

Role of Size, Condition, and Lipid Content in the Overwinter Survival of Age-0 Colorado Squawfish

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Abstract.—Small, medium, and large (mean total lengths of 30, 36, and 44 mm, respectively) hatchery-reared age-0 Colorado squawfish *Ptychocheilus lucius* were held at winter temperatures (3–5°C) in aquaria for 210 d to assess the role of size, condition factor, and lipid content on overwinter survival. Fish of each size-class were either fed dry pellets or starved. Fish in all size-classes fed at winter temperatures. The fish grew little, and condition declined as length of exposure to winter conditions increased. Condition declined more rapidly in starved than in fed fish of all size-classes. Lipid content of fish was inversely related to winter duration for all size-classes and feeding regimes. Percent survival at the end of 210 d was significantly lower in starved small (3.3%) and medium (6.7%) fish than in fed small (95.1%) and medium (98.4%) fish. Large fish showed 100% survival regardless of feeding regime. In years of large, prolonged runoff that delays the seasonal warming of the upper Colorado River, late spawning by Colorado squawfish leaves age-0 fish with only 2 months to grow and accumulate fat reserves before the onset of winter. These small age-0 fish may be unable to accumulate adequate lipid reserves to survive until the following spring.

The endangered Colorado squawfish *Ptychocheilus lucius* is a large piscivorous cyprinid native to the Colorado River basin. Once abundant throughout the basin, the species is now limited to the northern portion of its original range. Its decline has been attributed generally to the combined effects of dam construction, introduction of nonnative species, and poor land-use practices (Molles 1980; Behnke and Benson 1983; Carlson and Muth 1989).

In populations of temperate zone fishes near the northern limit of their range, the overwinter mortality of age-0 fish is often high (Oliver et al. 1979; Shuter and Post 1990). This mortality may result from hypothermia, predation, displacement by flooding, inadequate lipid reserves leading to

eventual starvation, and physical damage from anchor ice and frazil ice (Seelbach 1987).

As a result of confinement to northern portions of their historical range, remaining populations of Colorado squawfish spawn relatively late in the year. Hamman (1981) stated that Colorado squawfish spawn when water temperatures reach 20–22°C, which usually occurs during July or August in the upper Colorado River basin (Kaeding and Osmundson 1988). In the lower Colorado River basin (below Glen Canyon Dam), where Colorado squawfish were once abundant but have been extirpated, the spawning threshold of 20–22°C was usually reached in early May (Kaeding and Osmundson 1988). Haynes et al. (1984) estimated that Colorado squawfish may have spawned as late as 26 August in the upper Colorado River in 1981. Late spawning leaves age-0 fish only a brief period to grow and accumulate fat reserves before entering their first winter. The small size of age-0 Colorado squawfish as they enter winter might be an important factor affecting recruitment to the adult stock in the upper Colorado River basin (Kaeding and Osmundson 1988).

During winter, most temperate zone fishes un-

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dergo physiological changes that result in declining condition and depletion of energy reserves (Cunjak 1988). Oliver et al. (1979), Toney and Coble (1979), and Henderson et al. (1988) demonstrated that overwinter survival is directly related to fish size. Because weight-specific basal metabolism increases as fish size decreases, high metabolic demands of small age-0 fish exhaust energy supplies more quickly during winter (Shuter et al. 1980; Shuter and Post 1990). A positive relation between body size and lipid content has been demonstrated for yellow perch *Perca flavescens* (Toney and Coble 1979), smallmouth bass *Micropterus dolomieu* (Oliver et al. 1979; Isely 1981), and sand smelt *Atherina boyeri* (Henderson et al. 1988). Thus, the larger members of an age-0 cohort are more likely to survive their first winter (Gutreuter and Anderson 1985; Henderson et al. 1988). Kaeding and Osmundson (1988) speculated that the occurrence of comparatively larger age-0 Colorado squawfish in the Green River than in the Colorado River in fall may in part explain why adult Colorado squawfish are more abundant in the Green River.

Colorado squawfish stop growing when water temperatures fall below about 13°C (Kaeding and Osmundson 1988). This growth threshold of 13°C is usually reached in October in the upper Colorado River basin. In years of large, prolonged runoff that delays seasonal warming of the river, age-0 Colorado squawfish may have only 2 months to grow and accumulate fat reserves before the onset of winter.

We examined the role of size, condition factor, and lipid content in the overwinter survival of age-0 Colorado squawfish. Our objectives were to (1) determine the influence of size, condition factor, and lipid content on the overwinter survival of hatchery-reared age-0 Colorado squawfish held at simulated winter temperatures for 210 d; (2) compare size, condition, and lipid content of wild and hatchery-reared age-0 Colorado squawfish before and after the winter period; (3) compare condition, lipid content, and survival of hatchery-reared fish subjected to the two feeding regimes (either they were fed dry pellets or starved); and (4) estimate the amount of lipid that fish must maintain to survive the winter.

Methods

Age-0 Colorado squawfish used in this study were hatched in June 1988 at the Dexter (New Mexico) National Fish Hatchery and reared at Willow Beach (Arizona) National Fish Hatchery.

After fish reached desired lengths at Willow Beach, they were transferred to an experimental chamber at Fort Collins, Colorado, in three shipments (small fish arrived on 14 July, medium fish on 29 July, large fish on 21 September). Mean total lengths upon arrival were 30 mm (26–33 mm) for small, 36 mm (30–39 mm) for medium, and 44 mm (35–59 mm) for large fish.

Experimental design.—Fifteen 75.5-L aquaria were housed inside the environmental chamber. Each aquarium held only one size-class of fish (small, medium, or large). Aquaria were located on three tiers of shelves, and fish size-classes were randomly assigned within each tier. In the final experimental setup, five aquaria held 60 small fish, five held 45 medium fish, and five held 20 large fish. The initial biomass in all aquaria was about the same (range, 0.12–0.16 g/L). Fish were held at 20°C before water temperature was lowered to the simulated winter temperature (3–5°C) over a period of 24 to 48 h. Berry (1988) reported low mortality among 40-d-old Colorado squawfish subjected to either abrupt (5 min) or gradual (4–5 h) temperature decreases of 15°C. Following acclimation of the fish to reduced temperatures, water temperature was maintained between 3 and 5°C by adjusting ambient air temperature inside the chamber. Photoperiod (10 h light : 14 h darkness) was regulated by timers for the full 210-d experimental period. The first and last 0.5 h of the light phase were only 50% as bright to allow fish to adjust to changes in illumination.

The 15 aquaria constituted a closed system in which dechlorinated city water circulated continuously. Water was pumped from a biological filter tank through a 30-W ultraviolet sterilizer into 1.3-cm-diameter polyvinyl chloride piping, which delivered water to all aquaria. Inflow to each aquarium was controlled by individual valves; outflow was through a slotted standpipe. Water drained from the three levels into drainpipes suspended below the bottom tier of shelves. Water in the drainpipes flowed by gravity to a slotted spray bar that distributed water evenly over the biological filter media. The biological filter was housed inside a 207.6-L aquarium and consisted of two layers: a top layer of lava rock (20–30-mm diameter) and a bottom layer of crushed coral mixed with gravel (1–3-mm diameter). The filter medium was inoculated with nitrifying bacteria (primarily *Nitrosomonas* sp. and *Nitrobacter* sp.) that convert ammonia and nitrite into nitrate. Ammonia levels were monitored daily. Dissolved oxygen, pH, and nitrite levels were checked bimonthly. After pass-

ing through the biological filter, water was pumped back through the system.

Fish were subjected to two feeding regimes. Fish of each size-class in three aquaria (total, nine aquaria) were fed dry pelleted fish food (Silver Cup Fish Feed, Murray, Utah) twice weekly. The weight of pellets furnished at each feeding was equivalent to 2% of the total biomass of the fish remaining in the aquarium. The biweekly ration was adjusted every other feeding to account for mortality and fish removed for lipid analysis. The amount of pelleted food furnished was always in excess of the amount consumed. Following each feeding, food was left in aquaria for 24 h. After 24 h, remaining food and feces were siphoned out. Fish of each size-class in two aquaria (total, six aquaria) were not fed.

On days 70 and 140 of the experiment, 25% of the surviving fish in each aquarium were removed, measured, and weighed, and frozen for later lipid analysis. On day 210, all remaining fish were measured, weighed, and analyzed for lipids. Throughout the 210-d experiment, both dead and dying fish (those showing loss of equilibrium or uncoordinated swimming movements) were removed daily, measured, weighed, and analyzed for lipid content. The total length of each fish was measured to the nearest millimeter. Fish were blotted dry on a paper towel and then weighed to the nearest 0.01 g. Condition factor (K) was calculated by the formula (Weatherley and Gill 1987)

$$K = (W \times 10^5) / L^3;$$

W is weight (g) and L is total length (mm).

The length of the winter period (210 d) was determined from mean daily water temperatures recorded for the Colorado River at the Colorado-Utah state-line gage, where Colorado squawfish still occur. The beginning of the winter period was defined as the first day in fall when mean water temperature fell below 13°C and remained there for seven consecutive days. The end of the winter period was defined as the first day when mean water temperature rose above 13°C and remained there for seven consecutive days. The winter period averaged 210 d for 1983–1984, 1985–1986, and 1987–1988 (range, 202–223 d); data for the 1986–1987 winter period were not available.

Percent survival.—Daily percent survival of fish in the three size-classes and feeding regimes was calculated throughout the 210-d winter period with the formula

$$\text{Percent survival} = \frac{X}{N - A};$$

X is the number of fish in a size-class alive at the end of a given day, N is the number of fish in that size-class on day 0, and A is the total number of fish in that size-class removed for lipid analysis on days 70 and 140.

Lipid analysis.—Because the fish were small, we pooled several fish within each size-class and feeding regime to provide enough material for lipid extraction. About 11 small fish, 8 medium fish, or 4 large fish were pooled to provide material for each extraction. Pooled groups were prepared for extraction by a slightly modified version of the technique described by Wicker and Johnson (1987). Samples were extracted for 6–7 h with diethyl ether. Fat content, determined by weight loss, was expressed as a percent of the original dry weight of the fish (Wicker and Johnson 1987).

Collection of wild fish.—Wild age-0 Colorado squawfish were collected from the Colorado River (river kilometers 74.2–159.5, measured upstream from the confluence of the Green River and Colorado River) in October 1988 and March 1989. Fish were captured with beach seines (4.6 m long \times 1.2 m deep; 0.32-cm ace mesh) in backwater habitats. The total lengths of all fish were determined, and a representative subsample was weighed and frozen for future lipid analysis.

Statistical analysis.—Mean total length, mean condition factor, and mean lipid content were calculated for fish removed on days 70, 140, and 210 from each size-class and feeding regime. One-way analysis of variance (ANOVA) was used to determine if mean total length, mean condition factor, and mean lipid content within each size-class changed significantly during the experimental period. When significant differences were found, Tukey's honestly significant difference (HSD) method of multiple comparison was used to determine which means were significantly different (Kleinbaum et al. 1988). Significance was set at $P \leq 0.05$ for all statistical tests.

Results

Changes in Size

Length measurements from the three size-classes of fish subjected to each feeding regime at the beginning (day 0) of the winter period and on days 70, 140, and 210 (end of winter period) showed that the Colorado squawfish grew little at winter temperatures (Table 1). Increases in total length over time were slight, and changes in length during 70-d intervals were not significant. High nitrite levels (6.1 mg nitrite-N/L on 23 August) during

TABLE 1.—Mean total lengths in millimeters (ranges in parentheses; number of fish in brackets) of age-0 Colorado squawfish of three initial sizes subjected to two feeding regimes while held under simulated winter temperatures for 0–210 d.

Fish size and feeding regime	Days of exposure to winter temperatures			
	0	70	140	210
Small				
Fed pellets	30.1 (26–33) [60]	30.1 (28–32) [28]	30.6 (27–34) [18]	31.4 ^a (28–34) [57]
Starved	30.1 (26–33) [60]	30.1 (28–32) [14]	—	—
Medium				
Fed pellets	35.7 ^b (30–39) [60]	33.6 (29–40) [27]	32.5 (29–37) [24]	33.9 (29–41) [72]
Starved	35.7 (30–39) [60]	32.6 (30–36) [19]	32.8 (31–35) [12]	—
Large				
Fed pellets	44.0 (35–59) [60]	43.3 (39–51) [15]	43.2 (36–47) [12]	44.0 (35–54) [30]
Starved	44.0 (35–59) [60]	44.6 (39–57) [10]	41.6 (36–54) [9]	42.7 (38–53) [20]

^a Significant increase from mean total length on day 0 ($P \leq 0.05$).

^b Day-0 lengths of medium fish cannot be validly compared with lengths on days 70, 140, and 210 (see text for explanation).

the first 28 d following the addition of the medium fish resulted in high mortality among those fish (68% of the original 225 medium fish died in the first 30 d). Those that died were replaced with slightly smaller fish. Consequently, our comparisons of length, condition factor, and lipid content for medium fish were valid only for days 70, 140, and 210. Small fish, though present in the system during the period of elevated nitrite levels, did not suffer unusually high mortality. Following discovery of heightened nitrite levels, we reinoculated the biological filter with nitrifying bacteria, and the water in the system was changed thrice weekly for 2 weeks. After this 2-week period, nitrite levels were again near 0.1 mg/L and remained at low levels for the remainder of the experiment. Ammonia levels ranged from 0.01 to 0.25 mg/L, pH remained between 7.1 and 8.0, and dissolved oxygen was at saturation throughout the experimental period.

Condition Factor

Mean condition of small and large fish decreased between days 0 and 210 (Figure 1). Among medium fish, mean condition declined between

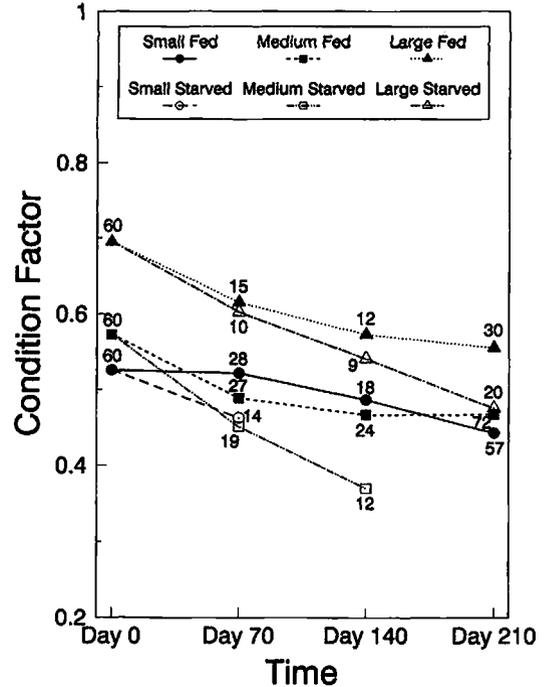


FIGURE 1.—Mean condition factors of pellet-fed and starved age-0 Colorado squawfish on days 0, 70, 140, and 210 of the winter period. Condition factors for small starved fish on days 140 and 210 and medium starved fish on day 210 are missing because of insufficient numbers of survivors. Numbers indicate sample size used to compute each mean value.

days 70 and 140 for both fed and starved fish, then remained unchanged between days 140 and 210 for fed fish. Condition declined more rapidly in starved fish than in fed fish. The mean condition factor of dying fish was 0.36 (small, 0.30–0.48, $N = 49$; medium, 0.28–0.42, $N = 59$), a value significantly lower than that of all surviving fish except for starved medium fish removed on day 140, which were very emaciated and near death.

Mean condition factors of wild age-0 Colorado squawfish collected from the Colorado River declined significantly between early October 1988 (mean, 0.75; $N = 30$) and mid-March 1989 (mean, 0.60; $N = 30$). Nonetheless, mean condition factors of wild age-0 Colorado squawfish after winter were still well above the mean value (0.36) determined for dying fish in our laboratory study.

Lipid Content

Mean lipid contents were inversely correlated with winter duration for fish of all size-classes and feeding regimes except for pellet-fed medium fish,

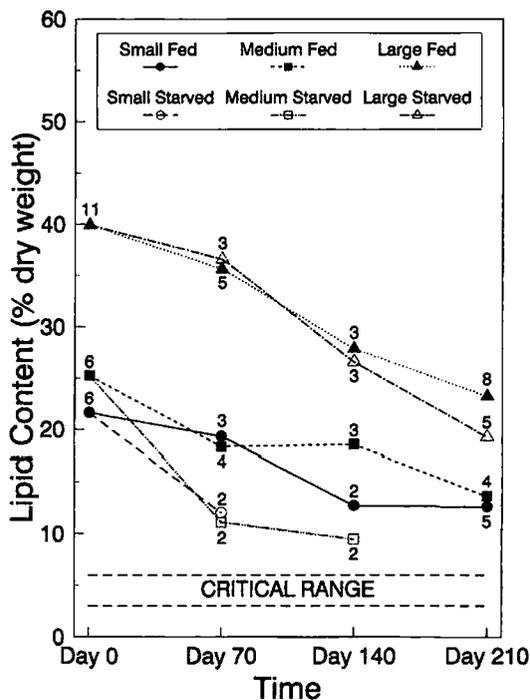


FIGURE 2.—Mean lipid content of pellet-fed and starved age-0 Colorado squawfish on days 0, 70, 140, and 210 of the winter period. The critical range represents the lipid content of starved small and medium fish that died during the winter period. Lipid content values for small starved fish on days 140 and 210 and medium starved fish on day 210 are missing because of insufficient numbers of survivors. Numbers indicate sample size used to compute each mean value.

whose mean lipid content remained unchanged between days 70 and 140 (Figure 2). Throughout the winter period, fed and starved large fish had significantly higher lipid contents than fed small or medium fish. Mean lipid contents of fed small and medium fish were not significantly different on days 0, 70, 140, or 210. On day 70 (the only day when both were measured), the mean lipid contents of starved small and medium fish were similar. The rate at which lipid reserves were depleted was greater for starved small and medium fish than for fed fish of these sizes. Rates of lipid decline were similar for large pellet-fed and starved fish, presumably because large fish seldom ate when pellets were offered.

Laboratory starvation suggested that age-0 Colorado squawfish must maintain lipid levels greater than 3–6% of their total dry weight to survive. The mean lipid contents of dying small and dying medium fish did not differ significantly. All dying fish had lipid levels 3–6% of their total dry weight;

these levels were significantly less than those of fish removed while still alive. Total length in millimeters (TL) was positively but weakly correlated with days to starvation (DS) for all dying fish; it was described by the relation ($r^2 = 0.40$, $N = 108$)

$$TL = 28.06 + 0.03DS.$$

All pellet-fed fish had higher lipid levels than wild fish of similar size. Before the winter period, the hatchery-reared fish (26–59 mm TL, $N = 180$) averaged 28.9% lipid by dry weight, whereas wild age-0 Colorado squawfish of similar lengths (30–58 mm, $N = 30$) averaged only 14.9% lipid. The mean lipid content of age-0 wild fish (36–54 mm TL, $N = 30$) collected in mid-March 1989 from the same stretch of the Colorado River was 13.6%, which was not significantly different from the fall lipid value. Although there was a trend toward increasing lipid content with increasing total length of wild fish, small sample sizes prohibited detection of significant differences.

Survival

For both small and medium fish, feeding determined whether a fish survived the 210-d winter period (Figure 3). At day 210, only 2 of the original 61 starved small fish were alive, but only 5 of the original 103 pellet-fed small fish had died. At day 210, only 6 of the original 90 starved medium fish were alive, but only 2 of the original 125 pellet-fed medium fish had died. No large fish in either feeding regime died because of exhausted energy reserves during the 210-d experimental period.

Body Water Content

As percent lipid content (% LC) decreased in age-0 Colorado squawfish, percent body water (% BW) increased linearly ($r^2 = 0.92$, $N = 62$):

$$\% LC = 220.89 - 2.54\% BW.$$

Discussion

Our laboratory results support the hypothesis that overwinter survival of age-0 Colorado squawfish depends on fish size. The lipid content of hatchery-reared Colorado squawfish increased as total length increased. For starved fish, the relation between fish length and amount of stored energy (lipids) determined whether a fish survived overwinter. Fish in all size-classes and feeding regimes depleted their lipid reserves over time, but only starved small and medium fish died. Large fish had higher initial lipid contents and therefore

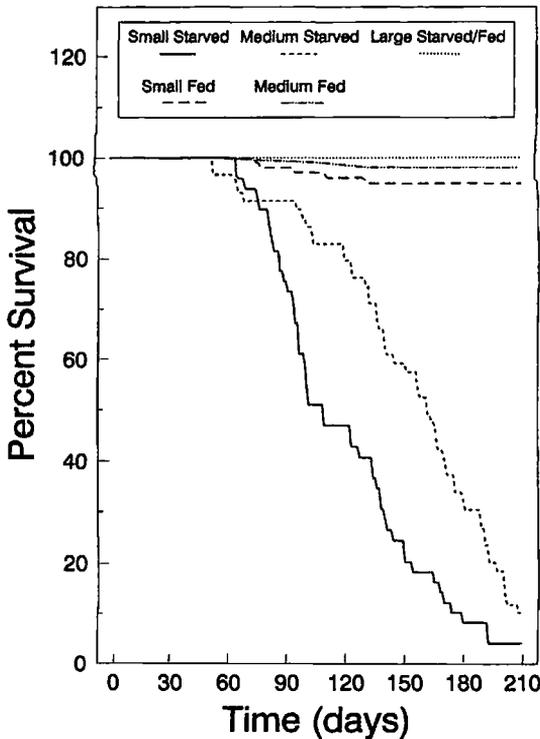


FIGURE 3.—Percent survival of age-0 Colorado squawfish during the 210-d winter period.

had sufficient energy reserves to survive the winter, regardless of feeding regime.

Hoar (1983) stated that an animal must maintain a "constant element" of fat to survive. Newsome and Leduc (1975) found that this critical fat content for yellow perch was about 2.2% of the total dry weight of the fish. In our study, the significantly lower lipid content of dying age-0 Colorado squawfish compared with that of surviving fish suggests that death was due to exhaustion of energy reserves. Other workers have similarly found that mortality of age-0 fish during winter results from exhaustion of stored energy reserves (Oliver et al. 1979; Isely 1981; Henderson et al. 1988).

Whether an age-0 Colorado squawfish survived the winter was a function of fish length and feeding regime. Some of our captive Colorado squawfish were offered food throughout the winter period. After an initial phase of 2–3 weeks following acclimation to winter temperatures, when fish fed little, fish of all size-classes fed readily. Feeding was inversely related to fish size, and small fish exhibited the most active feeding behavior. Cunjak (1988) stated that "early winter is a stressful

period of acclimatization to rapidly changing environmental conditions" for brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*. We believe that the initial 2–3-week phase of non-feeding exhibited by Colorado squawfish corresponded to this stressful early winter period. After 3 weeks, fish were sufficiently acclimated to winter conditions to begin feeding.

The low survival of starved small and medium fish demonstrates that, to survive through their first winter, age-0 Colorado squawfish must either accumulate a certain critical amount of lipid before winter or feed during winter to partly offset the drain on lipid reserves typical of this period. Shul'man (1974) noted that fish take up and accumulate lipids during periods of decreasing water temperatures. Pierce et al. (1980) found that age-0 gizzard shad *Dorosoma cepedianum* deposit lipids in late summer until their prewinter energy reserves exceed amounts required for normal maintenance. Larger age-0 sand smelt switched energy input from somatic growth to fat reserves before winter (Henderson et al. 1988). Smaller sand smelt that channeled their energy input into somatic growth were able to accumulate enough fat reserves to survive through the winter. Henderson et al. (1988) concluded that the rate of accumulation of fat reserves was size dependent, because either smaller fish directed more energy into somatic growth and maintenance, or larger fish had the advantage of a wider size range of available food. Further studies are needed to determine if lipid accumulation in late fall is size dependent for Colorado squawfish.

At 7.1°C, captive age-0 smallmouth bass fed lethargically and consumed virtually no food (Oliver 1977). Our observations showed that captive age-0 Colorado squawfish feed readily and remain active at 4°C. Cunjak and Power (1987) determined that wild brook trout and brown trout feed continuously throughout the winter, yet the condition factor in both species declines to the yearly low in winter. Declining condition factor during winter has also been reported for rainbow trout *Oncorhynchus mykiss* (Reimers 1963) and brook trout (Hunt 1969). Cunjak and Power (1987) hypothesized that low condition in winter is due either to the inability of the trout to effectively assimilate ingested food or to insufficient energy intake to balance metabolic costs. The metabolic costs of our captive Colorado squawfish were undoubtedly lower than those of wild fish. The aquarium-held fish lived in a comparatively benign environment, free from currents, tempera-

ture fluctuations, and predators or competitors. Despite these circumstances, with the exception of fed medium fish during the final 70 d of the winter period, condition declined in all size-classes and feeding regimes as the simulated winter progressed.

Although small fish were present in the system when the failure of the biological filter resulted in high nitrite levels, they did not experience unusually high mortality. Because small fish had been present in the system for several weeks prior to the addition of the medium fish, we presume the small fish were able to acclimate to the gradually rising nitrite levels. Lewis and Morris (1986) reported that after 5–7 d at high nitrite levels, salmonids showed little change in mortality, presumably because they developed resistance to nitrite toxicity. The medium fish in our study were transferred into a system with elevated nitrite levels and were unable to acclimate to the combination of cold temperature and high nitrite.

Before the onset of winter, the mean lipid content of the hatchery-reared fish (28.9%) was almost twice that of wild fish (14.9%) of similar size. Wood et al. (1957) found that lipids in hatchery-reared salmonids were higher than those of wild fish. If wild, age-0 Colorado squawfish depleted their lipid reserves at the same rate as our starved, hatchery-reared fish, the majority of the wild fish would exhaust their energy stores and perish during the winter. However, unlike our laboratory fish, wild age-0 Colorado squawfish did not show significant lipid declines during the winter period (14.9% in October 1988 versus 13.6% in March 1989).

Several factors may have contributed to our failure to detect significant differences between fall and spring lipid levels in wild fish. If overwinter mortality occurred in the Colorado River in the stretch that we sampled, spring lipid values would be high, because only surviving fish (which presumably would have had higher lipid content than fish that died) were analyzed. Second, our fall sample was collected before water temperatures had fallen below the growth threshold of 13°C. The fish may have accumulated additional lipid reserves between the time of collection on 1 October 1988, when backwater temperatures ranged from 12.2 to 25.0°C (mean, 16.9°C), and the beginning of winter (when water temperatures fell below 13°C in late October). Third, age-0 Colorado squawfish in the Colorado River may slow their rate of lipid depletion by feeding during all or part of the winter. Our laboratory observations

of active swimming and feeding by age-0 Colorado squawfish demonstrated that they will feed at winter temperatures if food is available. Although age-0 fish that feed during the winter still deplete their lipid reserves, the rate of depletion is not as fast as that of starved fish. As a result of the slowed rate of lipid loss, age-0 fish that feed have a much higher probability of surviving until spring. Stomach analyses conducted by the Larval Fish Laboratory at Colorado State University on age-0 Colorado squawfish collected from the Green River showed that 15 of 18 fish (83%) collected during November 1987 had food in their stomachs. Our observations of active feeding under simulated winter conditions in the laboratory, combined with the presence of food in the stomachs of wild fish after the onset of winter water temperatures in the Green River, clearly show that age-0 Colorado squawfish feed during winter.

High mortality rates for early life stages of Colorado squawfish in the upper Colorado River basin may be a factor contributing to the decline of this endangered species (Kaeding and Osmundson 1988). Although our study demonstrates that overwinter mortality of age-0 Colorado squawfish may occur, such mortality is probably most important in habitats in upstream river reaches (e.g., northern reaches of the Colorado River in western Colorado) where fish spawn late in the summer. In these marginal habitats, small age-0 Colorado squawfish might be unable to accumulate adequate lipid reserves to survive until the following spring despite overwinter feeding.

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