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The Impact of Squawfish on Salmonid Populations: A Review

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Abstract

Examination of the available literature on the effects of squawfish (*Ptychocheilus* spp.) predation and competition on salmonid populations indicates that: (1) squawfish may prey extensively on young salmon in lakes, but there is little evidence that this predation has much impact on the number of returning adults; (2) squawfish do not appear to be significant predators of salmon and trout in streams except under highly localized, seasonal or unusual circumstances; and (3) there is little evidence to indicate that squawfish compete strongly with salmonids. Areas of research are suggested that would clarify the role of squawfish in regulating salmonid populations and elucidate their position in the aquatic ecosystems of western North America.

Squawfish (*Ptychocheilus* spp.) have gained reputations in the western United States as both predators and competitors of salmon and trout. Concern over the impact of squawfish on salmonid populations has been considerable and has led to development of a variety of control methods including electrical barriers and traps (Maxfield et al. 1969, 1970), a combined program of dynamiting, spot treatment with rotenone, and drawdown (Jeppson 1957), and a selective piscicide, Squoxin (MacPhee and Ruelle 1969). While these techniques may succeed in reducing squawfish numbers, control operations are often undertaken on the basis of anecdotal evidence or inconclusive studies. Usually the presence of large numbers of squawfish in a habitat containing salmonids seems to be enough evidence to justify a control program. Presumably, the main reason for this attitude is that the limited amount of literature available on squawfish biology appears to support the belief that squawfish are significant predators or competitors of salmon and trout. This paper critically examines the studies often cited to establish the negative impact of squawfish on salmonid populations to determine under what conditions, if any, squawfish control is warranted.

Systematics and Distribution

Squawfish are predatory members of the family Cyprinidae and the largest members of that family native to North America. There are four species, each characteristic of a major drainage basin. The Colorado squawfish (*P. lucius*) of the Colorado River system is the largest of the four. Fish weighing up to 36 kg have been reported. The range of this species has been drastically reduced because of the many dams and diversions on the Colorado River, and it is now on both federal and state endangered species lists (Deacon et al. 1979). Because of its status, nothing more will be said about it except to note, somewhat ironically, that it was once the object of eradication measures, but now a population is being maintained in a federal fish hatchery in Arizona where they are fed largely on hatchery-reared trout (Toney 1974). The Sacramento squawfish (*P. grandis*) is found in the Sacramento-San Joaquin, Russian River, and Pajaro-Salinas River drainages of central California (Moyle 1976). This squawfish has only recently received much attention as a predator and/or competitor with salmonids. The Umpqua squawfish (*P. umpquae*) is found only in the Umpqua and Siuslaw rivers in Oregon (Bond 1980). The northern squawfish (*P. oregonensis*) is distributed throughout the Columbia River system, the Harney-Malheur Basin of Oregon, and various coastal drainages of Washington and British Columbia north to the Nass River. It is also found east of the Continental Divide in the Peace River of Canada (Wallace 1980). The northern squawfish, because of its wide association with commercially important salmonid species, is the most studied of the four species. However, because Umpqua and Sacramento squawfish appear to be very similar to northern squawfish ecologically, it is probably safe to assume that observations made on one species will be applicable to the other two.

Feeding Habits and Predation

Squawfish have been characterized as opportunistic predators on whatever invertebrate or vertebrate prey are most abundant (Thompson 1959; Casey 1962; Falter 1969; Moyle 1976; Eggers et al. 1978). However, the size and types of prey taken vary with the age and size of the fish. Falter (1969) found that fish and crayfish became an important component of the diet (>50%) for northern squawfish 18 cm FL (fork length) long or larger. Smaller fish consumed insects, other small invertebrates, and plant material. Thompson (1959) noted a similar transition in the Columbia River, with fish and crayfish becoming important in the diet of squawfish between 23–25 cm (FL). Taft and Murphy (1950) examined 36 stomachs of Sacramento squawfish 3–18 cm (FL) and found only aquatic insects. Data collected by Moyle et al. (1979) suggested a transition from a diet of insects to crayfish and fish at a size of 20–30 cm.

Squawfish apparently feed most heavily around dusk and dawn but full stomachs are often found throughout the day and night (Steigenberger and Larkin 1974). Recent studies on northern squawfish have shown that they have very rapid digestion rates. Steigenberger and Larkin (1974) determined that fish held in cages in their natural habitat digested fish at a rate of 14% per hour at temperatures of 10–12 C. Two-thirds of their experimental fish were able to evacuate the digestive tract in 24 hours or less. Their experiments also revealed that digestive rates increased substantially with temperature, increasing from about 5% per hour at 4–6 C to 40–50% per hour at 24 C. Falter (1969) also noted this increase in digestive rate with temperature. Digestive rates may be even faster since the fish were force fed, possibly slowing digestion. These data indicate that squawfish may feed more heavily and frequently than the high percentage of empty stomachs, characteristic of most dietary studies of squawfish, suggests. The frequency of empty stomachs may result in part from the tendency of large squawfish to regurgitate when captured by most methods. On the other hand, little is known about the frequency of feeding by large squawfish. Their growth, however, is slow (Moyle 1976), suggesting either high metabolic demands, a large diversion of energy into reproduction, or, most likely, infrequent feeding.

Concern over the predatory nature of the squawfish is most apparent when salmonids are the prey species. Squawfish are considered to be a particular problem in streams during the out-migration of smolts. Thompson's (1959) study of the food habits of the northern squawfish in the lower Columbia River is often cited as proof of squawfish predation on salmonids. Thompson found that, out of 1,272 countable fishes found in the squawfish stomachs he examined, 1,102 (87%) were salmon. However, a point often overlooked when this study is cited is the correlation of salmon consumption to periods of smolt release from hatcheries. In all but one instance, the occurrence of salmon in squawfish stomachs was preceded by a nearby hatchery release. Recent work on the Columbia River revealed that large populations of squawfish are often present below dams (Sims et al. 1977, 1978). The percentage of these squawfish consuming salmonids during migration varied from 20% in 1976 to 88% in 1977. A similar pattern has been observed in the Sacramento River where Sacramento squawfish may prey heavily on newly released salmon, especially immediately after the salmon pass over a large irrigation diversion dam at Red Bluff, California (A. Pickard, personal communication). Below dams, the flow patterns and constant availability of confused or injured small fishes seem to concentrate squawfish.

Other studies in streams indicated that, under natural conditions, salmonids are not major prey items of squawfish. Buchanan et al. (1980, 1981) studied northern squawfish in the lower free-flowing sections of the Willamette River, Oregon, during periods of salmon out-migration in 1976 and 1977. During this period, 1,127 squawfish stomachs were examined and only 2% contained salmonid remains. An unscheduled hatchery release of steelhead (*Salmo gairdneri*) in the study area may have inflated the percentage of stomachs containing salmonids. If these data are ignored the percentage decreases to 1.4%. Of the squawfish that were consuming salmonids, 75% were over 30 cm (FL), indicating that only a portion of the population may pose a threat to salmonids. The major prey in 14.4% of the stomachs were sculpins (*Cottus*). Sculpins were also the major food item in 449 squawfish stomachs from the St. Joe River, Idaho (Falter 1969). No salmonid remains were found although salmonids were present in the river. The importance of sculpins as prey of squawfish is of interest because sculpins are often considered to be predators and competitors of salmonids as well (Moyle 1979). Moyle et al. (1979) examined 100 adult Sacramento squawfish collected from six locations and found salmonids in the stomachs from only two of the locations. Salmonids made up 33% and 24% of the stomach contents. However, the first sample was small (N = 5) while the second sample (N = 31) consisted of fish taken below the Red Bluff Diversion Dam, a location where unusual hydrological conditions favored squawfish predation on salmon. All other fishes consumed were non-salmonids, including other squawfish.

A possible reason for the lack of significant predation on smolts by squawfish, even during the vulnerable migration period, is that young salmon exhibit behavioral adaptations that may reduce the impact of predation. Natural populations of smolts may cut their losses either by migrating in large concentrations at night (Foerster 1968; Sims et al. 1977, 1978) or during times of high flow and increased turbidity. As a result of such strategies the predator population is saturated with prey at times when prey are difficult to capture. Ginetz and Larkin (1976) demonstrated that the efficiency of predation by rainbow trout (*Salmo gairdneri*) on migrant fry of sockeye salmon (*Oncorhynchus nerka*) was reduced under conditions of low light, high flows, and high turbidity. Patten (1971) showed that predation on coho salmon (*Oncorhynchus kisutch*) fry by torrent sculpin (*Cottus rhotheus*) in stream tanks was greater on moonlit nights than on dark nights. Various studies have demonstrated that naive salmon begin to exhibit predator avoidance responses within several days of exposure to predators (Kanid'yev 1970; Ginetz and Larkin 1976; Patten 1977). Furthermore, Patten (1977) has found that when inexperienced coho salmon in the company of experienced fry are exposed to a predator, all individuals behave like experienced fry. This suggests that predator-avoidance responses are quickly learned. Presumably, experience with predators reinforces innate behavioral responses. While the above studies did not utilize squawfish as the predator, the results are general enough so that they should be applicable to squawfish predation in streams.

Although squawfish do not seem to be significant predators of salmonids in streams (at least under natural conditions), the situation in some lakes may be different. In fact, northern squawfish predation on young sockeye salmon in lakes is perhaps the best-documented example of the impact of squawfish predation on salmonids. The situations in Cultus Lake, British Columbia and Lake Washington, Washington, are particularly well known (Ricker 1933, 1941; Foerster and Ricker 1941; Foerster 1968; Hartman and Burgner 1972; Eggers et al. 1978). In Cultus Lake, squawfish exist as part of a predator species complex which includes arctic charr (*Salvelinus malma*), cutthroat trout (*Salmo clarki*), and coho salmon. Foerster (1968) compared the effectiveness of each predator and found that arctic charr, cutthroat trout, and coho salmon consumed more sockeye salmon per individual than squawfish over a 12-month period by factors of 3, 5, and 4, respectively. He concluded that these salmonids were more effective as predators than the squawfish, although the squawfish population was much larger. Also, Cultus Lake lacked high concentrations of buffer forage species such as sticklebacks (*Gasterosteus aculeatus*), pond smelt (*Hypomesus olidus*), and pygmy whitefish (*Prosopium coulteri*) which often dominate the diet of predators in other systems (Hartman and Burgner 1972), and may have caused overemphasis of squawfish as sockeye predators compared to other areas. In contrast, Lake Washington has a more complex fish community. Eggers et al. (1978) analyzed the fish production of that lake and determined that northern squawfish had a considerable impact on juvenile sockeye salmon populations. It was estimated that 3 million sockeye salmon were consumed by squawfish from June 1972 to May 1973. Nevertheless, sockeye salmon only made up 10–30% of the diet of squawfish, with prickly sculpin (*Cottus asper*) being the major item (70%).

One source of evidence that might demonstrate the importance of squawfish predation are removal studies. If squawfish are significant predators, then salmon populations should increase following significant control programs. Such a program was attempted at Cultus Lake from 1936 through 1938 (Foerster 1968). Predator populations (including other species besides squawfish) were reduced to one-tenth of their 1935 levels. This reduction was correlated with a 3-fold increase in smolt production. Both Thompson (1959) and Taft and Murphy (1950) cited this program as an example of the rewards of squawfish control, although the effects of squawfish control could not be separated either from the control of the other predators or other factors affecting the survival and ultimate contribution of smolts to an adult population (Hartman and Burgner 1972; Foerster 1968).

An increase in smolt production may not always lead to an increased production of adults. Ricker (1937a) noted an inverse relationship between the size of the population of young sockeye salmon and August zooplankton abundance, suggesting the presence of intraspecific competition for food at high sockeye salmon concentrations. Ricker (1937b) also presented evidence that, as the juvenile sockeye salmon population increases relative to the food supply, the available food per individual decreases, resulting in a smaller size at seaward migration. Ricker (1962) also has shown that ocean mortality increases with a decreasing size of migrating smolts. Small smolts may take an extra year to mature, increasing the time exposed to mortality factors in the sea (Foerster 1968). It is possible that decreased predation in the nursery lakes may be more than compensated for by increased mortality at sea. Finally, there are indications the predator-control program at Cultus Lake led to an increase in the population of threespine stickleback (*Gasterosteus aculeatus*), a probable competitor of sockeye salmon (Foerster 1968). It is apparent that a lacustrine squawfish control program in a lake can have a variety of impacts, but whether or not such a program can increase the production of adult salmon has yet to be conclusively demonstrated. It is worth noting, too, that sockeye salmon in lakes also have evolved effective predator-avoidance mechanisms (Eggers 1978), with predation becoming heavy only at high levels of sockeye abundance (Foerster 1968; Eggers et al. 1978). In some lakes fish may be unimportant in the squawfish diet. Casey (1962) found that only 3% of the squawfish stomachs from an Idaho reservoir contained fish, none of them salmonids.

The main conclusion that can be drawn from feeding habits of squawfish is that they do prey on salmonids in some situations and are capable of consuming them in large numbers. Probably they are most effective as predators on salmon in lakes. In streams, they consume large numbers of juvenile salmonids mostly after daytime hatchery releases or where dams and diversions have created unusually favorable environments for predation. However, the current evidence does not prove that squawfish predation has a major impact on salmon or trout production in either environment.

Competition

Although there is no doubt that squawfish prey on salmonids under certain conditions, their role as salmonid competitors is poorly documented. The evidence that does exist consists primarily of food studies that show similarities in diet to trout. A major problem with such studies is that food items are rarely identified beyond the order level, obscuring differences in diet. More importantly, dietary-overlap studies cannot be used to show competition unless it can be demonstrated that the food organisms are in limited supply. Nevertheless, early researchers tended to conclude that competition between squawfish and salmonids was occurring. For example, Burns (1966, pp. 525–526) stated:

> "Although squawfish may remain in the forage class for a year or more their competitive and predatory habits far outweigh their value as forage. They compete for food with trout and prey on their young. A more subtle realm of competition is for space, since squawfish occupy a niche similar to trout in relatively warm waters."

The fact that squawfish often utilize food resources similar to those known to be used by trout is fairly well documented (Jeppson and Platts 1959; Thompson 1959; Casey 1962; Falter 1969). However, no food-overlap studies comparing trout and squawfish from the same environment have been done. Furthermore, diet similarity does not necessarily mean trout and squawfish are feeding by the same means or in the same place. Most studies on squawfish and salmonid distributions indicate a distinct partitioning of the physical environment. Falter (1969) observed that northern squawfish occupied the large pools of the St. Joe River in Idano and trout were found in areas of faster current. Dettman (1976) found physical factors such as stream velocity and water temperatures to be the most important factors explaining the abundance of Sacramento squawfish and rainbow trout in a zone of distributional overlap in Deer Creek, California. Similarly, Smith (in press) found that juvenile squawfish and rainbow trout largely occurred in different microhabitats in two small California streams. Competition for food and space seemed possible only in a few riffle areas in which both species were present. These waters reached temperatures stressful to the trout, indicating they were only of marginal quality as trout habitat. Other studies of Sacramento squawfish and trout associations also indicated the greater importance of physical factors over biological factors (Moyle and Daniels, in press; Moyle and Nichols 1973). The indications are that lentic populations of juvenile squawfish and salmonids also are spatially segregated, during the summer at least, with few salmonids being taken in areas where squawfish are abundant (Casey 1962; Foerster 1968; Hartman and Burgner 1972). In Lake Washington, young squawfish were found in littoral areas but young sockeye were limnetic (Eggers et al. 1978).

Despite strong indications of both micro- and macro-habitat segregation by squawfish and salmonids, they occur together often enough so that competition is theoretically possible, especially under fluctuating environmental conditions. Unfortunately, food limitation is very hard to demonstrate and has never been addressed in any squawfish-related research. Behavioral data indicate that trout populations are more likely to be space limited than food limited. Intraspecific competition for feeding territories, whose size may depend on food availability, is of great importance (Chapman 1966; Slaney and Northcote 1974; Bohlin 1977). There is no evidence that squawfish are territorial or even particularly aggressive. Preliminary experiments with Sacramento squawfish and rainbow trout in laboratory streams indicate that trout are more aggressive than squawfish and dominate them (Li 1975). This information suggests that squawfish cannot exclude trout from feeding territories although the reverse may be true.

If squawfish competition limits trout production, then removal of squawfish should increase growth and production of trout. Unfortunately, there have been few documented cases of the effects of squawfish removal on presumed competitors. Jeppson and Platts (1959) reported on the results of a squawfish control program utilizing gill nets, dynamite, and rotenone undertaken at Hayden Lake, Idaho. The catch index for trout doubled; however, the increased number of marked hatchery rainbows in the catch made it difficult to determine the contribution of the control program to increased trout production.

Inverse correlations between the abundance of squawfish and trout can often result from noncompetitive factors such as overfishing of trout stocks or alterations to the environment by man that result in physical conditions unfavorable to trout. For example, fishing is a form of selective predation that can have a severe effect on gamefish populations. Li (1975) demonstrated this with a simple mathematical model utilizing modified Lotka-Voltera competition equations. The initial conditions for the trout and sucker populations used were: (1) an insignificant level of interspecific competition ($\alpha = 0.00015$), (2) a stream-carrying capacity of 1,000 suckers and 1,000 trout, (3) an initial population size of 1,000 of each species, and (4) a 10% harvest applied to the trout population. In 24 years, an asymptotic value of 600 trout was reached but the sucker population remained at 1,000 fish—the reduced trout population being the result of fishing. Thus, an increase in the ratio of squawfish to trout does not necessarily demonstrate that competition is occurring.

Changes in the environment also can favor either squawfish or salmonids. Northern squawfish have an upper incipient lethal temperature of about 29 C (Black 1953), appear to prefer water of 16–22 C but are often found in warmer waters, and can tolerate dissolved oxygen levels as low as 0.8 mg/liter (Dimick and Merryfield 1945). Rainbow trout have a preferred temperature range of 13–21 C and avoid temperatures above 22 C (Coutant 1977). Also, trout require high oxygen concentrations for normal growth (Moyle 1976). Trout-stream alterations (e.g., channelization, removal of riparian vegetation, impoundment) tend to raise water temperatures and lower dissolved oxygen levels, creating conditions more likely to favor squawfish than trout.

Impoundments may have other effects. When flows in streams below dams are suddenly reduced, trout may be forced to abandon territories or established feeding stations. Such behavior is known to increase their vulnerability to predation (Symons 1974) and might also result in lower food intake. Reduced flow rates may allow squawfish to forage in areas previously unavailable to them. Squawfish, especially at lower temperatures, are unable to maintain their position (and presumably feed) in fast currents often utilized by trout (Dettmann 1976; D. M. Baltz and P. Moyle, unpublished data). Upstream changes also may occur as a result of impoundment (Erman 1973); reservoirs may act as overwintering grounds for squawfish populations, and allow populations to increase (Adams and Moyle 1975), but there is no firm documentation for this phenomenon.

Conclusions

Four main conclusions can be drawn from this review:

1) In streams, squawfish do not appear to be significant predators of salmon and trout except under highly localized, seasonal, or unusual circumstances that are often related either to the design of dams and diversions or to poorly planned releases of hatchery smolts.
2) In lakes with large squawfish populations, squawfish (along with other predators) can reduce juvenile salmon populations, but it is not clear if this predation has any impact on the number of adult salmon returning to the system.
3) The available evidence is insufficient to determine if interspecific competition is occurring between squawfish and trout. The evidence that exists indicates that it is rarely a serious problem.
4) The interactions between squawfish and salmonids either are poorly understood or misunderstood. This seems to be largely the result of studies that were not of sufficient scope to adequately address the nature of the interactions. Most of the studies either start with the premise that squawfish eat or compete with salmonids or analyze unusual situations where squawfish have been perceived to be a problem (and the results then generalized).

It should be obvious from this review that there is need for more research on squawfish to determine under what situations, if any, squawfish control or management is needed. Some possible areas of study are:

1) It would be useful to have energy budgets constructed for squawfish at different temperatures to learn how much they eat, how often they eat, how efficient their digestion is, and how these factors relate to growth rates. With such a budget, it might be possible to predict the impact of a squawfish population on local salmonids through a study of stomach contents and growth rates.
2) The role of squawfish in the fish communities of which they are part needs to be clarified. Are they a 'keystone' predator that determines community structure or does their predation have little impact on the populations of other fish species? If squawfish are a keystone species, removal of squawfish from a community may cause an increase in other potential competitors or predators of salmon and trout.
3) Comparative studies of the feeding habits and microhabitat preferences of different size classes of trout and squawfish, in situations where they are sympatric, are needed to see under what circumstances, if any, they compete for food and space.
4) More needs to be known about how dams and diversions increase the impact of squawfish predation on salmon and trout populations to find ways to reduce that impact.
5) The circumstances under which squawfish prey on out-migrating salmon needs to be determined so that hatchery releases can be planned to reduce the impact of such predation.

Only when answers to such questions as these are found will the significance of squawfish predation and competition with salmonid populations become known. However, it seems to us that, in situations where it can be demonstrated that squawfish predation or competition is having a negative impact on salmonid populations, squawfish control will be at best a temporary solution and perhaps even detrimental over the long term (see Buchanan et al. 1981). In such situations, the "unbalanced" populations are likely to be symptoms of the more fundamental problems caused by man-made perturbations to the environment.

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