

Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids

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I experimentally tested two predictions of the hypothesis that the positive relationship between habitat diversity and species diversity arises from a reduction in the negative effects of interspecific competition. By allowing species to partition habitat and avoid competition, habitat diversity should 1) facilitate the addition of an ecologically intermediate species into an existing community, and 2) reduce the negative effects of that species on existing members of the community. I tested these predictions with juveniles of three sympatric salmonid species: coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarki*), which in natural streams occupy deep low-velocity pools, shallow high-velocity riffles, and intermediate habitats, respectively. I introduced two (coho and steelhead) and three species communities into each of three artificial stream habitats: pools, riffles, and diverse. The results provide partial support for the predictions. Cutthroat trout grew fastest in the diverse stream habitat. Though habitat diversity did not eliminate the negative effects of competition, in the three species community coho and steelhead grew as fast in the diverse habitat as in either homogeneous habitat. The results are consistent with data on species number and evenness from natural communities, where variation along other niche axes confounds the relationship between habitat diversity, interspecific competition, and species diversity.

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Few ideas in ecology enjoy the historical legacy, intuitive appeal, and empirical support as does that of a causal relationship between habitat diversity and species diversity (Elton 1933, MacArthur and MacArthur 1961, Pianka 1966, MacArthur 1972, Ricklefs and Schluter 1993, Rosenzweig 1995). The pattern has evolutionary and ecological explanations, each of which involves the partitioning of habitat (defined here as “the physical arrangement of objects in space” following McCoy and Bell (1991)) and/or consumable resources by ecologically similar species (MacArthur and Wilson 1967, Rosenzweig 1995). Habitat diversity may promote speciation if traits related to differential habitat utilization strengthen reproductive isolation between phenotypically divergent forms (Mayr 1963, Rosenzweig 1978, Futuyma 1986, Schluter 1996). If species

have different habitat requirements, habitat diversity may increase species diversity regardless of competitive interactions. Alternatively, habitat diversity may increase species diversity by reducing the negative effects of interspecific competition and the chance of competitive exclusion (MacArthur and Levins 1964, 1967, Levins 1968, Schoener 1974, Abrams 1983).

Empirical support for the “competition hypothesis”, that habitat diversity increases species diversity by reducing the negative effects of interspecific competition, is unsatisfying for two related reasons. First, habitat diversity is usually directly or indirectly related to productivity (MacArthur 1964, Pianka 1967, Whiteside and Harmsworth 1967, Kohn 1968, Orians 1969, Murdoch et al. 1972, Anderson 1978, Gorman and Karr 1978, Tonn and Magnussen 1982, Lawton 1983, Green-

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stone 1984, Kohn and Walsh 1994, Siemann et al. 1998, Hansen 2000), which can independently influence species interactions and species diversity (Connell and Orias 1964, MacArthur 1972, Brown 1973, Davidson 1977, Tilman 1982, Abramsky and Rosenzweig 1984, Huston 1985, Abrams 1988, 1995, Rosenzweig and Abramsky 1993, Rosenzweig 1995, Srivastava and Lawton 1998). Second, changes in habitat diversity are usually related to variation along other environmental niche axes (e.g., consumable resources, predators, parasites, climate, disturbance regimes) that can influence competitive interactions, species' vital rates, and species diversity.

The distinction between habitat diversity and other types of environmental variation is clarified by considering Hutchinson's (1957) definition of the niche "hypervolume" and the conceptually analogous partitioning of interspecific competition along different environmental axes (Birch 1957, Park 1962, May 1975). A species' "fundamental" niche is a volume within a multidimensional space whose axes are different abiotic and biotic conditions (Hutchinson 1957). Species may compete for habitat and resources, resources but not habitat, or habitat but not resources. The latter cases correspond to the two traditional forms of interspecific competition, exploitation and interference, invoked in the competition hypothesis (Birch 1957, Park 1962, Case and Gilpin 1974). Testing whether habitat diversity increases species diversity by reducing the strength of interspecific competition requires that variation along other environmental axes be controlled. I know of no field studies that have done so, and laboratory experiments widely cited as supporting the competition hypothesis actually involve species interactions other than traditional forms of competition (Crombie 1945, Huffaker 1958, Huffaker et al. 1964, Reed 1978).

I used a simple community of three salmonid species (*Oncorhynchus* spp.) to experimentally test two predictions of the competition hypothesis. By allowing ecologically similar species to partition habitat, habitat diversity should: 1) facilitate the addition of an ecologically intermediate species into an existing community, and 2) reduce the negative competitive effects of the additional species on the existing members of the community.

The system

Juvenile coho salmon (*O. kisutch*), steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarkii*) rear in coastal streams in the Pacific Northwest of North America. All three species are anadromous (both trout species also exhibit non-anadromous life histories); coho are semelparous and spend 18 to 30 months in freshwater; both trout species are optionally iteroparous and spend 2 to

5 years in freshwater (Hartman 1965, Trotter 1989, Sandercock 1991). As yearlings all three species forage on insect drift and engage in intra- and interspecific interference competition to acquire and defend energetically favorable positions in the water column (Chapman 1962, Hartman 1965, Fausch 1984, Nielsen 1992, Sabo and Pauley 1997). Favorable foraging positions can result in higher juvenile growth and survival rates, making juvenile growth rate a measure of fitness relevant to populations' vital rates and community composition (Bilton et al. 1982, Quinn and Peterson 1996, Harvey and Nakamoto 1997).

Few streams support populations of all three species; small, low-gradient streams often contain only coho and/or cutthroat, whereas larger, high-gradient streams are dominated by steelhead, with few coho or cutthroat (Hartman and Gill 1968, Reeves et al. 1993). In communities with all three species cutthroat trout are often rare (Bisson et al. 1988, Reeves et al. 1993) and the species partition habitat in a predictable way. Coho occupy energetically favorable pools (deep, low velocity), steelhead occupy energetically demanding riffles (shallow, high velocity), and cutthroat utilize intermediate depths and velocities (Bisson et al. 1988). As in many systems, there is observational evidence that habitat diversity is positively related to species diversity (Reeves et al. 1993), but the hypothesis that habitat diversity reduces the strength of interspecific competition remains untested.

In this experiment I control productivity and variation along other environmental niche axes to test the two predictions of the competition hypothesis: that habitat diversity will 1) increase the growth rate of cutthroat in a three-species community, and 2) reduce the negative effect of cutthroat on coho and steelhead growth rates compared to homogeneous pool and riffle habitats.

Methods

In the spring of 1999, I collected wild fry of all three species soon after emergence from the egg stage. Because of conservation concerns, only coho were taken from natural streams. On 19 March, I collected ≈ 300 cutthroat from a trout hatchery located near the Fraser River in British Columbia, Canada (49°N, 122°W). The fish were a random sample from the offspring of 10 families (one female, one male) of wild cutthroat trout. On 23 April, I pole seined ≈ 400 coho from the Chilliwack River, a tributary to the Fraser River. On 25 May, I collected ≈ 400 steelhead from the Chilliwack River hatchery. The fish were a random sample from the offspring of 12 families (one female, one male) of wild steelhead trout. All fish were held in allopatry in groups of ≈ 100 in identical rearing troughs (3.7 m

length \times 0.35 m width \times 0.20 m depth) from collection until the experiment began on 18 June. Cutthroat and coho were held at 9.5°C and fed maintenance rations of standard hatchery feed (Moore-Clark™ #1 Crumble) from collection until 25 May. From 25 May until 10 June all fish were held at 11°C and fed to satiation one to three times daily. From 11 June to 17 June all fish were held at 11°C and fed to satiation once daily.

The experimental design consisted of three habitat treatments (pool, riffle, and diverse) crossed with two communities (coho and steelhead, all three species) with the six treatments replicated once in each of three blocks ($n = 18$). The experimental units were small stream channels screened at both ends (wetted surface area: 4 m length \times 0.9 m width). The blocks were arranged so filtered water flowed from a common head tank into the six channels of block one, from each of those channels into block two, then into block three. I manipulated the amount and location of gravel (6 cm diameter from a local quarry) to create two of each habitat type in randomly chosen channels within each block. Pools were uniformly deep with low water velocities. Riffles were uniformly shallow with high water velocities. Diverse habitats were created by splitting the channel into four quadrants with pool and riffle areas on alternate sides in the front and back of the channel with a small riffle transition zone in the center (Table 1). Within each block the two replicates of each habitat type were randomly assigned one of two communities. The two species community consisted of nine coho and nine steelhead; the three species community contained an additional five cutthroat. The entire experimental setup was covered with burlap to simulate canopy

shade and prevent avian predation (I observed none).

I recorded the temperature (to 0.5°C) at the outflow of each channel every 3 d during the experiment. A repeated measures ANOVA revealed that water temperature did not change from block one to block two, but that block three was warmer than the other two (block, $P < 0.0001$) on some days (block \times time, $P < 0.0001$). However, the mean temperatures of the three blocks (calculated as the mean of the six channel means over the 13 sample dates) were similar (blocks 1, 2 = 11.4°C, block 3 = 11.5°C).

The experiment lasted 40 d. On 18 June, I anesthetized fish with tricaine methanesulfate, recorded their standard length (mm) and weight (g) and placed them in the channels (Table 1). From 19 June to 26 July, belt feeders introduced 0.45 g of food (same as above) to each of the 18 channels throughout the day (\approx 0900–1500 hours). On 27 July, fish were removed from the channels using minnow traps, dip netting, and electroshocking, and their standard lengths and weights recorded. I was able to recover all of the fish from only two of the experimental channels. Of the remaining 16 channels, I observed all of the fish in 10 channels, all but one fish in four channels, and all but two fish in the remaining two. In no case were less than four cutthroat, or less than seven coho or steelhead recovered. I used the fish recovered from each channel to calculate the mean absolute growth rate (g/day) for each species as (mean weight out – mean weight in)/40. Preliminary analyses revealed that within communities (two or three species) the mean growth rate of each species did not depend on the number (con-, heterospecific, total) of fish seen or recovered (numbers used as covariates in ANCOVA, all $P > 0.2$). Thus, I assume that the num-

Table 1. Habitat conditions and initial fish sizes of the six treatments. Each number represents the mean of the mean values of the three treatment replicates. The mean values and coefficients of variation (C.V.) for water depth and velocity are based on the same 12 evenly distributed points for each channel. Full factor ANOVAs on body length and size revealed only species effects. Steelhead (mean = 35.7 mm) were longer than coho (35.0, $P = 0.02$) but neither was longer than cutthroat (35.5, $P > 0.1$). Coho (mean = 0.64 g) were heavier than steelhead (0.59, $P = 0.06$) but not cutthroat (0.61, $P > 0.2$).

Variable	Two-species community			Three-species community		
	Pool habitat	Riffle habitat	Diverse habitat	Pool habitat	Riffle habitat	Diverse habitat
Mean depth (cm),	16.6	4.9	9.3	16.4	5.1	9.3
Mean C.V. of depth	12	18	61	13	11	49
Mean velocity (cm/s),	5.7	12.9	10.6	6.4	13.4	8.6
Mean C.V. of velocity	22	14	39	22	14	32
Mean coho length (mm),	34.7	35.0	35.2	35.0	35.1	34.9
Mean S.D. of coho length	1.1	1.4	1.5	1.4	1.6	1.4
Mean coho weight (g),	0.62	0.63	0.65	0.63	0.65	0.63
Mean S.D. of coho weight	0.09	0.12	0.12	0.12	0.13	0.11
Mean steelhead length,	35.6	36.1	35.7	35.5	35.5	35.7
Mean S.D. of sh length	1.6	2.1	1.9	1.7	1.8	1.6
Mean steelhead weight,	0.59	0.61	0.60	0.59	0.59	0.59
Mean S.D. of sh weight	0.11	0.10	0.11	0.09	0.12	0.08
Mean cutthroat length,	NA	NA	NA	35.6	35.3	35.6
Mean S.D. of ct length				1.4	1.6	1.3
Mean cutthroat weight,	NA	NA	NA	0.60	0.59	0.63
Mean S.D. of ct weight				0.1	0.12	0.07

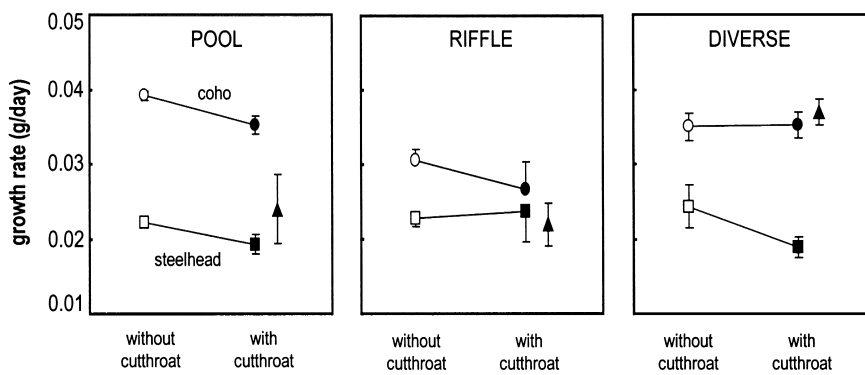


Fig. 1. The mean growth rates of the three species in the two- and three-species communities in each of the three habitats. Coho are the circles, steelhead the squares, and cutthroat the triangles. Each point represents the mean (± 1 SE) of three estimates of the mean growth rate of the species. Open symbols are for the two-species community (coho and steelhead), closed symbols for the three-species community (coho, steelhead, and cutthroat).

ber of fish placed in the channels represented the number during the experiment and the calculated growth rates accurately estimate the actual mean growth rates.

I tested the two predictions of the competition hypothesis using ANOVA (Type III sums of squares) with block (random), habitat, and community composition as main effects. To determine if habitat diversity facilitated invasion by an ecological intermediate, I tested for a significant habitat effect on the mean growth rate of cutthroat trout in the three species community ($n = 9$). To test if habitat diversity reduced the negative effect of cutthroat on the existing members of the community, I tested for a significant habitat \times community interaction effect on the mean growth rates of coho and steelhead using ANOVA ($n = 18$) and MANOVA ($n = 36$).

Results

Habitat diversity facilitated invasion of the community by a rare ecological intermediate. Cutthroat trout grew 54 and 68% faster in the diverse habitat than in pool and riffle habitats, respectively (Fig. 1) ($F_{2,4} = 6.93$, $P = 0.05$). Coho salmon grew significantly faster in pool and diverse habitats than in riffle habitat ($F_{2,10} = 9.55$, $P < 0.005$), but their growth rates were not significantly reduced by the presence of cutthroat trout ($F_{1,10} = 2.30$, $P = 0.16$) in any of the habitat types ($F_{2,10} = 0.69$, $P = 0.52$). Steelhead growth rates were uniformly low and not significantly affected by habitat ($F_{2,10} = 0.93$, $P = 0.43$), the presence of cutthroat ($F_{1,10} = 2.79$, $P = 0.13$), or their interaction ($F_{2,10} = 1.82$, $P = 0.21$). When the growth rates of coho and steelhead are considered together using MANOVA, habitat influenced the effect of cutthroat trout on the two species (habitat \times community: Wilks' lambda = 0.33, $F_{4,18} = 3.3$, $P = 0.03$). In pools the addition of cutthroat depressed the growth rates of both coho and steelhead (by 11 and 10%,

respectively). In riffles the addition of cutthroat reduced the growth rate of only coho (by 11%), whereas in the diverse habitat the addition of cutthroat reduced the growth rate of only steelhead (by 26%). This habitat by community interaction effect is seen more clearly in the effect of cutthroat on the ratio of coho to steelhead growth rates across the three habitat types (Fig. 2). With $\log_{10}(\text{ratio})$ as the dependent variable, ANOVA revealed significant habitat ($F_{2,10} = 25.6$, $P < 0.001$) and habitat \times community interaction effects ($F_{2,10} = 7.85$, $P < 0.01$).

In summary, the results offer partial support for the two predictions of the competition hypothesis. Cutthroat trout grew fastest in the diverse habitat. Though habitat diversity did not eliminate the negative effects of competition, in the three species community the

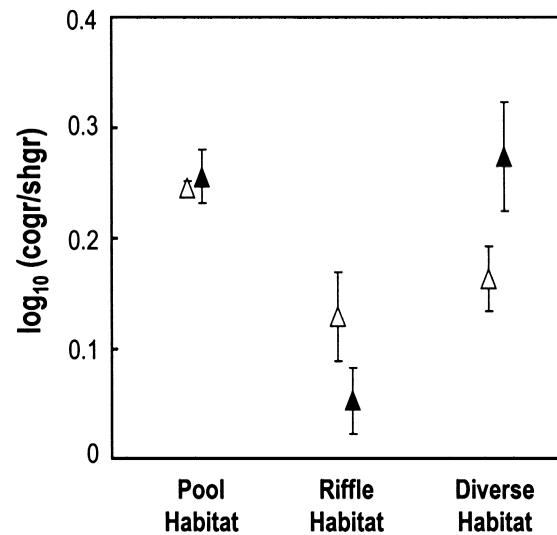


Fig. 2. The ratio of mean coho growth rate to mean steelhead growth rate (\log_{10}) in the three habitat types in the absence (open symbols) and presence (closed symbols) of cutthroat trout. Error bars are ± 1 SE.

growth rates of coho and steelhead in the diverse habitat were as high as in either homogeneous habitat (Fig. 1).

Discussion

This experiment provides one of first explicit tests of the hypothesis that the positive relationship between habitat diversity and species diversity results from a reduction in the strength of interspecific competition. To test the two predictions of the competition hypothesis, I used a simple community of three species with known habitat associations, eliminated predation, and controlled variation along two environmental axes, productivity and resource diversity, that usually confound the relationship between habitat diversity, interspecific competition, and species diversity.

Cutthroat trout, the rare ecological intermediate, grew significantly faster in the diverse habitat. Because cutthroat were not reared in allopatry, we cannot reject the hypothesis that cutthroat grow faster in diverse habitat regardless of interspecific competition. Evidence supports the alternative interpretation that habitat partitioning in the diverse habitat allowed cutthroat to avoid the negative competitive effects of coho. First, cutthroat prefer pool habitat in allopatry, but not in the presence of coho (Glova 1986). Second, coho are not displaced from their preferred pool habitat by either cutthroat (Glova 1986) or steelhead (Hartman 1965). Third, juvenile growth rates of all three species are highest in energetically favorable pool habitat (Quinn and Peterson 1996, Harvey and Nakamoto 1997, Rosenfeld and Boss 2001). If interspecific competition were not important, cutthroat (and steelhead) should have grown fastest in the pool habitat. That cutthroat grew slower in pools, and both coho and steelhead were negatively affected by their presence, suggests that interspecific competition was stronger in this homogeneous habitat. That coho growth was not reduced by the presence of cutthroat in the diverse habitat suggests habitat partitioning reduced the negative effects of interspecific competition between these two species.

The effect of cutthroat on the growth rates of coho and steelhead depended on habitat type. Cutthroat reduced the growth rates of both species in pools, that of coho in riffles, and that of steelhead in the diverse habitat. While habitat diversity did not eliminate the negative effects of cutthroat on coho and steelhead, in the full community all three species grew as fast or faster in the diverse habitat as in the homogeneous habitats. In the energetically demanding riffle habitat, cutthroat reduced the growth rate of coho but not steelhead, which achieved their highest growth rate relative to the other species. In the diverse habitat, where cutthroat had their highest growth rate, steelhead

growth rates were reduced, whereas coho were unaffected. Though I was unable to observe habitat utilization patterns during the experiment, this result suggests that cutthroat were able to successfully intercept drift items from the intermediate habitats between pools and riffles. In the two species community, steelhead did not experience an increased growth rate in the diverse habitat, suggesting they were unable, unwilling, or did not profit from utilizing those same intermediate habitats.

How habitat mediated interspecific competition affects juvenile growth rates likely depends on species' densities and variation along other niche axes, both of which were controlled in this experiment. Were densities increased, coho may have moved into the physically intermediate zones in the diverse habitat, which could reduce their mean growth rate and increase their competitive effect on cutthroat. Predation can influence juvenile foraging behavior and habitat selection (Grand and Dill 1997, Reinhardt 1999), and may affect the three species differently (Abrahams and Healey 1993). Productivity (Hill and Grossman 1993) and resource diversity (Nielsen 1992) can vary with habitat and may independently or interactively affect competitive interactions (Slaney and Northcote 1974) and growth rates (Nielsen 1992). Factorial experiments using this and other communities will help clarify how species' densities, productivity, and variation along other niche axes affect the relationship between habitat diversity, interspecific competition, and species diversity.

I designed this experiment to test the competition hypothesis and the connection between these results and species number and species evenness, the two variables that contribute the traditional indices of species diversity (e.g. the Shannon-Wiener index, H'), is necessarily tenuous. Community composition depends not only on habitat dependent competition between juveniles, but on estuarine habitat (Hartman and Gill 1968) and interspecific differences in marine survival rate, female fecundity, and adult spawning and juvenile emergence success. Still, the congruence between the present results and data from natural communities is encouraging. Steelhead had their highest relative growth rate in the riffle habitat and are numerically dominant in high gradient/velocity streams. Coho had their highest relative growth rate in pools and are numerically dominant in low gradient/velocity streams. In the diverse habitat all three species achieved growth rates equal to or greater than in homogeneous habitats, and natural streams with diverse habitat tend to contain all three species (Hartman and Gill 1968, Bisson et al. 1988, Reeves et al. 1993).

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