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Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients

Yoshinori Taniguchi, Frank J. Rahel, Douglas C. Novinger, and Kenneth G. Gerow

Abstract: Competitive ability changed across a range of 3–26°C among three fish species that show longitudinal replacement in Rocky Mountain streams: brook trout (*Salvelinus fontinalis*) at high elevations, brown trout (*Salmo trutta*) at middle elevations, and creek chub (*Semotilus atromaculatus*) at low elevations. Competitive ability was measured by food consumption and aggression in a stream tank. At ≤20°C, the trout species were competitively equal, and both were competitively superior to creek chub. Creek chub began to have competitive success against brook trout at 22°C and brown trout at 24°C, temperatures stressful but not lethal for the trout. Creek chub became competitively dominant over brook trout at 24°C and brown trout at 26°C, temperatures lethal to a portion of each trout species. We examined whether reduced food consumption was due to appetite loss or the presence of other species. For brook trout, interactions influenced feeding behavior at ≤22°C, but appetite loss became important at 24°C. For brown trout, interactions influenced feeding behavior at ≤24°C, but appetite loss became important at 26°C. For creek chub, there was an interaction between behavioral interactions and appetite in determining food consumption. Field data support a transition from trout to non-trout fishes at 22–25°C.

Résumé : Dans une plage de températures allant de 3 à 26°C, nous avons constaté un changement de compétitivité entre trois espèces de poissonsdont la distribution dénote un phénomène de remplacement longitudinal dans les cours d'eau des montagnes Rocheuses : l'omble de fontaine (*Salvelinus fontinalis*), qu'on trouve en haute altitude, la truite brune (*Salmo trutta*), qui se rencontre à moyenne altitude, et le mulet à cornes (*Semotilus atromaculatus*), qui se retrouve à faible altitude. Nous avons évalué la compétitivité de chacune de ces espèces en observant la consommation de nourriture et l'agressivité de spécimens gardés dans un bassin aménagé au fil de l'eau. À une température ≤20°C, l'omble de fontaine et la truite brune manifestaient la même compétitivité, laquelle était supérieure à celle du mulet à cornes. Celui-ci a commencé à exercer sa prépondérance sur l'omble de fontaine à 22°C et sur la truite brune à 24°C, des températures qui produisent un stress mais non un effet létal chez ces deux espèces. Le mulet à cornes a eu la prédominance sur l'omble de fontaine à 24°C, et sur la truite brune à 26°C, des températures létales, respectivement, pour une partie des poissons de chacune de ces deux espèces. Nous avons cherché à déterminer si la diminution de la consommation de nourriture était due à une perte d'appétit ou à la présence d'autres espèces. Chez l'omble de fontaine, les interactions avec les autres espèces ont eu une influence sur l'alimentation à une température ≤22°C, mais la perte d'appétit est devenue un facteur important à 24°C. Chez la truite brune, les interactions ont influé sur l'alimentation à une température ≤24°C et la perte d'appétit est devenue importante à 26°C. Enfin, chez le mulet à cornes, nous avons constaté que l'interaction avec les autres espèces et l'appétit influaient de manière interactive sur la consommation de nourriture. Les données recueillies sur le terrain concordent avec l'hypothèse du remplacement de l'omble de fontaine et de la truite brune par le mulet à cornes à des températures comprises entre 22 et 25°C.

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Introduction

Species distribution patterns often are the result of biotic interactions mediated by abiotic conditions. For example, a species may be excluded from some habitats by aggression from other species but persist in other habitats because they are more tolerant of abiotic stress than the aggressively dominant species (Baltz et al. 1982). A species may be eliminated by predators in some areas but persist across the landscape by inhabiting refuges where severe abiotic conditions exclude predators (Rahel 1984; Sih 1987). In many cases, the outcome of competition among species can be influenced by changes in abiotic conditions, a process referred to

as condition-specific competition (Dunson and Travis 1991; Warner et al. 1993; De Staso and Rahel 1994). The influence of abiotic conditions on competitive interactions should be most important in regions with strong abiotic gradients. Examples of such gradients include salinity changes in estuaries (Horne and Goldman 1994), changes in light availability with increasing depth in lakes (Spence 1982), and differences in hydroperiod among ephemeral ponds (Wilbur 1987).

Streams exhibit gradients in abiotic factors such as temperature, current speed, and substrate composition as they flow downstream (Vannote et al. 1980). Streams also are characterized by replacement of species along longitudinal gradients (Rahel and Hubert 1991; Fausch et al. 1994). We examined the potential for water temperature to influence competitive interactions among a group of stream fishes that replace each other along elevational gradients in streams of the Rocky Mountain region of North America. Such streams often are dominated by brook trout (Salmonidae: *Salvelinus fontinalis*) at high elevations, followed by brown trout (Salmonidae: *Salmo trutta*) at middle elevations and finally creek chub (Cyprinidae: *Semotilus atromaculatus*) at low elevations (Vincent and Miller 1969; Rahel and Hubert 1991).

Fishes in the family Salmonidae compete through interference competition for foraging sites (Fausch 1988; Nakano 1995). For example, brook trout in a Michigan stream were excluded from preferred resting positions by brown trout (Fausch and White 1981). Creek chub compete with brook trout for food in lake environments (Magnan 1988). In streams, brook trout, brown trout, and creek chub feed extensively on drifting invertebrates (Moshenko and Gee 1973; Allan 1981); thus, competition among the three species is likely to be important in determining which species are successful in a particular environment.

We explored how temperature might mediate the outcome of competition among these three species by testing the hypothesis that brook trout would be the competitively superior species at cold water temperatures, brown trout would be competitively superior at moderate water temperatures, and creek chub would be competitively superior at warm water temperatures. This hypothesis was based on the distribution of these species along elevational gradients in Rocky Mountain streams (Rahel and Hubert 1991) and differences in physiological performance with respect to temperature (Brett 1956; Eaton et al. 1995). We also examined whether the competitive inferiority of a species at a particular temperature was due primarily to loss of appetite or to interactions with the other species. This was done by sequentially removing dominant fish at a particular temperature to see if remaining fish would change their feeding behavior. If the mechanism is primarily loss of appetite, then removal of one fish should have little influence on the performance of remaining individuals. By contrast, if the mechanism is primarily through competition for food, then subordinate fish should consume more food after dominant fish are removed.

Materials and methods

Fish collection and experimental stream
Fish were collected from streams in Albany County, Wyoming. Prior to experiments, fish were held separately by species in 360-L

tanks at 10°C and fed mealworms (*Tenebrio molitor*) and frozen brine shrimp (*Artemia salina*). Experiments were conducted in an oval laboratory stream tank at the Red Buttes Environmental Biology Laboratory of the University of Wyoming (described in De Staso and Rahel 1994). Flow was generated by submersible pumps. Water temperatures were maintained at ±0.2°C by mixing cold and hot well water.

During each experiment, the observer sat in the darkened center of the oval and monitored fish behavior. Two experimental sections (2.0 m long and 0.6 m wide) were created by isolating portions of the stream tank with plastic screen. Each section featured a riffle–pool–riffle transition from upstream to downstream. Water depths were 19 cm in riffles and 29 cm in pools. Water velocities ranged up to 32 cm/s in the headwater riffle, 0–18 cm/s in the pools, and 1–17 cm/s in the tailwater sections. Substrate was a mixture of gravel ranging from 5–25 mm in diameter. Photoperiod was 12L:12D with dawn and dusk simulated by turning on and off two 60-watt incandescent bulbs 20 min before and after the main lights were activated.

Influence of temperature on competitive interactions
Observations were made at seven water temperatures: 3, 6, 10, 20, 22, 24, and 26°C. Fish were held at 10°C at least 2 weeks prior to the onset of thermal acclimation for each experiment. For thermal acclimation, selected fish were placed into individual 360-L acclimation tanks and the temperature was raised or decreased 1°C per day until the test temperature was reached (De Staso and Rahel 1994). Fish then were held at the test temperature for 6 days to ensure thermal acclimation. During acclimation, fish were fed mealworms and brine shrimp once daily.

For each replicate, one fish of each species was placed into the stream tank. To minimize size influences on behavioral dominance, the three species did not differ by more than 10% in fork length within a replicate. The size range of fish across all the replicates was 107–165 mm fork length. Each fish was used in only one replicate. Density of fish in the stream tank was 2.5 fish/m², which is within the range reported for juvenile salmon (Grant and Kramer 1990).

The number of replicates was 10 at 3–20°C, 8 at 22°C, 5 at 24°C, and 6 at 26°C. This variation was due to mortality of some species during thermal acclimation. As discussed in the Results section, this mortality provided insight into differences in thermal tolerances among the species. Each replicate consisted of three components: days 1–2 when dominance relations among the species formed; days 3–4 when we observed aggressive interactions and feeding behavior among all three species; and days 5–8 when dominant fish were removed and behavioral changes in remaining fish were observed. Because our objective was to observe behavioral interactions among the three species, fish were not allowed to emigrate from the stream reach. Food consumption and aggressive interactions were quantified during a 2-h period on days 3–8.

Competitive superiority was based on which species consumed the most food items because food intake often is considered a limiting factor for drift-feeding, stream fishes (Chapman 1966; Hill and Grossman 1993). During the 2-h observation period each day, a mealworm was placed at the upstream end of the tank every 10 min, yielding a total of 13 worms per observation period. Presentation of mealworms was standardized by injecting an air bubble using a hypodermic needle. This caused the mealworms to be buoyant and drift along the water surface. The species that consumed each food item was recorded and the species that ate the most food items on days 3 and 4 within a replicate was considered the superior competitor.

In addition to food consumption, we recorded the number of aggressive interactions initiated by each species during the 2-h observation period because such interactions often are correlated with successful resource acquisition in fish (Bachman 1984; Adams and

1896

Can. J. Fish. Aquat. Sci. Vol. 55, 1998

Fig 1. (*a*) Food consumption in relation to temperature for brook trout, brown trout, and creek chub. Values are mean ± 1 SE for the number of food items eaten by each species during a 2-h period on days 3–4. Values are slightly offset at each temperature for clarity of presentation. (*b*) Aggression in relation to temperature for brook trout, brown trout, and creek chub. Values are mean ± 1 SE for the $\log_{10}$ (number of aggressive acts + 1) initiated by each species during a 2-h period on days 3–4. Values are offset at each temperature for clarity of presentation.
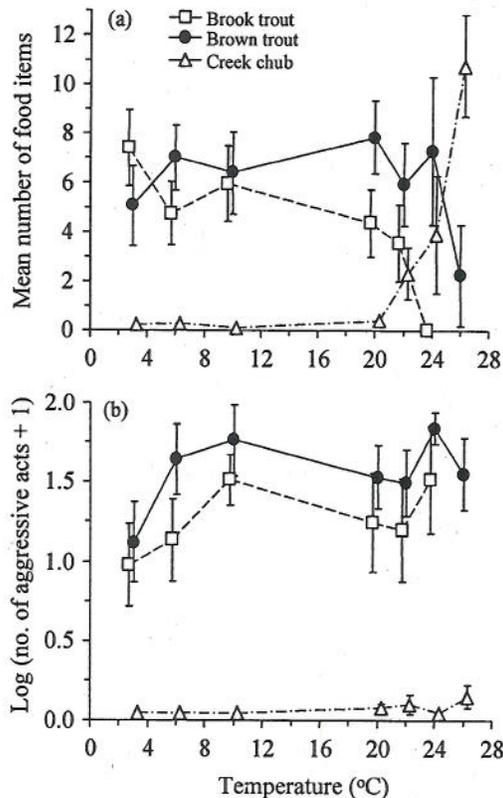
Huntingford 1996). These interactions consisted of chases, nips, and threats as described by Noakes (1980). For all statistical analyses, the number of aggressive acts was transformed by the $\log_{10}$ (number of aggressive acts + 1) to achieve normality in the data.

Statistical analysis involved analysis of covariance (ANCOVA) with the number of food items consumed or the number of aggressive acts as the dependent variable, species identity as the main effect, and temperature as the covariate. We also analyzed the food consumption data in terms of the proportion of food items (arcsine transformed) eaten by each species. Results were similar to the ANCOVA for the number of food items eaten and we present only the ANCOVA results. A significant interaction between species identity and temperature was evidence that competitive superiority depended on water temperature. To determine which species were most aggressive at each temperature, we did one-way analysis of variance (ANOVA) using the number of food items eaten or the number of aggressive acts as response variables and species identity as the treatment variable. Pairwise comparisons were done using Tukey's H.S.D. and an experimentwise error rate of 0.05 except for the trials at 26°C where comparisons were based on *t*-tests because only brown trout and creek chub survived at that temperature.

Assessing appetite loss versus competitive interactions

Removal experiments were conducted on days 5–8 to determine if the performance of competitively-inferior fish was primarily due

to loss of appetite or competition with the other species. We used the removal experiments to distinguish between the following two hypotheses: (A) the low amount of food eaten by the competitively inferior species during a trial was due to the presence of other species or (B) the low amount of food eaten by the competitively inferior species during a trial was due to a loss of appetite reflecting physiological stress. Hypothesis A could reflect interference competition (one species aggressively prevents the other species from access to food) or exploitation competition (one species eats food before the other species can). If hypothesis A is true, food consumption should increase following removal of the other species. If hypothesis B is true, food consumption should not increase following removal of the other species.

The order of species removals varied across replicates depending on the order of species competitive superiority in that replicate. After observations were completed on day 4, the dominant species in each trial was removed, and the remaining two species were observed for the next two consecutive days in the same manner as described above. The number of food items eaten by each species was used to assess competitive superiority. After observations were completed on day 6, the competitively superior fish was removed from the stream tank and another two days of observations were conducted on the remaining individual. The number of food items eaten by this fish was recorded for days 7 and 8.

We determined the change in food consumption for a fish by subtracting the average number of food items consumed in the presence of a competitively superior species from the average number of food items consumed after all competitively superior species were removed. For each species at each temperature, we calculated 95% confidence intervals for the mean change in the number of prey items eaten. Inclusion of zero in the confidence interval would be evidence that a species did not significantly increase its food consumption once other fish were removed. This would indicate that appetite loss, rather than the presence of other species, was responsible for low levels of food consumption by a species at that temperature.

Field distributions in relation to summer water temperature

The laboratory experiments indicated the temperature range where there should be a transition in competitive dominance between trout and creek chub. To determine if this temperature range corresponded with a shift from trout to creek chub in the field, we examined summer temperature data in relation to the occurrence of trout and creek chub in the Horse Creek drainage of southeastern Wyoming. Data on stream temperature and fish community composition at 53 sites were taken from two previous studies (Eifert and Wesche 1982; Hubert and Rahel 1989). Fish community data were based on multiple-pass electrofishing of 100 m reaches. Temperature was measured in midstream with a hand-held thermometer during midday (1200–1700 h) in the summer months of July and August. When multiple temperature records were available for a site, we used the highest temperature because we were interested in maximum summer temperatures in relation to fish distributions. Sites were grouped into three categories: only trout present, both trout and creek chub present, and only creek chub present.

Results

Temperature-related fish mortality

Mortality of fish during thermal acclimation indicated the species could be ranked in order of increasing thermal tolerance as follows: brook trout < brown trout < creek chub. None of the species experienced mortality during acclimation to 3–22°C. During acclimation to 24°C, 2 of 10 brook

Table 1. Analysis of variance comparing the number of food items eaten and the $\log_{10}$ (number of aggressive acts + 1) initiated by each species within a temperature. BKT = brook trout; BRN = brown trout; CKC = creek chub.

| Temperature (°C)	ANOVA results			Species pairwise comparisons
	F	df	P	
Number of food items eaten				
3	7.98	2	0.002	BKT = BRN > CKC
6	10.42	2	<0.001	BKT = BRN > CKC
10	7.07	2	0.003	BKT = BRN > CKC
20	10.00	2	0.001	BKT = BRN > CKC
22	1.57	2	0.232	BKT = BRN = CKC
24	2.70	2	0.108	BKT = BRN = CKC
26	2.92	10	0.015	BRN < CKC
Number of aggressive acts				
3	8.43	2	0.001	BKT = BRN > CKC
6	18.26	2	<0.001	BKT = BRN > CKC
10	35.61	2	<0.001	BKT = BRN > CKC
20	14.06	2	<0.001	BKT = BRN > CKC
22	11.27	2	<0.001	BKT = BRN > CKC
24	23.02	2	<0.001	BKT = BRN > CKC
26	5.98	5	0.002	BRN > CKC

trout died but no mortalities occurred for brown trout or creek chub. During acclimation to 26°C, all 10 brook trout died and 4 of 10 brown trout died, but no mortalities occurred among creek chub. Thus, creek chub were tolerant of even the warmest temperature. Because fish were held individually in separate tanks during thermal acclimation, mortalities reflected thermal stress and not aggressive interactions among the species.

Although no mortality of creek chubs occurred during the thermal acclimation phase, seven creek chubs died during the observation phase when all three fish species were present in the stream tank. Mortalities occurred at all test temperatures except 26°C and were attributable to attacks from trout. Creek chubs lost scales nearly every time they were nipped by trout. Creek chubs that died typically had lost most of the rays in their caudal, dorsal, and anal fins, and hemorrhages were commonly observed.

Influence of temperature on competitive interactions

Reversals in competitive ability were evident based on patterns of food consumption across the temperature range of 3–26°C (Fig 1). For the ANCOVA of food items consumed, the species by temperature interaction was highly significant ($F_{[2,165]} = 10.67$, $P < 0.001$). At temperatures ≤20°C, there was no difference in food consumption between the two trout species, but both consumed significantly more food than creek chub (Fig. 1, Table 1). However, as temperature increased, food consumption by creek chub increased, and the three species did not differ in food consumption at 22°C. At 24°C, the three species again did not differ in food consumption based on the one-way ANOVA (Table 1), although it should be noted that brook trout ate no food items at this temperature. The lack of statistical difference between brook trout and the two other species at 24°C is a reflection of the variability in the food consumption data

Fig 2. Change in food consumption after competitively superior species were removed from the stream tank. Shown are the mean change and 95% confidence intervals for the mean change in the number of food items eaten during a 2-h period. Positive values indicate an increase in food consumption after removal of dominant fish. (a) Number of replicates for brook trout was 4 at 3°C, 8 at 6°C, 4 at 10°C, 4 at 20°C, 4 at 22°C, 5 at 24°C. (b) Number of replicates for brown trout was 17 for 3–24°C and 4 for 26°C. (c) Number of replicates for creek chub was 9 at 3°C, 10 at 6°C, 6 at 10°C, 5 at 20°C, 4 at 22°C, 3 at 24°C. At 26°C, $n = 1$, thus a confidence interval could not be calculated.
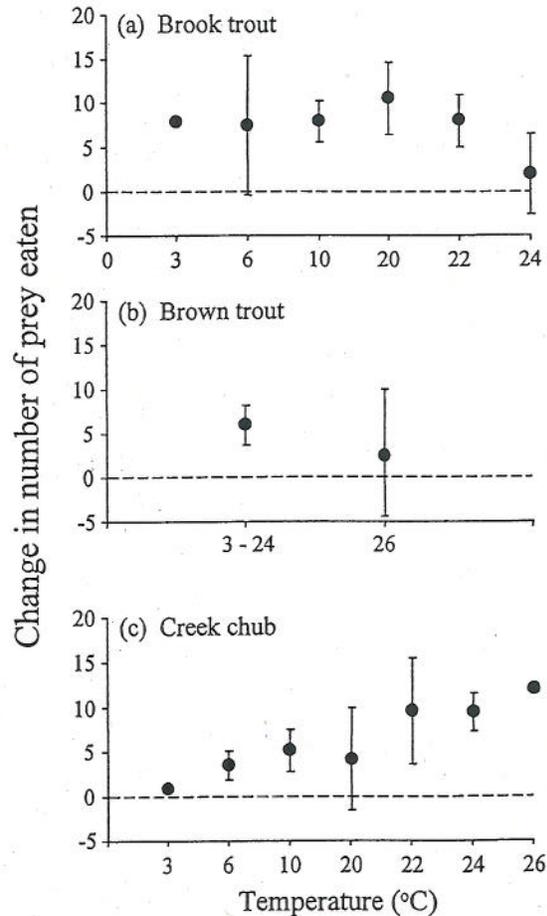
for the other species. At 26°C, creek chub consumed more food than brown trout. Food consumption data could not be collected for brook trout at this temperature because none survived the acclimation process.

The species differed in their level of aggressive behavior (Fig. 1). For the ANCOVA of number of aggressive acts initiated by each species, the species by temperature interaction was not significant ($F_{[2,165]} = 0.18$, $P = 0.836$) and there was no effect of temperature on aggressive behavior ($F_{[1,165]} = 2.26$, $P = 0.135$). However, there was a significant effect of species identity on aggressive behavior ($F_{[2,165]} = 24.67$, $P <0.001$). From 3–24°C, pairwise comparisons indicated that brook trout and brown trout did not differ in the number of aggressive acts initiated, but both species were significantly more aggressive than creek chub (Table 1). At 26°C, brown trout continued to show aggression toward creek chub, al-

Fig 3. Histograms showing the number of sites having (*a*) trout only (*n* = 20), (*b*) brown trout and creek chub (*n* = 7), or (*c*) creek chub only (*n* = 26) in relation to midday summer water temperatures in the Horse Creek drainage in southeastern Wyoming. BKT = brook trout; BRN = brown trout.
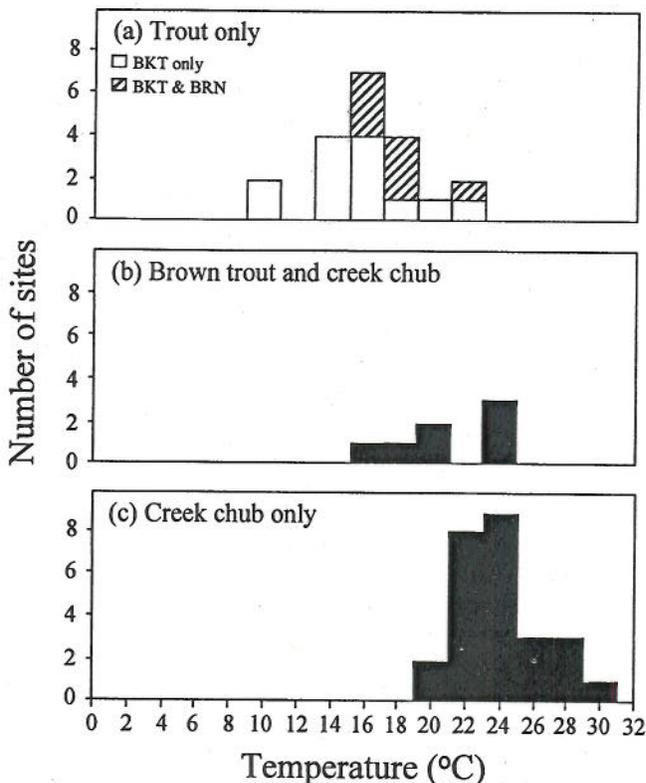
though the intensity of the interactions was reduced. Brown trout maintained positions at the head of the pool whereas creek chub swam throughout the stream tank. Occasionally, a creek chub would approach a brown trout and swim parallel to it, sometimes even bumping into the trout. Sometimes trout would react aggressively and chase the creek chub a short distance and these were recorded as aggressive acts by brown trout against creek chub. Other times, trout would swim away from the creek chub and the creek chub would follow the trout for a short distance. Because the approach by creek chub toward brown trout did not involve nips or aggressive displays, and because the creek chub's behavior could be interpreted as schooling behavior, we did not consider these behaviors to be aggressive acts toward brown trout.

Assessing loss of appetite versus competitive interactions

Changes in food consumption after removal of competitively dominant fish varied with temperature and differed among the three species. For brook trout, there was a significant increase in food consumption at temperatures below 24°C (Fig. 2). This indicates that the presence of other fish species, not loss of appetite, was the reason for low food consumption in trials where brook trout was not the dominant species in the stream. However, at 24°C, there was no significant increase in food consumption and in three of five

replicates brook trout consumed no food items even when they were the only species present. Therefore, at 24°C, lack of appetite, not behavioral interactions, was the likely reason that brook trout did not eat in the presence of other species.

Because brown trout generally consumed more food items and were more aggressive than brook trout or creek chub at all temperatures below 26°C (Fig. 1), they were usually the first species removed. Consequently, the number of replicates where we could observe food intake by brown trout after removal of other species was limited. As a result, we combined the data into two temperature categories: unstressful temperatures (3–24°C) where no mortality occurred during thermal acclimation and a stressful temperature (26°C) where 40% of brown trout died during thermal acclimation. For the temperature range of 3–24°C, brown trout ate significantly more food when competitively dominant fish were removed (Fig. 2). This indicates that behavioral interaction, not lack of appetite, was the reason for low food consumption in trials where brown trout was not the dominant species in the stream at temperatures of 3–24°C. At 26°C, brown trout were under physiological stress and did not significantly increase their food consumption. In fact, in three of four replicates at 26°C, brown trout did not feed, even when they were the only species in the stream tank.

Creek chub increased their food consumption when trout were removed and the magnitude of the change increased with temperature (Fig. 2). Thus, there was an interaction between behavioral and physiological factors in determining the extent of food consumption by creek chub.

Field distributions in relation to midday summer water temperature

At sites that contained only trout in the Horse Creek drainage, brook trout were the only species present below 15°C, whereas both brook trout and brown trout were present in the range of 15–23°C (Fig. 3). A few sites contained both brown trout and creek chub, and recorded temperatures at these sites did not exceed 25°C. No sites contained both brook trout and creek chub. At sites with creek chub but no trout present, temperatures ranged up to 31°C. Thus, the transition in competitive ability from 22–24°C in the laboratory experiments was supported by a transition in community composition from trout to creek chub at a similar temperature range in the field.

Discussion

Temperature mediation of competitive interactions was evident among the three fish species. The two species of trout were competitively superior to creek chub at temperatures ≤20°C as demonstrated by their greater food consumption and aggression toward creek chub. However, creek chub began to have competitive success against the brook trout at 22°C and the brown trout at 24°C (Fig. 1), temperatures that were stressful but not lethal for those species. By 26°C, a complete reversal in competitive dominance occurred with creek chub a superior competitor over brown trout. Reversal in competitive dominance due to temperature also was reported for sculpins and dace in a California stream (Baltz et al. 1982). Laboratory experiments and field observations re-

vealed that riffle sculpin (*Cottus gulosus*) were aggressively dominant over speckled dace (*Rhinichthys osculus*) at cool temperatures. However, sculpin could not tolerate the warm temperatures typical of a downstream site in summer and lost their competitive advantage over dace during that season. In winter, water temperatures cooled and sculpin became dominant again.

The failure of brook trout to be competitively dominant over brown trout at cold temperatures in our laboratory experiments is at odds with observations that brook trout often exist allopatrically in high elevation reaches of streams dominated by brown trout downstream (Vincent and Miller 1969; Gard and Flittner 1974; Rahel and Hubert 1991). Several factors could explain the discrepancy between these field observations and our laboratory results. First, there may be differences in foraging success or aggressive behavior at temperatures below 3°C and competitive reversal might occur at temperatures colder than we could create in our stream tank. Second, even if the species consume the same amount of food at cold temperatures, differences in energy assimilation efficiency may allow brook trout to grow faster which would give them a competitive edge (Brett and Groves 1979). Third, winter is a stressful time for fish and brook trout may be better able to resist starvation during long periods of low food availability at cold temperatures (Shuter and Post 1990). Species differences in behavioral and physiological responses to extreme cold would be a fruitful area of research because water temperatures in Rocky Mountain streams may remain near 0°C for up to 6 months of the year (Allan 1982). Finally, it may be that factors other than temperature favor brook trout over brown trout at high elevation sites. Such factors could include high stream gradient or limited areas of spawning gravel (Fausch 1989).

The changes in feeding success and the pattern of mortality during thermal acclimation indicate that the three species can be ranked in order of increasing thermal tolerance as follows: brook trout, brown trout, and creek chub. These rankings are supported by studies of physiological performance in relation to temperature. The upper thermal limit for both brook trout and brown trout has been reported to be near 25°C but the temperature at which growth is maximum is lower for brook trout (14.4°C) than for brown trout (18.0°C) (Eaton et al. 1995). Although the temperature of maximum growth for creek chub has not been investigated, they have an upper lethal temperature of 30°C (Brett 1956) and thus are tolerant of warmer temperatures than either of the trout species.

Our laboratory observations of competitive interactions and the field data on species distributions in relation to water temperature both indicate that the transition from trout to creek chub dominance occurs in the temperature range of 22–25°C. Other studies have reported a similar thermal limit for the occurrence of trout in streams. Barton et al. (1985) reported that maximum summer water temperature below 22°C was the main factor distinguishing trout from non-trout streams in Ontario, Canada. Meisner (1990) monitored fish distributions in two southern Ontario streams and found the upper thermal limit of brook trout was 23–24°C. A compilation of fish distributions and stream temperature data

throughout the U.S. found that the highest weekly mean temperature associated with the presence of brook trout was 22.3°C, and for brown trout, 24.1°C (Eaton et al. 1995).

In our experiments, the mechanism of competition was different for the two trout species in comparison to the cyprinid species. Brook trout and brown trout defended territories and forcefully evicted intruders through chases and nips. The territories were generally at the head of the pool and gave the behaviorally dominant fish first access to food drifting from the upstream riffle area. This is a classic example of interference competition whereby individuals aggressively defend resources and make them unavailable to competitors. Interference competition is a dominant feature of interactions among stream salmonids (Noakes 1980; Fausch 1988). By contrast, exploitation competition appears to be the mechanism by which creek chub obtained food at 22–26°C. Creek chub did not defend feeding territories in the same manner as the trout species. Instead, at warm water temperatures, creek chub swam actively around the stream tank, avoiding attacks by the trout and attempting to reach drifting food items before the trout. As water temperature increased, creek chubs had increasing success at capturing food items and depressing resource levels for the other species, a classic example of exploitation competition. Exploitation competition also appears to be the mechanism by which creek chubs successfully compete with brook trout in lakes (Magnan 1988).

In streams, defense of choice feeding locations would give trout a competitive advantage over species such as cyprinids that generally do not exhibit highly aggressive behavior. In fact, behavioral dominance of trout over cyprinids in streams has been reported (Li 1975; Symons 1976; Grossman and Boule 1991), but these studies were done at temperatures near the physiological optimum for trout. Our results indicate that reversals in competitive dominance between trout and cyprinids should occur at temperatures near the upper thermal limit for trout. Under these conditions, cyprinids should have the competitive advantage through exploitative competition for food items. Reeves et al. (1987) observed a similar reversal of competitive mechanisms between rainbow trout (*Oncorhynchus mykiss*) and redside shiner (*Richardsonius balteatus*) due to water temperature. At cool temperatures (12–15°C), rainbow trout were strongly territorial and limited access to food by redside shiner through interference competition. At warm temperatures (19–22°C), redside shiner were more active and captured food more quickly than rainbow trout and thus prevailed by exploitative competition.

In conclusion, our results indicate that temperature-mediated competitive interactions likely play a role in the transition from trout to cyprinids that is common in streams of the Rocky Mountain region. At water temperatures below 22–25°C, trout would be dominant because of their aggressive behavior and defense of feeding territories. As temperatures warm to 22–25°C, trout would experience thermal stress that would allow other species such as creek chub to obtain food resources. The increase in water temperature as streams flow from high to low elevations would mediate competitive interactions and thus influence patterns of species replacements in stream ecosystems.

Acknowledgments

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