Occupancy of invasive Northern Crayfish (*Faxonius virilis*) in northern streams is associated primarily with water temperature

Victoria A. Van Mierlo[1,4], **Stephanie J. Green**[2,5], **Craig A. Emmerton**[2,3,6], **Mina Nasr**[3,7],
Cristina Buendia[3,8], **Faye R. Wyatt**[3,9], **and Mark S. Poesch**[1,10]

[1]Department of Renewable Resources, University of Alberta, 433 South Academic Building, Edmonton, Alberta, Canada T6G 2G7
[2]Biological Sciences Department, University of Alberta, CW405 Biological Sciences Building, Edmonton, Alberta, Canada T6G 2E9
[3]Alberta Environment and Parks, Government of Alberta, 9-9888 Jasper Avenue, Edmonton, Alberta, Canada T5J 5C6

Abstract: Invasive species are the 2nd-greatest threat to global freshwater biodiversity. Crayfish are especially robust invaders due to their omnivorous nature and ability to compete both directly (resource procurement) and indirectly (habitat occupation and modification) with native species. The Northern Crayfish (*Faxonius virilis* Hagen, 1870) was introduced to the North Saskatchewan River basin (Alberta, western Canada) and has persisted there since the early 1990s. *Faxonius virilis*' impacts on native fish assemblages in the North Saskatchewan River have yet to be assessed, even though the watershed is ecologically, economically, and culturally valuable and home to multiple sensitive and at-risk fish species. We aimed to identify the instream environmental characteristics associated with *F. virilis* occupancy in the North Saskatchewan River basin and to determine which currently unoccupied tributaries are most vulnerable to *F. virilis* invasion. We used occupancy modeling to meet these objectives. We deployed 24-h baited crayfish traps and measured water temperature, turbidity, flow velocity, and physical complexity at 37 sites along the Alberta portion of the North Saskatchewan River basin. We detected *F. virilis* at 13/37 sites with no occurrences detected in the upper basin. Occupancy model selection and averaging revealed that water temperature alone was associated with occupancy of *F. virilis* in the North Saskatchewan River basin. Streams with mean summer water temperatures >~19°C were ≥50% more likely to be occupied by *F. virilis* than cooler streams and are at highest risk of invasion. Further, we found that streams with mean summer water temperatures <~15°C had a <25% chance of becoming occupied by *F. virilis* than warmer streams. Coldwater streams may thus have some natural protection against *F. virilis* invasion. The results from this study provide practical guidelines for watershed management of invasive *F. virilis* populations in western Canadian river basins. Managing *F. virilis* is particularly important and time sensitive because *F. virilis*' range will likely expand when water temperatures in the basin rise because of climate change.

Key words: *Faxonius virilis*, aquatic invasive species, North Saskatchewan River, occupancy modeling, watershed management, crayfish, northern ecosystems, water temperature, rivers

Nonnative species are species that occur in an environment that is not part of their natural range. Nonnative species are described as invasive species when they become established in a novel environment and cause negative ecological, economic, or human-health impacts (Mack et al. 2000). Invasive species have had a substantial adverse impact on global freshwater biodiversity, second only to habitat destruction (Mack et al. 2000, Dudgeon et al. 2006). Aquatic invasive species are an especially problematic group because they are challenging to detect and difficult to control and contain (Ruppert et al. 2017).

Crayfish are particularly difficult to manage because they are habitat generalists, highly adaptable, and omnivorous. They can modify habitats by increasing turbidity via

---

E-mail addresses: [4]vanmierl@ualberta.ca; [5]stephanie.green@ualberta.ca; [6]craig.emmerton@gov.ab.ca; [7]mina.nasr@gov.ab.ca; [8]crisbuendia@gmail.com; [9]Present address: Met Office, Fitzroy Road, Exeter, United Kingdom EX1 3PB, Faye.wyatt@metoffice.gov.uk; [10]poesch@ualberta.ca.
ORCIDs: Van Mierlo, https://orcid.org/0000-0002-9472-793; Emmerton, https://orcid.org/0000-0001-9511-9191; Buendia, https://orcid.org/0000-0001-5966-3202; Poesch, https://orcid.org/0000-0001-7452-8180

Received 26 December 2021; Accepted 8 June 2022; Published online 6 October 2022. Associate Editor, Seth Wenger.

Freshwater Science, volume 41, number 4, December 2022. © 2022 The Society for Freshwater Science. All rights reserved. Published by The University of Chicago Press for the Society for Freshwater Science. https://doi.org/10.1086/722576

macrophyte consumption and bioturbation (Usio 2000, Usio et al. 2009). They can also compete indirectly for important microhabitats like shelters that small and juvenile fish use to evade predators (Light 2005). Because crayfish are generalist feeders, they can compete with native fauna on multiple trophic levels simultaneously. For example, crayfish can reduce the abundance of herbivorous benthic invertebrates (Hanson et al. 1990), including native snails (Dorn and Wojdak 2004), via predation and competition. They can also directly affect the young-of-year of threatened fish species—e.g., they consume the eggs and fry of sunfish (Dorn and Mittelbach 2004), lake sturgeon (Caroffino et al. 2010), and arctic charr (Setzer et al. 2011) among others.

Northern Crayfish (*Faxonius virilis* Hagen, 1870), also known as the Virile Crayfish, are native to large portions of Canada and the northern United States. *Faxonius virilis* is native to Canada from Quebec to Saskatchewan and as far north as the 55th parallel (Aiken 1968, Williams et al. 2011), but established invasive populations are causes for concern in many places, including Eastern New Brunswick and Alberta (McAlpine et al. 2007, Williams 2012). Generally, crayfish prefer warm (Wetzel and Brown 1993, Bowman 2019), well-oxygenated (Haddaway et al. 2015) waters with moderate turbidity (Rosewarne et al. 2014). Crayfish tend to be less active under high stream flow velocities (Light 2003, Hazlett et al. 2006). In fact, some dams are specifically designed to increase flow velocity to prevent movement of invasive crayfish species into unoccupied systems (Frings et al. 2013). *Faxonius virilis* is less tolerant of high-flow velocities than other crayfish species (Maude and Williams 1983, Foster and Keller 2011). The life functions of most crayfish are impeded by low water temperatures. For example, *Procambarus clarkii* (Girard, 1852) experience ~3× slower embryonic development at water temperatures <18°C (Jin et al. 2019). More specifically, *F. virilis* experiences delayed sexual maturity and higher juvenile mortality at temperatures <16°C (Wetzel and Brown 1993). Further, the lower thermal limit of *F. virilis*, where crayfish become inactive and molting is slowed or halted completely, is thought to be 10 to 12°C (Momot 1967, Rogowski et al. 2013). Physical complexity (i.e., the overall rugosity of the riverbed) has been associated with increased crayfish abundance, survival, and growth. For example, crayfish find shelter and forage in substate crevasses and vegetation (Hill and Lodge 1994, Olsson and Nyström 2009).

In Alberta, *F. virilis* has been introduced to several watersheds including the Athabasca, Battle, Oldman, Bow, Milk, and North Saskatchewan rivers (Williams 2012). The North Saskatchewan River runs through Edmonton, Canada's 5th-largest city and, with a population of >1.5M, North America's northern-most metropolis. The basin has culturally valuable fisheries and provides essential ecosystem services such as water filtration and flood mitigation (Yeakley et al. 2016). Additionally, the basin supports aquatic species at risk (e.g., Bull Trout [*Salvelinus confluentus* Suckley, 1859] and Plains Sucker [*Catostomus platyrhynchus* Cope, 1874]), economically important sport fisheries (e.g., Northern Pike [*Esox lucius* Linneus, 1758]), and culturally important species (e.g., Lake Sturgeon [*Acipenser fulvescens* Rafinesque, 1817]). Aquatic invasive species threaten these and other critical resources of the North Saskatchewan River basin (Dudgeon et al. 2006, Poos et al. 2010). Understanding the distribution of *F. virilis* and the characteristics of the North Saskatchewan basin that facilitate its spread can be used to improve aquatic invasive species management by informing rapid response techniques in the future. In turn, improved *F. virilis* management can be used to protect the basin's ecosystem services and the aquatic species that it supports.

The goals of this study were to determine the environmental characteristics that are most strongly associated with *F. virilis* occupancy in the North Saskatchewan River basin and identify which currently unoccupied tributary reaches are most susceptible to *F. virilis* invasion. Specifically, our objectives were to identify 1) the suite of local (instream) habitat features (water temperature, physical complexity, flow velocity, turbidity, or their interactions) that best predict *F. virilis* occupancy in tributaries of the North Saskatchewan River basin, 2) if flow velocity or tributary depth affect *F. virilis* detection, and 3) which currently unoccupied tributary reaches in the North Saskatchewan River basin should be prioritized for additional monitoring to prevent subsequent invasion. We used occupancy modeling to achieve these objectives. Occupancy models have been used to identify the distributions of crayfish as well as the ecological characteristics that best predict their occupancy while accounting for imperfect detection (e.g., Ficetola et al. 2011, Magoulick et al. 2017, Yarra and Magoulick 2018). Given our knowledge on *F. virilis*' habitat preferences, we hypothesized that water temperature (Momot 1967, Rogowski et al. 2013), flow velocity (Maude and Williams 1983), turbidity (Wetzel and Brown 1993), and instream physical complexity (Olsson and Nyström 2009) would best predict *F. virilis* occupancy. We further hypothesized that tributary depth and flow velocity would be inversely related to *F. virilis* detection because increasing depth would act as a physical survey barrier and increasing flow would alter the bait odor plume (Zimmer-Faust et al. 1995).

METHODS

Field methods

Study area and tributary reach selection The study area included tributaries of the Alberta portion of the North Saskatchewan River basin in western Canada. The basin is a glacier-fed watercourse that begins in the Rocky Mountains at the Saskatchewan Glacier. From the headwaters, the river's mainstem flows through Edmonton and continues to the Alberta–Saskatchewan border, just north of Lloydminster, Alberta. The basin includes multiple natural regions including alpine, subalpine, montane, foothills, parkland, and prairie biomes. From west to east, the major tributaries of the basin are the Clearwater, Brazeau, Sturgeon, and Vermilion rivers. Prior to *F. virilis* invasion, no decapod species were endemic to the basin (Williams 2012).

We collected field data from 43 reaches in the North Saskatchewan River basin located within tributaries of Strahler stream orders 4 to 6 (Fig. 1). We collected our data during the warmest months of the year (June, July, and August with average maximum monthly air temperatures of 15.5, 18.2, and 17.6°C, respectively) in 2020. We did not collect data at any mainstem Saskatchewan River sites because of dangerous sampling conditions including high water velocity and depth. We collected field measurements throughout a 200 to 300-m stretch (hereinafter referred to as reach) within each sampled tributary. We selected reaches throughout the foothills, parkland, and prairie natural regions of the North Saskatchewan River basin, but not in the alpine, subalpine, or montane natural regions, which were difficult to access. We selected reaches to ensure an even distribution of sampling locations throughout the basin and among natural basin features and anthropogenic land uses.

Crayfish sampling We used modified minnow traps with 5.7-cm diameter openings to sample *F. virilis* in each tributary reach (Mangan et al. 2009, De Palma-Dow et al. 2020). Individual traps were tied to nylon rope 3 m apart in sets of 6 to form a trapline (Rosewarne et al. 2014). We baited individual traps of the traplines with perforated film canisters filled with Friskies® salmon-based cat food (Purina®, St Louis, Missouri; 1 canister/trap; Mangan et al. 2009). We then affixed each trapline to the riverbank with a loop and rebar stake on the upstream end. We deployed 4 traplines at each reach for a total of 24 traps/reach. We numbered traplines from 1 to 4 and deployed them in order along the riverbank in an upstream direction. We placed each trap line 50 m apart to reduce spatial overlap between surveys and reduce spatial random effects (Acosta and Perry 2000). We considered a single trapline as the measurement unit for a single crayfish survey (Fig. 2A). We left baited traplines overnight to increase the chance of capture because crayfish are nocturnal (Styrishave et al. 2007). The morning following deployment, we retrieved traplines from the water and recorded presence/absence (p/a) data as well as crayfish counts/trapline. All captured crayfish were humanely euthanized by placing crayfish in an ice bath for 15 min and then pithing them following animal handling and ethics regulations of the Government of Alberta (Research License No. 20-3812 RL) and the University of Alberta (Animal Use Protocol No. AUP00003578). We did not return any crayfish to the water because they are a regulated invasive species in Alberta, and all captured individuals must be euthanized on site (Alberta Government 2021). We compiled *F. virilis* p/a data by trapline to create a detection history for each reach. For example, the detection history for a reach would be coded as 1011 if we detected crayfish in the 1st, 3rd, and 4th traplines (Fig. 2A, B).

Environmental variable sampling We measured 10 covariates to model *F. virilis* occupancy and detection: water

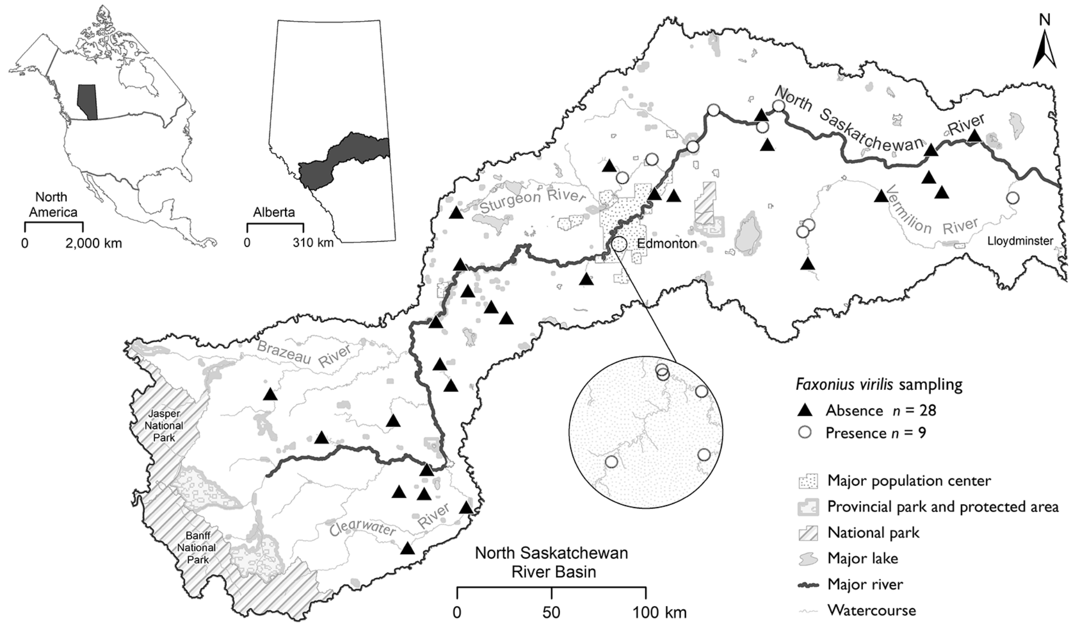

Figure 1. Tributary reaches where crayfish traplines were deployed throughout the North Saskatchewan River basin (Alberta, western Canada) during June to August 2020. *Faxonius virilis* presence and absence are represented by circular and triangular symbols, respectively. Projected coordinate system: NAD38 10TM AEP forest (https://epsg.io/3400).

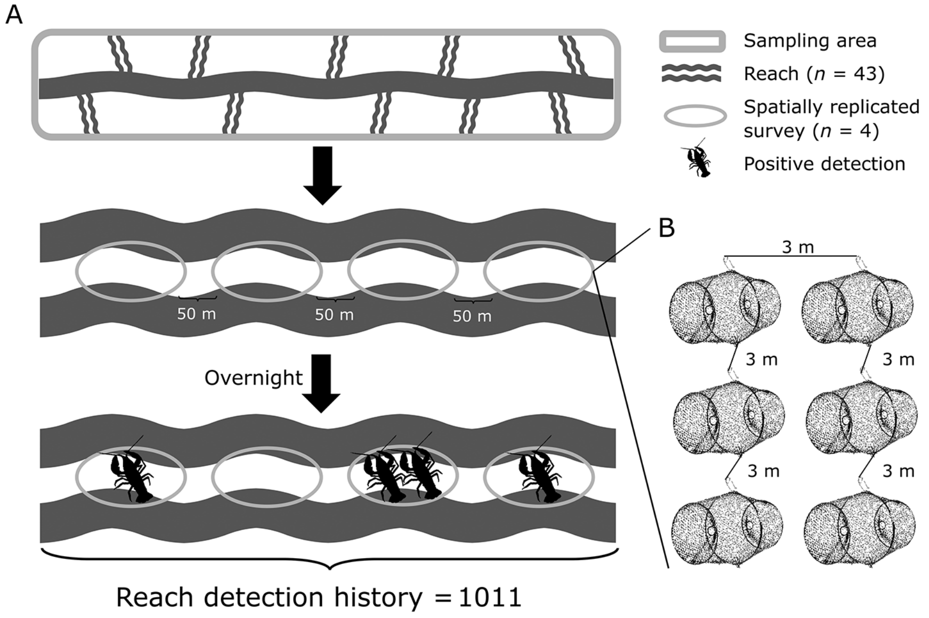

Figure 2. Field sampling methods for *Faxonius virilis* reach occupancy modeling. Tributary reaches 200 to 300 m in length are selected as sampling reaches within the study area of North Saskatchewan River basin in Alberta, western Canada (A). Four spatially replicated crayfish surveys (baited traplines) were conducted within each reach (B). Traplines were set 50 m apart along the river's edge, secured with a rebar stake, and left overnight. The following day, *F. virilis* presence (1) or absence (0) in each trapline were recorded as the reach detection history.

temperature (°C), turbidity (nephelometric turbidity unit [NTU]), flow velocity (m/s), p/a of woody debris, p/a of instream boulders, p/a of overhanging banks, % rocky substrate cover, % macrophyte cover, % sand/silt cover, and water depth (cm). We measured these factors after we retrieved the traplines to avoid disturbing crayfish at the reach prior to sampling. We used a DataSonde® 5X Multiprobe (Hydrolab®, Loveland, Colorado) to measure water temperature and turbidity at each trapline to the nearest 0.1°C and NTU, respectively. The sampling summer was typical in terms of water temperature (Fig. S1). We measured water depth in 5 locations near each trapline with a 4-ft wading rod (United States Geological Survey, Rickly Hydrological, Columbus, Ohio). We also measured flow velocity in 5 random locations near each trapline at 60% depth (standard method for measuring mean channel flow velocity) with a Flo-Mate™ 2000 (Marsh-McBirney, Frederick, Maryland) (Flinders and Magoulick 2005, Vacher 2005). We visually assessed the p/a of woody debris, overhanging banks, and instream boulders within the vicinity of each trapline. Woody debris was defined as wood substrate (e.g., downed trees) that was totally or partially submerged in the water and was ≥15 cm in diameter (Zale et al. 2012). Overhanging banks were defined as riverbanks with eroded bottom portions that cause the top of the bank to hang over a portion of the river's surface (Zale et al. 2012). Instream boulders were defined as rocky substrate that was ≥30 cm in diameter and was fully or partially submerged in the water. Finally, we visually assessed the proportion of rocky cover, macrophyte cover, and sand/silt cover within 50 cm of the water's edge during sampling. We defined these variables as the area covered by the substrate type divided by the total area along the length of where the trapline was placed. Rocky substrate included rock particles of cobble, gravel, and pebble size classes following the Wentworth Scale (Bunte and Abt 2001). We checked visual estimates against field site photos for accuracy prior to analysis. We acknowledge that visual estimation of substrate cover and proportion can be subject to bias and inaccuracy especially under turbid or deep river conditions (Gibson et al. 1998) and could influence our subsequent physical complexity analyses. However, visual estimation has been deemed an adequate method of describing substrate coarseness (Gibson et al. 1998) and has been used in other crayfish studies (e.g., Dorn and Wodjak 2004).

Statistical analyses

We used 37/43 reaches in analyses because 6 reaches had missing covariate data. We conducted our analyses in R (version 4.2.0; R Project for Statistical Computing, Vienna, Austria). A workflow of all statistical analyses conducted during this study is available in the supplementary materials (Fig. S2).

Physical complexity gradient To reduce the total number of covariates and increase the parsimony of our models, we combined our 6 physical complexity covariates (p/a woody debris, p/a instream boulders, p/a overhanging banks, % rocky substrate cover, % macrophyte cover, % sand/silt cover) into a single gradient of instream physical complexity. We used Principal Coordinate Analysis (PCoA) instead of other multivariate statistical analyses (e.g., principal component analysis) because the distributions of our variables were either binary or non-normally distributed. PCoA has been used to create synthetic components that combine ecological characteristics (Heino et al. 2015). We used a Gower's distance matrix because of the binary nature of some of our variables (Legendre and Legendre 2012). It is important to note that % sand/silt cover was not included in the calculation as this variable is equivalent to the lack of % rocky substrate cover or % macrophyte cover and, therefore, would have produced a singular matrix. We used the pcoa function in the *ape* package (version 5.6–2; Paradis 2022) to perform a PCoA ordination with reaches standardized with scaling of 1. We visually inspected the 1st PCoA axis (PCoA 1) in relation to covariate vectors and found it to be a good representation of the physical complexity gradient with positive values associated with high physical complexity and negative values associated with low physical complexity. We then replaced the 6 original physical complexity covariates with the complexity vector values from PCoA 1 for each reach. These PCoA vector values became the covariate representing instream physical complexity for occupancy modeling.

Occupancy modeling and selection The standard occupancy model assumes that the abundance of the target species is homogenous across all sample reaches (MacKenzie et al. 2017). However, it was apparent that *F. virilis* relative abundance was highly variable between reaches. For this reason, we elected to use the Royle–Nichols occupancy model with the occuRN function in the *unmarked* package (version 1.2.5; Chandler et al. 2021) because it accounts for effects of heterogeneity in target species abundance between reaches on the detection probability parameter (p; Royle and Nichols 2003). Detection probability may be greater in reaches with higher abundance because more individuals are present and thus, the species is more likely to be detected. The Royle–Nichols model's occupancy parameter is denoted by lambda (λ) in lieu of psi (Ψ), which is used to denote the occupancy parameter in the standard occupancy model (MacKenzie et al. 2017). We used a global additive model with the following covariate structure for occupancy estimation: temperature (temp) + flow velocity (flow) + turbidity (turb) + complexity (comp). We based the covariate structure for occupancy on hypotheses derived from the literature (Table 1).

The detection estimation portion of the model included a flow + depth covariate structure. We included depth as a detection probability covariate because deeper reaches may have prevented traplines from reaching the riverbed, which would make the trapline inaccessible (physical survey barrier) to crayfish and therefore negatively impact detection (Table 1). We also included flow velocity as a detection probability covariate because high flow velocity could alter the bait odor plume (Zimmer-Faust et al. 1995) and act as a physical barrier by preventing *F. virilis* from traveling upstream and into the traps of the trapline (Table 1). Thus, the complete global model was λ(temp + comp + flow + turb), p(depth + flow).

We used Pearson's parametric bootstrapped χ^2 test to assess goodness of fit of the global model to the data (MacKenzie and Bailey 2004). If overdispersion was detected, SE values were inflated by the square root of the overdispersion correction value (c-hat) to reduce the probability of a Type I error (MacKenzie and Bailey 2004). We then fit models representing all possible subsets of covariates. We used 2$^{\text{nd}}$-order, bias-corrected Quasi Akaike Information Criterion (QAICc) to compare models, which is recommended for models with reasonable overdispersion ($1 < \text{c-hat} < 4$) and $n/K < 40$ where n is the number of observations and K is the total number of parameters in the model (Burnham and Anderson 2004, MacKenzie et al. 2017). We calculated ΔQAICc as the difference in QAICc between each model

Table 1. Hypothesized relationships of covariates included in the global occupancy model for *Faxonius virilis* detection and occupancy and literary support for hypotheses. Physical survey barrier is defined as any factor that physically impedes or prevents target species access to the survey unit (e.g., sufficient tributary depth may prevent some traps within a trapline from reaching the riverbed, thus preventing crayfish entry into traps). Symbols + and – indicate expected positive and negative relationships, respectively. NTU = nephelometric turbidity unit, PCoA1 = principal coordinate axis 1.

Covariates	Model aspect	Hypothesis	Source
Flow velocity (m/s)	Detection	–	Zimmer-Faust et al. 1995, physical survey barrier
Depth (cm)	Detection	–	Physical survey barrier
Flow velocity (m/s)	Occupancy	–	Maude and Williams 1983, Light 2003
Turbidity (NTU)	Occupancy	–	Rosewarne et al. 2014
Water temperature (°C)	Occupancy	+	Momot 1967, Wetzel and Brown 1993, Rogowski et al. 2013, Bowman 2019
Physical complexity (PCoA 1)	Occupancy	+	Hill and Lodge 1994, Olsson and Nyström 2009, Simon and Cooper 2014

and the best-ranked model (i.e., the one with the lowest QAICc). Models have substantial support (strong) when $\Delta\text{QAICc} \le 2$, less support (moderate) when $4 \le \Delta\text{QAICc} \le 7$, and no support (weak) when $\Delta\text{QAICc} > 10$ (Burnham and Anderson 2004). We considered all models with $\Delta\text{QAICc} \le 3$ to be plausible. Then, we calculated the variance inflation factor (VIF; Allison 1999) for each covariate within the global model and all plausible models that included ≥2 covariates. We considered $\text{VIF} \ge 2.5$ as an indication of problematic multicollinearity (Johnston et al. 2018).

We calculated 95% CIs for all parameter estimates. We calculated the trapline and reach probabilities of detecting ≥1 crayfish from the detection intercept value from the best model (smallest QAICc) and principles of probability equations. The probability of detecting ≥1 crayfish is equal to 1 minus the probability of not detecting a single crayfish in each of the 4 traplines at a reach. If the failure to detect a crayfish in trapline 1, 2, 3, and 4 is represented by $p(A')$, $p(B')$, $p(C')$, and $p(D')$, respectively, then the detection probability at a reach is $P(\text{reach}) = 1 - [p(A')p(B')p(C')p(D')]$. We calculated the probability of failing to detect a crayfish ($p(X')$) in a trapline at a reach where crayfish are present as $1 - p(X)$, with $p(X)$ being the detection intercept value from the best model. The detection failure probability of a single trapline was then subbed into the reach detection probability equation, $P(\text{reach}) = 1 - (p(X'))^4$, which resulted in the detection probability for a reach that contained 4 traplines.

Water temperature standardized occupancy modeling To further investigate covariate-occupancy relationships, we controlled for the effect of water temperature by repeating the above occupancy modeling procedures on a subset of the data ($n = 19$) restricted to reaches with water temperature measurements ≥18°C (maximum = 22.2°C). This analysis allowed us to achieve a standardized water temperature range spanning 4.2°C. The aim of this analysis was to identify potential relationships between occupancy and turbidity, flow velocity, and physical complexity that may otherwise be masked by the effect of the strong water temperature gradient of the basin.

Generalized linear mixed modeling of abundance and other sources of variation To investigate potential random spatial effects that were unaccounted for in the occupancy model, we used the glmmTMB function in the *glmmTMB* package (version 1.1.3; Brooks et al. 2021) to create a generalized linear mixed model (GLMM) with the same covariate structure for occupancy estimation as the global occupancy model (λ [temp + comp + flow + turb]), with the addition of reach as a random effect ($n = 37$). We chose a Poisson error distribution with a log link function for the GLMM because the response variable for this analysis was crayfish count/reach (relative abundance) (Bolker et al. 2009). Random effect structure was assessed in 2 candidate global models, which differed in their random effect variable structures. The 2 global models possessed either no random effects or reach as a random effect. To choose a model, we calculated and compared the 2$^{\text{nd}}$-order AICc, which is recommended for models with a small sample size that are not overdispersed (Burnham and Anderson 2004). The most parsimonious model with the smallest AICc value was the global model that included reach as a random variable. We selected this model as the final global GLMM.

We used the testZeroInflation function in the *DHARMa* package (version 0.4.5; Hartig and Lohse 2021) to assess zero inflation in the global model. We visually inspected simulated residual plots and found them to be normal, indicating proper model specification (Zuur et al. 2009). We iterated the global model and used model selection analysis to determine which covariates contributed positively to model parsimony. We then used AICc to identify all similar and plausible ($\Delta\text{AICc} < 2$) models. We used these similar models to identify and explain any deviation from the relationships found by the occupancy model that could result from random spatial effects. Covariate estimate standard errors were multiplied by 1.96 and added or subtracted from the estimate value to determine the upper and lower 95% CI boundaries, respectively. We used a log-likelihood ratio test with a χ^2 statistic to determine the significance of the random effect variable reach for all best models.

Model averaging for prediction To make management-relevant predictions about *F. virilis* occupancy based on environmental variable gradients within sampled streams, we used the modavg and modavgPred functions in the *AICcmodavg* package (version 2.3–1; Mazerolle 2020) to perform model averaging of the predictor covariate parameter estimates and calculate the model averaged predictions and 95% CIs based on the strongest ($\Delta\text{QAICc} \le 3$) models (Buckland et al. 1997). Average occupancy probability was then plotted as a function of those predictors with 95% CIs. We estimated the 50% probability of occupancy threshold from the plots.

We then used our model to map predicted probabilities of occupation in 19 tributaries monitored by Alberta Environment and Parks that were not sampled in our study. We calculated the mean summer temperature from the June to August water temperature measurements from the last 5 y of available data (2015–2020). Each tributary was designated as either of concern or less vulnerable to *F. virilis* occupation if the 5-y mean summer water temperature was greater or less than that corresponding to ~50% occupancy probability, respectively.

Model validation To validate the reliability of our models, we used the leave-one-out cross-validation method (crossVal function in the *unmarked* package) where the number of testing data sets is maximized and equal to the total number of observations (Hastie et al. 2009). We selected leave-one-out cross-validation because it is a reliable, low-bias estimator of model accuracy that is used often in ecological modeling (Hastie et al. 2009, Ratajc et al. 2022). The root-mean-square error (RMSE) is calculated from leave-one-out cross-validation and is a measure of the average distance between model predicted estimates and actual dataset values. Because observed occupancy and absence are denoted as 1 and 0, respectively, RMSE can be interpreted as the proportion of error in model prediction. In turn, 1 – RMSE can be interpreted as the mean accuracy of model occupancy prediction. Leave-one-out cross-validation was conducted on each of the top (within $\Delta\text{QAICc} \leq 3$) models. Lastly, to further investigate the accuracy of our predictive models, we calculated the mean sensitivity (true positive rate) and specificity (true negative rate) of each top model. Sensitivity was calculated as TP / (TP + FN) and specificity was calculated as TN / (TN + FP), where TN is total true negatives, TP is total true positives, FN is total false negatives, and FP is total false positives (Allouche et al. 2006).

RESULTS

We captured a total of 239 *F. virilis* individuals over the study period. We positively detected *F. virilis* in 14/43 reaches (mean = 17 ind./reach, range = 1–38). We did not detect any individuals in the upper basin, west of the city of Edmonton, Alberta (Fig. 1).

Water temperature, flow velocity, tributary depth, turbidity, and aspects of riverbed complexity varied substantially across the 37 sampled reaches. Water temperature ranged from 9.4 to 23.2°C with a mean of 17.4°C. The average flow velocity was 0.18 m/s with maximum and minimum flow velocities of 1.42 and 0 m/s, respectively. Stream depth was an average of 42.6 cm deep (range = 3–107) and average turbidity was 18.91 NTU (range = 0–174). The mean proportion of rocky cover, macrophyte cover, and sand/silt cover were 21.4, 28.5, and 49.0%, respectively (ranges = 0–100). Finally, course woody debris, instream boulders, and overhanging banks were present at 27, 25, and 21 of the 37 sampled reaches, respectively.

Physical complexity gradient

Our PCoA based on Gowers distance matrix of physical complexity variables produced 2 principal coordinate axes. The x-components of 4/5 vectors were positive. In contrast, the % macrophyte vector had a negative x-component and was somewhat orthogonally and negatively positioned relative to the % rocky and boulder vectors. PCoA 1 explained 54.1% of the variance in the data and spanned a gradient of high (dominated by rocky substrate and boulders), medium (dominated by woody debris and overhanging banks), and low (dominated by sand/silt and macrophyte cover) substrate complexity (Fig. 3). Positive vector values from the PCoA 1 gradient were associated with high physical complexity, whereas negative loadings were associated with low physical complexity. We chose not to use PCoA 2 to represent the physical complexity gradient because it explained less variance in the data (39.5%) compared with PCoA 1 . We used the loadings from PCoA 1 in subsequent analyses as a single covariate for instream physical complexity, hereafter referred to as physical complexity.

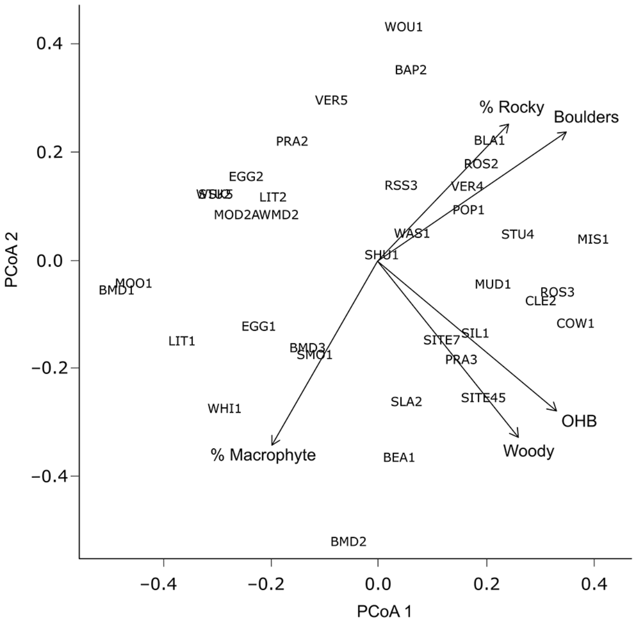

Figure 3. Principal coordinate analysis (PCoA) ordination of sample reaches with reaches standardized with scaling of 1 based on 5 physical complexity variables. PCoA 1 represents the instream physical complexity gradient from reaches with high complexity (positive values) to those with low complexity (negative values). Reach identity and location within the ordination space are represented by unique reach codes. Vectors are defined as % rocky = % rocky cover, boulders = presence or absence (p/a) instream boulders, OHB = p/a overhanging banks, woody = p/a woody debris, % macrophyte = % macrophyte cover.

Faxonius virilis occupancy and environmental variables

Full-occupancy model The goodness-of-fit test indicated a good fit of the global model (λ[temp + comp + flow + turb], p[depth + flow]) to the data (p = 0.20) and slight overdispersion (c-hat = 2.22). Iteration of the global model resulted in 1 model that was strongly supported by the data and 5 models that were moderately supported by the data (Table 2). To account for the effect of overdispersion found in the global model, the square root of c-hat was added to SEs in each of the best models prior to 95% CI calculation. VIF ranged from $1.00 \geq \text{VIF} \leq 1.14$, indicating negligible multicollinearity within models. The detection intercept value for the best model was 0.67, which translated to a very high reach detection probability of 0.998 or 98.8%.

Table 2. Global and best occupancy models ranked by bias-corrected Quasi Akaike Information Criterion (QAICc) weights within ΔQAICc ≤ 3 and corresponding covariate relationship estimates. Flow velocity (flow), turbidity (turb), physical complexity (comp), and water temperature (temp) were predictor variables for the occupancy parameter (λ). Water depth (dep) and flow velocity (flow) were predictor variables for the detection probability parameter (p). Strong covariate relationships, defined as those with 95% CIs that do not include 0, appear in bold. NTU = nephelometric turbidity unit.

	Detection estimates			Occupancy estimates				Ranking statistics		
Model	Intercept	Depth (cm)	Flow (m/s)	Flow (m/s)	Turbidity (NTU)	Physical complexity	Water temperature (C°)	QAICc	ΔQAICc	Weight
λ(temp), p(.)	0.67	–	–	–	–	–	**0.376**	48.08	0.00	0.406
λ(temp), p(flow)	1.16	–	−2.730	–	–	–	**0.379**	50.30	2.22	0.134
λ(temp + turb), p(.)	0.65	–	–	–	−0.008	–	**0.418**	50.37	2.29	0.129
λ(temp+ comp), p(.)	0.67	–	–	–	–	–0.596	**0.371**	50.64	2.56	0.113
λ(temp + flow), p(.)	0.66	–	–	0.918	–	–	**0.377**	50.69	2.61	0.110
λ(temp), p(dep)	0.47	0.004	–	–	–	–	**0.373**	50.74	2.66	0.106
global: λ(temp + comp + flow + turb), p(depth + flow)	1.27	0.000	−4.41	4.710	−0.013	−1.911	**0.467**	97.18	49.10	–

The best model lacked any detection covariates. Flow velocity and water depth appear as detection covariates in the 2nd and 6th models, respectively. However, these estimates are not related to detection probability (0 ⊂ 95% CI), indicating negligible effects of depth or flow velocity on detection. Water temperature was identified as an occupancy predictor in all 6 best models (Table 2). The parameter estimates for water temperature in all 6 best models and the global model were positive (λmax = 0.418, λmin = 0.371) and strongly related to occupancy (95% CI = 0.130, 0.621; Table 2). Physical complexity was identified as a predictor only in the 4th-best model (ΔQAICc = 2.55); however, the parameter estimate was not related to occupancy (λ = −0.596, 95% CI = 1.562, −2.755). Turbidity and flow velocity were identified in the 3rd- and 5th-best models, respectively (Table 2). Neither covariate estimate was related to occupancy in either of the models (0 ⊂ 95% CI).

Temperature standardized occupancy model The goodness-of-fit test of the global temperature standardized model (data subset of reaches with ≥18°C) indicated poor fit ($p > 0.05$) and slight overdispersion (c-hat = 1.91). To account for overdispersion, we added the square root of c-hat to SEs in each of the best models prior to calculating the 95% CI. VIF ranged from 1.01 ≤ VIF ≤ 1.02, indicating negligible multicollinearity within models.

Iteration of the global model resulted in 3 models that were strongly supported by the data (Table S1). The best model (QAICc = 38.65) did not include the water temperature covariate, indicating successful temperature standardization. Water temperature was present (λ = 0.480) but not related to occupancy in the 2nd model (0 ⊂ 95% CI). The 3rd model included flow velocity as a detection covariate, but the CI contained 0, indicating negligible effect on detection probability. No other covariate relationships were present, indicating that the strong effect of water temperature in the basin was not masking any other occupancy–covariate relationships, and it was reasonable to make inferences on the full-occupancy model results (Table S1).

Faxonius virilis *abundance and other sources of variation* As the detection probability of the best model was very high (98.8%), imperfect detection was deemed to be negligible. Therefore, use of GLMM that does not account for imperfect detection is a reasonable approach to investigate spatial random effects. Iteration of the global GLMM resulted in 3 best models that were strongly supported by the data (Table 3). Water temperature was the only covariate present in the 1st and 3rd models, whereas both water temperature and physical complexity were present in the 2nd model. The water temperature parameter estimate was positive and strongly related to *F. virilis* relative abundance in all 3 models (1st = 95% CI = 0.289, 1.207; 2nd = 95% CI = 0.296, 1.258; 3rd = 95% CI = 0.309, 1.187) while the physical complexity gradient was not related to *F. virilis* relative abundance (0 ⊂ 95% CI) (Table 3). Flow velocity was absent from the 1st and 2nd models but present and positive in the 3rd-best model; however, flow velocity was not related to *F. virilis* relative abundance (0 ⊂ 95% CI). Variances and SDs of the reach random effect variable were 6.016 and 2.453, 5.474 and 2.340, and 5.635 and 2.374 in the 1st, 2nd, and 3rd models, respectively. The log-likelihood ratio test indicated that the random effect of reach explained a substantial amount of variance in *F. virilis* relative abundance ($p < 0.001$) in all best GLMM models.

Model averaging

Prediction with occupancy model averaging We performed model averaging on the full-occupancy model

Table 3. Generalized linear mixed models ranked by Akaike Information Criterion corrected for small sample size (AICc) weights within ΔAICc <2 and corresponding covariates relationship estimates. Flow velocity (flow), turbidity (turb), physical complexity (comp), and water temperature (temp) were fixed predictor variables (F), whereas reach code was the random (R) variable in the model. Strong covariate relationships, defined as those with 95% CIs that do not include 0, appear in bold. NTU = nephelometric turbidity unit.

	Fixed abundance estimates				Random effects		Ranking statistics		
Model	Flow (m/s)	Turbidity (NTU)	Physical complexity	Water temperature (C°)	Variance	SD	AICc	ΔAICc	Weight
F(temp + comp), R(site)	–	–	–	**0.75**	6.016	2.453	143.68	0	0.487
F(temp + comp), R(site)	–	–	−3.08	**0.77**	5.474	2.340	144.58	0.90	0.311
F(temp + flow), R(site)	4.21	–	–	**0.75**	5.635	2.374	145.45	1.77	0.201

but not on the temperature standardized occupancy model. Model averaging of the water temperature occupancy parameter from the 6 best occupancy models (ΔQAICc ≤ 3) indicated that the probability of *F. virilis* occupancy of a stream reach is >50% where mean summer water temperatures are ≥18.7°C and <25% where mean summer water temperatures are ≥15°C (Fig. 4A). In contrast, the model averaged occupancy probabilities were held nearly constant (~30%) over all measurements of turbidity, physical complexity, and flow velocity because they were present only in the 3rd-, 4th-, and 5th-best models, all of which were far less heavily weighted than the best 2 models (Fig. 4B, C, D). Therefore, the occupancy probability is maintained near the value consistent with mean water temperature (17.3°C) over all sampled reaches (Fig. 4B, C, D).

Model validation RMSE estimate values obtained from leave-one-out cross-validation ranged between 0.33 and 0.34 for the 6 best occupancy models, which translates to ~67% overall accuracy in the models' occupancy predictions. Model sensitivity ranged from 0.53 to 0.59 with a mean of 0.55, whereas specificity ranged from 0.80 to 0.89 with a mean of 0.85.

We used our model to map predicted probabilities of occurrence in 19 tributaries monitored by Alberta Environment and Parks that were not sampled in our study. We identified 4 of these tributaries (Strawberry Creek, Sturgeon River, Redwater River, and Vermillion River) as reaches of concern (>18°C mean summer water temperature) that should be prioritized for *F. virilis* prevention, monitoring, and management (Fig. S3).

DISCUSSION

Understanding the factors that drive invasive species occupancy is an integral aspect of providing effective invasive species management. Our aims were to identify 1) which local (instream) habitat features best predict occupancy of invasive *F. virilis* in tributaries of the North Saskatchewan River basin, 2) if flow velocity or tributary depth affect *F. virilis* detection, and 3) which unoccupied tributary reaches in the North Saskatchewan River basin should be prioritized for additional monitoring to prevent subsequent invasion. Our analyses revealed that *F. virilis* occupancy is positively and strongly related to water temperature. In contrast to our expectations, flow velocity, turbidity, and physical complexity were not related to *F. virilis* occupancy in tributaries of the North Saskatchewan River basin. We found that the *F. virilis* detection probability obtained from the 4-trapline crayfish sampling method was very high (99.8%). This result in addition to the lack of relationships between detection probability and flow velocity and depth in the strongest models indicates that imperfect crayfish detection was negligible (Appendix S1).

Flow velocity and turbidity

Our study streams did not experience flow velocity and turbidity in the ranges that affect the survival, growth, and reproduction of crayfish in the lab or in the field (Maude and Williams 1983, Foster and Keller 2011, Rosewarne et al. 2014). We initially hypothesized that flow velocity would be negatively correlated with crayfish occupancy; however, the mean flow velocity among study reaches was determined to be 0.18 m/s, which is nearly ½ that of the average slip speed for *F. virilis* found by Maude and Williams (1983) in the lab and Foster and Keller (2011) in the field. Therefore, the average flow velocities in the North Saskatchewan River basin were outside of the range in which they would preclude *F. virilis* from occupying and establishing a population at a given reach, which may explain why we did not find a negative relationship between *F. virilis* occupancy and flow velocity.

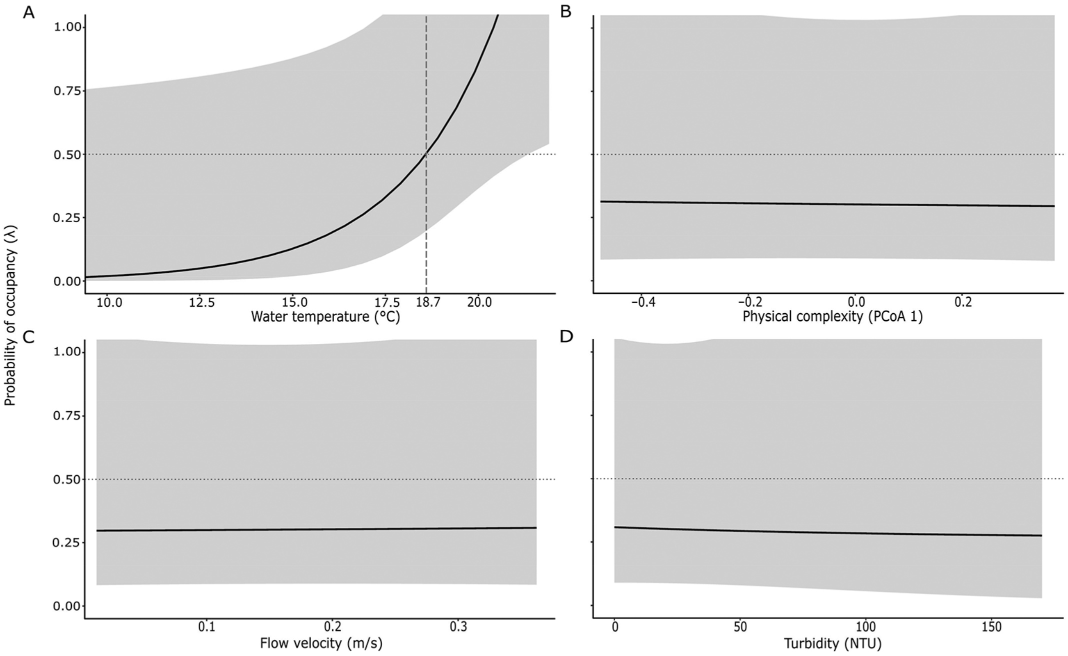

Figure 4. Model averaged predictions of probability of occupancy (λ) as a function of environmental covariates with 95% CIs about occupancy (gray bands) and reference lines indicating a 50% probability of occupancy (dotted) estimates. The probability of occupancy as a function of water temperature (°C) is represented with a vertical dashed reference line at 18.7°C (A). Remaining panels pertain to the probability of occupancy as a function of environmental covariates that were unrelated to occupancy in the 6 strongest models: physical complexity (principal coordinate analysis axis 1 [PCoA1]) (B), flow velocity (m/s) (C), and turbidity (nephelometric turbidity unit [NTU]) (D).

In the case of turbidity, we hypothesized that turbidity would be negatively correlated with occupancy because crayfish gills are susceptible to fouling by suspended solids, bacteria, and parasites in the water column (Bauer 1998). Further, gill function of the White-clawed Crayfish (*Austropotamobius pallipes* Lereboullet, 1858) and Signal Crayfish (*Pacifastacus leniusculus* Dana, 1852) was impaired at high suspended solid concentrations, specifically 133 mg/L, which is equivalent to 399 NTU (Rosewarne et al. 2014). In comparison, mean and maximum turbidity within our study reaches were 19 and 174 NTU, respectively. Thus, mean and maximum North Saskatchewan River basin turbidity values are ~21 and 2.3× lower than the concentration of suspended solids in which crayfish begin to experience gill fouling. Generally low suspended solids across sites likely explain why turbidity was not a driver of *F. virilis* occupancy in this study.

Water temperature

Water temperature alone was the most important driver of *F. virilis* occupancy at tributary reaches along the North Saskatchewan River basin. In all 6 best models, water temperature was strongly positively related to occupancy. The basin has a strong water temperature gradient from west to east, with high altitude coldwater streams originating in the Rocky Mountains and foothills regions and low altitude warmwater streams originating in the prairies. As poikilotherms, crayfish cannot regulate their own body temperature and rely on external water temperature to meet their physiological and biochemical requirements. Water temperature requirements and preferences of crayfish vary with species, and *F. virilis* demonstrate preference for warmer water temperatures in the 21 to 25°C range (Westhoff and Rosenberger 2016). In the Snake River drainage, Larson et al. (2018) observed that *F. virilis* were found in warmer low-elevation streams but were absent from colder headwater rivers. Their study did not evaluate water temperature's relationship to *F. virilis* occupancy specifically but provides anecdotal evidence of *F. virilis*' preference toward warm water temperatures that is consistent with our results (Larson et al. 2018).

In a laboratory setting, *F. virilis* have demonstrated a preference for 22°C water temperature when exposed to a temperature gradient tank ranging between 18 and 22°C (Bowman 2019). Further, Wetzel and Brown (1993) exposed 3rd-instar *F. virilis* to water temperatures of 10, 15, 20, 25, and 30°C for 21 d and consistently monitored their survival and growth. They found that the *F. virilis* group subject to 10°C demonstrated the lowest survival at 53% and experienced the most stunted growth in both body length and weight (Wetzel and Brown 1993). Low instar survival at coldwater temperatures may be driving the strong positive relationship of occupancy with water temperature. Specifically, juvenile *F. virilis* may suffer high mortality in westerly coldwater streams, preventing *F. virilis* populations from establishing. In addition to coldwater treatments, Wetzel and Brown (1993) found that 3rd-instar survival and growth were maximized at 25°C. Moreover, crayfish sperm production and embryonic development is optimized at 27 to 29°C and 25°C, respectively (Bugnot and López Greco 2009, Jin et al. 2019). Warmer water temperatures promote crayfish growth and decrease age of sexual maturity, thereby increasing egg production and abundance (Wetzel and Brown 1993, Whitmore and Huryn 1999). These findings are consistent with our model averaging results that indicate that the probability of *F. virilis* occupancy approaches 50% at water temperature of ~19°C and approaches 100% at ~21°C. This strong relationship of occupancy to water temperature may explain the weak relationship between occupancy and physical complexity.

Physical complexity

Counter to our original hypothesis, physical complexity was not related to occupancy in any of the plausible models. Our results contrast with previous studies that demonstrated the importance of physical complexity on crayfish growth, survival, and reproduction. Specifically, Simon and Cooper (2014) found that habitat suitability for Northern Clearwater Crayfish (*Faxonius propinquus* Girard, 1852) was highly correlated with rocky substrate and the presence of instream boulders and not related at all to landscape or reach level variables like landcover or wetted width). Further, Olsson and Nyström (2009) report a positive effect of rocky substrate on juvenile crayfish survival and recruitment in mesocosm experiments. We contend that the lack of relationship between physical complexity and *F. virilis* occupancy in our results is likely a consequence of the inverse relationship between the geomorphic and temperature gradients within the basin. As mentioned previously, the North Saskatchewan River flows from the Rocky Mountains, through the foothills, and into the prairies of eastern Alberta. As such, the geomorphology of high-elevation headwater streams is predominantly associated with boulders, rocky substrate, and downed tree woody debris. Therefore, reaches located in headwater streams were associated with high physical complexity in the PCoA ordination (Fig. 3). However, *F. virilis* cannot occupy these highly complex reaches because the coldwater temperatures exceed their thermal niche and temperature tolerance. In contrast, the geomorphic structure of reaches located in downstream prairie tributaries is dominated by overhanging banks, some aquatic macrophyte cover, and a large amount of sand, silt, and detritus, resulting in lower overall physical complexity values. These reaches also possess optimal water temperatures for *F. virilis* survival and growth (Bugnot and López Greco 2009, Jin et al. 2019). Rocky substrates are preferred but not essential for *F. virilis* survival (Hill and Lodge 1994). If these substrates were essential, *F. virilis* would be unable to occupy any part of North Saskatchewan River basin reaches because of coldwater temperatures in the west and low physical complexity in the east.

Faxonius virilis is associated with cobble dominated habitats under otherwise suitable conditions (Hill and Lodge 1994). However, when *F. virilis* coexists with a rival invader and competitor, *F. virilis* presence appears to be unrelated to rocky substrate but instead is positively associated with silt, detritus, and especially live vegetation beds (Smith et al. 2019). Likewise, in the western tributaries of the North Saskatchewan River, cold temperatures may be preventing *F. virilis* from occupying more physically complex steams. Instead, in lower-gradient streams, *F. virilis* populations appear to occupy less physically complex, but thermally more suitable, streams that are dominated by macrophyte cover, sand, silt, and detritus.

Faxonius virilis abundance and environmental variables

The GLMM indicated that crayfish relative abundance had a strong positive relationship with water temperature in all 3 best models. As discussed above, warmer water temperatures maximize *F. virilis* growth and reproduction. Also, similar to the occupancy model results, physical complexity was weakly negatively related to crayfish relative abundance. In the western reaches, coldwater temperatures may be excluding *F. virilis* from occupying habitats with preferred rocky substate. However, rocky substrates are not essential for *F. virilis* survival, therefore, *F. virilis* can readily occupy the sand, silt, and macrophyte-dominated easterly reaches which offer optimal warmwater temperatures. In this way, water temperatures in the basin may be defining the habitat options available to *F. virilis* to use and restricting them to only soft substrate, low-complexity reaches. *Faxonius virilis*' use of habitats with soft substrate and low complexity may also explain some of the PCoA results. In particular, the % macrophyte vector was somewhat orthogonally and negatively positioned relative to the % rocky and boulder vectors as well as pointed toward reaches in Blackmud Creek and Beaver Creek (BMD2, BMD3, and BEA1; Fig. 3), which demonstrated among the highest relative *F. virilis* abundances. This vector may therefore be reflecting the benefit of macrophyte cover to *F. virilis* survival and reproduction within warmer water, low-complexity reaches (Garvey et al. 2003).

Management and broader implications

Understanding the local instream environmental characteristics that drive crayfish occupancy is essential for managing and preventing current and future *F. virilis* invasive populations. Sensitivity and specificity indicate that our models are ~55% accurate at correctly predicting *F. virilis* presence and ~85% accurate at predicting *F. virilis* absence. Few ecological occupancy studies report the sensitivity and specificity values of their models, making it difficult to compare the accuracy of our models to others. Nonetheless, our model accurately predicts *F. virilis* occupancy the majority of the time, further supporting our results and management recommendations. Our results indicate that *F. virilis* can tolerate a wide range of instream physical complexity and that both turbidity and flow velocity ranges within the basin are within the tolerance limits of *F. virilis*. However, *F. virilis*' water temperature requirements dictate that they may only occupy eastern warmwater streams as the coldwater streams of the headwaters are outside of their thermal niche. Thus, rather than a suite of factors, temperature appears to be the single local environmental variable associated with crayfish occupancy in the basin.

Coldwater streams may thus have some natural protection against invasion by *F. virilis*. North Saskatchewan River streams with mean summer water temperatures ≥18°C should therefore be prioritized for *F. virilis* monitoring and introduction prevention, and occupied streams with mean summer water temperatures ≥18°C should be prioritized for targeted *F. virilis* invasive species management.

Climate change is projected to shift the affect the thermal regime, streamflow, discharge volume, snowpack, and other features of the North Saskatchewan River basin (Kienzle et al. 2012, Carr et al. 2019). As climate change progresses, western coldwater streams in the basin could potentially warm to the point where *F. virilis* can occupy them. Mean annual air temperatures in the upper basin are projected to increase by 2 to 6°C in the near (by 2050) and far (by 2080) future (Anis and Sauchyn 2021), and, because air and water temperatures follow each other closely, river water temperatures will warm along this trend. Watershed managers should therefore consider the likely effects of climate change and the need for water temperature monitoring when prioritizing tributaries for *F. virilis* monitoring and management. Our mapping exercise revealed at least 4 tributaries of the North Saskatchewan River basin that should be prioritized for current and future *F. virilis* introduction prevention and management. The identification of these tributaries provides an excellent starting point for invasive species management within the basin, and our findings provide a practical framework through which other tributaries in the North Saskatchewan River basin and in other basins of western Canada can be identified and prioritized for invasive *F. virilis* management.

Our findings could be extended to other basins in western Canada that have similar temperature and geomorphic regimes as the North Saskatchewan River basin. For example, *F. virilis* capture data in the Lake Winnipeg River basin showed that *F. virilis* occupied 92% of reaches (81/88) with water temperatures ≥18°C (Rosenberg et al. 2010; Fig. S4). In addition, tributaries of the Oldman and Bow River watersheds occupied by *F. virilis* (Williams et al. 2011) have water temperatures within the range of occupancy susceptibility (≥18°C; D. Watkinson, Fisheries and Oceans Canada, personal communication) indicating that our management recommendations could be applied to those and similar watersheds as well. Our study design could be applied to determine the relationships between environmental characteristics and occupancy of other invasive crayfish species in locations such as the Pacific Northwest where the number of alien crayfish exceed that of native species (Larson and Olden 2011). Regarding future research directions, our GLMM results highlight the need to consider wider landscape covariates (e.g., human population density, etc.) on *F. virilis* occupancy to gain a clearer picture of all the drivers of *F. virilis* occupancy. Consideration of landscape scale covariates and application of our study design to other regions and crayfish species will improve occupancy estimations and invasive crayfish management recommendations.

ACKNOWLEDGEMENTS

Author contributions: VVM, SJG, CAE, CB, FRW, and MSP conceptualized the study. CB, FRW, CAE, MSP, and SJG acquired project funding. VVM, SJG, CAE, and MSP developed methodology for field sampling and analysis of field data. VVM led field data collection, analyzed the data, coordinated manuscript contributions, and led manuscript writing and revisions. CAE and MN performed additional analyses. SJG, CAE, and MSP verified the analytical methods. All authors reviewed, provided feedback, and edited all versions of the manuscript. Project administration and was provided by CAE, CB, SJG, and MSP.

We thank Rebecca Huang, Lauren Perras, Matthew Cunningham, and Jesse Shirton for their effort in field data collection. Thanks goes to the Alberta Government Environment and Parks water quality and quantity field staff for field support and equipment and to EPCOR Utilities for additional station data. Funding of this project was provided by Alberta Innovates Water Innovation Program (Project No. 2614) with additional funding support from the Government of Canada through the Alexander Graham Bell Canada Graduate Scholarship – Master's. All sampling followed animal handling and ethics regulations of the Government of Alberta (Research License No. 20-3812 RL) and the University of Alberta (Animal Use Protocol No. AUP00003578). R code for all analyses is available at https://doi.org/10.5281/zenodo.6837103.

LITERATURE CITED

Acosta, C. A., and S. A. Perry. 2000. Effective sampling area: A quantitative method for sampling crayfish populations in freshwater marshes. Crustaceana 73:425–431.

Aiken, D. E. 1968. The crayfish *Orconectes virilis*: Survival in a region with severe winter conditions. Canadian Journal of Zoology 46:207–211.

Alberta Government. 2021. 2021 Alberta guide to sportfishing regulations. Alberta Government, Alberta Environments and Parks, Alberta Conservation Association, Sherwood Park, Alberta, Canada. (Available from: https://albertaregulations.ca/fishingregs/)

Allison, P. D. 1999. Multiple regression: A primer. Pine Forge Press, Thousand Oaks, California.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Anis, M. R., and D. J. Sauchyn. 2021. Ensemble projection of future climate and surface water supplies in the North Saskatchewan River Basin above Edmonton, Alberta, Canada. Water 13:2425.

Bauer, R. T. 1998. Gill-cleaning mechanisms of the crayfish *Procambarus clarkii* (Astacidea: Cambaridae): Experimental testing of setobranch function. Invertebrate Biology 117: 129–143.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bowman, A. 2019. Chemosensory behavior and temperature preferences of Northern Crayfish (*Faxonius virilis*) and Rusty Crayfish (*Faxonius rusticus*). Master's Thesis. Plymouth State University, Plymouth, New Hampshire.

Brooks, M., B. Bolker, K. Kristensen, M. Maechler, A. Magnusson, M. McGillycuddy, H. Skaug, A. Nielsen, C. Berg, K. van Bentham, N. Sadat, D. Lüdecke, R. Lenth, J. O'Brien, C. J. Geyer, and M. Jagan. 2021. *glmmTMB*: Generalized linear mixed models using template model builder. (Available from: https://cran.r-project.org/web/packages/glmmTMB/index.html)

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: An integral part of inference. Biometrics 53:603–618.

Bugnot, A. B., and L. S. López Greco. 2009. Sperm production in the Red Claw Crayfish *Cherax quadricarinatus* (Decapoda, Parastacidae). Aquaculture 295:292–299.

Bunte, K., and S. R. Abt. 2001. Sampling surface and subsurface particle-size distributions in wadable gravel-and cobble-bed streams for analyses in sediment transport, hydraulics, and streambed monitoring. General Technical Report RMRS-GTR-74. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. (Available from: https://www.fs.usda.gov/treesearch/pubs/4580)

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Caroffino, D. C., T. M. Sutton, R. F. Elliott, and M. C. Donofrio. 2010. Predation on early life stages of Lake Sturgeon in the Peshtigo River, Wisconsin. Transactions of the American Fisheries Society 139:1846–1856.

Carr, M., L. Li, A. Sadeghian, I. D. Phillips, and K.-E. Lindenschmidt. 2019. Modelling the possible impacts of climate change on the thermal regime and macroinvertebrate species of a regulated prairie river. Ecohydrology 12:e2102.

Chandler, R., K. Kellner, I. Fiske, D. Miller, A. Royle, J. Hostetler, R. Hutchinson, A. Smith, M. Kery, M. Meredith, A. Fournier, A. Muldoon, and C. Baker. 2021. *unmarked*: Models for data from unmarked animals. (Available from: https://cran.r-project.org/web/packages/unmarked/index.html)

De Palma-Dow, A., J. Curti, and E. Fergus. 2020. It's a trap! An evaluation of different passive trap types to effectively catch and control the invasive Red Swamp Crayfish (*Procambarus clarkii*) in streams of the Santa Monica Mountains. Management of Biological Invasions 11:44–62.

Dorn, N. J., and G. G. Mittelbach. 2004. Effects of a native crayfish (*Orconectes virilis*) on the reproductive success and nesting behavior of sunfish (*Lepomis* spp.). Canadian Journal of Fisheries and Aquatic Sciences 61:2135–2143.

Dorn, N. J., and J. M. Wojdak. 2004. The role of omnivorous crayfish in littoral communities. Oecologia 140:150–159.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Ficetola, G. F., M. E. Siesa, R. Manenti, L. Bottoni, F. D. Bernardi, and E. Padoa-Schioppa. 2011. Early assessment of the impact of alien species: Differential consequences of an invasive crayfish on adult and larval amphibians. Diversity and Distributions 17:1141–1151.

Flinders, C. A., and D. D. Magoulick. 2005. Distribution, habitat use and life history of stream-dwelling crayfish in the Spring River Drainage of Arkansas and Missouri with a focus on the imperiled Mammoth Spring Crayfish (*Orconectes marchandi*). The American Midland Naturalist 154:358–374.

Foster, H. R., and T. A. Keller. 2011. Flow in culverts as a potential mechanism of stream fragmentation for native and nonindigenous crayfish species. Journal of the North American Benthological Society 30:1129–1137.

Frings, R. M., S. C. K. Vaeßen, H. Groß, S. Roger, H. Schüttrumpf, and H. Hollert. 2013. A fish-passable barrier to stop the invasion of non-indigenous crayfish. Biological Conservation 159: 521–529.

Garvey, J. E., J. E. Rettig, R. A. Stein, D. M. Lodge, and S. P. Klosiewski. 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. Ecology 84:3339–3348.

Gibson, R. J., K. G. Hillier, and R. R. Whalen. 1998. A comparison of three methods for estimating substrate coarseness in rivers. Fisheries Management and Ecology 5:323–329.

Haddaway, N. R., R. J. G. Mortimer, M. Christmas, and A. M. Dunn. 2015. Water chemistry and endangered White-clawed Crayfish: A literature review and field study of water chemistry association in *Austropotamobius pallipes*. Knowledge & Management of Aquatic Ecosystems 416:1.

Hanson, J. M., P. A. Chambers, and E. E. Prepas. 1990. Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. Freshwater Biology 24:69–80.

Hartig, F., and L. Lohse. 2021. *DHARMa*: Residual diagnostics for hierarchical (multi-level/mixed) regression models. (Available from: https://cran.r-project.org/web/packages/DHARMa/index.html)

Hastie, T., R. Tibshirani, and J. Friedman. 2009. The elements of statistical learning – Data mining, inference, and prediction. Springer, Berlin, Germany.

Hazlett, B. A., P. Acquistapace, and F. Gerardi. 2006. Responses of the crayfish *Orconectes Virilis* to chemical cues depend upon flow conditions. Journal of Crustacean Biology 26:94–98.

Heino, J., J. Soininen, J. Alahuhta, J. Lappalainen, and R. Virtanen. 2015. A comparative analysis of metacommunity types in the freshwater realm. Ecology and Evolution 5:1525–1537.

Hill, A. M., and D. M. Lodge. 1994. Diel changes in resource demand: Competition and predation in species replacement among crayfishes. Ecology 75:2118–2126.

Jin, S., L. Jacquin, F. Huang, M. Xiong, R. Li, S. Lek, W. Li, J. Liu, and T. Zhang. 2019. Optimizing reproductive performance and embryonic development of Red Swamp Crayfish *Procambarus clarkii* by manipulating water temperature. Aquaculture 510:32–42.

Johnston, R., K. Jones, and D. Manley. 2018. Confounding and collinearity in regression analysis: A cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. Quality & Quantity 52:1957–1976.

Kienzle, S. W., M. W. Nemeth, J. M. Byrne, and R. J. MacDonald. 2012. Simulating the hydrological impacts of climate change in the upper North Saskatchewan River basin, Alberta, Canada. Journal of Hydrology 412–413:76–89.

Larson, E., R. Egly, and B. Williams. 2018. New records of the nonnative virile crayfish *Faxonius virilis* (Hagen, 1870) from the upper Snake River drainage and northern Bonneville Basin of the western United States. BioInvasions Records 7:177–183.

Larson, E. R., and J. D. Olden. 2011. The state of crayfish in the Pacific Northwest. Fisheries 36:60–73.

Legendre, P., and L. Legendre. 2012. Numerical ecology. 3rd edition. Elsevier, Amsterdam, The Netherlands.

Light, T. 2003. Success and failure in a lotic crayfish invasion: The roles of hydrologic variability and habitat alteration. Freshwater Biology 48:1886–1897.

Light, T. 2005. Behavioral effects of invaders: Alien crayfish and native sculpin in a California stream. Biological Invasions 7: 353–367.

Mack, R. N., W. M. Lonsdale, D. Simberloff, L. H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California.

Magoulick, D. D., R. J. DiStefano, E. M. Imhoff, M. S. Nolen, and B. K. Wagner. 2017. Landscape- and local-scale habitat influences on occupancy and detection probability of stream-dwelling crayfish: Implications for conservation. Hydrobiologia 799:217–231.

Mangan, B. P., J. J. Savitski, and N. T. Fisher. 2009. Comparison of two traps used for capturing wild crayfish. Journal of Freshwater Ecology 24:445–450.

Maude, S. H., and D. D. Williams. 1983. Behavior of crayfish in water currents: Hydrodynamics of eight species with reference to their distribution patterns in Southern Ontario. Canadian Journal of Fisheries and Aquatic Sciences 40:68–77.

Mazerolle, M. J. 2020. *AICcmodavg*: Model selection and multimodel inference based on (Q)AIC(c). (Available from: https://cran.r-project.org/web/packages/AICcmodavg/index.html)

McAlpine, D. F., A. H. E. McAlpine, and A. Madden. 2007. Occurrence of the potentially invasive crayfish, *Orconectes virilis* (Decapoda, Cambaridae) in eastern New Brunswick, Canada. 80:509–511.

Momot, W. T. 1967. Population dynamics and productivity of the crayfish, *Orconectes virilis*, in a Marl Lake. The American Midland Naturalist 78:55–81.

Olsson, K., and P. Nyström. 2009. Non-interactive effects of habitat complexity and adult crayfish on survival and growth of juvenile crayfish (*Pacifastacus leniusculus*). Freshwater Biology 54:35–46.

Paradis, E., S. Blomberg, B. Bolker, J. Brown, S. Claramunt, J. Claude, H. S. Cuong, R. Desper, G. Didier, B. Durand, J. Dutheil, R. Ewing, O. Gascuel, T. Guillerme, C. Heibl, A. Ives, B. Jones, F. Krah, D. Lawson, V. Lefort, P. Legendre, J. Lemon, G. Louvel, E. Marcon, R. McCloskey, J. Nylander, R. Opgen-Rhein, A.-A. Popescu, M. Royer-Carenzi, K. Schliep, K. Strimmer, and D. de Vienne. 2022. *ape*: Analyses of phylogenetics and evolution. (Available from: https://cran.r-project.org/web/packages/ape/index.html)

Poos, M., A. J. Dextrase, A. N. Schwalb, and J. D. Ackerman. 2010. Secondary invasion of the Round Goby into high diversity Great Lakes tributaries and species at risk hotspots: Potential new concerns for endangered freshwater species. Biological Invasions 12:1269–1284.

Ratajc, U., M. Breskvar, S. Džeroski, and A. Vrezec. 2022. Differential responses of coexisting owls to annual small mammal population fluctuations in temperate mixed forest. Ibis 164: 535–551.

Rogowski, D. L., S. Sitko, and S. A. Bonar. 2013. Optimising control of invasive crayfish using life-history information. Freshwater Biology 58:1279–1291.

Rosenberg, D. M., M. A. Turner, W. Jansen, T. Mosindy, and D. A. Watkinson. 2010. Threats to Lake of the Woods and the Winnipeg River by the Rusty Crayfish (*Orconectes rusticus*), an aquatic invader. Technical Workshop Report TWR-005. (Available from: Ontario Ministry of Natural Resources, Northwest Science & Information RR 1, 25th Side Road Thunder Bay, Ontario P7C 4T9 Canada)

Rosewarne, P. J., J. C. Svendsen, R. J. G. Mortimer, and A. M. Dunn. 2014. Muddied waters: Suspended sediment impacts on gill structure and aerobic scope in an endangered native and an invasive freshwater crayfish. Hydrobiologia 722:61–74.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84: 777–790.

Ruppert, J. L. W., C. Docherty, K. Neufeld, K. Hamilton, L. MacPherson, and M. S. Poesch. 2017. Native freshwater species get out of the way: Prussian Carp (*Carassius gibelio*) impacts both fish and benthic invertebrate communities in North America. Royal Society Open Science 4:170400.

Setzer, M., J. R. Norrgård, and T. Jonsson. 2011. An invasive crayfish affects egg survival and the potential recovery of an endangered population of Arctic charr. Freshwater Biology 56: 2543–2553.

Simon, T., and N. Cooper. 2014. Habitat suitability index relationships for the Northern Clearwater Crayfish, *Orconectes Propinquus* (Decapoda: Cambaridae). Fisheries & Aquaculture Journal 5:1–7.

Smith, K. R., B. M. Roth, M. L. Jones, D. B. Hayes, S. J. Herbst, and N. Popoff. 2019. Changes in the distribution of Michigan crayfishes and the influence of invasive Rusty Crayfish (*Faxonius rusticus*) on native crayfish substrate associations. Biological Invasions 21:637–656.

Styrishave, B., B. H. Bojsen, H. Witthøfft, and O. Andersen. 2007. Diurnal variations in physiology and behaviour of the Noble Crayfish *Astacus astacus* and the Signal Crayfish *Pacifastacus leniusculus*. Marine and Freshwater Behaviour and Physiology 40:63–77.

Usio, N. 2000. Effects of crayfish on leaf processing and invertebrate colonisation of leaves in a headwater stream: Decoupling of a trophic cascade. Oecologia 124:608–614.

Usio, N., R. Kamiyama, A. Saji, and N. Takamura. 2009. Size-dependent impacts of invasive alien crayfish on a littoral marsh community. Biological Conservation 142:1480–1490.

Vacher, H. L. 2005. Visualizing averages – The 60% relative depth rule for stream velocity. Journal of Geoscience Education 53: 478–481.

Westhoff, J. T., and A. E. Rosenberger. 2016. A global review of freshwater crayfish temperature tolerance, preference, and optimal growth. Reviews in Fish Biology and Fisheries 26: 329–349.

Wetzel, J. E., and P. B. Brown. 1993. Growth and survival of juvenile *Orconectes virilis* and *Orconectes immunis* at different temperatures. Journal of the World Aquaculture Society 24: 339–343.

Whitmore, N., and A. D. Huryn. 1999. Life history and production of *Paranephrops zealandicus* in a forest stream, with comments about the sustainable harvest of a freshwater crayfish. Freshwater Biology 42:467–478.

Williams, B. W. 2012. A molecular assessment of range expansion of the northern or virile crayfish (*Orconectes virilis*), crayfish-based community co-structure, and phylogeny of crayfish-affiliated symbionts. PhD Dissertation. University of Alberta, Alberta, Canada.

Williams, B. W., H. C. Proctor, and T. Clayton. 2011. Range extension of the Northern Crayfish, *Orconectes Virilis* (Decapoda, Cambaridae), in the Western Prairie Provinces of Canada. Crustaceana 84:451–460.

Yarra, A. N., and D. D. Magoulick. 2018. Stream permanence is related to crayfish occupancy and abundance in the Ozark Highlands, USA. Freshwater Science 37:54–63.

Yeakley, J. A., D. Ervin, H. Chang, E. F. Granek, V. Dujon, V. Shandas, and D. Brown. 2016. Ecosystem services of streams and rivers. Pages 335–352 *in* D. J. Gilvear, M. T. Greenwood, M. C. Thoms, and P. J. Wood (editors). River science: Research and management for the 21st century. John Wiley & Sons, Hoboken, New Jersey.

Zale, A. V., D. L. Parrish, and T. M. Sutton (editors). 2012. Fisheries techniques. 3rd edition. American Fisheries Society, Bethesda, Maryland.

Zimmer-Faust, R. K., C. M. Finelli, N. D. Pentcheff, and D. S. Wethey. 1995. Odor plumes and animal navigation in turbulent water flow: A field study. The Biological Bulletin 188:11 1–116.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York.