50 mm fork length; Lawrence, unpublished data) to the ocean-type subyearling Chinook salmon that bass preyed heavily upon in other studies (i.e. mean 57 mm fork length; Fritts & Pearsons, 2004). Northern pikeminnow, a native predator present in our survey extent, may also prey on subyearling Chinook salmon in the NFJDR, but they were far less abundant than smallmouth bass in the study area (Lawrence, unpublished data). Finally, temperature-mediated competition with other species, such as redside shiner, who feed on drift with subyearling Chinook salmon, but prefer warmer temperatures, may also reduce the growth or exclude subyearling Chinook salmon from the lower survey extent as water temperatures seasonally warm (Reeves, Everest & Hall, 1987). Further study is needed to weigh the relative influence of these mechanisms on subyearling Chinook salmon seasonal distribution and to more fully understand the implications of bass and Chinook salmon sympatry.

Degree days >10 °C, an ecologically relevant temperature threshold above which bass are generally active and growth occurs (Shuter & Post, 1990), was the primary determinant of bass abundance at both reach and channel-unit scales. Our results revealed strong year-to-year consistency in the influence of water temperature in the distribution of bass in the NFJDR in both early and late summer. This consistency, and previous research (summarised by Armour, 1993), suggests that water temperature determines bass distribution in cold-water rivers. Given this mechanistic underpinning, it is likely that these results could be applied to many other river systems experiencing upstream range expansions of smallmouth bass.

Our multiscale analysis suggests that bass selected habitat based on antecedent thermal history at a broad scale, and if satisfactory temperature conditions were met, mesoscale habitat features (i.e. channel-unit type and depth) played an additional role in determining bass abundance. In the lower, warmer section of the NFJDR, bass were more abundant in deeper channel units and typically those with slow (i.e. pools and glide-like pools) and intermediate (i.e. glide-like riffles) water velocity. Depth was also a significant predictor of adult bass density in spatially extensive (Dauwalter *et al.*, 2007) and temporally intensive (Dauwalter & Fisher, 2008) studies of smallmouth bass in their native range. Water depth is important in the early summer period because bass must avoid constructing nests in channel reaches that are susceptible to dewatering (leaving eggs and fry stranded)

as stream discharge declines into the summer. In the late summer, when the NFJDR was at base flow and riffle habitat was extremely shallow, longitudinal patterns in bass abundance were influenced by channel-unit type (i.e. riffles versus non-riffle units) and channel depth. Riffles at this discharge would impede adult bass movement and occupancy, whereas in non-riffle habitat, water depth is important to provide cover for bass and to allow for their movement within the channel unit. Prior studies demonstrate that adult bass typically do not occupy riffle habitat (Schlosser, 1987; Ebert & Filipek, 1991).

Water temperature may operate through several mechanisms to limit bass upstream extent in cold-water river systems such as the NFJDR. In the early summer, bass spawn and therefore must not only select temperatures that are suitable for their own physiology, but also establish their nests in areas with temperatures that are appropriate for the development of their young. Temperature directly affects the development of bass eggs and the growth of young-of-the-year bass (Shuter *et al.*, 1980). Temperature–growth relationships differ for adult and young-of-the-year bass; young-of-the-year bass grow optimally at temperatures significantly greater (29 °C; Shuter & Post, 1990) than those that provide optimal growth for adult bass (22 °C; Whitledge, Hayward & Rabeni, 2002). This difference is likely to influence how far bass move upstream prior to spawning. Young-of-the-year growth is particularly important in north temperate river systems, where bass must obtain a minimal size to survive a winter starvation period (Shuter *et al.*, 1980). Bass nesting in areas with temperature regimes that are not sufficient to achieve this growth minimum would be selected against because their offspring would not survive to spawn. In a central Appalachian river, Martin & Petty (2009) found bass in cold streams in relatively close proximity to warm streams, but not in cold streams separated by significant distances from warm segments. They attributed this pattern to a similar mechanism, that is, the need for adult bass to spawn in water with temperatures suitable for the development of their young.

In the late summer, adult temperature–growth relationships are likely to govern the upstream extent of bass. After spawning, a portion of the bass population continued to move upstream of their nesting grounds, as evidenced by the difference between their early versus late summer upstream extent. The water temperature observed at the uppermost occurrence of bass during this time was similar in 2009 and 2010 (i.e. 7DAD mean 18 and 19 °C, respectively). This consistency suggests that these may be the coolest water temperatures that bass can occupy and still maintain positive growth given the availability of food in the NFJDR. As upstream temperatures become increasingly cold, bass would have reduced, zero or negative growth regardless of food availability (Whitledge, Hayward & Zweifel, 2003).

In addition to water temperature, channel morphology may also play an important role in determining the upstream extent of bass in mountainous regions. Our spatially continuous sampling technique revealed that a geomorphic discontinuity may restrict the upstream movement of bass in the NFJDR during late summer. In both survey years, bass were not found above a highly confined, high-gradient canyon segment at RKM 100. In 2009, bass were present in a pool immediately downstream of this feature. We conducted an extensive survey of the peer-reviewed literature to determine the highest stream gradient that bass could overcome; however, given that most studies of bass are in relatively low gradient river systems in their native range, this gradient threshold is unknown. Brewer *et al.* (2007) surveyed almost 2000 reaches in Missouri and found that smallmouth bass rarely occupied areas with gradients exceeding 10 m km^{-1} (i.e. eight out of 1994 reaches) and were not found in reaches with channel gradients >25 m km^{-1}. Dauwalter *et al.* (2007) measured smallmouth bass abundance in 1800 channel units of streams in Oklahoma and found that bass were absent from any units exceeding 10 m km^{-1} gradient. Although bass may not reside in relatively high-gradient stream segments, they could potentially pass through them. Burton & Odum (1945) found that bass did not occur in reaches with gradients ranging from 8 to 10 m km^{-1}, but they were present upstream of them. The authors reported occurrence, not abundance, so it is unknown how many bass were able to overcome these high-gradient segments. The high-gradient segment in the NFJDR was 8 m km^{-1}, which may deter bass from moving farther upstream, especially because this feature coincided with cold-water temperatures. However, based on the limited literature available, it is unlikely to completely prevent their movement. Year-to-year variation in upstream water temperature will probably determine whether bass move far enough upstream to encounter this high-gradient feature, and thus will alter its influence on bass upstream movement – that is, in some years, cold-water temperatures downstream of this feature will prevent bass upstream movement before bass encounter this high-gradient segment. This appeared to happen in 2010, when a late snow melt delayed the warming of water temperatures in the upper NFJDR, and so bass upstream extent was 11 km below this high-gradient feature. However, climate-related warming is projected to increase stream tempera-

tures in the John Day River (Ruesch *et al.*, in press) and many other rivers in the Pacific Northwest (Isaak *et al.*, 2012), and therefore, high-gradient features that become more common upstream are likely to play an increasingly prominent role in determining bass upstream range expansions.

Managers may be able to prevent or at least limit upstream range expansions of bass in salmon-bearing rivers by (i) capitalising on aspects of the life history of bass (i.e. the need for sufficient age 0 growth to overcome winter starvation) and (ii) using natural landscape knickpoints such as high-gradient discontinuities to deter the upstream movement of bass. Managers could establish target temperature criteria to prevent over-winter survival of young-of-the-year bass in salmon-rearing areas (e.g. the United States Environmental Protection Agency has water temperatures standards above which salmonids are physiologically and competitively disadvantaged; EPA, 2003). Chu *et al.* (2006) found that young-of-the-year survival had the greatest influence on population dynamics of bass; thus, by reducing recruitment, managers may be able to slow the invasion by non-native bass populations in rivers. Also, with relatively limited geographical information (e.g. gradient derived from a topographic map), managers could identify moderate- to high-gradient knickpoints on the landscape that naturally deter upstream movements of bass. These locations could function as a 'first front' to prevent range expansions by bass. For example, this information could be used to spatially prioritise protection (e.g. conservation of intact riparian vegetation) or restoration activities (e.g. revegetation of riverbanks) to maintain cold-water temperatures above these geomorphic features. This could provide multiple disincentives to bass to further penetrate salmon-rearing grounds. Similar strategies could be applied to limit the upstream range expansion of bass in other river systems, and these approaches may constrain upstream movements of other non-native cool- and warm-water predatory species.

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