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4 **Movement rule selection through eco-genetic modeling: Application to diurnal vertical**  
5 **movement**  
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43

## Abstract

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46 Agent-based, spatially-explicit models that incorporate movement rules are used across  
47 ecological disciplines for a variety of applications. However, appropriate movement rules may be  
48 difficult to implement due to the complexity of an individual's response to both proximate and  
49 ultimate cues, as well as the difficulty in directly assessing how organisms choose to move  
50 across their environment. Environmental cues may be complex and dynamic, and therefore,  
51 movement responses may require tradeoffs between preferred levels of different environmental  
52 variables (e.g, temperature, light level, and prey availability). Here, we present an approach to  
53 determine appropriate movement rules by setting them as heritable traits in an eco-genetic  
54 modeling framework and allowing movement rules to evolve during the model rather than  
55 setting them *a priori*. We modeled yellow perch, *Perca flavescens*, movement in a simulated  
56 environment and allowed perch to move in response to high-resolution vertical gradients in  
57 temperature, dissolved oxygen, light, predators, and prey. Evolving movement rules ultimately  
58 increased fish growth and survival over generations in our model, indicating that evolving  
59 movement rules led to improved individual performance. We found that emergent movement  
60 rules were consistent across trials, with evolved movement rules incorporating different weights  
61 of these environmental factors and the most rapid selection on temperature preference. This case  
62 study presents a flexible method using eco-genetic modeling to determine appropriate movement  
63 rules that can be applied to diverse scenarios in spatially-explicit ecological modeling.

64

## Introduction

65

66

67 Defining appropriate movement rules is a central challenge for spatially-explicit  
68 ecological modeling that includes individual movement (Bélisle and Desrochers, 2002; Tang and  
69 Bennett, 2010). However, accurate implementation of movement rules has significant  
70 consequences for modeling and interpreting animal movement (Humston et al., 2004;  
71 Kristiansen et al., 2009; McLane et al., 2011). Accurately modeling how an animal moves not  
72 only provides insight into its ecology. Accurate modeling also facilitates prediction of how  
73 species distributions may change with perturbations in habitat, such as anthropogenic  
74 disturbances, that cause habitats to diverge from preferred physiological conditions of local  
75 species. Movement rules are an integral component of a diversity of ecological models  
76 considering processes such as short, sub-daily migrations (Rinke and Petzoldt, 2008; Tarling et  
77 al., 2000) to broad-scale dispersal (North et al., 2008; Revilla et al., 2004). A more complete  
78 understanding of appropriate movement rules has the potential to improve accuracy of a number  
79 of ecological modeling frameworks and to increase the utility and predictive power of models in  
80 a dynamic environment.

81 Sub-daily migrations such as diel vertical migration (DVM) are particularly difficult to  
82 understand and model. Many fish and other aquatic organisms display this daily movement  
83 pattern, but the driving forces behind DVM are difficult to disentangle (Mehner, 2012). Drivers  
84 of DVM in freshwater fish may include proximate cues such as light and water temperature in  
85 addition to ultimate causes including bioenergetic efficiency, increased feeding rates, and  
86 predator avoidance (Mehner, 2012). Yellow perch and related Eurasian perch have been

87 observed to perform DVM, potentially as responses to light and temperature (Imbrock et al.,  
88 1996; Nakayama et al., 2018; Rudstam and Magnuson, 1985).

89         Most models assume that animals move in response to either ultimate cues that increase  
90 overall evolutionary fitness or proximate cues that are immediately sensed by the organism.  
91 Many models that incorporate ultimate cues program animal movement by considering fitness,  
92 e.g., by minimizing the ratio of mortality to growth (Brönmark et al., 2008; Gilliam and Fraser,  
93 1987) or density-dependent factors including prey availability (DeAngelis et al., 2010; Fretwell  
94 and Lucas, 1969). Some models utilize a game theory approach to simulate predator-prey  
95 interactions to integrate tradeoffs between risks and benefits (Hugie and Dill, 1994; Sainmont et  
96 al., 2013). Although ultimate cues are useful in determining habitat choice over the lifespan of an  
97 organism, they pose a problem for fine-scale, process-based models, as animals are likely not  
98 capable of sensing long-term effects of fitness given their surrounding environment. Instead,  
99 animals react to environmental variables that they can sense in their immediate vicinity. Fish, for  
100 example, respond rapidly to predator presence (Eklöv and Persson, 1996), ambient temperature  
101 (Reynolds, 1977), oxygen concentration (Johansen et al., 2006), or vertical orientation  
102 determined by ambient pressure (Holbrook and Burt de Perera, 2009). Response to proximate  
103 cues has likely evolved over time to increase fitness, thus, an approach to modeling movement  
104 rules that integrates both proximate and ultimate cues may greatly increase the flexibility and  
105 accuracy of movement rules in ecological models.

106         Both proximate and ultimate cues can be used to program rules that match movement  
107 patterns in a natural environment, but it remains challenging to set movement rules *a priori*  
108 without knowledge of complex animal behavior. Animals are capable of processing a great deal  
109 of complex information to inform decisions about orientation and movement (Braithwaite & Burt

110 De Perera 2006), therefore, animals likely incorporate many different factors that are not easily  
111 captured in simple movement rules. In addition, animals are simultaneously subjected to  
112 selection based on long-term fitness that they cannot sense or predict. Movement rule robustness  
113 can be tested using pattern-matching approaches that compare similarity between model output  
114 and field data (Grimm and Railsback, 2012). However, pattern-matching does not guarantee that  
115 movement rules specific to one system at one time are consistent across applications or that they  
116 reflect actual responses to proximate cues in the environment (i.e., pattern matching is not  
117 equivalent to process accuracy).

118         One way to account for difficulty in choosing *a priori* movement rules is to allow  
119 movement behaviors to emerge from the model itself. Genetic algorithms, for instance, are  
120 analytical approaches that mimic natural selection to expedite model convergence (Holland,  
121 1989). In a behavioral ecology context, they can allow complex behaviors to be selected and  
122 passed down to offspring, and allow new behaviors to arise through random changes (mutations)  
123 (Forrest, 1993; Goldberg, 1989; Holland, 1992). A related approach is eco-genetic modeling.  
124 Eco-genetic models are a subset of genetic algorithms that allow genetic traits to evolve while  
125 taking ecological factors into account that may influence phenotypic responses, effectively  
126 incorporating elements of both genetic evolution by natural selection and response to dynamic  
127 environmental variables (Dunlop et al., 2009, 2007). Eco-genetic modeling has been used for a  
128 variety of applications in aquatic systems, including fisheries-induced evolution (Dunlop et al.,  
129 2009, 2007; Thériault et al., 2008; Wang and Höök, 2009), energy allocation (Ivan and Höök,  
130 2015), and habitat selection (Middaugh, 2011). Similar individual-based movement models that  
131 incorporate genetic algorithms have also been applied to larval fish dispersal (Fiksen et al., 2007;  
132 Huse and Giske, 1998).

133           We developed an individual-based eco-genetic model to allow movement rules based on  
134 five proximate cues (temperature, dissolved oxygen, light, predators, and prey) to evolve over  
135 generations. We used species-specific physiological parameters paired with high-frequency  
136 environmental conditions simulated with a limnological model. Our five proximate cues  
137 represent an array of environmental constraints that influence fish physiology and behavior,  
138 therefore affecting vertical distribution of fish. Temperature influences the rate of many  
139 physiological processes, including metabolism, gastric evacuation rate, consumption, growth,  
140 and swimming speed (Brett, 1971; Claireaux et al., 2006; Fonds et al., 1992; Persson, 1981).  
141 Limited dissolved oxygen (DO) may impact fish through direct mortality (Townsend &  
142 Edwards, 2003), decreased growth (Wang et al., 2009), or decreased consumption (Pichavant et  
143 al., 2000, 2001; Zhou, Wu, Randall, & Lam, 2001). Light levels primarily affect foraging  
144 behaviors through altered reactive distance to prey (Rickel and Genin, 2005). Fish may actively  
145 avoid areas with high predation risk or choose areas with high prey availability (Brown and  
146 Kotler, 2004; Sims et al., 2006). Several of these environmental variables interact with one  
147 another and there are often tradeoffs between environmental cues. For example, temperature and  
148 dissolved oxygen are closely related in ecosystems with chronic hypoxia that develops with  
149 thermal stratification such as in Lake Erie's Central Basin (LECB) (Diaz, 2001; Edwards et al.,  
150 2005). Furthermore, low DO and high temperature may limit access to the hypolimnion during  
151 low DO periods while also limiting access to near-surface water when temperatures are elevated  
152 beyond the thermal preference of the fish (Arend et al., 2011). Additionally, environmental  
153 influences on movement behavior often act on predator and prey species concurrently,  
154 reinforcing the need for a novel modeling approach to test movement rule combinations that  
155 incorporate interactive effects and tradeoffs between environmental cues.

156 We allowed movement rules to emerge using an eco-genetic modeling approach (Dunlop  
157 et al., 2007) of yellow perch, *Perca flavescens*, in LECB. The model is structured in a one-  
158 dimensional, individual-based bioenergetic modeling framework where fish can move vertically  
159 through a stratified water column that includes dynamic gradients of temperature, light, DO, prey  
160 resources, and predation risk on a high-frequency (ten minute) time step. This framework  
161 integrates both proximate cues that the fish can respond to on a short time scale, and ultimate  
162 determinants of its overall fitness, including survival, growth, and fecundity. This model is not  
163 meant to simulate actual development of fish cognitive processes, but rather is a programming  
164 method that applies principles from evolutionary biology to improve aspects of individual-based  
165 models involving animal movement. We tested the development of movement rules when (1)  
166 fish were exposed to realistic environmental conditions from LECB based on historical data and  
167 reactions to all five environmental variables evolving simultaneously, (2) movement preference  
168 based on one environmental variable was allowed to evolve at a time while other movement  
169 preferences were fixed, and (3) one environmental variable at a time was held constant and  
170 movement preference rules based on all five environmental variables were allowed to adapt. The  
171 first set of simulations were meant to allow movement rules to evolve, whereas the second and  
172 third sets of simulations were designed to test model robustness.

173

174

## Methods

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### Model Description

177

178 The following outline describes a one-dimensional, individual-based eco-genetic  
bioenergetics model to simulate vertical movement of yellow perch (*Perca flavescens*) in LECB.

179 We follow the “Overview, Design concepts, and Details” (ODD) protocol to describe individual-  
180 based models (Grimm et al., 2010, 2006).

181

## 182 **Overview**

183

### 184 *Purpose*

185

186 The purpose of this model was to explore movement rules that increase fitness for yellow  
187 perch in LECB during late summer and early fall. Movement rule combinations were tested by  
188 structuring movement preferences in an eco-genetic framework (Dunlop et al., 2007) and  
189 allowing fish to reproduce based upon their growth and survival, therefore selecting movement  
190 rules that allow for enhanced survival and growth in a vertically-structured, dynamic  
191 environment. This framework allowed appropriate movement rules to emerge from the model  
192 rather than setting them *a priori*.

193

### 194 *State Variables and Scales*

195

196 The model LECB environment represented a 24 m column of water divided into 48, 0.5  
197 m vertical sections. It included vertical gradients of predation pressure (proportional volume  
198 searched by a predator species), prey density ( $\text{g}\cdot\text{m}^{-3}$  for zooplankton and  $\text{g}\cdot\text{m}^{-2}$  for chironomids),  
199 light (Langley), temperature ( $^{\circ}\text{C}$ ), and dissolved oxygen ( $\text{mg}\cdot\text{L}^{-1}$ ). Zooplankton prey  
200 encompassed three size classes: microzooplankton represented rotifers and copepod nauplii,  
201 mesozooplankton represented adult copepods, and macrozooplankton represented large



202 cladocerans. High-frequency environmental conditions were extracted from a published  
203 limnological model based on historical Lake Erie data (Rucinski et al., 2014).

204 We modeled yellow perch as super-individuals (SIs) to decrease computation time by  
205 representing many individuals with a single entity (Scheffer et al., 1995). SIs were initialized to  
206 represent a specified number of individuals and included a parameter to define the number of  
207 individuals represented by a SI that could change with mortality (each individual represented by  
208 a single SI was identical). Therefore, a successful SI would represent a greater proportion of the  
209 total population than an SI with less successful movement rules. SIs were described by the  
210 number of actual fish they represented (declined with mortality), sex, age (years), total length  
211 (mm), total mass (g, indicates both storage and structural mass), current location (which cell they  
212 occupy), and genetic parameters which defined movement preferences. Movement preferences  
213 were weighted for preferred light, temperature, dissolved oxygen, prey density, and predator  
214 avoidance.

215

### 216 *Process Overview and Scheduling*

217

218 This model updated in ten minute, daily, and annual increments. Every 10 minutes, the  
219 fish moved according to their specified habitat preference, foraged, grew according to  
220 bioenergetics equations, and their survival was evaluated. In addition, at each 10-minute time  
221 step, light transmission and zooplankton depth and distribution were updated. Temperature, DO,  
222 and total prey biomass (zooplankton and chironomids) in each 0.5 m cell were updated on a daily  
223 increment. Each year, reproductive capacity was evaluated and individuals mated with an  
224 individual of the opposite sex. While reproduction included a stochastic element, larger SIs

225 (higher mass) and SIs that represented more actual individuals were likely to produce the most  
226 offspring. Simulations progressed from August 1 to October 31 and the entire population was  
227 replaced with new offspring each year to increase speed of selection. This limited timeframe  
228 allowed us to examine movement rules for specific seasonal conditions when the lake was  
229 stratified and hypoxic, and allowed enough growth to differentiate fitness measures between  
230 individuals. While this annual population replacement does not mimic natural yellow perch  
231 generation time, it allowed our modeled population to evolve more rapidly to determine  
232 appropriate movement rules for adult yellow perch in the modeled environment. Offspring were  
233 introduced into the population at age two. This abbreviated lifespan further accelerated selection  
234 because only the most successful individuals would reach reproductive size and therefore pass  
235 down movement preferences to subsequent generations. We randomly chose environmental  
236 conditions for each simulation year from one of 18 different years (1987-2005, excluding 1998  
237 due to highly anomalous input data) simulated in a previous study (Rucinski et al., 2014).

238

### 239 **Design concepts**

240

241 See Appendix 1 for Basic principles, Emergence, Adaptation, Objectives, Sensing, Interaction,  
242 and Stochasticity portions of the ODD description.

243

### 244 **Details and sub-models**

245

246 See supplementary material for full details on initialization, model structure, and sub-  
 247 models as well as specific parameter values (Appendix 1). An abbreviated description is  
 248 presented below.

249

250 *Initialization*

251

252 All yellow perch were initialized at age two and were randomly designated as males or  
 253 females. Initial size was determined as a distribution around average size for male and female  
 254 LECB yellow perch (Appendix 1).

255

256 *Movement*

257

258 Fish had perfect knowledge of their current cell, plus three cells above and three cells  
 259 below their location. This distance was constricted in our model to limit fish from sampling the  
 260 entire water column each time step even though adult yellow perch in a natural environment  
 261 could move vertically more than 3.5 m within ten minutes. We modeled movement preference in  
 262 each cell as an additive equation, where fish weighted environmental parameters by five separate  
 263 heritable traits:

264

$$265 \quad Q_{cell} = \beta_{DO} * Pref_{DO} + \beta_{pred} * Pref_{pred} +$$

$$\beta_{temp} * Pref_{temp} + \beta_{light} * Pref_{light} + \beta_{prey} * Pref_{prey}$$

266

Eq. 1

267 where  $Q_{cell}$ =overall cell quality, while  $\beta_{DO}$ ,  $\beta_{pred}$ ,  $\beta_{temp}$ ,  $\beta_{light}$ , and  $\beta_{prey}$  ranged from zero to one  
 268 and represented heritable weights given to movement cues that accounted for dissolved oxygen,  
 269 predators, temperature, light, and prey.  $\beta$  values were re-weighted for each super-individual to  
 270 sum to 1.0 and their proportions in the population changed over time as better movement rule  
 271 combinations developed.  $Pref_{DO}$ ,  $Pref_{pred}$ ,  $Pref_{temp}$ ,  $Pref_{light}$ , and  $Pref_{prey}$  represented habitat  
 272 quality based on yellow perch preferred levels of each environmental variable according to the  
 273 literature and each scaled from zero to one. Movement rules were inherited at the end of the  
 274 simulation year through the partially-stochastic reproduction process described above. Incoming  
 275 individuals in the new simulation year entered the population at age two.

276  $Pref_{DO}$  was a function of the critical minimum dissolved oxygen level,  $DO_{critmin}$ , and the  
 277 minimum dissolved oxygen level required for growth,  $DO_{crit}$  and calculated as

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285

$$0, \begin{cases} \text{when } DO_{amb} < DO_{critmin} \\ DO_{Fi} = \frac{DO_{amb} - DO_{critmin}}{DO_{crit} - DO_{critmin}}, \text{ when } DO_{critmin} \leq DO_{amb} \leq DO_{crit} \\ 1, \end{cases} \begin{cases} \text{when } DO_{amb} > DO_{crit} \end{cases}$$

286

Eq. 2

287  $DO_{amb}$  was the ambient DO (in  $\text{mg}\cdot\text{L}^{-1}$ ),  $DO_{critmin}$  was set at 1.5-2.5  $\text{mg}\cdot\text{L}^{-1}$ , and  $DO_{crit}$  was set at  
 288 3.5-5.5 depending on acclimation (Arend et al., 2011).

289  $Pref_{pred}$  was calculated as  $1 - VS_{walleye}$ , where  $VS_{walleye}$  was the relative volume searched by  
 290 a predator and is described in the mortality sub-model (Appendix 1). Although perch greater than  
 291 200 mm were not susceptible to predation in this model, large yellow perch in the model  
 292 continued to move to avoid perceived predators.

293  $Pref_{temp}$  was calculated as the temperature with the highest scope for growth for yellow  
 294 perch. Maximum scope for growth was defined as the cell with the highest growth potential  
 295 calculated as maximum respiration subtracted from maximum consumption at a given  
 296 temperature using a bioenergetics model (Hanson et al., 1997) parameterized with values from a  
 297 previous study (Kitchell et al., 1977).

298  $Pref_{light}$  was determined by scaling a walleye-specific light preference curve (Lester et al.,  
 299 2004) to match yellow perch distributions (Almeida, 2016). This scaling factor,  $LF_{perch}$ , was  
 300 given by

$$301 \quad LF_{perch} = 0.0561 * \sqrt{light * 0.4^{1.2}} * e^{-0.0434 * \sqrt{light * 0.4}} * 0.67 + 0.3$$

302 Eq. 3

303

304 where  $light$  was light level in a given cell (lux).

305  $Pref_{prey}$  was calculated as the attack probability from the foraging sub-model (Appendix  
 306 1) weighted by prey numerical density and energy density.

307 Cell quality,  $Q_{cell}$ , was then assigned to each of the seven cells that the fish can sense.  
 308 Fish then oriented themselves toward the highest quality cell. Their swimming speed,  $SS$  was  
 309 calculated as

$$310 \quad SS = \frac{\alpha_S T_{accl} + \beta_S}{\gamma_S L_{fish}} \quad \text{Eq. 4}$$

311 (Breck, 1993; Hergenrader and Hasler, 1967) where  $T_{accl}$  was acclimation temperature for yellow  
 312 perch,  $L_{fish}$  was the total length of the individual (mm), and  $\alpha_S$ ,  $\beta_S$ , and  $\gamma_S$  were constants (Table  
 313 A1). This equation calculated swimming speed in body lengths  $\cdot s^{-1}$ , so it was converted to  $mm \cdot s^{-1}$   
 314 using fish length. After orientation was determined based on habitat quality, super-individuals

315 were assigned a random number weighted by their swimming speed that determined how many  
316 cells they moved up or down.

317

### 318 *Growth and Survival*

319

320 Fish grew according to prey consumed and bioenergetic processes, corrected for hypoxic  
321 stress that impacted respiration rates. Mortality could occur from predation, starvation, or  
322 suffocation (prolonged exposure to hypoxia). An individual was subtracted from the number of  
323 individuals that an SI represented when mortality occurred.

324

### 325 *Reproduction*

326

327 The probability that a super-individual reproduced was proportional to the product of  
328 fecundity (a function of size) and the number of individuals represented by the SI (Appendix 1).  
329 Super-individuals were sampled with replacement. After one male and one female was chosen to  
330 mate, they produced offspring that express a value for each movement preference as a function  
331 of their parents' traits. Their phenotype ( $\beta_{DO}$ ,  $\beta_{pred}$ ,  $\beta_{temp}$ ,  $\beta_{light}$ , and  $\beta_{prey}$  in Eq. 1) was chosen  
332 randomly from a normal distribution around the parental mean with a variance of 0.1. However,  
333 parental genotypes (original, unweighted  $\beta$  values) were conserved and one of two inheritance  
334 models took effect. For independent inheritance, each of the five genes was evaluated  
335 independently, and either the mother's or father's gene for each trait was carried by the offspring  
336 to be passed down the next year. In the linked inheritance model, it was randomly determined  
337 whether all of the mother's genes or all of the father's genes were carried down to the next

338 generation. This process repeated until the entire initial population of perch was replaced for the  
339 following year of simulations. Once reproduction occurred, adults were removed from the  
340 simulations and replaced by two-year-old offspring for the next growing season. This pattern of  
341 complete population replacement each year resulted in more rapid selection and simplification.

342

343

### 344 **Simulations**

345

346 We executed six replicates of full model scenarios with independent inheritance, where  
347 each of the five movement preference parameters was inherited randomly from either the mother  
348 or father. These baseline simulations contained unmanipulated input variables directly from  
349 limnological model output, and we allowed all movement preferences, i.e.,  $\beta$  values (for light,  
350 temperature, dissolved oxygen, predator avoidance, and prey), to evolve simultaneously. We  
351 initialized 2000 yellow perch SIs that were each composed of 500 individuals, resulting in a total  
352 of 1,000,000 individuals. The number of individuals per SI varied after initialization as a result  
353 of mortality events. Simulations were executed from August 1 to October 31 to encompass a  
354 thermally stratified and potentially hypoxic period. Simulations continued for 100 years. We  
355 initialized yellow perch as two-year-olds and allowed complete population replacement each  
356 year with new two-year-olds (2000 SIs). No time lag was necessary due to full population  
357 replacement each year.

358 We then performed six full 100-year simulations as described above, but with a linked  
359 inheritance model rather than independent inheritance to test the sensitivity of our inheritance  
360 model. In the case of linked inheritance, all movement preference parameters were randomly

361 inherited from either the mother or father rather than a mix of traits from each. Inheritance model  
362 structure is a key underlying mechanism of eco-genetic models that may influence speed of  
363 evolution and model outcomes (Dunlop et al., 2009).

364 We evaluated differences in survival (mean number of individuals per SI at the end of  
365 simulation year) and growth (mean final weight of individuals at the end of simulation year) over  
366 time (generations) using linear regressions. Increasing survival and growth over time would  
367 indicate fitness-driven movement rule evolution. We used paired t-tests (paired by simulation  
368 replicate) to test for differences in final movement preferences in full 100-year simulations.  
369 Significant differences between movement preferences indicated that, on average, fish weigh one  
370 preference over another at the end of simulations.

371 To examine model robustness and to test proximate cues with limited effects of  
372 interactions between cues, we performed a set of simulations where one movement preference  
373 evolved while the other four parameters were held constant at an intermediate value of 0.5. Three  
374 replicates were performed for each of the five movement traits (i.e., 15 total simulations) using  
375 an independent inheritance model. We ran these simulations for 30 years because full model  
376 scenarios revealed that movement preferences had fully diverged at this point.

377 Next, we performed a series of simulations that fixed a single environmental variable at a  
378 constant value to further examine responses of movement preferences when the influence of one  
379 habitat variable was effectively removed. We performed three replicates for each of five trials  
380 where one environmental variable (light, temperature, dissolved oxygen, predator pressure, or  
381 prey density) was held constant. For trials with constant dissolved oxygen, we set dissolved  
382 oxygen at 8.0 mg/L, a level much higher than potential negative direct or indirect effects of  
383 hypoxia (Bejda et al., 1992; Pichavant et al., 2001). We set temperature throughout the water



384 column at 24°C for temperature trials, the preferred temperature of yellow perch (Ferguson,  
385 1958). For light trials, we set light at 1000 Langley, a relatively high value in this model to allow  
386 high reactive distance. We removed predation by eliminating predation mortality, and equalized  
387 prey density by setting the same density of zooplankton in each cell and removing chironomids,  
388 which are found exclusively in benthic cells. Each simulation with a constant environmental  
389 variable utilized the independent inheritance model and simulated 30 generations.

390 To examine distributional outcomes of evolved movement rules, we performed truncated  
391 simulations and tracked fish depth throughout a 24-hour period. We chose three days to examine  
392 that spanned the duration of our simulation year: the first (August 1), middle (September 16),  
393 and final day (October 31) of simulations. These dates represent the spectrum of environmental  
394 conditions included in the simulations. We initialized three groups of individuals for each day.  
395 One group weighted proximate cues equally in their movement decisions, one group was  
396 initialized with mean movement rules at the end of 100-year simulations with an independent  
397 inheritance model, and one group was initialized with traits derived from 100-year simulations  
398 with a linked inheritance model. 2000 SIs were placed randomly throughout the water column,  
399 then given 24 hours to move to their preferred location before depth was tracked (by 0.5 m cell)  
400 for 24 hours on the target date. Each daily simulation used input data from the year 2000 to  
401 ensure consistent environmental conditions between trials. Results were reported as median  
402 depth (m) of individuals on a ten-minute time step to demonstrate where fish would move in the  
403 water column over the course of one day given each set of movement rules.

404

405

## Results

406

407 Modeled yellow perch displayed distinct, consistent evolution in the weighting of different  
408 environmental factors in determining movement rules in baseline simulations. Specifically,  
409 modeled yellow perch evolved to prioritize suitable light levels and predator avoidance. The  
410 weighting of dissolved oxygen tended to remain constant, while the importance of prey  
411 availability in determining movement decreased and the importance of temperature declined  
412 precipitously over successive generations for simulations using both independent and linked  
413 inheritance models (Fig. 1). Trait preferences generally evolved to level values over 100-year  
414 simulations, demonstrating that 100 generations were sufficient time for movement rules to  
415 evolve and the most severe selection occurred in the first 20 years of simulations (Fig. 1).  
416 Movement preferences had diverged by the end of simulations with highest weight toward  
417 preferred light levels and predation levels, followed by prey availability or DO preference, with a  
418 very low weighting of temperature (Fig. 2). We observed significant differences between most  
419 pairwise combinations of final movement rule weights except predator and light preferences in  
420 simulations with independent inheritance (Fig. 2).

421 Both survival and growth increased over several generations of simulations,  
422 corroborating that movement rule evolution was fitness-driven. Although mean individual  
423 growth and mean number of individuals per SI were considerably variable across replicates,  
424 years, and simulations (Fig. 3), growth showed significant increases over time for the first 30  
425 years of full simulations using independent inheritance (slope = 0.239;  $t_{28} = 2.51$ ;  $p = 0.018$ ) and  
426 linked inheritance (slope = 0.364;  $t_{28} = 4.38$ ;  $p = 0.0001$ ). Survival also demonstrated a  
427 significant increase over time for independent (slope = 3.28;  $t_{28} = 3.29$ ;  $p = 0.002$ ) and linked  
428 (slope = 4.26;  $t_{28} = 3.99$ ;  $p = 0.0004$ ) inheritance models. Independent and linked inheritance  
429 models showed very little difference in evolved movement preferences after 100 simulation

430 years, suggesting that results of this model are not very sensitive to choice of inheritance model  
431 (Figs. 1-4). However, the speed of evolution and the variability between replicates were both  
432 higher in linked inheritance models (Fig. 2; slopes in Fig. 3).

433         Sub-daily movement demonstrated cyclical patterns of moving deeper in the water  
434 column during the day. Movements were sensitive to minor changes in movement traits (Fig. 4).  
435 Evolved movement traits from both independent and linked inheritance models allowed  
436 individuals to better access habitat lower in the water column late in the season when hypoxia  
437 was present (Fig. 4).

438         In simulations where only one movement trait evolved while the other four remained  
439 fixed at 0.5, general trajectories of trait evolution were similar to full models with concurrent  
440 evolution of all five movement traits. Movement toward preferred light and predator densities  
441 increased, while temperature preference decreased rapidly and dissolved oxygen preference  
442 remained fairly constant (Fig. 5), providing support for the consistency of accurate movement  
443 traits. In contrast, when the movement trait related to prey densities was allowed to evolve on its  
444 own it increased, while in full models, values of this movement trait decreased.

445         In simulations with one environmental variable held constant, movement traits evolved  
446 similar to full models. Temperature preference generally evolved the fastest. When we set DO to  
447 8.0 mg/L throughout the water column at all times, DO preference remained constant, while  
448 temperature and prey preference decreased over time, predator avoidance and light preference  
449 increased, similar to full simulations (Fig. 6A). Constant light produced an environment where  
450 predator avoidance (i.e. a function of light level) did not evolve. Other traits evolved similarly to  
451 full simulations (Fig. 6B). When temperature was fixed at 24°C throughout the water column,  
452 traits diverged little from initial values (Fig. 6C), demonstrating the high importance of thermal

453 stratification to related environmental factors and movement rules that enhance fitness. Negative  
454 trajectory of temperature preference in other simulations combined with lack of evolution in  
455 simulations where temperature was constant may suggest that our definition of “preferred”  
456 temperature for yellow perch (24°C) is not accurate for LECB, but that temperature preference  
457 has a strong link to fitness. Removal of predation pressure produced trends in temperature and  
458 light preference similar to full simulations (Fig. 6D). However, DO preference appeared to  
459 decrease over time and prey preference remained close to initial values. Surprisingly, predator  
460 preference continued to evolve, potentially indicating interactive effects among movement traits.  
461 Movement rules evolved in similar trajectories to full simulations when prey was constant  
462 throughout the water (Fig. 6E).

463

464

## Discussion

465

466 We developed a modeling approach of explicitly testing movement responses to realistic,  
467 high-resolution environmental factors within an eco-genetic framework. Other models have used  
468 complex spatially-explicit proximate cues to predict movement rules (Goodwin et al., 2006;  
469 Humston et al., 2004) or tested movement preferences as heritable traits (Huse and Giske, 1998;  
470 Middaugh, 2011), however, to our knowledge, few have used high spatial and temporal  
471 resolution environmental data to explore the relationships between interacting proximate cues in  
472 a dynamic environment (but see Fiksen, Jørgensen, Kristiansen, Vikebø, & Huse, 2007 for an  
473 example with larval marine fish dispersal). We tested interacting effects between movement  
474 preferences, emphasizing the importance of considering both proximate cues and their overall  
475 influence on fitness to understand fish movement decisions. Trends in movement rules were

476 generally robust to an alternate inheritance model. Increased growth and survival over time in  
477 full simulations also corroborated the general approach of our model. Simulations in which we  
478 limited evolution to a single trait or held one environmental variable constant generally  
479 supported full model results, but revealed some possible interactive effects, particularly between  
480 prey availability and other factors. These results highlight the importance of considering  
481 interactive effects of movement stimuli, and developing a framework to select appropriate  
482 movement rules for a variety of applications in spatially-explicit individual-based modeling.

483         Over generations, movement rules developed into differential preferences for our five  
484 environmental cues: temperature, DO, prey, predators, and light. Modeled yellow perch  
485 movement evolved rapidly, likely because movement rules affect fitness at each ten-minute time  
486 step. Fish quickly decreased their weighting of preferred temperature, as defined by maximum  
487 scope for growth according to maximum consumption and temperature-regulated respiration  
488 (Hanson et al., 1997; Kitchell et al., 1977). One potential explanation for rapid temperature  
489 selection is that the calculated preferred temperature of yellow perch in our model overlapped  
490 with high rates of walleye predation, adding to the impetus for movement away from the  
491 temperature that produces maximum growth. This type of tradeoff can be accounted for in the  
492 eco-genetic framework without explicit programming of the relationship between temperature  
493 and predation. Flexibility of the eco-genetic model framework allowed a somewhat unexpected  
494 temperature response to develop, despite initially defining the “best” temperature based on  
495 bioenergetics equations.

496         Weighted preference for DO demonstrated stabilizing selection. DO preference changed  
497 very little over time in our model with a consistent value close to the starting mean of 0.5.  
498 Remaining in low DO can cause direct mortality in fish (Townsend & Edwards, 2003), but more

499 often causes decreased growth and consumption (Hrycik et al., 2017). These lethal and sub-lethal  
500 effects cause fish to preferentially move out of hypoxic areas (Brady and Targett, 2013; Herbert  
501 et al., 2011). However, avoiding hypolimnetic hypoxia limits access to energy-rich benthic prey  
502 that yellow perch may consume except for short forays into the hypolimnion (Keast, 1977;  
503 Roberts et al., 2012, 2009). However, such forays are unlikely to show up during the longer (ten  
504 minute) time step, which may obscure the evolution of the DO tolerance trait value. In addition  
505 to physiological effects on yellow perch, DO preference may be regulated by hypoxia severity.  
506 Hypoxia in LECB is variable across years and occurs only for a brief period of time each year  
507 (Zhou, Obenour, Scavia, Johengen, & Michalak, 2013) and, therefore, may not be a strong  
508 selection factor in our model. Although we chose to simulate a period that included hypoxia, the  
509 fish did not experience hypoxia for the entire duration of the simulations. Hypoxia is also limited  
510 to the lower part of the water column and is correlated with other environmental variables. A less  
511 flexible modeling approach may have overestimated the importance of DO variation.

512         Simulated populations developed a lower habitat selection preference for prey relative to  
513 other environmental cues. This was likely the result of having sufficient prey for survival and  
514 growth during the time period tested. During most simulation years, both zooplankton and  
515 benthic invertebrate prey remain at moderate levels in August through October (Botts, 1997;  
516 Makarewicz, 1993), so prey availability may not be a limiting factor on yellow perch growth.  
517 With year-round simulations including zooplankton and chironomid abundance, we would  
518 expect that seasonal prey preference may be stronger during other seasons. In addition, we did  
519 not explicitly model density-dependent prey interactions because the limnological model  
520 accounted for fish predation in modeling daily zooplankton density. If we had explicitly

521 incorporated prey depletion in the eco-genetic model, we may have seen differences in  
522 movement strategies such as specialization within the population.

523         Modeled yellow perch evolved preference for limiting predation risk, which is a common  
524 behavior to program into movement rules (Srinivasan et al., 2010; Wood and Ackland, 2007).  
525 Predation avoidance corroborates results from field studies where predation risk structures prey  
526 distributions (Hammerschlag et al., 2010; Swain et al., 2015). Predator avoidance continued to  
527 evolve when predation pressure was removed, although not to as high of a degree in full  
528 simulations. This suggests that movement that effectively allows fish to avoid predation also  
529 increases movement toward habitat that provides other benefits to growth or survival. One  
530 potential mechanism for movement away from high predation areas that may also increase  
531 growth is simultaneous movement toward cooler temperatures. Cooler temperatures decrease  
532 metabolism and therefore promote growth (Byström et al., 2006; Larsson et al., 2005; Munday et  
533 al., 2008). Growth may also be increased through movement toward maximum prey densities in  
534 the benthos that are located far from maximum risk of predation, i.e., towards the top of the  
535 water column where light is greatest.

536         Attraction to preferred light levels increased over time across simulations. Light directly  
537 affects foraging patterns, namely through increased reactive distance (Rickel and Genin, 2005).  
538 Preferred light levels result in increased growth and therefore fitness in our model. Light also  
539 influences predation pressure from walleye. Light is an important regulatory factor of walleye  
540 behavior (Ryder, 1977), and our model contained considerable overlap of yellow perch and  
541 walleye optimal foraging conditions. The interplay of increased foraging by yellow perch at  
542 preferred light levels but also increased exposure to predation potentially regulated selection on  
543 light preference in movement rules, displaying another example in which tradeoffs between

544 movement preferences emerged without explicit coding for interaction between the two  
545 variables.

546         The five proximate cues in our model interacted to produce movement rules that allowed  
547 individuals to react to high-frequency changes in their environmental conditions on a sub-daily  
548 time step. Daily cyclical movement patterns varied in magnitude according to ambient  
549 conditions, but overall, indicated a preference for deeper waters during the day, consistent with  
550 yellow perch avoidance of high light levels in surface waters (Rudstam and Magnuson, 1985).  
551 Additionally, our model allows for complex interactions between proximate cues and a dynamic  
552 environment. For instance, sub-daily movement may be linked to complex predator-prey  
553 interactions in accordance with foraging arena theory in which prey vulnerability shifts over time  
554 and space, providing a dynamic foraging arena for predators (Walters & Juanes, 1993; Walters,  
555 Christensen, & Pauly, 1997; Walters & Korman, 1999) . Yellow perch in our model were  
556 considered both predators as well as prey, and as such, were subjected to multiple levels of  
557 predator-prey relationships, in addition to influences of light on foraging capabilities and  
558 influences of physiological limitations from ambient temperature and DO. By including these  
559 various relationships, the eco-genetic model described herein was able to identify appropriate  
560 movement rules, while bypassing the need to explicitly model interactions between  
561 environmental cues.

562         Our LECB yellow perch movement model has some limitations based on the assumptions  
563 and simplifications we made in programming, as is the case with all models. The movement  
564 rules in our model simulations pertain to LECB yellow perch during late summer/early autumn  
565 hypoxic conditions. Movement rule determination for other seasons, lakes, or environmental  
566 conditions would require more extensive environmental data. Similarly, our model does not



567 explicitly allow for encountering novel environments like more complex behavioral models (e.g.,  
568 Budaev, Giske, & Eliassen, 2018). However, the benefit of our eco-genetic framework is that it  
569 can be implemented for any species and environment for which there is sufficient physiological  
570 and environmental data. Future modeling endeavors could be further improved by determining  
571 physiological parameters for the population of interest such as hypoxia tolerance and temperature  
572 preference, as these parameters may be population-specific (Eliason et al., 2011; Timmerman  
573 and Chapman, 2004).

574         Eco-genetic modeling represents a departure from modeling approaches typically used to  
575 determine movement rules in individual-based modeling. Some individual-based movement  
576 models have explicitly tested a high number of scenarios to determine appropriate movement  
577 rules (Tracey et al., 2014), while others carefully consider realistic decisions of the agents in  
578 question (Cohen et al., 2014; Kleinmann and Wang, 2017). Eco-genetic modeling gives us the  
579 ability to allow mechanistic interactions such as movement rules to emerge from the model itself  
580 by emphasizing the increase of fitness over time rather than programming movement rules as  
581 individual decisions. Other models that take a similar approach in allowing behavioral traits to  
582 emerge from models use artificial neural networks (Strand et al., 2002; Tracey et al., 2011),  
583 fuzzy cognitive maps (Bhattacharjee et al., 2018), hedonic modeling (Giske et al., 2003), or  
584 emotional bookkeeping (Evers et al., 2014). However, these methods add a layer of complexity  
585 in programming and interpretation that may not be needed if emergent traits are meant to  
586 correspond directly with behavior. An eco-genetic approach combined with a high-frequency  
587 time step can be applied to understanding animal movement in response to many ecological  
588 changes. Here, we examined sub-daily movement responses in a hypoxic ecosystem and  
589 observed differentiation of movement traits based on weighted preferences of light, DO,

590 temperature, predators, and prey. Eco-genetic modeling of movement rules could be more widely  
591 applied to countless other scenarios where proximate cues are dynamic and challenging to  
592 interpret simultaneously. Spatially-explicit eco-genetic modeling allows researchers to test  
593 hypotheses about responses to complex environmental changes using established physiological  
594 parameters of individuals and defined determinants of fitness.

595

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597

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602

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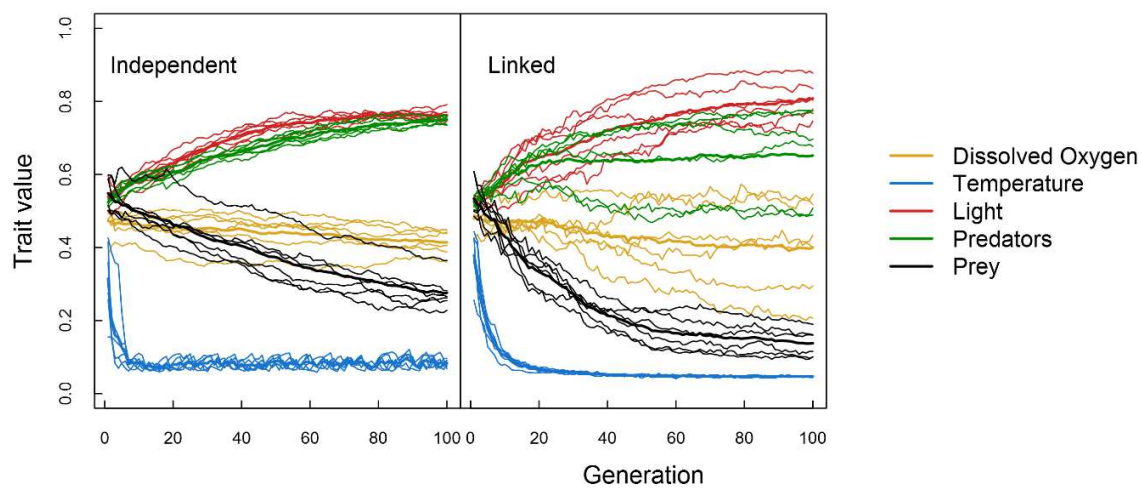
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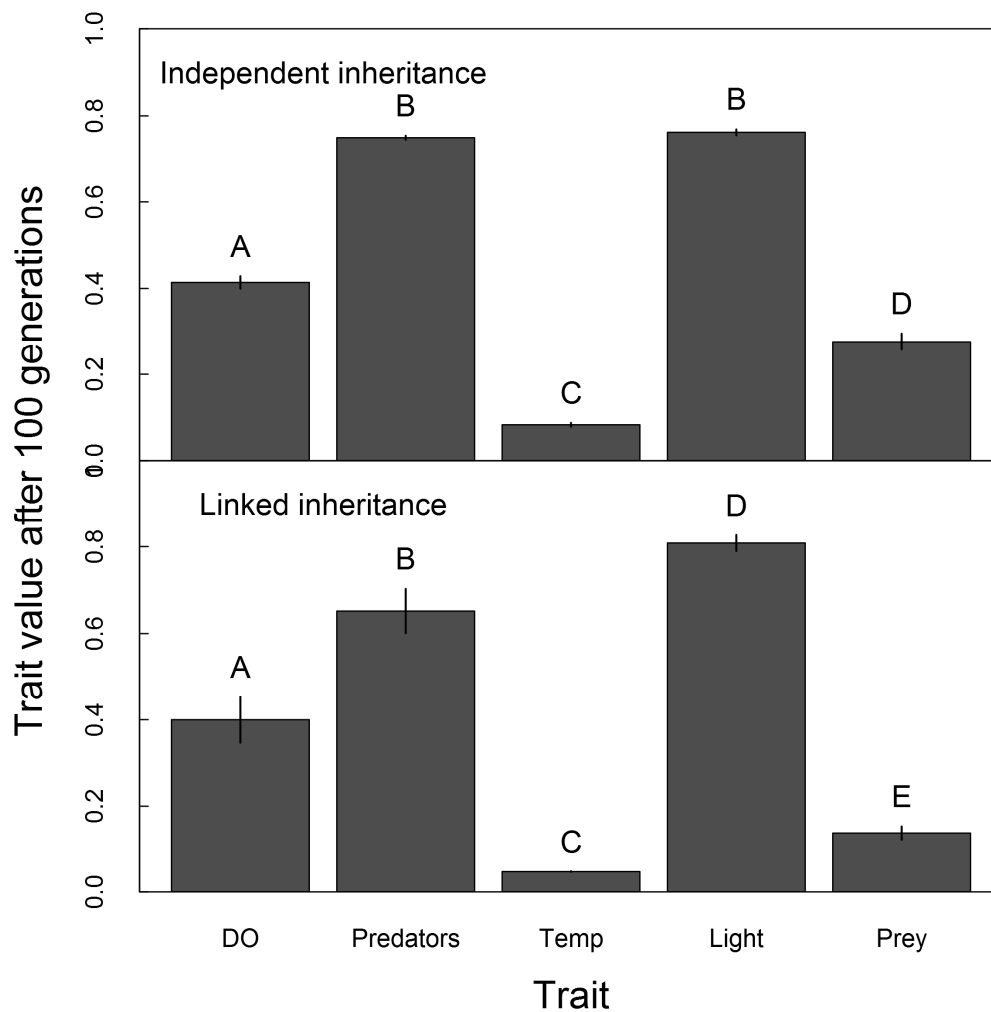
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## Tables and Figures



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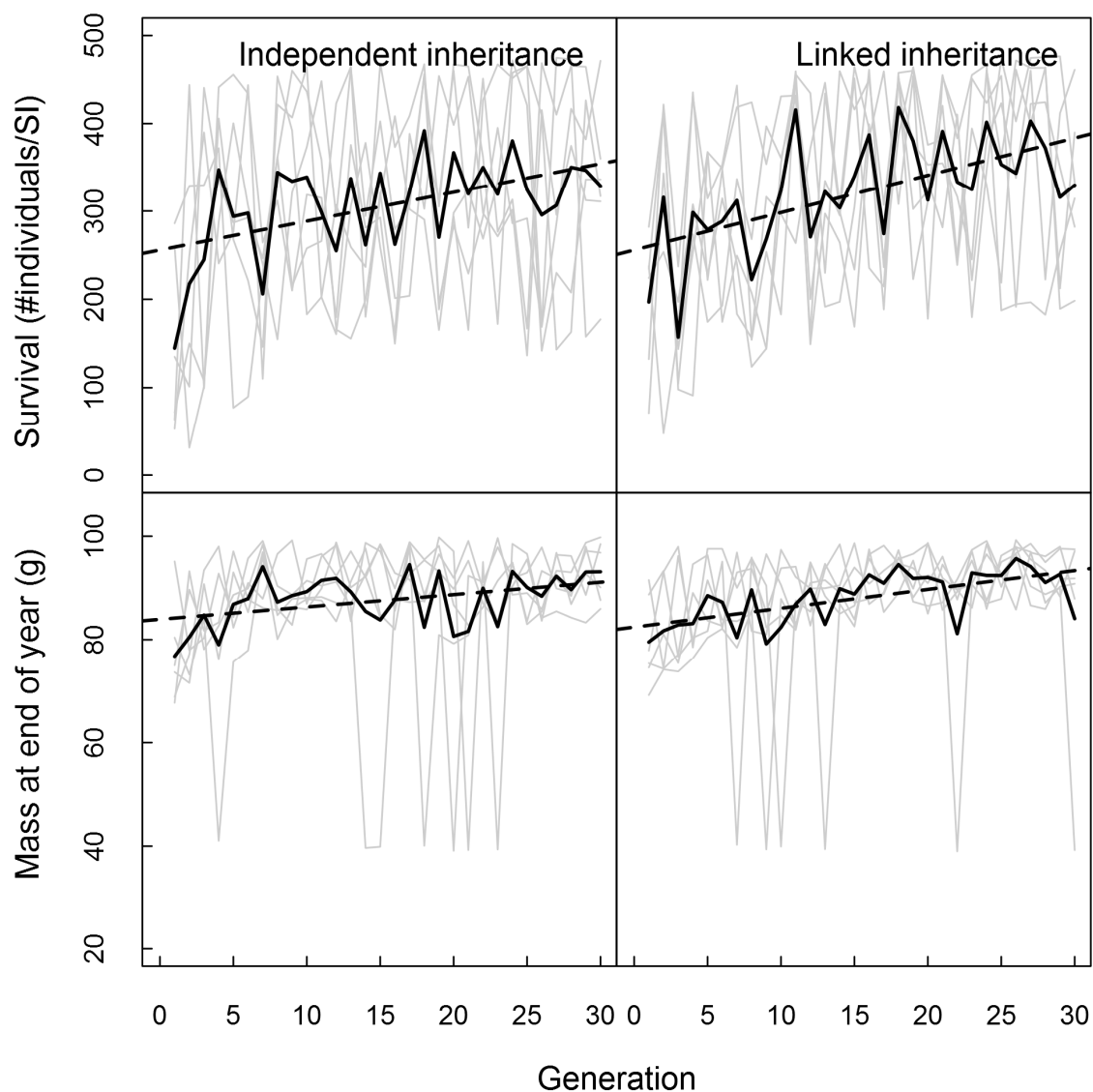
889 Figure 1. 100-year simulations with all traits evolving simultaneously and environmental  
 890 variables changing naturally with an independent inheritance reproduction model and a linked  
 891 inheritance model. Thin lines represent replicates (N=6) and thick lines represent averages across  
 892 replicates.



893

894 Figure 2. Trait values at the end of 100-year full simulations with an independent inheritance  
 895 model and a linked inheritance model. Error bars represent standard error (N=6), and letters  
 896 denote significant differences between trait means within each inheritance model group  
 897 according to paired t-tests ( $\alpha=0.05$ ). Dissolved oxygen is abbreviated as “DO” and temperature is  
 898 abbreviated as “Temp.”

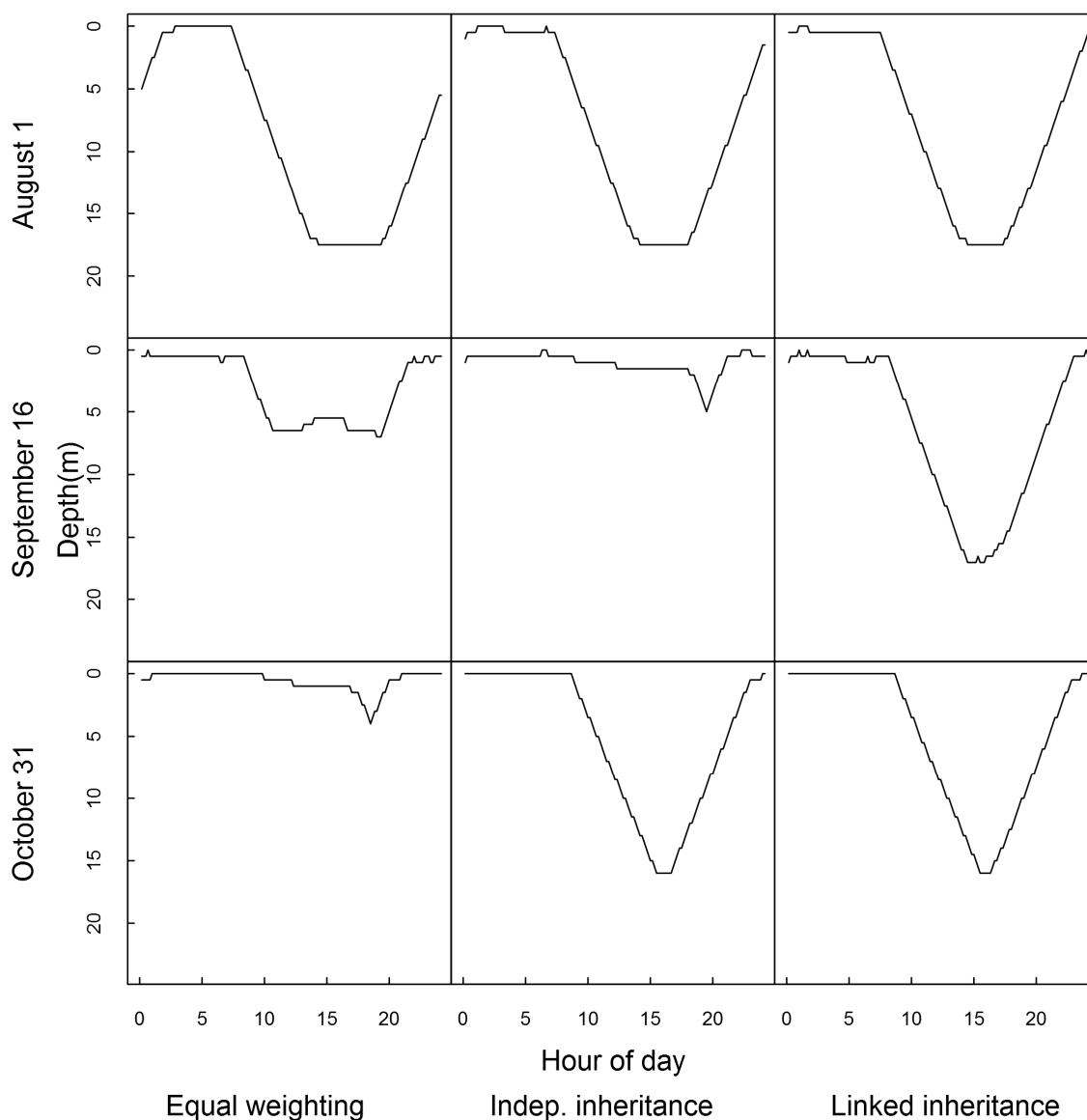




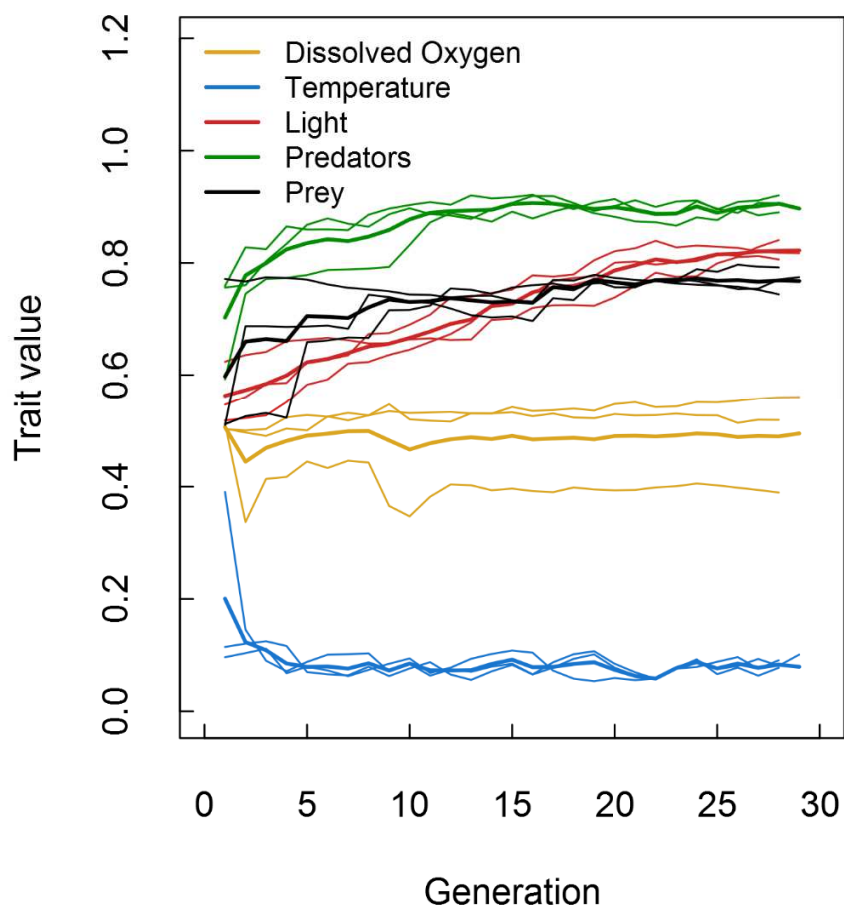
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900 Figure 3. Average survival and mass of SIs at the end of each simulation year for the first 30  
 901 years of simulations using an independent inheritance model and a linked inheritance model.  
 902 Light gray lines represent replicates (N=6), solid black lines represent mean of replicates, and  
 903 dotted black lines are linear regressions using all replicates.

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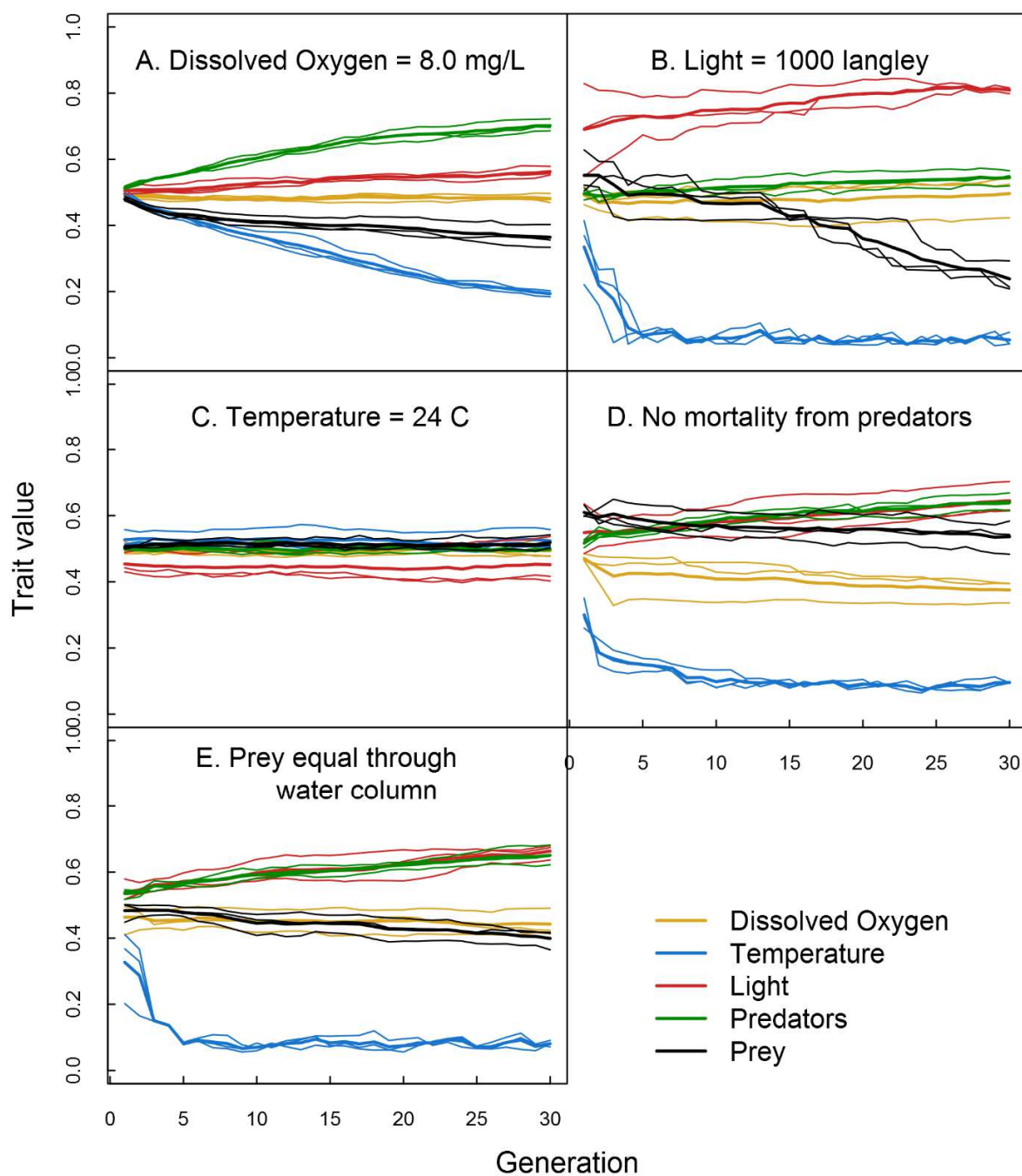
905  
 906 Figure 4. Examples of daily movement preferences of modeled yellow perch on first (August 1),  
 907 middle (September 16), and final (October 31) days of a simulation using year 2000 input data  
 908 and three different sets of movement rules. Each line represents the median depth of 2000 SIs  
 909 with identical movement rules. Individuals with equally-weighted movement rules retained  
 910 values of 0.5 for each habitat preference, while individuals with individual inheritance or linked  
 911 inheritance had movement preference values equal to the mean values of all individuals at the  
 912 end of 100-year simulations for their respective reproduction model.  
 913



914

915 Figure 5. Evolution of single traits when all other trait values were held constant at 0.5. Thin  
 916 lines represent replicates (N=3) and thick lines represent the average trait values across all  
 917 simulations. Note that each panel represents a separate set of simulations.

918



919

920 Figure 6. Evolution of movement traits when each environmental variable was held constant  
 921 throughout simulations. Thin lines represent replicates for each simulation (N=3) and thick lines  
 922 represent the average trait values across all simulations.

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925