A SIMULATION MODEL TEST OF THE POTENTIAL ROLE FOR SIZE-STRUCTURED, AGONISTIC, INTRASPECIFIC INTERACTIONS IN THE ONTOGENETIC NICHE SHIFTS OF SIGNAL CRAYFISH (*PACIFASTACUS LENIUSCULUS* DANA)

by

AMANDA E. MARTIN

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FACULTY OF FORESTRY

UNIVERSITY OF BRITISH COLUMBIA

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ABSTRACT

Ontogenetic niche shifts generally coincide with changes in size, morphology, behavior, and/or feeding preferences during development, resulting in a shift in preferred habitat. In aquatic species, these ontogenetic niche shifts are often associated with habitat-dependent changes in competition and/or predation dynamics, expressed as a size-depth relationship where the larger-bodied adults occupy deeper habitats while the smaller-bodied juveniles primarily reside in shallower regions. While the influence of interspecific interactions on size-structured habitat occupancy has been well studied, few have examined the potential role of intraspecific agonistic interactions between size classes in ontogenetic niche shifts. A simulation model was developed to test whether the size-specific habitat occupancy observed in signal crayfish can be explained by the size-structured individual responses to agonistic interaction, where the smaller-bodied juvenile responds to the interaction with an escape movement, to avoid engagement and the risk of mortality or injury from the adult. The simulated movements of signal crayfish resulted in higher juvenile occupancy of riffles relative to pools reflecting a greater rate of escape from adults into riffles, away from the higher densities of adults in their preferred habitat (i.e. pools). This provides evidence that the juvenile escape response to size-structured, intraspecific, agonistic interactions may contribute to ontogenetic niche shifts.

Keywords: *habitat selection; escape behavior; turn angle; density dependence*

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mean movement distance in riffles relative to pools for juveniles ($\bar{x}_{riffle} = 17.2$ cm $\pm$ 4.2, $\bar{x}_{pool} = 8.6$ cm $\pm$ 4.2) and for adults ($\bar{x}_{riffle} = 41.8$ cm $\pm$ 6.4, $\bar{x}_{pool} = 20.9$ cm $\pm$ 6.4). Other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° ($\pm$ 30), and 90 time steps per trial. The dotted line represents the null condition where individuals have an equal probability of being in either habitat type, and (*) denote significant differences from the reference condition (A) for juveniles and (•) for adults.

Figure 8. The mean proportion of juveniles and adults in pools ($\pm$ standard deviation) under four escape distance scenarios: (A) the base condition ($\bar{x} = 5.9$ cm $\pm$ 4.2); (B) half of the base condition ($\bar{x} = 2.95$ cm $\pm$ 2.4); (C) 50% over the base condition ($\bar{x} = 8.85$ cm $\pm$ 4.2); and (D) double the base condition ($\bar{x} = 11.8$ cm $\pm$ 4.2). Other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° ($\pm$ 30), and 90 time steps per trial. The dotted line represents the null condition where individuals have an equal probability of being in either habitat type, and (*) denote significant differences from the reference condition (A) for juveniles.

Figure 9. The mean proportion of juveniles in pools as a function of the interaction distance (m) and the total density of crayfish in the stream segment (per m^2). While interaction distance and the initial density of the total crayfish population were varied, all other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° ($\pm$ 30), and 90 time steps per trial. Color bands denote changes in the proportion in pools at an interval of 0.02.

Figure 10. The final density of juveniles in pools (per m^2), as a function of the interaction distance (m) and the initial density of randomly distributed juveniles in pools (per m^2). While interaction distance and the initial density of the total crayfish population were varied, all other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° ($\pm$ 30), and 90 time steps per model iteration. Color bands denote changes in the final density in pools at an interval of 0.5.

INTRODUCTION

Habitat selection is largely driven by the evolutionary impetus of organisms to maximize fitness (Morris 2003). Ontogenetic niche shifts, where a species utilizes different habitats at different developmental stages, generally coincide with changes in size, morphology, behavior, and/or feeding preferences which in turn alter the habitat characteristics required to optimize fitness (Werner and Gilliam 1984). Ontogenetic niche shifts are generally attributed to shifts in the trade-offs between maximizing growth potential and minimizing mortality risk for a given habitat type, making previously preferred habitat less suitable than an alternative (Werner and Gilliam 1984). Thus the life stage-specific resource requirements and biotic interactions are important determinants of habitat selection at different life stages.

Ontogenetic niche shifts in aquatic systems may be largely influenced by changes in the predation and competition dynamics that occur with increasing organism size (Werner and Gilliam 1984). Avoidance of predators has been shown to be a powerful motivator for habitat selection. For example, young of the year (YOY) cutthroat trout (*Oncorhynchus clarki*) show preferences for pools in the absence of larger trout, but are displaced to riffles in the presence of larger conspecifics (Rosenfeld and Boss 2001). Similarly, juvenile bluegill sunfish (*Lepomis macrochirus*) occupy littoral zones over energetically favorable pelagic regions, to avoid the increased mortality risk inherent to the pelagic (Werner and Hall 1988). This suggests that small-bodied individuals for a given species may choose poorer foraging habitats in a trade-off for reduced risk of predation by piscivorous predators or conspecifics.

A size-depth pattern is often found for stream- and lake-dwelling fish, such that larger individuals are predominately in deeper waters and smaller individuals in shallower regions, corresponding to a change in the dominant predation threat with size; smaller individuals are generally more susceptible to piscivorous fish relative to terrestrial predators, while this relationship is reversed for larger size classes (Power 1987). Crayfish species distribution may be subject to the same spatial variation in predation pressure. Movement to shallower depths in the presence of predacious fish has been observed in several crayfish species including the rusty crayfish (*Orconectes rusticus*), northern crayfish (*Orconectes virilis*), phallic crayfish

(*Orconectes putnami*), and eastern crayfish (*Cambarus bartoni*), suggesting crayfish will alter their distribution to avoid predators (Englund 1999; Magoulick 2004; Davis and Huber 2007). A declining response to aquatic predators with size is also evident in the literature; the addition of predatory fish to laboratory aquaria lead to size-dependent changes in behavior of the northern clearwater crayfish (*Orconectes propinquus*), with greater suppression of active behaviors and increases in defensive behaviors as size decreased (Stein and Magnuson 1976). Similarly, the presence of predatory fish caused small, but not large, eastern and phallic crayfish to move to shallower waters, while the presence of terrestrial predators such as raccoons and wading birds was related to movement of larger crayfish into deeper waters (Englund and Krupa 2000).

Despite evidence suggesting that size-class distributions of crayfish depend on changes in the dominant predation risk, Englund and Krupa (2000) observed that interspecific predation alone could not fully explain the distribution of juvenile crayfish; juvenile crayfish maintained their preference for shallower depths in the absence of fish. Our species of interest, the signal crayfish (*Pacifastacus leniusculus* Dana) shows a similar size class distribution, with adults preferring pools and juveniles preferring riffles (Guan and Wiles 1996).

A shift in feeding ecology is one proposed explanation for habitat preference differences between large and small crayfish. Crayfish species including the noble crayfish (*Astacus astacus*) and the red swamp crayfish (*Procambarus clarkia*) have shown shifts in food preferences during development, evidenced by an increasing contribution of plant material relative to animal matter in crayfish gut contents with increasing size (Abrahamsson 1966, Pérez-Bote 2005). Although shifts in food preference may play a role in distribution of crayfish species, it is unlikely that this factor alone is enough to explain the size-specific distribution of signal crayfish in the absence of predatory fish. Diet analysis of juvenile and adult signal crayfish have revealed only minimal differences between size classes, and these differences are only evident for food sources that are minor components of the total intake (Guan and Wiles 1998; Bondar et al. 2005). However, more recent study suggests that signal crayfish may undergo ontogenetic shifts in food preferences at earlier developmental stages (i.e. smaller sizes) than previously assessed; when YOY crayfish were contrasted with adults there was evidence for a shift towards consumption of leaf litter with size (Bondar and Richardson, 2009b). However, an ontogenetic

shift in food preference from more carnivorous to herbivorous diets with size may not promote general shifts in habitat between size classes. In many cases both organic matter and animal matter accumulates in pools over riffles (Wohl et al. 1995), therefore even if subtle differences in food preferences exist, it is likely the most abundant sources for both juveniles and adults will be found in pools.

Intraspecific agonistic interactions between adult and juvenile crayfish may provide, at least in part, an explanation for juvenile avoidance of deeper stream habitats that persists in the absence of interspecific predators. Signal crayfish readily engage in agonistic interactions; in comparison with three *Orconectes* species, the signal crayfish was the most aggressive, spending significantly more time fighting and exhibiting a greater prevalence of aggressive behaviors (Tierney et al. 2000). The smaller individual engaged in an agonistic interaction is likely to fare poorly, as size is a major determinant of the interaction's outcome (Edsman and Jonsson 1996), and fighting often resolves more quickly as size asymmetries increase (Davis and Huber 2007). Furthermore, smaller individuals may avoid interactions with larger individuals by choosing to retreat rather than engage in potentially costly combat (Harrison et al. 2006, Pavey and Fielder 1996). Olsson and Nyström (2009) observed that the behavior of juveniles changes in the presence of adults, with reductions in activity, which indicates that smaller-sized crayfish adopt behaviors to avoid interactions with larger individuals. In addition to risking damage during interaction, mortality risk for juveniles may come from intraspecific predation; signal crayfish are cannibalistic, with the incidence of cannibalism increasing with size (Guan and Wiles 1998, Bondar et al. 2005). Additionally, juvenile signal crayfish may be displaced from preferred habitat during interactions for shelters. Studies with the golden crayfish (*Orconectes luteus*) and spothand crayfish (*Orconectes punctimanus*) have shown that the addition of large individuals to laboratory aquaria result in smaller individuals being expelled from shelters, and the smaller size-classes shift away from the preferred, shelter-rich habitat (Rabeni 1985).

Despite the potent risk for juveniles from larger conspecifics, the role of agonistic interactions in ontogenetic niche shifts has been largely ignored in the scientific literature. Preliminary data on the movement behaviors and intraspecific agonistic interactions of adult and juvenile signal crayfish suggests a possible mechanism for segregating the size-classes; in

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adult-juvenile interactions adults showed little movement, while juveniles consistently retreated (Harrison et al. 2006). The current study seeks to simulate the individual movements and interactions of the adult and juvenile signal crayfish within a stream reach comprised of alternating pools and riffles, to determine whether or not agonistic interactions can generate size-specific habitat preferences in signal crayfish. Based on the findings of Harrison et al. (2006) the predicted outcome is that a size-structured distribution of the signal crayfish population in the modeled stream reach will develop over time, such that the adults will dominate their preferred habitat (i.e. pools) and juveniles will retreat to riffles. Additionally, the model will be used to assess the potential impact of various parameters on the final distribution of the modeled crayfish population.

METHODS

MODEL CREATION

     To model the agonistic interactions of signal crayfish, a model simulating the movements of individual crayfish within a stream was created using the Visual Basic programming language. The model structure was based on the stochastic movement models of Siniff and Jessen (1969) which describe individual movement paths as a function of a set of parameters, where stochastic variability in parameter values conforms to probability distributions derived from field observations of the movements for the species or population to be modeled. The individual movements in the simulation model for signal crayfish were based on two movement parameters – movement length and turn angle – under the simplifying assumption that, although animals typically follow circuitous paths, these paths can be approximated by a series of straight line segments connecting the individual's location at consecutive time steps (Figure 1; Kareiva and Shigesada 1983). The model employed a Cartesian coordinate system to track and specify movements in two dimensions, (1) "longitudinal" movements in an up-downstream direction and (2) "lateral" movements between stream banks. Movement lengths and turn angles were transposed into two-dimensional vectors using trigonometric functions, where each movement formed a right-angled triangle, with the movement length vector as the hypotenuse and the longitudinal and lateral movement vectors as the remaining triangle sides (see Equations 1 and 2). The position of each individual at the end of each time step was calculated by adding the longitudinal and lateral movement vectors to the existing position of the individual.

$$l_{long} = l_t \times \cos(\theta) \qquad \text{(Equation 1)}$$
$$l_{lat} = l_t \times \sin(\theta) \qquad \text{(Equation 2)}$$

Where l_{long} is the longitudinal movement vector, l_{lat} is the lateral movement vector, l_t is the movement length, and θ is the turn angle.

     The theoretical signal crayfish population consisted of two discrete size classes, "adult" and "juvenile", which were characterized by a separate set of movement parameters and behavior during agonistic interaction. The model environment consisted of a simplified stream
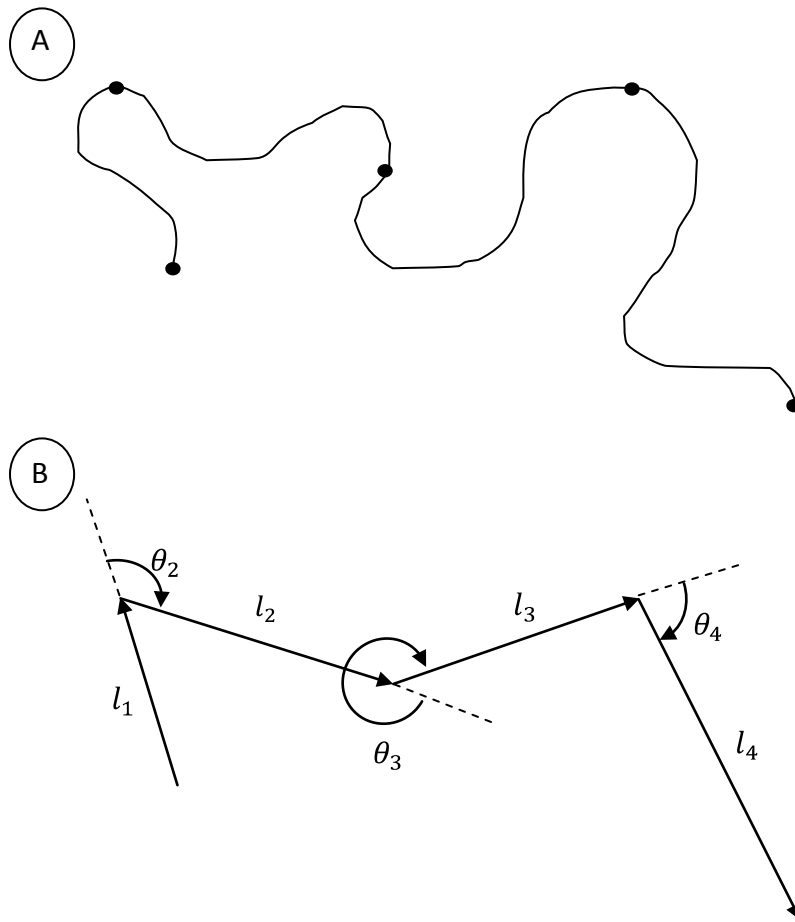
Figure 1. A. The hypothetical movement path of an organism (−), with • corresponding to the organism's position at each time step. B. The model of an organism's movement path through successive time steps (t), based on movement length (l_t) and turn angle (θ_t).

with a series of alternating habitats, three "pools" and three "riffles", each of constant width (3 m) and length (2 m). Stochasticity of movements between individuals and through time was incorporated into the modeled movements using Gaussian distributions to represent the range of possible values for the movement lengths and turn angles. Separate distributions were created to specify the movement lengths of the adult and juvenile size classes, and within a size class for the movement lengths in pools versus riffles. The turn angle was also represented as a distribution. Creation of Gaussian Distributions in Visual Basic required the use of the Box-Muller transformation, to translate the uniform distribution generated by the random number generation function into a standard Gaussian distribution. Separate distributions were differentiated by the mean and standard deviation incorporated into the normal distribution

through Equation 3. Thus the individual's movement in a given time step depended on the

$$x = sz + \bar{x} \qquad \text{(Equation 3)}$$

Where z is the value from the standard Gaussian distribution, $\bar{x}$ is the mean, and s is the standard deviation.

position of the individual at the end of the previous time step, the habitat type occupied at this position, the size class, the value drawn from the appropriate movement length distribution, and the value drawn from the turn angle distribution.

Differences in the lengths of movement between habitat types for a given size class created a habitat preference, such that the habitat in which the movements were shorter was favored. Movement lengths and turn angles were not biased to favor movements in any particular direction relative to the model stream; that is, the movement and distance distributions used to determine movements at each time step were not dependent on whether the individual is moving downstream, upstream, or across the width of the stream. The literature describing directional movements in crayfish was not conclusive, with various studies reporting no bias, an upstream bias, or a downstream bias (see Appendix A).

Movements were restricted to the stream via two mechanisms, (1) reflecting boundaries at stream banks and (2) creation of a closed loop system at the upstream and downstream bounds of the modeled stream segment. The reflecting boundary served to ensure no individuals crossed the lateral boundaries at the land-water interface for the stream. In instances where the calculated position of the organism fell outside the width, a new position was calculated such that the length of movement vector was conserved, and the individual was reflected at an equal but opposite angle (Figure 2). The closed loop system ensured that individuals moving outside the modeled stream segment entered into the other end at an equivalent position. This assumes that individuals were equally likely to enter the downstream end of the segment as to leave the upstream end, and vice versa.

The general movement model described above was further modified to include agonistic interactions. As the purpose of this model was to assess the implications for interactions between the size classes, the interactions were simplified by assuming that there were no adult-adult nor juvenile-juvenile interactions. In each adult-juvenile interaction, the
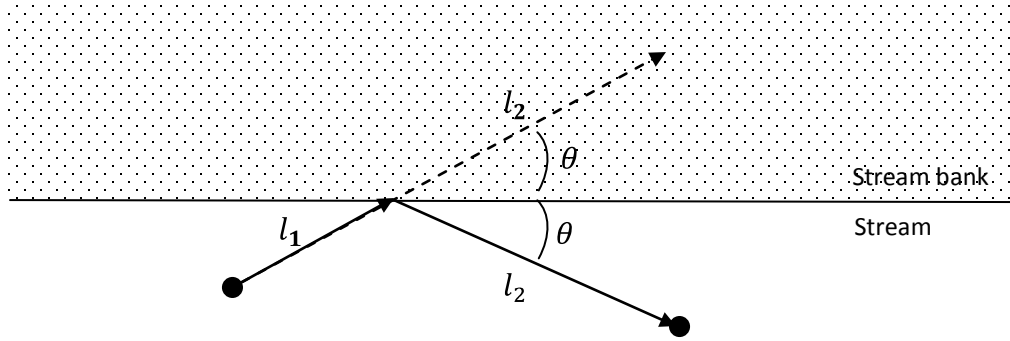
Figure 2. The hypothetical movement of an organism encountering the reflecting boundary at the stream-land interface. The new position represents a mirror reflection of the position outside the boundary, with the length of the movement vector ($l_1 + l_2$) conserved, at an equal but opposite angle (θ).

juvenile responded by making an escape movement while the adult remained stationary, as was indicated by Harrison et al. (2006). If the distance between an adult and juvenile was less than a threshold "interaction distance" the juvenile made an escape response directly away from the adult, and a new juvenile position was calculated using a movement length drawn from a separate distribution representing the escape distance. Each juvenile was restricted to one escape movement per time step.

The initial position of each member of the model population was randomly assigned within the total length and width of the model stream segment. The initial movement direction was also selected at random. For each time step, the model repeated the procedure of calculating new positions for each member of the population and assessing the agonistic interactions. To produce data for analysis the simulation model was repeated in 1000 trials for a given set of parameters. The model then generated as output the number of adults and juveniles present in pools and in riffles after the final time step for each of the 1000 trials.

SIMULATION OF SIGNAL CRAYFISH MOVEMENTS AND AGONISTIC INTERACTIONS

Model Parameterization

A base set of parameter values were established to simulate the movements and interactions of the signal crayfish size classes (see Table 1 for all parameter values). Mean and error estimates from Harrison et al. (2006) were used to parameterize the Gaussian distributions representing the movement lengths for the adult and juvenile size classes, and within a size class for the

movement lengths in pools versus riffles. As movement lengths between the two habitat types were not significantly different for juveniles in Harrison et al. (2006), data for juveniles were averaged to produce a single value, used in both the pools and riffles. Harrison et al. (2006) also supplied parameter values for the juvenile escape distance distribution. Signal crayfish densities vary widely (e.g. 1.3 ± 0.6 adults/m^2 and 1.4 ± 0.9 juveniles/m^2 in California [Light 2003], to greater than 20 crayfish/m^2 in suitable habitat in Britain [Bubb et al. 2006]), and densities for signal crayfish in their native habitat in British Columbia range from approximately 1 to 4 adults/m^2 or 4 to 12 juveniles/m^2 (Bondar et al. 2005). Thus a conservative density was utilized as the base condition and the influence of density on model outcome was tested (see Experiment 4). The population was assumed to contain equal numbers of adults and juveniles. A search of the literature did not produce values for the interaction distance, so again a conservative value was selected and the influence of interaction distance on the model outcome was tested (see Experiment 4). Two parameters were considered likely to be highly influential over the model outcome, thus the base parameter values were left to be determined by preliminary model testing: (1) the number of time steps and (2) the mean and standard deviations for the turn angle distribution.

Table 1. The base set of parameter values to be utilized in the simulation modeling of signal crayfish movements and adult-juvenile agonistic interactions. Values in brackets represent standard deviation from the mean.

Parameter	Values
Crayfish density	2.5 crayfish/m^2
Adult movement lengths in pools	20.9 cm (± 6.4)
Adult movement lengths in riffles	46.5 cm (± 7.3)
Juvenile movement lengths in pools	8.6 cm (± 4.2)
Juvenile movement lengths in riffles	8.6 cm (± 4.2)
Juvenile escape distance	5.9 cm (± 2.4)
Juvenile-adult interaction distance	15 cm

Selection of Base Parameter Values

<u>Selecting the Number of Iterations</u>

The number of time steps utilized in each model run had the potential to largely influence model outcomes, as a result of the initially random distribution of individuals throughout the theoretical stream segment. It was expected that the initial random distribution

would reach an equilibrium condition after some number of time steps, such that further increases in the number of iterations would no longer influence the model outcome. To assess the influence of different numbers of iterations, the model was run under 10 scenarios, in which the number of time steps was increased from 10 to 100 in increments of 10. The rest of the parameters were kept constant at base conditions, and the turn angle distribution was set to 0° (± 15). The base number of time steps was chosen to represent some point after equilibrium.

<u>Selecting Values for the Turn Angle Distribution</u>

A search of the literature did not return any potential mean and error estimates for the turn angle distribution. Studies of turning behavior in crayfish were restricted to those monitoring crayfish orientation in response to specific stimuli such as odor (e.g. Wolf et al. 2004), tactile stimulation (e.g. Copp and Watson 1988), or predation (e.g. Breithaupt et al. 1995). These estimates are not indicative of the general turning behavior of crayfish during daily movements, as in these experiments turns are in response to specific, experimentally introduced source stimuli.

Although the literature did not directly provide values for the turn angle distribution, evidence from other invertebrate taxa indicated that a mean angle of 0° was appropriate. A mean of 0° is common to the turning behavior of many assessed terrestrial invertebrates (e.g. Levin et al. 1971, Jones 1977) and has been utilized in similar simulation models for movements of terrestrial invertebrates (e.g. Kitching 1971, Cain 1985). Additional support for the use of a mean of 0° for simulation of crayfish movements was derived from T-maze choice experiments, where individuals must choose to move down the left or right arm of a maze. Crayfish in these choice experiments exhibit a lack of directional bias, and are equally likely to turn left as right (McMahon et al. 2005, Shuranova 2008).

The influence of changing the other value required for the turn angle distribution, standard deviation, was assessed by running the simulation model under 10 scenarios, where the standard deviation for the turn angle distribution was given a value of: 5, 10, and from 15 to 120 in increments of 15. The rest of the parameters were kept constant at base conditions, and

utilized the number of iterations selected from the previous investigation. The base value for the turn angle was selected from the outcome of this modeling exercise.

<u>Assessing the Influence of Habitat Preferences on the Relationship Between the Turn Angle and Model Outcome</u>

The influence of habitat preference strength in conjunction with the width of the turn angle distribution was further assessed for the adult size class only, as the outcome of these variations was not confounded by the agonistic interaction (i.e. only juveniles respond when an interaction occurs). In this case, three levels of habitat preference strength were created by varying the mean movement length for adults in riffles: (A) the movement length in riffles set equal to that in pools (20.9 cm ± 6.4); (B) the movement length in riffles set 50% higher than in pools (31.4 cm ± 6.4); and (C) double the movement length in riffles relative to pools (41.8 cm ± 6.4). For each level of habitat preference, five values of standard deviation for the turn angle distribution were examined: 5, 30, 60, 90, and 120. The rest of the parameters were kept constant at base conditions, and utilized the number of iterations selected from the previous investigation.

Experiment 1: Assessing the Model Outcome under the Base Conditions

In the first simulation, the model was run under the base conditions described in Table 1, and the number of iterations and turn angle parameter values selected from the preliminary investigations.

Experiment 2: Assessing the Influence of Habitat Preferences

To assess the influence of habitat preferences on the distribution of juveniles and adults, we varied the mean movement lengths of the size classes in pools and riffles. Four scenarios were assessed: (A) equal movement lengths for adults and juveniles in both habitat types, set at the base value for the juveniles; (B) equal movement lengths in both habitat types for a given size class but different movement lengths for adults and juveniles, set at the base movement length for adults in pools and the base value for juveniles respectively; (C) habitat preference for pools in the adult size class only, setting the mean movement length for riffles at double the value of the base movement length for adults in pools and keeping the juvenile size

class at the base value; and (D) habitat preference for pools in both size classes, increasing the mean movement length for juveniles in riffles to double the base movement length (see Table 2 for values). All other parameters were kept constant at the base conditions.

Table 2. Movement length parameter values for the four scenarios assessing the effect of habitat preferences on model outcome. Values represent the mean in centimeters (± standard deviation) for the Gaussian distribution.

Movement Length Parameter	A	B	C	D
Adult size class in pools	8.6 (± 4.2)	20.9 (± 6.4)	20.9 (± 6.4)	20.9 (± 6.4)
Adult size class in riffles			41.8 (± 6.4)	41.8 (± 6.4)
Juvenile size class in pools		8.6 (± 4.2)	8.6 (± 4.2)	8.6 (± 4.2)
Juvenile size class in riffles				17.2 (± 4.2)

Experiment 3: Assessing the Influence of Escape Behavior

To assess the importance of the length of the escape movements during agonistic interactions on the final distribution of juveniles between pools and riffles, the simulation model was run under four scenarios, each with a different value for the mean escape distance distribution: (A) the mean escape distance at the base value drawn from the literature (Harrison et al. 2006); (B) the mean escape distance at half the base parameter value (2.95 cm ± 2.4); (C) the mean escape distance 50% higher than the base value (8.85 cm ± 2.4); and (D) mean escape distance at double the base value (11.8 cm ± 2.4). All other parameters were kept constant at the base conditions.

Experiment 4: Assessing the Influence of the Crayfish Population Density and Agonistic Interaction Distance

The influence of crayfish population density and the interaction distance on the distribution of juveniles between the two stream habitat types were co-varied. The total density of crayfish was evaluated at densities from 0.5 crayfish/m^2 to 5.0 crayfish/m^2 in increments of 0.5, maintaining equal numbers of adults and juveniles at each density. For each value of density, the interaction distance was varied from 5 to 25 cm in increments of 5. All other parameters were kept constant at the base conditions.

DATA ANALYSIS

For each experiment testing the model outcome, the raw data were expressed as the proportion of the size class occupying either pools or riffles. Analysis of the different occupancy of the two habitat types required only consideration of either the proportion of juveniles in pools or proportion in riffles, not both; since the population size was kept constant and only two habitat types were available, the proportion of individuals in one habitat type was always equivalent to one minus the proportion in the other habitat type. Thus all analyses considered only the number of individuals found in pools during the final time step, as any significant difference will necessarily show the opposite trend in the riffle habitat.

All proportions were arcsine square root transformed to account for the non-normal effects of a data set bounded by zero and one. The data collected for the experiment varying the crayfish density and interaction distance was also expressed as the density of the juvenile size class in pools at the final time step. Preliminary Anderson-Darling and Levene's tests were conducted for all data sets to test for the assumptions of normality and equality of variance respectively. The data sets failed to satisfy one or both of the assumptions required for use of parametric statistical tests (see Appendix B for details). However parametric tests were still used, as these are considered relatively robust to violations and to avoid the difficulties inherent to the use of non-parametric methods. All data analyses employed Minitab (Version 15.1) (State College, Minitab Inc.), and significant differences were evaluated at a confidence level of 95%.

The displacement of juveniles from pools as a result of agonistic adult-juvenile interactions was tested using a one-tailed t-test, evaluating whether or not the mean proportion of juveniles in pools was less than the null condition of 0.5, which corresponds to a uniform distribution of juveniles between the two habitats. A one-way t-test was also used to test whether or not the proportion of adults in pools was significantly greater than 0.5, as habitat preferences introduced through asymmetric movement lengths in pools and riffles was expected to favor pools.

The influence of varying the width of the turn angle distribution was assessed using regressions for both the juvenile and adult proportions. The further variation of both the turn angle parameter and the strength of habitat preference were assessed using a two-way analysis of variance (ANOVA) for the proportion of adults in pools. Post hoc regression analyses were planned, to determine trends for each of the three habitat preference conditions and further describe the findings of a significant ANOVA.

ANOVA tests were also used to investigate the influence of varying the strength of habitat preference for juveniles and adults, and varying the mean length for the escape distance distribution. In each case a one-way ANOVA was used to assess the effects of the varied parameter on the proportion in pools, and post hoc Bonferroni Simultaneous tests were utilized to compare each scenario to a reference condition. For the strength of habitat preference experiment, the reference condition was where all movement length distributions were equal for adults and juveniles. For the escape distance experiment, the reference condition corresponded to the base condition for the escape distance distribution.

The effects of simultaneously varying the crayfish population density and the interaction distance on the proportion of juveniles in pools were tested using a two-way ANOVA. A second two-way ANOVA evaluated the effects of these two factors on the final density of juveniles in pools.

RESULTS

SELECTION OF BASE PARAMETER VALUES

Selecting the Number of Iterations

Changes in the proportions of juveniles and adults in pools as the number of time steps per trial increased revealed that beyond 60 time steps the movements of individuals in both size classes reach an asymptote, and further increases in the number of time steps did not appreciably change the outcome of the simulation model (Figure 3). This equilibrium suggests that at least 60 time steps were required for the initial randomly distributed individuals to reach a distribution based on the model parameters. From these findings, a conservative value of 90 time steps was chosen for all further model runs.
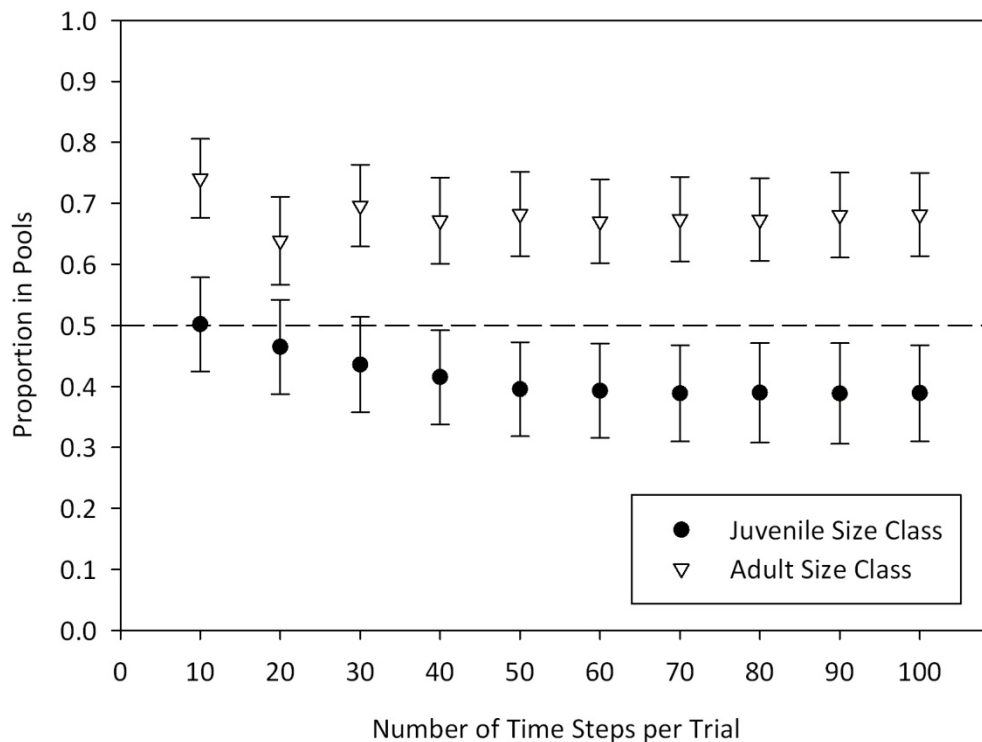
Figure 3. The mean proportions of juveniles and adults in pools (± standard deviation) as a function of the number of time steps per simulation trial. Other model parameters were kept constant at the base parameter conditions and a turn angle distribution centered at 0° (± 15). The dotted line represents the null condition, where individuals have an equal probability of being in either habitat type.

Selecting Values for the Turn Angle Distribution

Increasing the standard deviation used to define the turn angle distribution influenced the model outcome for both the juvenile and adult size classes. As the standard deviation for the turn angle distribution increased, the proportion of juveniles in pools increased asymptotically towards 0.5; the turn angle explained 25.3% of the variability in a significant logarithmic regression for the arcsine square root transformed data ($F_{[1, 9998]} = 3387.92$, $p < 0.001$; Figure 4). The proportion of adults in pools also exhibited an increasing trend, as evidenced by the significant linear regression of the transformed data ($F_{[1, 9998]} = 3678.38$, $p < 0.001$, $R^2 = 27.0\%$; Figure 4). A conservative value for the standard deviation parameter was chosen on the basis of the regression trend for the juvenile size class; in order to avoid choosing either a parameter value likely to produce a highly significant response, or one likely to produce
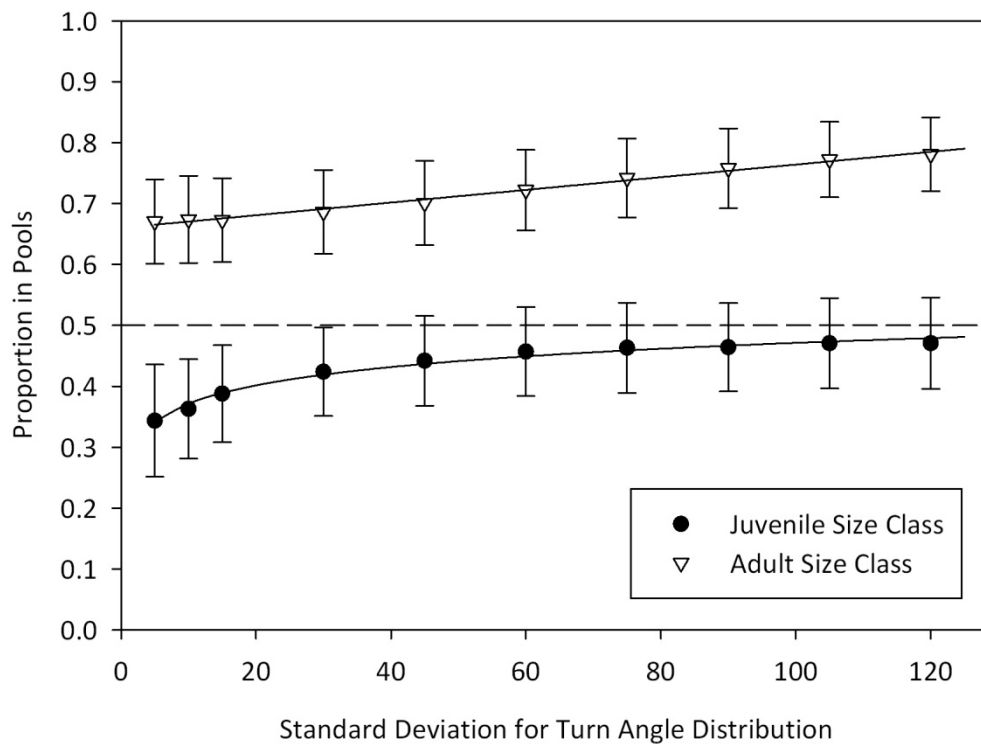
Figure 4. Regression of the mean proportions of juveniles and adults in pools (± standard deviation) as a function of the standard deviation for the turn angle distribution. Other model parameters were kept constant at the base parameter conditions and 90 time steps per trial. The dotted line represents the null condition, where individuals have an equal probability of being in either habitat type.

a value close to the asymptote of 0.5, a standard deviation of 30 was chosen, as this value is approximately half way between the origin and where the regression line begins to level off.

Assessing the Influence of Habitat Preferences on the Relationship Between the Turn Angle and Model Outcome

Further investigation of the influence of habitat preferences on the relationship between the proportion of adults in pools and the standard deviation for the turn angle distribution suggested that the strength of habitat preference for pools modulated the strength of the influence of the turn angle parameter on the model outcome ($F_{[8, 14985]}$ = 108.17, $p < 0.001$; Figure 5), with significant main effects of the habitat preference condition ($F_{[2, 14985]}$ = 9594.74, $p < 0.001$) and the turn angle distribution width ($F_{[4, 14985]}$ = 361.12, $p < 0.001$). Individual linear regression analyses for the change in the proportion of adults in
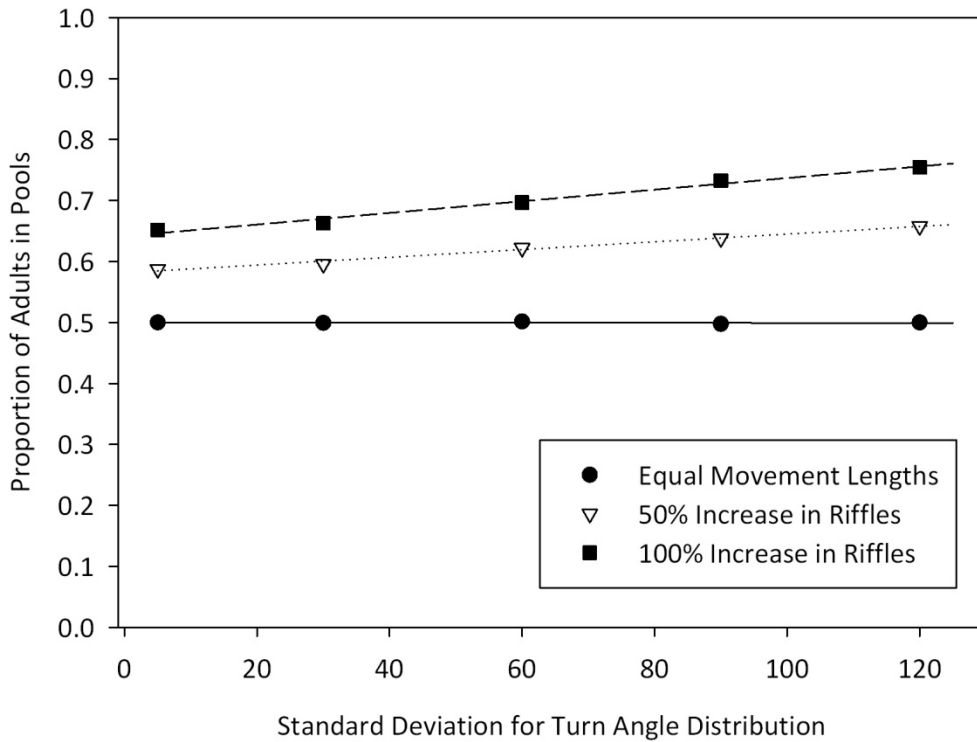
Figure 5. The regression of the mean proportion of adults in pools (± standard deviation) as a function of the standard deviation for the turn angle distribution, under three different conditions for the movement distance distribution: equal mean movement distances ($\bar{x}_{pool} = \bar{x}_{riffle}$ = 20.9 cm ± 6.4), a 50% increase in the mean movement distance in riffles over pools ($\bar{x}_{pool}$ = 20.9 cm ± 6.4, $\bar{x}_{riffle}$ = 31.4 cm ± 6.4), and double the higher mean movement distance in riffles over pools ($\bar{x}_{pool}$ = 20.9 cm ± 6.4, $\bar{x}_{riffle}$ = 41.8 cm ± 6.4). Other model parameters are kept constant at the base parameter conditions and 90 time steps per trial.

pools with increasing standard deviation under each habitat preference scenario can further clarify this influence. When adults had equal mean movements in pools and riffles the linear regression was non-significant and explained none of the variability ($F_{[1, 4998]} = 0.08$, $p = 0.774$). However, as the habitat preference for pools was strengthened the linear relationship explained more of the variability and the regression line became significant; when the average riffle movement was increased by 50% the average pool movement R^2 becomes 11.2% ($F_{[1, 4998]} = 629.56$, $p < 0.001$) and when the average riffle movement was set at double the average pool movement R^2 rose to 24.5% ($F_{[1, 4998]} = 1623.84$, $p < 0.001$).

EXPERIMENT 1: ASSESSING THE MODEL OUTCOME UNDER THE BASE CONDITIONS

The model outcome under the base set of parameters showed that individual movements and size-class interactions result in an uneven distribution of the size-classes
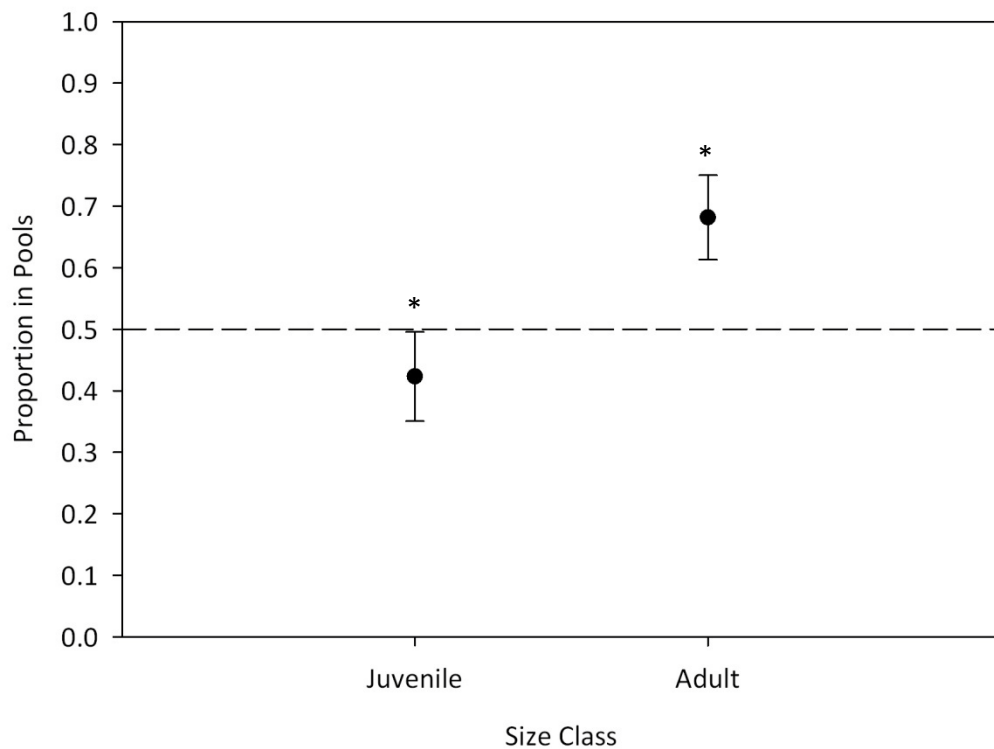
Figure 6. The mean proportions of juveniles and adults in pools (± standard deviation) at the base movement parameter conditions, a turn angle distribution centered at 0° (± 30), and 90 time steps per trial. The dotted line represents the null condition where individuals have where individuals have an equal probability of being in either habitat type. Significant differences from the null condition are denoted by (*).

between habitat types. Significantly fewer juveniles and more adults were found in pools
(t = -33.24, df = 999, p < 0.001; t = 79.40, df = 999, p < 0.001) relative to the null expectation of
an equal probability of being in either habitat type (Figure 6).

EXPERIMENT 2: ASSESSING THE INFLUENCE OF HABITAT PREFERENCES

Varying the habitat preferences by increasing the mean movement distances of adults
and juveniles in riffles over pools showed that adult preference for pools decreased the juvenile
occupancy of pools when juvenile movement lengths are equal, but not when juvenile
movement lengths are similarly increased in riffles. Changing the average values for the
movement length distributions used for juveniles and adults in pools and riffles significantly
altered model outcome for the juvenile size class ($F_{[3, 3996]}$ = 967.83, p < 0.001; Figure 7).
Increasing the mean movement distance for adults over juveniles did not change the juvenile
pool occupancy relative to the reference condition of equal mean movements across size-
classes and habitat types (Bonferroni Simultaneous test, t = -0.64, p = 1.000) while doubling the
mean distance movement for adults in riffles relative to pools significantly decreased the
proportion of juveniles in pools (t = -19.40, p < 0.001). Doubling the mean movement length for
juveniles in riffles significantly increased the proportion of juveniles in pools (t = 33.47,
p < 0.001) relative to the reference condition.

Altering the average values for the movement distance distribution also influenced the
proportion of adults in pools ($F_{[3, 3996]}$ = 1670.59, p < 0.001; Figure 7). Differences in the mean
movement lengths between juveniles and adults without a habitat preference did not change
the outcome relative to the reference condition (Bonferroni Simultaneous test, t = -1.532,
p = 0.377) however the model produced significantly higher proportions of adults in pools after
introducing an adult habitat preference for pools in the final two scenarios (t = 48.140,
p < 0.001; t = 50.372, p < 0.001) relative to the reference condition.

EXPERIMENT 3: ASSESSING THE INFLUENCE OF ESCAPE BEHAVIOR

The model showed that increasing the distances moved by juveniles in the escape
response to agonistic interactions reduced the final occupancy of the pool habitat by juveniles.
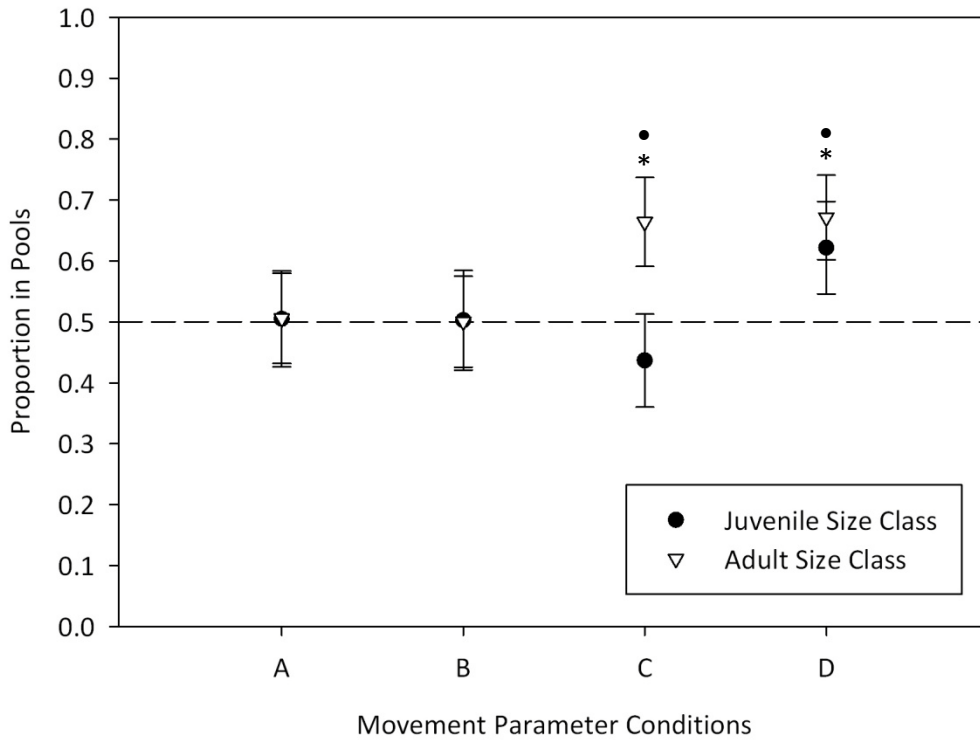
Figure 7. The mean proportion of juveniles and adults in pools (± standard deviation) under four movement parameter conditions: (A) equal mean movement distances for juveniles and adults in riffles and pools ($\bar{x} = 8.6$ cm $\pm$ 4.2); (B) equal mean movement distances in riffles and pools for juveniles ($\bar{x} = 8.6$ cm $\pm$ 4.2) and in riffles and pools for adults ($\bar{x} = 20.9$ cm $\pm$ 6.4); (C) equal mean movement distances in riffles and pools for juveniles ($\bar{x} = 8.6$ cm $\pm$ 4.2) and double the mean movement distance in riffles relative to pools for adults ($\bar{x}_{riffle} = 41.8$ cm $\pm$ 6.4, $\bar{x}_{pool} = 20.9$ cm $\pm$ 6.4); and (D) double the mean movement distance in riffles relative to pools for juveniles ($\bar{x}_{riffle} = 17.2$ cm $\pm$ 4.2, $\bar{x}_{pool} = 8.6$ cm $\pm$ 4.2) and for adults ($\bar{x}_{riffle} = 41.8$ cm $\pm$ 6.4, $\bar{x}_{pool} = 20.9$ cm $\pm$ 6.4). Other model parameters were kept constant at the base conditions, a turn angle distribution centered at $0°$ (± 30), and 90 time steps per trial. The dotted line represents the null condition where individuals have an equal probability of being in either habitat type, and (*) denote significant differences from the reference condition (A) for juveniles and (•) for adults.

Changes in the average value for the escape distance distribution significantly altered model outcome for the juvenile size class ($F_{[3, 3996]}$ = 155.73, p < 0.001), but not adults ($F_{[3, 3996]}$ = 0.22, p = 0.886; Figure 8). Halving the mean escape distance significantly increased the proportion of juveniles in pools (Bonferroni Simultaneous test, t = 6.45, p < 0.001), while increasing the mean escape distance by 50% or 100% significantly decreased the final proportion of juveniles in pools (t = -6.75, p < 0.001; t = -14.07, p < 0.001).

Figure 8. The mean proportion of juveniles and adults in pools (± standard deviation) under four escape distance scenarios: (A) the base condition ($\bar{x} = 5.9$ cm $\pm$ 4.2); (B) half of the base condition ($\bar{x} = 2.95$ cm $\pm$ 2.4); (C) 50% over the base condition ($\bar{x} = 8.85$ cm $\pm$ 4.2); and (D) double the base condition ($\bar{x} = 11.8$ cm $\pm$ 4.2). Other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° ($\pm$ 30), and 90 time steps per trial. The dotted line represents the null condition where individuals have an equal probability of being in either habitat type, and (*) denote significant differences from the reference condition (A) for juveniles.

EXPERIMENT 4: ASSESSING THE INFLUENCE OF THE CRAYFISH POPULATION DENSITY AND AGONISTIC INTERACTION DISTANCE

Varying the total density of crayfish and the threshold distance for agonistic interactions showed that increasing the interactions reduces the final density of juveniles in pools. Increasing the total density of crayfish significantly decreased the proportion of juveniles in pools ($F_{[9, 49950]} = 452.82$, $p < 0.001$), as did increasing the interaction distance ($F_{[4, 49950]} = 1865.82$, $p < 0.001$), and these two factors interacted to alter the final proportion of juveniles in pools ($F_{[36, 49950]} = 21.53$, $p < 0.001$; Figure 9). The final proportion of juveniles in pools (Figure 10). Density of juveniles in pools at the end of the simulation was significantly altered by an interaction of the initial density of the crayfish population and the interaction distance ($F_{[36, 49950]} = 186.50$, $p < 0.001$), with significant decreases in the final density of

juveniles in pools with increases in total density ($F_{[9, 49950]} = 40513.94$, $p < 0.001$) and the interaction distance ($F_{[4, 49950]} = 3819.99$, $p < 0.001$; Figure 10).

Figure 9. The mean proportion of juveniles in pools as a function of the interaction distance (m) and the total density of crayfish in the stream segment (per m^2). While interaction distance and the initial density of the total crayfish population were varied, all other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° (± 30), and 90 time steps per trial. Color bands denote changes in the proportion in pools at an interval of 0.02.

Figure 10.The final density of juveniles in pools (per m^2), as a function of the interaction distance (m) and the initial density of randomly distributed juveniles in pools (per m^2). While interaction distance and the initial density of the total crayfish population were varied, all other model parameters were kept constant at the base conditions, a turn angle distribution centered at 0° (± 30), and 90 time steps per model iteration. Color bands denote changes in the final density in pools at an interval of 0.5.

DISCUSSION

THE POTENTIAL ROLE OF ESCAPE BEHAVIOR IN THE ONTOGENETIC NICHE SHIFTS OF SIGNAL CRAYFISH

The individual-based simulation model of adult-juvenile agonistic interactions in signal crayfish indicates that escape behavior by juveniles during interactions with larger individuals can result in an asymmetric distribution of juveniles between the two habitat types modeled (riffles and pools). Agonistic interactions between adults and juveniles resulted in a decrease in juvenile abundance in pools, the habitat type preferred by adults. Manipulation of the movement length parameters suggested an adult habitat preference for pools over riffles was essential for creating an uneven distribution of juveniles between habitat types. This result is intuitive; a uniform distribution of adults throughout the stream would result in juveniles facing roughly equivalent mortality risks from adults in both habitats. Habitat preferences for pools over riffles in adult crayfish were demonstrated by Guan and Wiles (1996) and (Harrison et al. 2006); the latter study was used to parameterize the model presented here. These findings are further supported by evidence that adult crayfish are more threatened by terrestrial than aquatic predators, as fish are gape-limited predators and are generally unable to consume crayfish above a threshold size (Stein and Magnuson 1976, Englund and Krupa 2000); thus adult crayfish may avoid the greater mortality risk in shallower waters, where predation from terrestrial consumers is more likely to occur, in favor of deeper waters.

The modeled agonistic interactions between adult and juvenile crayfish may explain the ontogenetic niche shifts observed in this species (Guan and Wiles 1996). Aggressive interactions between relatively large adults and smaller juveniles may represent significant mortality risk for juveniles. In signal crayfish, size is an important determinant of interaction success (Edsman and Jonsson 1996, Davis and Huber 2007). Thus, smaller-bodied individuals often avoid the danger of injury or mortality by retreating from aggressive interactions with adults (Edsmann and Jonsson 1996, Pavey and Fielder 1996, Harrison et al. 2006). Ontogenetic niche shifts are generally thought to result when physiological or behavioral changes alter the habitat requirements for optimal individual fitness, leading to a shift in preferred habitat from one life

history stage to another (Werner and Gilliam 1984). The habitat-specific tradeoffs for an individual at a given stage of development are a function of the physical characteristics of the habitat and the competitive and/or predation relationships that exist within that habitat for the individual (Morris 2003). The ability of individuals to detect and respond to changes in resource availability and mortality risk may mediate niche shifts, as individuals adaptively alter habitat use in response to habitat-specific changes in growth potential and predation risk as development continues through time (Lima and Dill 1990, DeRoos et al. 2002). Escape behavior by juvenile crayfish during adult-juvenile interactions may provide a mechanism by which a behavioral response results in an apparent habitat preference, as the increased probability of interaction in pools where adults exist in higher densities results in a net escape of juveniles to riffles.

DENSITY DEPENDENCE OF ONTOGENETIC NICHE SHIFTS MEDIATED BY AGONISTIC INTERACTIONS

The degree to which agonistic intraspecific interactions contribute to ontogenetic niche shifts may be density-dependent. In this model density interacted with interaction distance to alter the distribution of juveniles. Increasing the density and/or interaction distance resulted in a reduction in the proportion of juveniles occupying pools, indicating that the influence of agonistic interactions on the juvenile size-class distribution was a function of interaction frequency. At the lowest densities and interaction distances, the proportion of juveniles in pools approached 0.50, and at the highest densities and interaction distances, the proportion in pools approached 0.36. The asymptote of 0.5 indicated that agonistic interactions are not strongly influencing the distribution of juveniles, as there are approximately equal numbers in pools and riffles. This reflects the low mortality risk for juveniles posed by adult crayfish at low densities, as the probability of encountering an adult remains low even in pools, the preferred adult habitat. The asymptote approaching 0.36 reflected the random nature of the modeled crayfish movements in the model; although the strong rate of interactions with adults at higher densities increased the expulsion of juveniles to riffles, there was always movement of some juveniles into pools in any given time step. Thus, in this model, there can never be a complete removal of juveniles from pools. This is a reasonable result, as signal crayfish are known to be

mobile and capable of moving hundreds of metres over a few weeks (e.g. Light 2003, Bubb et al. 2006) and it is likely that some juvenile crayfish will continue to cross boundaries into pools during daily movements, despite the risk of agonistic interactions.

In this model, increases in the density of crayfish increased the probability of agonistic interaction, which in turn increased the net movement of juveniles into riffles as adults are concentrated in pools. The influence of density on the juvenile distribution is supported by theories of habitat selection. Habitat choice resulting from the drive of an organism to maximize the difference between growth potential and mortality risk (Morris 2003) can further be described as a habitat-dependent trade-off between fitness and density, as density-dependent changes in resource availability, competition, and predation risk varies between habitats (Morris 1988). Variable influences of density between habitats can result in a "switched preference" pattern, where one habitat is preferred at low density and another at higher density (Morris 1988). The increasing proportion of juveniles found in riffles as density increases in our model can be conceptualized as a possible mechanism by which this habitat switch occurs, as the probability of agonistic interactions disproportionately increase in pools as adult densities increase in that habitat.

THE POTENTIAL INFLUENCE OF JUVENILE HABITAT PREFERENCES

While the influences of adult habitat preferences and density on the distribution of juvenile crayfish were expected, when juvenile crayfish were modeled with the same strength of habitat preferences (i.e. higher rates of movement in riffles) the final distribution of juveniles unexpectedly showed a higher proportion of juveniles in pools. This finding suggests that preference for pools in the juveniles may reduce the influence of agonistic interactions on the juvenile distribution. If the rates of movement in riffles are sufficiently greater than in pools, juveniles may exhibit preferences for pools in spite of the higher probability of agonistic interactions with adults. This result is likely a function of changes in the probability of a movement displacing an individual from one habitat to another due to a relative increase in movement rate in that habitat type. Increasing the mean movement lengths in riffles relative to pools increases the probability of individuals leaving riffles and entering pools, leading to a greater pool occupancy. Thus, increasing the difference between movement lengths in riffles

and pools may diminish the influence of escape movements; although juveniles will still tend to escape from adults into riffles, with larger average movements in riffles it will generally take less time for an individual to move from a riffle back into a pool.

The influence of agonistic interactions may only function if juveniles have more niche flexibility than adults. The stage-structured cutthroat trout provides an example of this concept (Rosenfeld and Boss 2001). While both YOY and adult trout have greater growth rates in pools relative to riffles, YOY can maintain positive growth in riffles while adults cannot. The ability of juvenile cutthroat trout to maintain positive growth in both habitat types may play a role in the size-class distribution of this species; although juveniles experience sub-optimal growth in riffles, riffles may be the preferred habitat in the presence of adult trout, as YOY trout may trade-off enhanced growth potential for the decreased mortality risk of competition and/or predation from adults, which are largely confined to pools to by energetic constraints.

A greater flexibility in the juvenile life stage may also be the case for crayfish, as juveniles may be able to persist through time in a wider range of habitats than adults. For example, YOY golden crayfish will distribute themselves evenly between two available substrate types in the absence of adult crayfish, but will shift towards the habitat less-favorable to the adults after introduction of adults (Rabeni 1985). However, it is also possible that juvenile signal crayfish may have preferences for pools that persist in the presence of larger conspecifics not detected by statistical tests in the study on which our simulation model was based (Harrison et al. 2006). Although movement lengths for juveniles in pools and riffles were not significantly different, the observed behaviors of juveniles reported in Harrison et al. 2006 differed between habitat types, with fewer behaviors such as foraging or grooming in riffles. This suggests juvenile crayfish may have little motivation to remain in the riffle habitat, despite similar rates of movement in riffles and pools.

IMPLICATIONS OF AGONISTIC INTERACTION-MEDIATED ONTOGENETIC NICHE SHIFTS

Understanding size-specific signal crayfish dynamics and the role of agonistic interactions involved in the ontogenetic niche shift has important implications for

understanding stream system processes. Consideration of size-class implications can improve the understanding of community dynamics, as the impacts of density dependence on size-structured populations differ as a function of the different physiological and behavioral traits of the size classes, as well as the characteristics of their preferred habitat (e.g. Mittelbach and Osenberg 1993, Murdoch 1994, Rudolf 2006).

Size-structure considerations can further improve our understanding of the interactions of signal crayfish with other members of the stream community. This model of agonistic interactions investigates a potential mechanism by which ontogenetic niche shifts occur, and this may provide insight into the spatial resolution of these relationships within the stream community. For example, it is conventionally believed that predacious fish negatively affect crayfish through predation and behavioral changes associated with predator avoidance in small-bodied individuals (Englund and Krupa 2000, Stein and Magnuson 1976). However, studying the interactions between the size classes of each species reveal a more profound impact of signal crayfish on cutthroat trout, with negative consequences to YOY trout in the presence of both adult and YOY signal crayfish (Bondar and Richardson 2009b). The size-specific habitat choices of signal crayfish may have further implications for this relationship, as YOY trout and crayfish may be prone to high levels of interaction relative to across-size-class interactions, as both are likely to congregate in pools in the presence of adult conspecifics.

Behaviorally mediated ontogenetic niche shifts, when coupled with spatial variation in feeding ecology, may have habitat-specific influences on resource dynamics in streams. Preliminary studies suggest that signal crayfish, in their native range, have similar roles at the juvenile and adult stage with respect to their impacts on leaf detritus availability and the invertebrate community (Bondar and Richardson 2009a). This is supported by findings of similar diet compositions for adult and juvenile signal crayfish (Guan and Wiles 1998, Bondar et al. 2005). However, an ontogenetic niche shift in signal crayfish may lead to habitat-specific community effects, particularly in the context of density-dependence, as increases in crayfish density in the model stream lead to a disproportionate increase in the density of juveniles in riffles. Disproportionate increases in the density of juveniles in riffles may influence the riffle community, indirectly altering the invertebrate community composition through a functional

response to the reduced availability of leaf detritus, reducing the abundance of the shredding invertebrate guild (Bondar and Richardson 2009a). Thus understanding the dynamics of size-specific habitat preferences for juveniles may provide important insights into the role of crayfish in the stream community, as crayfish may have size-specific impacts on the stream community that function in a density-dependent fashion.

FUTURE RESEARCH DIRECTIONS

There are several key studies that, if conducted, would improve model parameterization and increase our understanding of the role of agonistic interactions in structuring the population distribution. One important element is to quantify the turning behavior of signal crayfish. Turning angle data was unavailable in the published literature, necessitating a largely arbitrary choice of turning angle for the current study. Turn angle was shown to have significant influence over the model outcome for both adults and juveniles; as the standard deviation was increased the proportion of adults in pools increased linearly, while the proportion of juveniles approached 0.5.

The influence of habitat preferences on the relationship between turn angle and the distribution of crayfish was further investigated for the adult size class, which was free of the potentially confounding influence of agonistic interaction. When movement lengths were equal for the two habitat types there was no significant change in the proportion of adults in pools with increasing standard deviation. However, increasing the difference between movements in pools and riffles was associated with greater rates of change for the relationship between pool occupancy and turn angle. The most likely explanation for this observed trend is that this increases the probability of movement from riffles to pools over the probability of moving from pools to riffles; as the turn angle distribution widens there is a greater chance that an adult who has stepped into the riffle will "turn around" and make a large movement into a pool, where the shorter movement lengths make it less probable that a given step will move the individual back into a riffle. The influence of the turn angle value on juveniles likely functions similarly, diminishing the influence of escape movements by increasing the chance that the next movement will return them to the habitat from which they just escaped. Selection of a turn

angle based on field observation can improve the model, producing a more realistic approximation of the signal crayfish movement paths.

In addition to determining appropriate values for missing parameters, applicability of this model to natural stream systems may require reassessment of the movement and escape behavior of signal crayfish in situ, as Harrison et al. (2006) conducted their assessments in artificial stream segments. Crayfish have been shown to exhibit a "fright response" to being captured and handled, leading to abnormal patterns of movement (Robinson et al. 2000). Crayfish also react to novel habitats presented in the experimental situation, resulting in initial increases in locomotion as the individual explores its surroundings (Shuranova et al. 2005). A fright response to handling and/or the influence of a novel habitat may have lead to an overestimation of movement lengths used in this simulation experiment. Additional study is required to determine whether or not this phenomenon is independent of habitat or habitat-specific (i.e. producing asymmetric increases in movements in one habitat type over the other). Experiment 2 highlighted the importance of unequal movement lengths between pools and riffles.

The length of the escape movement for juveniles during an agonistic interaction also had a significant impact on the distribution of juveniles. Decreasing the mean escape length resulted in a more uniform distribution of juveniles throughout the stream segment, while increasing the mean escape length enhanced the preference for riffles in the juvenile size-class.

A further study direction is to address how crayfish assess and respond to the riffle-pool interface during movements. Although a review of the current literature revealed no evidence thus far of boundary avoidance in crayfish, it has been documented for many other species including terrestrial invertebrates (e.g. Peltonen and Heliövaara 1998, Ross et al. 2005). In the stream system, where there is generally a gradation between habitat types, this avoidance response may be a function of depth, where decreases in depth are associated with increasing risk and/or decreasing growth potential. Avoidance behavior may limit the applicability of the current model, which allows free movement between the habitat types. Boundary responses could be modeled by altering the movement behaviors of individuals as they approach the boundaries of pools, where depth decreases and the pool grades into a riffle.

In addition to providing a means to investigate the mechanisms by which agonistic interactions create habitat-associated, size-structured population distributions in streams, changing the definition of the classes and other model parameters would allow this model to be used to understand how agonistic interactions can spatially structure the distribution of other species, through intraspecific or interspecific agonistic interactions. Evidence of adaptive responses to mortality risk has been observed in a range of taxa (see review in Lima and Dill 1990). Escape behavior during interactions where one individual is at significant risk of injury or mortality does not have to be limited to crayfish, nor to intraspecific interactions. Agonistic interactions may occur between species in competition or in predator-prey relationships. Avoidance of injury or mortality in the smaller-bodied class or species via escape behavior may be a mechanism by which uneven distributions occur in a variety of ecological scenarios, including size- or stage- structured populations and in the spatial distributions of communities in a heterogeneous landscape.

One potential application is to the study of how larger and/or more aggressive invasive species can negatively impact and outcompete a native species with similar habitat requirements. Signal crayfish are an invasive species in streams in Europe, Asia, Japan, and some areas of the United States (Hill and Lodge 1994; Svardson 1995; Usio et al. 2001; Light 2003). Agonistic interactions may play a key role in the replacement of native species by signal crayfish, as size asymmetries between invasive and native crayfish have been shown to contribute to the replacement of native species. For example, introduction of invasive rusty crayfish displaced smaller-bodied native clearwater crayfish and northern crayfish from refugia during the daytime, exposing these species to increased risk of predation (Hill and Lodge 1994). Signal crayfish are a relatively large-bodied species, known to be highly aggressive and to dominate in interactions with many of the species they are replacing, including *Orconectes* species (Tierney et al. 2000), the noble crayfish (Söderbäck 1995), and the Japanese crayfish (*Cambaroides japonicas*; Usio et al. 2001). Thus far, studies of the movements of invasive crayfish have largely focused on dispersal, tracking movements of signal crayfish on the scale of days (e.g.Bubb et al. 2004, Bubb et al. 2006) to weeks (e.g. Light 2003). Alteration of the current model, replacing the adult size class with the invasive signal crayfish and juveniles with the

native species may be useful in linking studies of specific interactions to the larger pattern of invasion and displacement of native crayfish.

CONCLUSIONS

This model provides evidence that agonistic interactions between different sizes of signal crayfish may contribute to the ontogenetic niche shifts, mediated by an escape reaction of juveniles to avoid injury or mortality from adults. Further field studies of the agonistic interactions within size-structured signal crayfish populations will improve the model parameterization, and will help define the potential role of agonistic interactions in relation to other factors that may influence habitat choice for juvenile crayfish. In addition to providing evidence that size-dependent agonistic interactions can contribute to asymmetric distribution of juvenile signal crayfish between riffles and pools, the escape behavior utilized in this simulation model may have implications for understanding how agonistic interactions can spatially structure the distribution of other species through similar escape responses to intraspecific or interspecific agonistic interactions.

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APPENDIX A

Selected literature review of studies investigating the directionality of crayfish movements in streams.

Species	Study Location	Tracking Method	Measurement Interval	Movement Behavior	Source
Austropotamobius pallipes	•Tuscany, Italy	•Mark-recapture •All sizes	•Every 3 hours for a period of 24 hours, for one day per season •Alternate weeks for one year	•No upstream-downstream bias for frequency of movements	Gherardi et al. 1998
Austropotamobius pallipes	•North Yorkshire, U.K.	•Mark-recapture •All sizes	•7+ days between sampling sessions, over 22 days	•No upstream-downstream bias for frequency of movements and mean distance travelled per day	Robinson et al. 2000
		•Radio-telemetry •Crayfish > 35 mm carapace length	•At least every other day until tag failure (mean day to failure was 34 days)		
Orconectes nais	•Oklahoma, U.S.	•Mark-recapture •All sizes	•Weekly, over a period of 7 weeks	•Bias towards upstream for frequency of movements	Momot 1966
Pacifastacus leniusculus	•California, U.S.	•Mark-recapture •Crayfish > 18 mm carapace length	•Weekly, over a period of 7 weeks	•No overall upstream-downstream bias for frequency of movements •Size-related bias for direction of movements; smaller tended to stay in the origin pool, mid-sized to move upstream, and the largest to move downstream	Light 2003

Pacifastacus leniusculus	• Northern England	• Radio-tracking • Crayfish between 31.9 – 63.8 mm carapace length	• 1-2 times per week, winter 2000/01 • Alternate days, summer and autumn 2001, summer 2002	• No upstream-downstream bias for frequency of movements • Bias in the length of movements; longer movements made downstream relative to upstream	Bubb et al. 2004
Pacifastacus leniusculus	• Northern England	• PIT-tagging • Crayfish between 21.0 – 67.3 mm carapace length	• Daily over 25 days	• Bias in frequency of movements towards upsteam direction • Bias in length of movements; longer movements made downstream relative to upstream	Bubb et al. 2006

APPENDIX B

Results of the preliminary assessment of data for the assumptions of parametric statistical tests, using the Anderson-Darling test for normality and Levene's test for homogeneity of variance.

Data Set		Anderson-Darling test for Normality	Levene's test for Homogeneous Variances	Outcome
Selection of the standard deviation for the turn angle distribution	Transformed proportion of juveniles in pools	$AD = 38.734$, $N = 10\,000$, $p < 0.005$	$W = 18.76$, $N = 10\,000$, $p < 0.005$	Violates assumptions of normality and homogeneity of variances
	Transformed proportion of adults in pools	$AD = 33.701$, $N = 10\,000$, $p < 0.005$	$W = 0.76$, $N = 10\,000$, $p = 0.666$	Violates assumption of normality
Assessing the influence of habitat preferences on the relationship between turn angle and model outcome	Transformed proportion of adults in pools	$AD = 33.030$, $N = 15\,000$	$W = 0.76$, $N = 15\,000$, $p = 0.715$	Violates assumption of normality
Assessing the model outcome under the base conditions	Transformed proportion of juveniles in pools	$AD = 3.924$, $N = 1000$, $p < 0.005$		Violates assumption of normality
	Transformed proportion of adults in pools	$AD = 5.176$, $N = 1000$, $p < 0.005$		Violates assumption of normality
Assessing influence of habitat preferences	Transformed proportion of juveniles in pools	$AD = 9.516$, $N = 4000$, $p < 0.005$	$W = 1.08$, $N = 4000$, $p = 0.355$	Violates assumption of normality
	Transformed proportion of adults in pools	$AD = 13.504$, $N = 4000$, $p < 0.005$	$W = 0.56$, $N = 4000$, $p = 644$	Violates assumption of normality
Assessing the influence of mean escape distance	Transformed proportion of juveniles in pools	$AD = 12.686$, $N = 4000$, $p < 0.005$	$W = 0.77$, $N = 4000$, $p = 0.513$	Violates assumption of normality
	Transformed proportion of adults in pools	$AD = 17.249$, $N = 4000$, $p < 0.005$	$W = 0.58$, $N = 4000$, $p = 0.613$	Violates assumption of normality
Assessing the influence of density and interaction distance	Transformed proportion of juveniles in pools	$AD = 186.977$, $N = 50\,000$, $p < 0.005$	$W = 203.56$, $N = 50\,000$, $p < 0.005$	Violates assumptions of normality and homogeneity of variances
	Final density of juveniles in pools	$AD = 254.889$, $N = 50\,000$, $p < 0.005$	$W = 175.49$, $N = 50\,000$, $p < 0.005$	Violates assumptions of normality and homogeneity of variances