

Demographic and phenotypic responses of juvenile steelhead trout to spatial predictability of food resources

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Abstract. We manipulated food inputs among patches within experimental streams to determine how variation in foraging behavior influenced demographic and phenotypic responses of juvenile steelhead trout (*Oncorhynchus mykiss*) to the spatial predictability of food resources. Demographic responses included compensatory adjustments in fish abundance, mean fish size, and size inequality. These responses paralleled shifts in individual foraging behavior, which increased the strength of exploitative competition relative to interference competition in streams with lower spatial predictability of food resources. Variation in the spatial predictability of food resources also favored different physiological phenotypes, as inferred from selection on an index of standard metabolic rate (SMR) based on fish otolith size. We observed positive directional selection on SMR in streams with spatially predictable food resources, disruptive selection for SMR at intermediate levels of spatial predictability, and negative directional selection for SMR in streams with the lowest level of spatial predictability of food resources. Thus, variation in the spatial predictability of food resources resulted in changes in individual behavior and modes of population regulation, and produced physiologically divergent cohorts of stream salmonids.

Key words: competition, exploitation, and interference; emigration; growth depensation; intraspecific competition; *Oncorhynchus mykiss*; phenotypic selection; population dynamics; regulation; spatial predictability; standard metabolic rate; steelhead trout.

INTRODUCTION

A critical challenge for ecologists is to understand individual and population responses to habitat heterogeneity. One important but understudied component of spatial habitat heterogeneity is the spatial predictability of resources, a measure of the consistency of relative habitat patch quality over time (Warner 1980). Spatial predictability of food resources is known to influence animal behavior (Grant 1993), but little is known about how behavioral changes induced along a gradient in spatial habitat predictability might influence population processes. When food resources are spatially predictable, competitively dominant individuals can effectively monopolize food resources through aggression and territoriality (Reid et al. 2011). Interference competition, mediated through territoriality, may act to regulate populations through density-dependent mortality, emigration, and growth in spatially heterogeneous but temporally static environments (Keeley 2001). In many environments, resource abundance is not static, however, and the quality of habitat patches can vary substantially over time (Martin-Smith and Armstrong 2002). A prediction from resource defense theory is that

aggressive defense of feeding territories will produce an energy deficit when the spatial predictability of food resources falls below a critical threshold (Brown 1964, Grant 1993). Under such conditions, animals with flexible foraging strategies may abandon territoriality in favor of alternative foraging tactics and exploitative rather than interference competition may predominate (Grand and Grant 1994). Such an environmentally induced shift in foraging behavior may alter population responses to food and space competition. For example, a reduction in territoriality may relax the constraints of space on animal abundance, resulting in habitats supporting a larger number of individuals for a given level of food resources, but with compensatory reductions in components of individual fitness such as body size. Consequently, mechanisms of population regulation may vary along gradients in the spatial predictability of food resources, but this hypothesis remains largely untested.

In addition to influencing individual behaviors and their linkages to population demography, variation in the spatial predictability of food resources may exert different selective pressures on populations. Under spatially predictable food regimes, individuals with traits that improve their ability to monopolize access to food are likely to be favored. Individual variation in energy metabolism is a potentially important trait in this regard, because standard metabolic rate (SMR) is positively associated with boldness, aggression, and

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competitive dominance in a wide range of taxa (Biro and Stamps 2010). Thus, individuals with faster rates of energy metabolism may be at an advantage in territorial contests for limited food and space when resources are economically defendable (*sensu* Brown 1964). In environments with low spatial predictability in food resources, however, individuals with low SMR may be favored if lower maintenance costs help to minimize energy loss during periods of food scarcity. SMR may, therefore, be a trait under strong selection in response to the spatial predictability of food resources.

In this study, we experimentally test how the spatial predictability of food resources influences behavior and early demography in a stream-dwelling salmonid, and we determine how individual performance is influenced by variation in SMR. We studied offspring of steelhead trout (*Oncorhynchus mykiss*), the anadromous form of rainbow trout (Behnke 2002). This species is a good candidate for such a study because juvenile salmonids have flexible foraging strategies, including both territorial and non-territorial tactics (Puckett and Dill 1985). Additionally, SMR varies several-fold among individuals within populations even after accounting for variation in body mass (Tyler and Bolduc 2008), and SMR is known to influence dominance during interference competition in salmonids (e.g., Metcalfe et al. 1995, McCarthy 2001, Reid et al. 2011). Consequently, there is strong potential for phenotypic selection on energy metabolism within populations due to variation in SMR, and a functional relationship between SMR and individual performance. To manipulate the spatial predictability of food resources, we created habitat patches within stream mesocosms and varied the consistency in patch quality, as defined by the quantity of patch-specific food inputs, over time. By monitoring how individuals and populations responded to the spatial predictability of food resources, we were able to determine how individual variation in physiology and behavior contributes to changes in abundance, growth, and emigration in stream-dwelling salmonids occupying heterogeneous habitats.

MATERIALS AND METHODS

Experimental animals

We used a full-sibling group of juvenile steelhead trout from the Siletz River, Oregon, USA, for the experiment. Fish were obtained as eggs by mating a single male and female of first-generation Siletz River winter steelhead trout hatchery stock. Eggs were incubated at 10°C at the Oregon Hatchery Research Center, Alsea, Oregon, and were transferred to Oregon State University's Salmon Disease Laboratory, Corvallis, as larval trout just prior to completing egg yolk absorption. All fish were housed in a single 100-L tank until yolk absorption was complete and fish were ready to feed exogenously.

Experimental setup

We constructed 12 stream mesocosms at OSU's Salmon Disease Laboratory. Each stream consisted of a 2.4×0.5 m rectangular channel with gravel substrate and a one-way fish emigration trap at the outflow (Sloat 2013; see Appendix B). Flow rate through the streams was ~ 2 m³/h and water depth was a uniform 15 cm. Three $14 \times 5 \times 8$ cm bricks were evenly spaced along the center of each stream to provide physical structure for fish orientation. Temperature was maintained at a constant of 13°C within all streams, consistent with mean temperatures experienced by the source population in the wild. Photoperiod was held constant at 14 h light:10 h dark, a regime typical for the source population during the 22-d experimental period (27 July–9 August 2011). Each stream received a total of 1.2 g/d of food in the form of floating flakes (BioDiet starter feed, Bioproducts, Warrenton, Oregon, USA). This amount of food represents $\sim 30\%$ of the maximum daily intake rate for the number and size of fish at the time of stocking, and was selected to match consumption rates observed for juvenile trout in natural streams (Railsback and Rose 1999). We supplied food via three programmable automated jitter feeders suspended above each stream channel. This allowed us to divide the food supply among three feeding patches of equal size that received a high, medium, or low proportion of the total amount of food delivered to a stream. Feeding patches were created by securing 1-mm mesh nylon netting that extended 5 mm beneath the water surface perpendicular to the stream channel. Netting retained floating food within each feeding patch while allowing fish to swim freely between patches. Jitter feeders dispensed equal amounts of food per feeding (0.06 ± 0.009 g, mean $\pm$ SD), with differences among patches in the daily quantity of food delivered controlled by differences in the number of food dispensations made between 08:00 and 18:00 hours each day. High food abundance patches received a total of 0.72 g of feed over 12 feedings per day, medium food abundance patches received a total 0.30 g over five feedings per day, and low food abundance patches received a total of 0.18 g over three feedings per day.

We manipulated the spatial predictability of food resources among streams by varying the spatial arrangement of high, medium, and low food patches over time. Four streams each were assigned to one of three levels of spatial predictability of food resources. In streams with high spatial predictability, the spatial arrangement of high, medium, and low food patches remained constant throughout the experiment (Appendix C). In streams with intermediate spatial predictability, the spatial arrangement of high, medium, and low food patches changed every three days, and in low predictability streams, the spatial arrangement of high, medium, and low food patches changed daily. Thus the daily timing and total amount of food delivered (i.e., temporal predictability) was the same for each stream, but

treatments varied in the consistency of the spatial arrangement of patch quality over time.

To begin the study, we stocked each stream with 60 juvenile steelhead trout (fork length 29.9 ± 0.5 mm, mean $\pm$ SD; mass 0.21 ± 0.02 g, mean $\pm$ SD). This level of stocking represented three to four times the carrying capacity for juvenile steelhead trout, based on previous studies using the same experimental system (Sloat 2013). When stocking fish into the experimental streams, we captured 5–10 individuals from the pool of fish that we reared from embryos and randomly assigned them to one of 12 holding containers. We repeated this procedure until we had 12 groups of 60 fish and then randomly assigned each group to an experimental stream. We determined the distribution of fish within each stream using scan observations to count the number of fish per patch in each stream. Three scan observations lasting ~ 30 s each were made at 2-h intervals every three days, during which time we counted the number of territorial fish (i.e., fish that maintained consistent focal positions from which they made short forays to feed or interact with other fish) within each feeding patch, as well as the number of non-territorial “floaters” (i.e., nonstationary fish that moved among feeding patches and fed while roaming; sensu Puckett and Dill 1985). We also performed focal animal observations of six fish per stream every three days. These observations were divided equally among the three feeding patches in each stream. To conduct focal observations, we selected a single individual from a randomly chosen quadrant within a feeding patch and observed territorial and feeding activity over a period of 3 min. During focal observations, we categorized fish into territorial and floater behavioral types based on their foraging tactics, and we mapped space use on scaled, planform drawings of experimental streams. To facilitate mapping of fish behavior, including the location of each feeding event and agonistic interaction (including whether aggression was initiated or received), we embedded a matrix of white marbles in the stream substrate and used this matrix as a visual reference to divide each stream into 5×5 cm cells. All observations were made from portals cut into the opaque curtain housing each stream in order to avoid disturbing the study animals.

Stream channels were opened to emigration after an acclimation period of four days. During acclimation, fish in streams with low spatial predictability of food resources experienced four changes in the spatial arrangement of high, medium, and low food patches. Those in streams with medium spatial predictability experienced one change in the spatial arrangement of food patches, and those in high predictability streams experienced a constant arrangement of food patches. Emigration was allowed into a one-way fish trap at the downstream end of each stream channel, which was monitored twice daily. To prevent “accidental” emigration, we anesthetized and marked each fish with a small

caudal fin clip upon their initial capture and returned them to the head of the stream channel after recovery (Keeley 2001). If a marked fish was captured in the trap a second time, we removed it from the experiment, euthanized it by overexposure to buffered anesthetic (Finquel MS-222; Argent Chemical, Redmond, Washington, USA), and preserved the fish in 90% ethanol. At the end of the experiment, we removed and euthanized all remaining fish from the streams, and measured their fork length to the nearest 1 mm and their wet mass to the nearest 0.01 g.

We used fish otolith microstructures as a proxy for individual variation in SMR in our study. In teleost fishes, otoliths are argonite (CaCO_3) structures of the inner ear for which mineral accretion is strongly and positively associated with SMR (Wright 1991, Hüsey and Mosegaard 2004, Fablet et al. 2011). Variation among fish in the size of otoliths at the onset of exogenous feeding (i.e., the time at which fish were stocked into experimental streams) reflects metabolic rate-dependent mineral accretion by fish prior to exogenous feeding, and provides a permanent index of relative SMR that can be retrospectively sampled (e.g., Titus and Mosegaard 1991, Yamamoto et al. 1998, Bochdansky et al. 2005). To improve identification of otolith size at the beginning of the experiment, otoliths of all fish were marked with alizarin complexone (Sigma-Aldrich, Saint Louis, Missouri, USA) prior to stocking (Zimmerman and Reeves 2000). To examine individual variation in otolith size, we extracted sagittal otoliths from all fish that were included in the experiment as well as 28 fish from the same family that were not included in the experiment. The latter sample was used to examine correlations between otolith size and body size at the beginning of the experiment, because body size may also influence competitive asymmetries. Otolith preparation followed procedures described in Zimmerman and Reeves (2000). We used a compound microscope and camera lucida to capture and import digital images of the prepared otoliths into image analysis software (Image-Pro version 7.0, Media Cybernetics, Rockville, Maryland, USA). Relative SMR for each individual at the beginning of the experiment was inferred by measuring individual differences in the total otolith area within the alizarin complexone mark.

Data analysis

We used repeated-measures analyses of variance (ANOVAR) to assess treatment effects on the demography of juvenile steelhead trout. When responses were measured on a specific group of fish at only a single point during the experiment, such as for those fish remaining in the streams at the end of the experiment, we used analysis of variance (ANOVA) to assess treatment effects. To quantify the degree of body size inequality among individuals within populations, we determined the relative mean size difference between all pairs of individuals within streams at the end of the

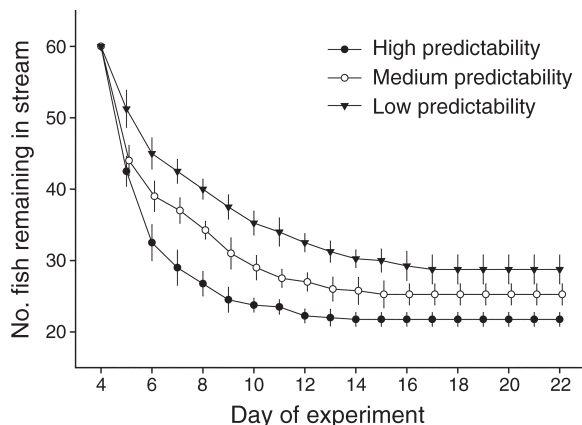


FIG. 1. Daily number (mean $\pm$ SE) of juvenile steelhead trout (*Oncorhynchus mykiss*) remaining in streams with high, medium, or low levels of spatial predictability of food resources.

experiment (Gini coefficient; Weiner and Solbrig 1984, Keeley 2001).

We compared otolith area measurements of all fish included in the experiment with those of fish that remained within the streams for the duration of the experiment to determine the effect of SMR on the probability of fish remaining within experimental streams. For each stream, SMR was standardized by subtracting the population mean value from each individual measurement, and then dividing by the standard deviation of SMR for the population at the beginning of the experiment (Lande and Arnold 1983). We used two approaches for measuring the strength of selection on SMR during the experiment. First, we performed logistic regressions to estimate directional and quadratic selection on SMR. Fish that remained within the streams for the duration of the experiment were assigned a value of 1, and emigrants were assigned a value of 0. Linear and quadratic equivalents of logistic regression coefficients were calculated (Janzen and Stern 1998) to estimate selection gradients describing micro-evolutionary change (e.g., Lande and Arnold 1983), and coefficients for quadratic terms were doubled (Stinchcombe et al. 2008); see Appendix A. Second, we complemented parametric statistical analyses of phenotypic selection by performing univariate cubic splines (nonparametric regressions) to visualize the form of selection acting on each population (Schluter 1988). We generated these splines using general additive models fit by generalized cross-validation using the program R (R Development Core Team 2010).

RESULTS

Numbers of fish remaining within streams declined through emigration over time in all treatments (ANOVAR, effect of time, $F_{11,73} = 641.70$, $P < 0.001$), but showed the largest and most rapid declines in the spatially predictable treatment (ANOVAR, effect of

treatment, $F_{11,73} = 65.51$, $P < 0.001$; Fig. 1). Emigration ceased after 11–17 d, with population abundance taking fewer days to stabilize in streams with increasing predictability of food resources (ANOVA, $F_{2,9} = 11.95$, $P = 0.003$; Fig. 1). The number of fish remaining within streams at the end of the experiment ranged from 22 to 31 individuals (a reduction of 43–63%), and decreased with increasing predictability in food resources (ANOVA, $F_{2,9} = 19.82$, $P < 0.001$; Fig. 1). Despite all three treatments receiving the same total amount of food, predictable streams supported 14–24% fewer fish at the end of the experiment than streams with intermediate ($P = 0.029$) or low predictability in food resources ($P < 0.001$), respectively.

Foraging behavior

Spatial predictability of food resources influenced the proportion of fish adopting territorial vs. floater foraging tactics within each stream (ANOVAR on arcsine-transformed proportions, $F_{2,81} = 95.11$, $P < 0.001$). With increasing spatial predictability of food resources, a higher proportion of fish held feeding territories, and the magnitude of the difference increased over time, giving rise to a significant treatment $\times$ time interaction (ANOVAR, $F_{2,81} = 6.56$, $P < 0.001$; Fig. 2).

For fish acquiring territories, mean territory size increased over time in all streams (ANOVAR, $F_{6,64} = 37.13$, $P < 0.001$; Fig. 3a–c), with no effect of treatment (ANOVAR, $F_{2,70} = 0.57$, $P = 0.58$) and no interaction of treatment $\times$ time (ANOVAR, $F_{6,64} = 0.80$, $P = 0.55$). In streams with spatially predictable food resources, territory size was smaller in feeding patches with higher food inputs (ANOVAR, $F_{2,70} = 5.60$, $P = 0.026$; Fig. 3a), but the magnitude of these differences did not increase over time and therefore did not produce time $\times$ patch quality interactions (ANOVAR, $F_{6,64} = 0.89$, $P = 0.56$). In streams with medium or low spatial predictability of food resources, there was no association between the amount of food delivered to a patch and territory size

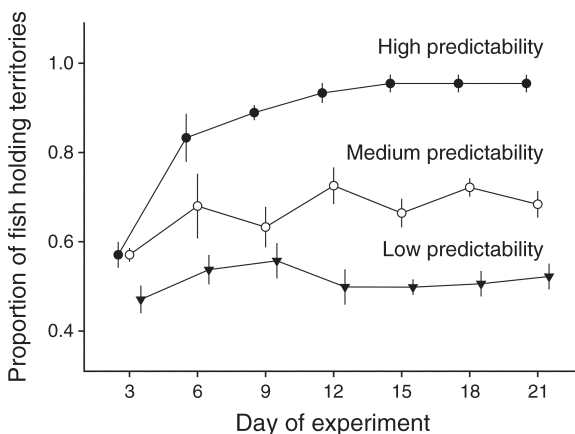


FIG. 2. Proportion (mean $\pm$ SE) of juvenile steelhead trout holding territories in streams with high, medium, or low levels of spatial predictability of food resources.

(ANOVAR, intermediate predictability, $F_{2,70}=0.43$, $P=0.66$; low predictability, $F_{2,70}=0.88$, $P=0.45$; Fig. 3b, c).

In all treatments, territory holders had a significantly higher number of foraging attempts than floaters (paired t tests, high predictability, $t_6=4.29$, $P=0.005$; medium predictability, $t_6=7.41$, $P<0.001$; low predictability, $t_6=3.73$, $P=0.01$; Fig. 4a, b). The difference between territory holders and floaters in the number of foraging attempts was greatest in streams with high spatial predictability of food resources (difference of 2.07 ± 1.18 foraging attempts/3 min, mean and 95% CI), and smallest in streams with the lowest spatial predictability (difference of 0.69 ± 0.45 foraging attempts/3 min, mean and 95% CI). Within foraging behavior types, treatment had a significant effect on the number of foraging attempts, with territory holders having more foraging attempts, on average, when the spatial predictability of food resources was higher (ANOVAR, $F_{2,70}=14.70$, $P=0.001$; Fig. 4a). Floaters had a significantly higher number of foraging attempts as the spatial predictability of food resources decreased (ANOVAR, $F_{2,70}=6.51$, $P=0.018$; Fig. 4b).

Territory holders and floaters also differed in their rates of agonistic interactions (Fig. 4c, d). In all treatments, territory holders had significantly fewer agonistic interactions, on average, than floaters (paired t tests, high predictability, $t_6=13.83$, $P<0.001$; medium predictability, $t_6=5.79$, $P=0.001$; low predictability, $t_6=4.21$, $P=0.006$; Fig. 4c, d). The difference in mean agonistic rates between territory holders and floaters was greatest in streams with high spatial predictability of food resources (difference of 5.42 ± 0.92 interactions/3 min, mean and 95% CI), and smallest in streams with the lowest spatial predictability of food resources (difference of 2.05 ± 1.19 interactions/3 min, mean and 95% CI). Differences between behavioral types in the direction of agonism were also apparent: across all treatments, floaters were the recipients of attacks in 92% of their agonistic interactions, whereas territorial fish were aggressors in 84% of their agonistic interactions. Within foraging behavior types, treatment had a significant effect on agonistic rates, with territory holders having higher agonistic rates, on average, when the spatial predictability of food resources was lower (ANOVAR, $F_{2,70}=7.82$, $P=0.011$; Fig. 4c). On average, floaters had significantly higher agonistic rates as the spatial predictability of food resources increased (ANOVAR, $F_{2,70}=12.45$, $P=0.003$; Fig. 4d).

Fish size

Growth of fish within the stream channels was also affected by the spatial predictability of food resources. For fish remaining within the stream channels until the end of the experiment, fish length was 42.4 ± 2.5 mm (mean $\pm$ SD), and fish mass was 0.71 ± 0.15 g (mean $\pm$ SD). Mean fish length increased with increasing spatial predictability of food resources (ANOVA, $F_{2,9}=15.76$, $P=0.001$). Fish in streams with spatially predictable

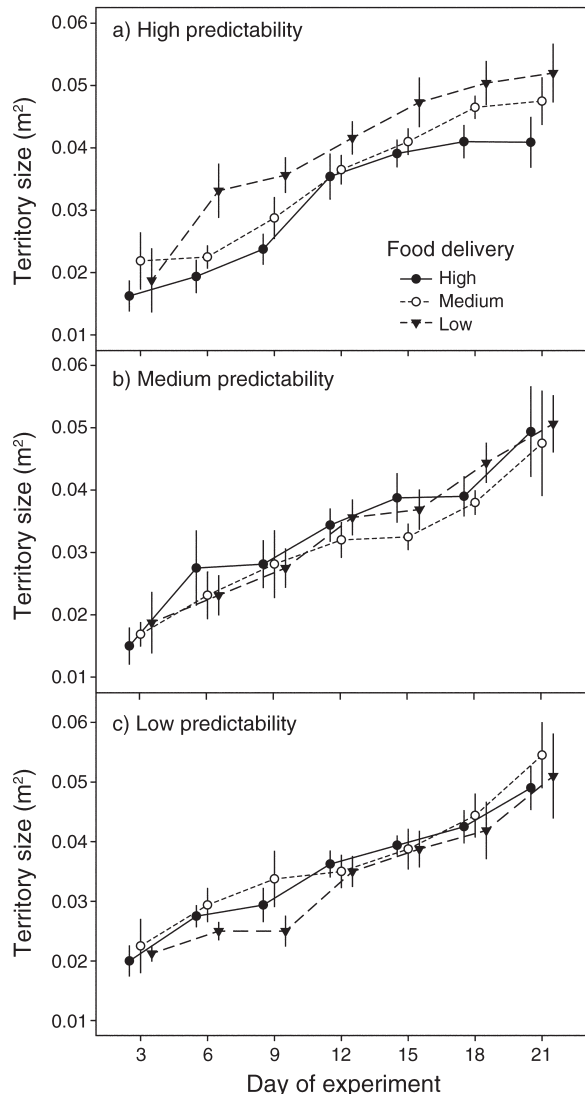


FIG. 3. Territory size (mean $\pm$ SE) for juvenile steelhead trout occupying high-, medium-, or low-quality food patches (food delivery) in experimental streams with (a) high, (b) medium, or (c) low levels of spatial predictability of food resources.

food resources were, on average, 6.4% (95% CI 1.3–8.0%) and 3.5% (95% CI 0.9–4.6%) longer than fish in streams where food resources had intermediate or low spatial predictability, respectively. We also detected treatment effects on mean fish mass (ANOVA, $F_{2,9}=6.34$, $P=0.019$), but significant differences were restricted to contrasts between the high and intermediate predictability treatments ($P=0.02$). In addition to treatment effects on mean values, length and mass frequency distributions showed significant differences in growth depensation among treatments (ANOVA, length, $F_{2,9}=13.83$, $P=0.002$; ANOVA, mass, $F_{2,9}=15.59$, $P=0.001$; Fig. 5a, b). Gini coefficients for length and mass variation were lowest in streams with high

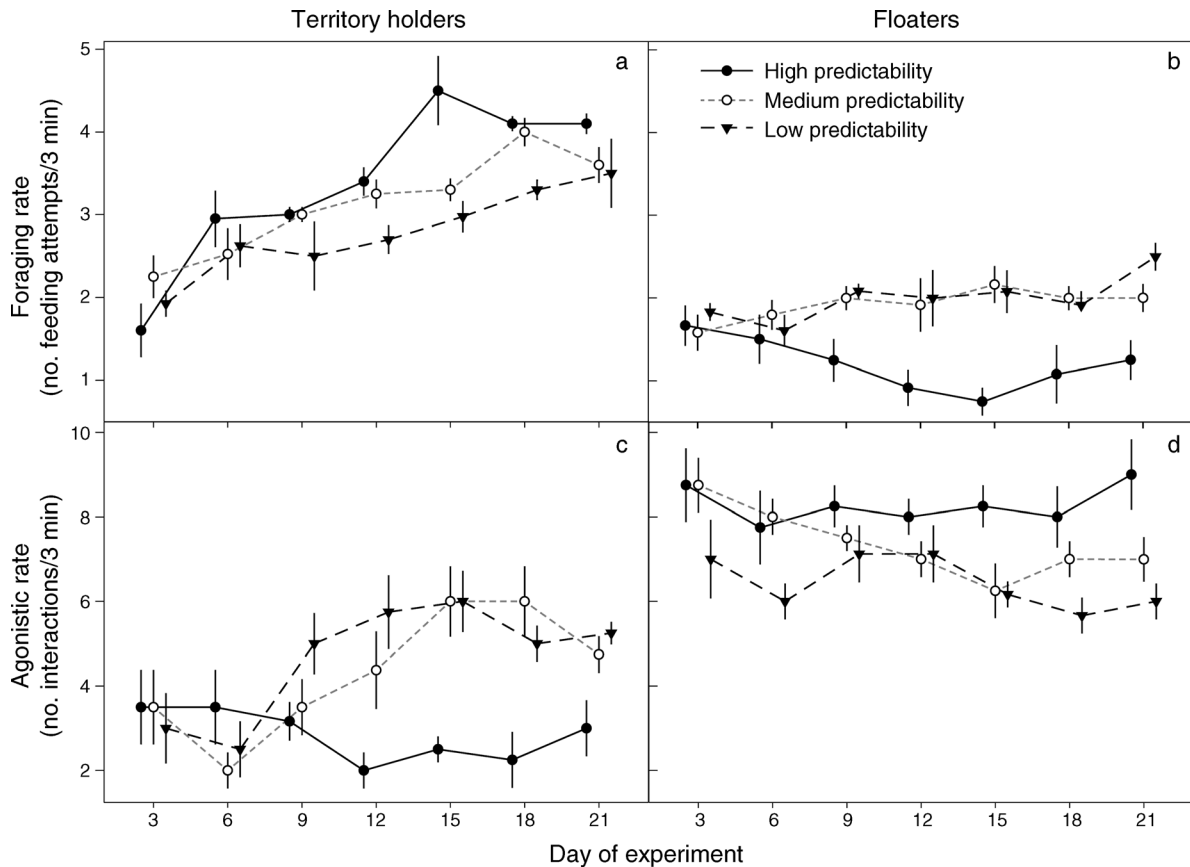


FIG. 4. Foraging rates (number of feeding attempts per 3-min observation period) for (a) territory holders and (b) floaters, and agonistic rates (number of agonistic interactions per 3-min observation period) for (c) territory holders and (d) floaters in streams with high, medium, and low levels of spatial predictability of food resources. Error bars show 95% CI.

spatial predictability of food resources (Fig. 5c), indicating that high spatial predictability in food resources reduced variation in body size. Because of the relatively small numbers of fish remaining within the streams at the conclusion of the experiment (Fig. 1), we pooled data from streams within each treatment to examine correlations between SMR and individual fish growth. Significant correlations between SMR and fish growth were limited to streams with high spatial predictability of food resources, where SMR, as measured by otolith size at the start of the experiment, was moderately and positively correlated with both fish fork length and mass ($n = 88$; for length, $r = 0.30$, $P = 0.005$; for mass, $r = 0.28$, $P = 0.010$). Total biomass per stream ranged from 14.8 g/m^2 to 21.0 g/m^2 by the end of the experiment, with treatment having no effect on mean biomass (ANOVA, $F_{2,9} = 0.08$, $P = 0.92$).

Selection on SMR

SMR, as measured by otolith size at the start of the experiment, and initial body size were not significantly related (linear regression, $F_{1,26} = 3.34$, $P = 0.08$). Logistic regression analysis of the relationship between SMR at the start of the experiment and the probability

of an individual remaining within a stream for the duration of the experiment revealed both directional and nonlinear selection acting on this trait (Table 1). In the spatially predictable treatment, directional selection gradients were positive in all stream replicates, indicating that individuals with high SMR at the time of stocking were more likely to remain within the streams. Quadratic (nonlinear) selection gradients were consistently positive, suggesting some selective loss of individuals with intermediate SMR, but these coefficients only approached statistical significance in formal analyses of selection when data from replicate streams were pooled (Table 1). In streams intermediate in the spatial predictability of food resources, directional coefficients were a mix of positive and negative values, with none differing significantly from zero. Quadratic coefficients were consistently positive and were statistically significant in two of the four streams, suggesting that individuals with extreme values of SMR were more likely to remain within streams than those with intermediate SMR (Table 1). In streams with low spatial predictability of food resources, directional coefficients were consistently negative and statistically significant in three of four streams, indicating that

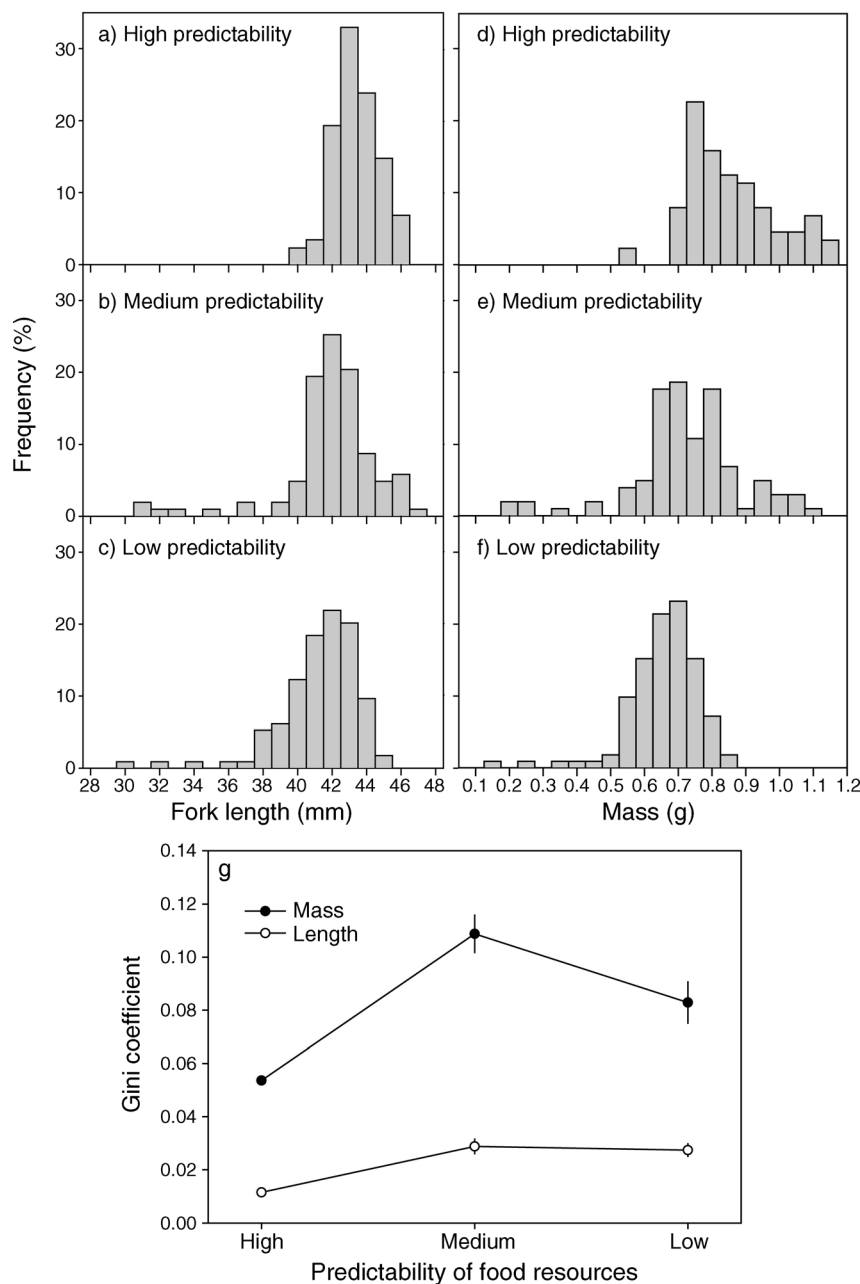


FIG. 5. Fork length (a–c) and mass (d–f) frequencies for juvenile steelhead trout within streams with high, medium, and low levels of spatial predictability of food resources. (g) Gini coefficients (mean $\pm$ SE) measuring variability within fork length and mass distributions.

individuals with lower SMR at the time of stocking were more likely to remain within streams (Table 1). Quadratic coefficients did not differ from zero in streams with low spatial predictability of food resources (Table 1).

Visualization of selection surfaces with cubic spline plots confirmed overall patterns of directional and quadratic selection on SMR identified by logistic regression (Fig. 6a–c). Selection on SMR was positively

directional and possibly disruptive in streams with high spatial predictability in food resources (Fig. 6a). In streams with intermediate spatial predictability, selection on SMR showed little directionality but demonstrated consistent evidence for disruptive selection (Fig. 6b). In streams with low spatial predictability of food resources, selection surfaces were directional, consistently negative, and showed little evidence for either disruptive or stabilizing selection (Fig. 6c).

TABLE 1. Directional (linear) and quadratic (nonlinear) selection acting on an index of standard metabolic rate (SMR) in juvenile steelhead trout (*Oncorhynchus mykiss*) stocked in experimental streams with varying levels of spatial predictability of food resources.

Spatial predictability of food	Directional selection gradients		Quadratic selection gradients	
	β	95% CI	γ	95% CI
Predictable				
Stream B	0.17	0.03 to 0.31	0.41	−0.13 to 0.30
Stream E	0.26	0.10 to 0.41	0.71	−0.15 to 0.38
Stream G	0.27	0.20 to 0.35	0.90	−0.10 to 0.45
Stream I	0.22	0.08 to 0.35	0.39	−0.14 to 0.30
Replicates pooled	0.20	0.13 to 0.27	0.54	−0.01 to 0.22
Intermediate				
Stream D	0.02	−0.11 to 0.15	0.14	−0.17 to 0.23
Stream F	0.01	−0.12 to 0.14	1.44	0.07 to 0.53
Stream H	−0.08	−0.22 to 0.05	0.20	−0.15 to 0.25
Stream K	−0.06	−0.19 to 0.07	1.16	0.01 to 0.50
Replicates pooled	−0.03	−0.09 to 0.04	0.68	0.05 to 0.25
Unpredictable				
Stream A	−0.24	−0.35 to −0.12	−0.10	−0.26 to 0.23
Stream C	−0.12	−0.25 to 0.02	0.11	−0.20 to 0.25
Stream J	−0.15	−0.29 to −0.01	0.82	−0.05 to 0.40
Stream L	−0.19	−0.34 to −0.04	0.10	−0.27 to 0.31
Replicates pooled	−0.16	−0.23 to −0.09	0.23	−0.07 to 0.17

Notes: Selection gradients for stream replicates and data pooled across treatment replicates are transformed from logistic regression coefficients (see Appendix A). Boldface entries indicate coefficients that were significant at $\alpha = 0.05$.

DISCUSSION

Although individual behavior has long been thought to influence ecological processes that regulate populations (e.g., Łomnicki 1988), empirical studies that test the mechanistic linkages between behavioral and population ecology have lagged behind theory (Anholt 1997; but see Anholt 1990, Levin et al. 2000). Our study is one of the first to determine how behavioral changes induced along a gradient in spatial predictability of food resources influence animal population regulation. In response to decreased spatial predictability of food resources, juvenile steelhead trout altered their foraging tactics. Nearly all fish remaining within spatially predictable streams established feeding territories that they defended through agonistic interactions with neighboring territory holders. In streams with intermediate or low spatial predictability of food resources, fewer fish were territorial, with approximately one-third to one-half of the experimental populations foraging as non-territorial “floaters” (Puckett and Dill 1985). Decreased dependence on feeding territories with decreasing predictability in food resources is expected under the economic defendability hypothesis because the potential benefits of energy spent in aggressively defending a territory are less certain (Brown 1964). With decreasing spatial predictability of food resources, there probably were fewer territories of sufficient quality to provide a net energy benefit to resource defense.

The reduction in territoriality among juvenile steelhead trout experiencing decreased spatial predictability of food resources may represent an environmentally induced shift in the relative strengths of interference and

exploitative competition within experimental populations. Because behavioral interactions can be an integral component of population demography (Levin et al. 2000), a shift in the form of intraspecific competition should result in changes in the modes of population regulation. Accordingly, in spatially predictable streams, steelhead trout populations were regulated to stable densities primarily through interference competition for feeding territories and selective emigration of subordinate individuals. Territory sizes were progressively smaller in feeding patches with higher food inputs, resulting in increased local fish densities in higher quality patches. Consequently, the distribution of fish among patches within predictable streams was consistent with the food input-matching expectations of the ideal free distribution, IFD (Fretwell and Lucas 1970). An apparent outcome of matching within-patch fish abundance and food quantity was an increase in the mean size and a decrease in size inequality of steelhead trout in predictable streams relative to streams with lower spatial predictability of food resources. Thus, despite a fourfold difference in the quantity of food delivered among patches within streams, variation in fish size was reduced through patch-specific adjustments in territory size and fish abundance when the spatial distribution of feeding patch quality was predictable.

Streams with lower predictability in the spatial distribution of food resources supported, on average, a greater number of smaller fish. Because food and space exert complementary controls on stream salmonid populations (Keeley 2001), the increased prevalence of floaters and decreased proportion of territory holders may have facilitated higher fish abundance in streams

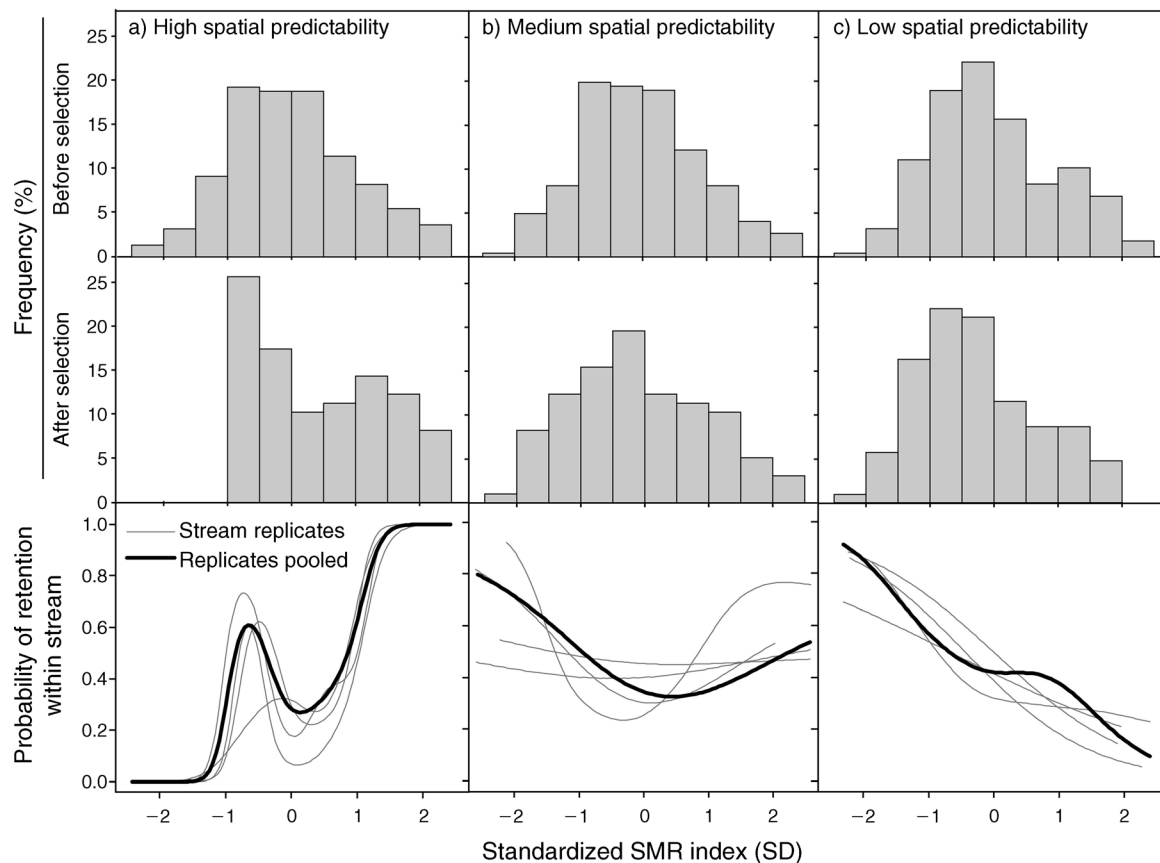


FIG. 6. Phenotype frequency for an index of standard metabolic rate (SMR) in juvenile steelhead trout at the beginning (top row) and end (middle row) of an experiment in streams with (a) high, (b) medium, and (c) low levels of spatial predictability of food resources. The bottom row shows results from cubic spline analysis of the probability of fish remaining within streams for the duration of the experiment as a function of standardized SMR expressed in units of standard deviations (SD) from a phenotypic mean of zero.

with lower predictability of food resources by relaxing the constraints of space on abundance. For example, floaters were less likely to be attacked by territory holders in streams with lower spatial predictability of food resources, suggesting that there was more undefended space available for floaters to exploit in these streams. Thus, even while the total input of food remained constant across treatments, streams with lower spatial predictability of food resources supported higher fish densities due to the reduced intensity of interference competition for space.

The increased abundance of fish in streams with lower spatial predictability of food resources was matched by a compensatory reduction in mean fish size and an increase in size inequality among individuals. Several factors may have contributed to the reduction in mean fish size, including density dependence in growth, and a mismatching of patch-specific fish abundance and food quantity. Our results suggest that the increased prevalence of floater foraging tactics in streams with lower spatial predictability in food resources also may have produced strong effects on size–frequency differences

among treatments. Floaters were less successful at acquiring food and experienced more agonistic interactions, and thus probably experienced growth relative to territory holders (Puckett and Dill 1985). The higher proportion of individuals adopting floater foraging tactics may explain the increasingly negatively skewed size–frequency distributions and greater degree of size inequality that accompanied declines in the spatial predictability of food resources. Although a pattern of increasing size inequality is often attributed to the intensity of competition (Keeley 2001), our results provide experimental evidence for predictions that the form of intraspecific competition also influences the distribution of animal sizes within populations (Łomnicki 1978).

In addition to effects on fish size frequencies, differences in the spatial predictability of food resources strongly influenced patterns of selection on physiological phenotypes within steelhead trout populations. Individuals with higher SMR were favored in streams with spatially predictable food resources, as evidenced by the selective retention of individuals having, on average,

larger otoliths at the time of stocking. The advantage of higher levels of SMR in spatially predictable habitats reflects the strong correlation between SMR and dominance during interference competition in salmonid fish that has previously been shown both through direct measurement of SMR (e.g., Metcalfe et al. 1995, McCarthy 2001) and by using otolith size as a proxy for individual differences in SMR (Titus and Mosegaard 1991, Metcalfe et al. 1992, Yamamoto et al. 1998). Consequently, individuals with higher SMR may offset their increased energy costs of maintenance by monopolizing food resources through territoriality, but apparently only in streams where food resources are economically defendable. This may help to explain the moderate, but significant, positive correlation between SMR and fish growth observed exclusively in spatially predictable streams, a result similar to a recent experimental analysis of juvenile Atlantic salmon *Salmo salar* (Hoogenboom et al. 2013).

The selective advantage of higher SMR should be reduced or neutralized when resources are less defendable and the energy costs of territoriality are not compensated by increased food acquisition (Hoogenboom et al. 2013). Consistent with this expectation, individuals with high SMR were selected against and those with low SMR were favored in highly unpredictable streams. Similarly, in streams with intermediate levels of spatial predictability in food resources, where selection on SMR tended to be disruptive, there was not a clear advantage of high SMR. Visualization of selection surfaces using cubic splines suggested consistent patterns of disruptive selection on SMR, although quadratic selection coefficients from parametric selection analyses were only statistically significant in two of the four streams. Disruptive selection on SMR may have occurred if individuals with intermediate levels of energy metabolism had neither a sufficient level of aggression to acquire a feeding territory, nor low enough maintenance energy demands to balance the lower food intake rates provided by the floater foraging tactic. Taken together, the alternative modes of selection that we observed indicate that variation in the spatial predictability of food resources during early ontogeny in stream salmonids may result in physiologically divergent cohorts.

Conclusions

Our results illustrate that individual and population responses to heterogeneous but spatially predictable food resources support several key predictions of IFD models (Fretwell and Lucas 1970). In spatially predictable environments, individuals that could monopolize resources through territoriality were favored, with territory size and within-patch animal density adjusting to habitat patch quality. These compensatory adjustments resulted in more even partitioning of resources among individuals and tended to reduce variance in components of fitness (e.g., growth) across heterogeneous environments. However, when the spatial predict-

ability of resources declined to a point at which resource defense became uneconomical for significant numbers of individuals, populations did not conform to IFD predictions. Low spatial predictability of resources resulted in a greater total abundance of animals, but a mismatch between patch-specific animal abundance and food quantity, greater discrepancy in the partitioning of food resources among individuals, and physiologically diverging populations. Our results indicate that the spatial predictability of food resources can be an important determinant of individual and population characteristics. We suggest that spatial predictability of resources is an important but understudied component of habitat structure. Studies that manipulate the spatial predictability of resources may be especially promising for integrating dynamics of individual behavior, habitat selection, and population demography.

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SUPPLEMENTAL MATERIAL

Appendix A

Summary of logistic regression selection analyses ([Ecological Archives E095-215-A1](#)).

Appendix B

Schematic of stream mesocosms and experimental layout ([Ecological Archives E095-215-A2](#)).

Appendix C

Schematic of experimental feeding regimes for stream mesocosms ([Ecological Archives E095-215-A3](#)).