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EFFECTS OF TURBIDITY ON FEEDING RATES OF LAHONTAN CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI HENSHAWI*) AND LAHONTAN REDSIDE SHINER (*RICHARDSONIUS EGREGIUS*)

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ABSTRACT.—The spawning population of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in Summit Lake, Nevada, has reportedly declined since the early 1970s, coincident with the appearance of Lahontan redside shiner (*Richardsonius egregius*) in the lake. We investigated the relative predatory abilities of these 2 fish species foraging on live *Daphnia magna* in turbidity conditions commonly observed in Summit Lake. Experiments were performed under controlled light and temperature conditions. In separate trials we fed trout and shiner 1 of 3 size classes of *D. magna* (1.7 mm, 2.2 mm, and 3.0 mm) at 6 levels of turbidity ranging from 3.5 to 25 NTU. Feeding rates for both species varied inversely with turbidity for all prey sizes. Feeding rates of shiner were greater than trout at all turbidity levels. In low turbidity (5 NTU), shiner consumed approximately 3% more prey during 2-h feeding trials. However, at high turbidity levels, the difference in feeding rates between species was proportionally higher (10%). At high turbidity levels (≥ 20 NTU) trout predation rates were relatively insensitive to prey size. However, shiner continued to consume more, larger prey at the highest turbidity levels. These results indicate that Lahontan redside shiner may be superior to Lahontan cutthroat trout as zooplankton predators at high turbidity levels, and may explain the recent success of shiner in Summit Lake.

Key words: Daphnia, *Lahontan cutthroat trout,* Oncorhynchus clarki henshawi, *Lahontan redside shiner,* Richardsonius egregius, *planktivory, predation, size selectivity, turbidity.*

The Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) is an inland subspecies endemic to the physiographic Lahontan basin in northern Nevada, eastern California, and southern Oregon. These trout were once widespread throughout the basins of Pleistocene Lake Lahontan (USFWS 1995). Currently, they occupy <1% of their former lacustrine range and 11% of their former stream habitat within the native range (USFWS 1995). Listed as endangered in 1970, the fish was subsequently reclassified as threatened in 1975. This facilitated management and permitted regulated angling (USFWS 1995).

Summit Lake is located in the Summit Lake Paiute Indian Reservation in northwestern Humboldt County, Nevada (41°N latitude 119°W longitude), at an elevation of 1828 m. Formed by a landslide about 20,000 years ago, Summit Lake is relatively shallow (maximum depth 12 m) and has historically been subject to high turbidity levels during summer months from suspended algae and silt (LaRivers 1962). It contains the most secure remaining lacustrine population of Lahontan cutthroat trout, and no other salmonids occur in the basin (Cowan and Blake 1989, Valeska 1989). Other lacustrine populations are either maintained by artificial stocking or are subject to higher levels of harvest and disturbance. Conservation of this population is compelling, and it has been identified as important for recovery of the subspecies (USFWS 1995).

Cutthroat trout spawning runs at Summit Lake have generally declined since the late 1970s (Cowan and Blake 1989). Collection of roe during the 1960s and 1970s and excessive loss of spawning habitat in Mahogany Creek from livestock overgrazing (Cowan and Blake 1989, Vinyard and Winzeler 1993) have been blamed. However, coinciding with the decline in trout, Lahontan redside shiner (*Richardsonius egregius*) also increased in abundance in the lake, suggesting a competition effect.

Redside shiner are native to the Great Basin, but they do not occur naturally in Summit Lake. Origins of the present shiner population in the lake are unknown, but they have been used frequently as live bait. Lahontan redside shiner feed on drift in streams and are zooplanktivorous in lakes (Vinyard and Winzeler 1993). Laboratory observations suggest they

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may also prey on larval trout (Vinyard and Winzeler 1993). Analysis of stomach contents suggests that Lahontan cutthroat trout and Lahontan redside shiner probably consume similar foods both in Summit Lake and in Mahogany Creek, the primary spawning tributary for trout from Summit Lake (Vinyard and Winzeler 1993). Both species consume drift in the stream, and mostly amphipods in Summit Lake (Cowan and Blake 1989). In contrast, similarly large Lahontan cutthroat trout in Pyramid Lake are piscivorous (USFWS 1995). Because most fish species depend on vision to locate prey (Hobson 1979, Guthrie 1986), it is possible that high turbidity in Summit Lake limits the visibility of prey and impedes the ability of trout to catch redside shiner and other large prey.

Our experiments compared the relationships of feeding rate, turbidity, and prey size for Lahontan cutthroat trout and Lahontan redside shiner, with the primary focus being to examine the relative performance of both species under various turbidity levels.

METHODS AND MATERIALS

Lahontan redside shiner were captured from Mahogany Creek, Humboldt County, Nevada, and transported to the University of Nevada. Lahontan cutthroat trout from the current Pyramid Lake stock were acquired from the Lahontan National Fish Hatchery, Gardnerville, Nevada. Although the historical origins of the existing Pyramid Lake stock are mixed, Summit Lake fish were heavily planted into Pyramid Lake for a number of years, and they likely constitute the dominant component of the population (USFWS 1995). Fish were housed in 19-L tanks and acclimated to local water conditions for at least 3 wk prior to experiments.

Experiments were conducted in a secluded section of a greenhouse at the University of Nevada. The experimental protocol was similar to that employed by Vinyard and Winzeler (1993) and Li et al. (1985). Visual isolation of experimental tanks was ensured by opaque black polyethylene sheeting (10 mil, 2.5 m high), which enclosed all sides of the experimental area and controlled external light. Temperatures ranged between 12°C and 17°C during the experiments, and diel variation never exceeded 4°C, a range easily tolerated by both species. Lighting was provided by a bank of three 56-watt fluorescent tubes controlled by an automatic timer (10L:14D). Light intensity at the water surface averaged 93 μE m^{-2} S^{-1}. An airstone in the center of each of four 38-L aquaria provided aeration and kept turbidity in suspension. Turbidity (nephelometric turbidity units, NTU) was measured with an HF Instruments Model DRT 15 turbidimeter. Six turbidity levels (3.5, 6, 10, 20, 22, and 25 NTU) were produced using suspensions of bentonite. Bentonite concentrations (mg/L) were significantly correlated with measured turbidity (NTU = 2.583 + 0.162 B, r^2 = 0.99). This material is nontoxic and remains in suspension for long periods.

Feeding rates were determined for fish exposed to single-sized groups of *Daphnia magna* at each turbidity level. Laboratory-reared *D. magna* were sorted into 3 size groups using a dissecting microscope: 1.7 mm, 2.2 mm, and 3.0 mm (top of head to base of tail spine, ± 0.3 mm). Before each feeding trial, a single fish was placed into each experimental tank and allowed to acclimate for 24 h. A group of 200 *Daphnia* were introduced into the tank and the fish allowed to feed for 2 h. Fish were then removed and the water and remaining prey siphoned through a 363-micron mesh net. Prey retained on the net were counted to determine consumption rates. This procedure was repeated for each of the 3 prey size classes and 6 turbidity levels with 4 fish from each species, yielding a total of 144 feeding trials. Fish used in the feeding trials ranged from 70 mm to 93 mm SL. Analysis of variance and linear regression were used to assess the effects of fish species, prey size, and turbidity level on predation rates.

RESULTS

An analysis of overall predation rates for both fish species consuming all prey sizes (Figs. 1a, 1b) indicates that feeding rates varied inversely with turbidity (multiple regression, F = 1894, $P < 0.001$) and between fish species (F = 28.4, $P < 0.001$), and that larger prey generally were consumed at greater rates (F = 38.3, $P < 0.001$). Significant results were observed for both the species*NTU and species*daphnia size interaction terms, indicating that the 2 fish species differ in their responses to these 2 variables. Lahontan redside shiner consumed significantly more prey than Lahontan cutthroat trout. At the lowest turbidity level (3.5 NTU), approximately 90% of all prey were consumed by both fish species. However, even small increases in turbidity reduced predation rates. This decrease in predation with turbidity was strongly linear, and there was no indication of a minimum value having been reached by 25 NTU. At that turbidity level, predation rates declined by approximately 80% for trout (Fig. 1a) and by 60% to 80% for shiner (Fig. 1b), depending on prey size. Predation rates for trout were significantly affected by prey size and turbidity (multiple regression $F = 2.67$, $P = 0.009$ for prey size; $F = 35.1$, $P < 0.001$ for turbidity). Similar results were observed for shiner (multiple regression $F = 6.54$, $P < 0.001$ for prey size; $F = 27.15$, $P < 0.001$ for turbidity).

At higher turbidity levels, differences in performance of the 2 fish species became most apparent. At turbidity levels of 20 NTU or more, prey of all sizes were consumed at virtually equal rates by Lahontan cutthroat trout (Fig. 1a). In contrast, Lahontan redside shiner showed increasing predation on 3-mm prey relative to the smaller sizes at high turbidity levels (Fig. 1b), and shiner showed the greatest differences in predation rates between prey of different size at the highest turbidity levels. Lahontan cutthroat trout exhibited the opposite trend, with greater differences in predation rates between prey of different sizes at low turbidity levels.

DISCUSSION

Foraging behavior and efficiency are affected by local visibility. Many workers have demonstrated reduced effectiveness by visual predators at elevated turbidity (Vinyard and O'Brien 1976, Li et al. 1985, Barrett et al. 1992, Gregory and Northcote 1993). Sigler et al. (1984) found that chronic high turbidity impedes growth and increases mortality of steelhead (*O. mykiss*) and coho salmon (*O. kisutch*). Evidence suggests that high turbidity or low light intensity reduces predator selectivity because relative differences in prey-detection distance for different sizes of prey are reduced (Vinyard and O'Brien 1976, Gregory and Northcote 1993). Gregory and Northcote (1993) observed log-linear declines in reactive distance with increased turbidity in chinook salmon (*O. tshawytscha*).

Our results demonstrate that turbidity reduces predation rates for all prey sizes for both Lahontan redside shiner and Lahontan cutthroat trout. Larger prey were generally consumed with greater frequency, although this frequency varies with turbidity and fish species. The effect of prey size was most consistent for Lahontan redside shiner. These fish consumed more large (3.0 mm) prey at all turbidity levels than did Lahontan cutthroat trout (Figs. 1a, 1b). In contrast, prey size had little effect on the relative numbers of prey of each size consumed by trout at turbidity levels of 20 NTU or above (Fig. 1a).

Redside shiner also consumed more prey of all 3 sizes combined over all turbidity levels. For all prey sizes combined, shiner consumed approximately 3% more prey than Lahontan cutthroat trout at low turbidity levels and approximately 10% more at high levels (Figs. 1a, 1b). Angradi and Griffith (1990) found predation by rainbow trout (*O. mykiss*) to be more selective for large prey in clear water, whereas selectivity was reduced in elevated turbidity. Similar effects on prey selection under reduced visibility conditions have been observed in bluegill sunfish (*Lepomis macrochirus*). Under low-light conditions bluegill sunfish consumed fewer zooplankton but proportionally more large individuals (Miner and Stein 1993).

Neither trout nor shiner have been shown explicitly to possess adaptations that might enhance their effectiveness as foragers in turbid waters. However, fish that feed nocturnally, such as walleye (*Stizostedion vitreum*), may perform equally well in either clear or turbid waters (Vandenbyllaardt et al. 1991). Walleye have higher densities of retinal cells and also develop scotopic vision earlier in life in comparison to salmonids (Vandenbyllaardt et al. 1991, Borgstrom et al. 1992, Hurber and Rylander 1992). Such species-specific factors may contribute to differences in visual performance.

Behavioral responses of fish to turbidity may also affect their feeding abilities or rates. In laboratory experiments, golden shiner (*Notemigonus crysoleucas*) showed increased flight responses with increased turbidity (Chiasson 1993). Juvenile chinook salmon apparently experienced reduced predation from piscivorous birds and fishes at elevated turbidity levels (Gregory 1993). During our experiments, redside shiner were observed to search faster

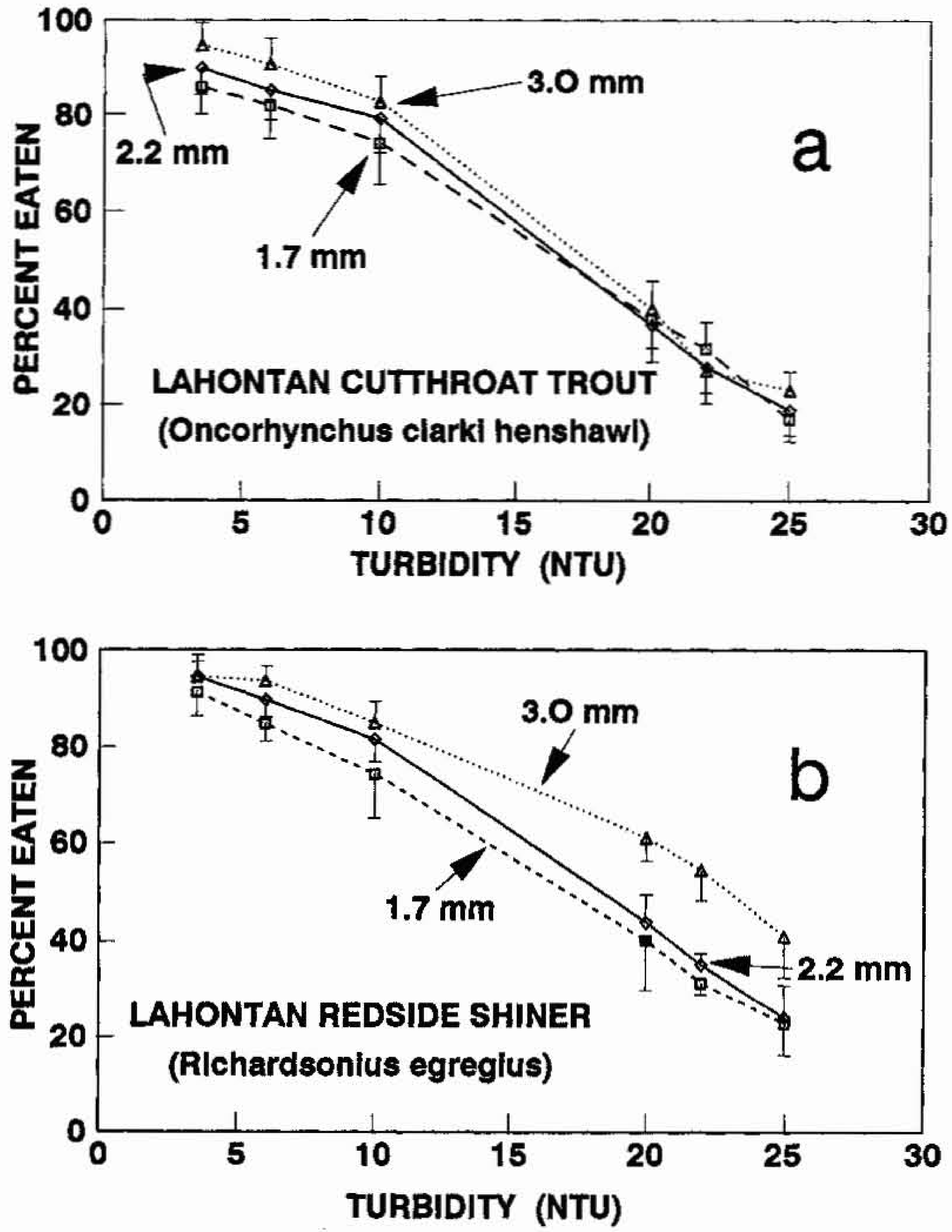

Fig. 1. Mean percent prey consumed in relation to turbidity. Upper panel (a) shows results from feeding trials with Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), and lower panel (b) shows results from Lahontan redside shiner (*Richardsonius egregius*). Four fish of each species were exposed to prey of a single size for 2-h feeding trials. *Daphnia magna* prey sizes are as indicated. Vertical bars indicate 1 standard deviation.

and more widely at higher turbidity. Elevated turbidity may have provided greater visual isolation and promoted greater mobility by predators as suggested by Confer et al. (1978) and Gradall and Swenson (1982). Increased activity may have compensated for reduced visual effectiveness, resulting in larger search volumes for shiner than for trout. In a study of brook trout (*Salvelinus fontinalis*) and creek chub (*Semotilus atromaculatus*), Gradall and Swenson (1982) found creek chub to be less affected by turbidity than brook trout. They suggested such differential effects may explain local disparities in fish density.

High turbidity in Summit Lake may decrease reactive distance and search volume unequally for shiner and trout. This may differentially reduce the probability of successful prey capture and could produce altered prey selection patterns under different turbidity conditions. Although our results are generally similar to those shown for other fishes (Vinyard and O'Brien 1976, Berg and Northcote 1985, Li et al. 1985), we document highly significant differences between potentially competing fish species. Because Lahontan cutthroat trout and Lahontan redside shiner consume the same prey in Summit Lake, competition for food may exist. Our results suggest that in elevated turbidity conditions Lahontan redside shiner may be a better competitor for food than Lahontan cutthroat trout. A factor contributing to the success of Lahontan redside shiner in Summit Lake may be that their predation rates are higher than those of cutthroat trout at elevated turbidity levels.

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