A Review of Seminatural Culture Strategies for Enhancing the Postrelease Survival of Anadromous Salmonids

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Abstract

The unnatural behavioral and morphological conditioning that occurs in the fish culture environment reduces the postrelease survival of hatchery-reared salmonids compared to their wild-reared counterparts. We review innovative culture techniques that offer development of fish with more "wild-like" behavior and morphology, and higher postrelease survival. These techniques include rearing fish over natural substrates that promote the development of proper camouflage coloration, training them to avoid predators, exercising them to enhance their ability to escape from predators, supplementing diets with natural live foods to improve foraging ability, reducing rearing densities, and utilizing oxygen-supplementation technology. In addition to enhancing postrelease survival, these seminatural culture strategies will minimize the shift in selection pressures associated with the artificial rearing environment. We conclude that these innovative culture techniques are effective and should be used in both enhancement and conservation hatcheries.

Introduction

The success of fish-culture programs for salmonids is now achieved primarily by increasing the prerelease survival of salmonid fishes. Artificial propagation may easily increase egg-to-smolt survival by more than an order of magnitude over that experienced by wild fish. Unfortunately, the postrelease survival of these cultured salmonids is often considerably lower than that of wild-reared fish (Greene 1952; Miller 1952; Salo and Bayliff 1958; Reimers 1963). While this low postrelease survival may be acceptable in put-and-take fisheries, it is intolerable in supplementation programs to increase salmonid stocks designed to rebuild self-sustaining natural runs and conserve genetic resources. Continued success of hatchery programs can be assured by implementing innovative fish culture techniques that increase the postrelease survival of hatchery salmonids.

When standard hatchery strains of brook trout (*Salvelinus fontinalis*) were released to recolonize vacant habitats they failed, while releases of wild strains usually succeeded (LaChance and Magnan 1990a). Similarly, the use of hatchery coho salmon (*Oncorhynchus kisutch*) to supplement natural runs caused a long-term decline in production (Nickelson et al. 1986). Low postrelease survival of hatchery salmonids compared to their wild cohorts may result from the behavioral and morphological differences that develop in cultured fish. For example, the practice of feeding pellets at the surface by hand or from vehicles results in hatchery brook trout and Atlantic salmon

(_Salmo_ _salar_) that are more surface oriented and more likely to approach large moving objects than wild fish (Mason et al. 1967; Sosiak 1978). This surface orientation makes these hatchery-reared salmonids more vulnerable to avian predators (e.g., herons, kingfishers, and mergansers). The conventional hatchery environment also produces brook trout, brown trout (_S_. _trutta_), and coho salmon with more aggressive social behavior than wild-reared fish (Fenderson et al. 1968; Bachman 1984; Swain and Riddell 1990). After release, the heightened aggressive tendencies of these hatchery fish put them at a greater risk from predation and often result in inefficient expenditure of energy in contests over quickly abandoned feeding territories. In addition, many hatchery salmonids exhibit inept foraging behavior that results in their stomachs containing fewer digestible items than those of their wild-reared counterparts (Miller 1953; Hochackka 1961; Reimers 1963; Sosiak et al. 1979; Myers 1980; O'Grady 1983). As adults, hatchery strains of coho salmon have better developed primary sexual characteristics (egg size and number), but less well-developed secondary sexual characteristics (kype size and nuptial coloration) than wild-reared strains (Fleming and Gross 1989). These reduced secondary sexual characteristics of hatchery strains may prohibit their ability to defend redd sites when spawning naturally. Although the effect on postrelease survival is unknown, the shape of hatchery and wild chinook salmon (_O_. _tshawytscha_) also differs at the juvenile stage (Taylor 1986).

Phenotypic differences observed between cultured and wild fish are both genetically and environmentally induced. The artificial culture environment conditions salmonids to respond to food, habitat, conspecifics, and objects in a different manner than the natural environment. Present culture techniques also alter selection pressures, which results in cultured strains becoming innately distinct from wild strains (Flick and Webster 1964; Fraser 1981, 1989; Lachance and Magnan 1990b; Mason et al. 1967; Reisenbichler and McIntyre 1977; Swain and Riddell 1990).

Theoretically, both environmental conditioning and shifts in evolutionary selection pressure produced by the artificial culture environment can be alleviated with culture practices that simulate a more natural rearing environment. In this paper, we review fish culture methods for increasing postrelease survival. The use of antipredator conditioning, foraging training, supplemental dissolved oxygen, and reduced rearing density will be examined.

Antipredator Conditioning

Predation may be a key factor in the poor postrelease survival of cultured salmonids. The ability of an animal to avoid predation is dependent on proper cryptic coloration to avoid detection by predators, ability to recognize predators, and stamina to flee from predators. Techniques presently exist for improving each of these antipredator attributes of cultured fish.

Cryptic Coloration

Postrelease survival of cultured fish can be increased by rearing them in an environment that promotes full development of the camouflage pattern they will need after release. Both the short- and long-term camouflage coloration of salmonids is primarily affected by the background color pattern of their environment. Short-term physiological color changes are accomplished by chromatophore expansion where pigment is dispersed within the chromatophore unit and color change occurs within minutes. In contrast, morphological color changes take weeks to complete as pigments and chromatophore units are developed to match the general background coloration (Fuji 1993). The cryptic coloration ability generated by these long-term stable color adaptations provides the greatest benefit for avoiding detection by predators.

Fish culturists have long recognized that fish reared in earthen-bottom ponds have better coloration than those reared in concrete vessels (Piper et al. 1982). However, only recently has it been understood that rearing salmonids over natural substrates, similar to those over which they will be released, increases postrelease survival by enhancing cryptic coloration. Groups of brook trout reared for 11 weeks over distinct background colors were less vulnerable to predators when challenged over background colors similar to those over which they were reared (Donnelly and Whoriskey 1991).

In our laboratory, fall chinook salmon reared in seminatural rectangular tanks with substrate, cover, and in-stream structure (plants and rootwads) had better cryptic coloration for the stream environment into which they were released than fish reared in barren grey tanks similar to the surroundings in conventional raceways. These seminaturally reared fish had almost 50% higher postrelease survival in a coastal stream than their conventionally reared counterparts (Figure 1). As there was no observed difference in size or disease status between the treatments, the difference in survival is probably attributable to coloration.

Similar relationships have been noted by other investigators. In one Lummi Indian Nation coho salmon enhancement project, fish reared in dirt-bottom ponds had higher smolt-to-adult survival than those reared in concrete vessels (K. Johnson, Idaho Department of Fish and Game, personal communication). Besides having better cryptic coloration, fish reared in earthen ponds are considered to have better health, fin condition, and overall quality than those reared in concrete vessels (Piper et al. 1982). This was recently verified by Parker et al. (1990) in a study that demonstrated that coho salmon fry reared over leaf litter had higher prerelease survival than those reared in barren-bottom tanks.

Predator Avoidance

Postrelease survival of cultured salmonids can also be increased by training them to recognize and avoid predators. Thompson (1966) first determined that salmonids can learn to avoid predators in the laboratory and then demonstrated that predator avoidance training is practical in production hatcheries. He conditioned production lots of fall chinook salmon to avoid predators by moving an electrified model of a predacious trout through raceways each day for several weeks. Salmon that approached the model too closely were negatively conditioned with an electrical shock. After they were released into a coastal creek, the in-stream survival of the salmon trained to avoid predators was significantly higher than that of their untrained cohorts.

In the laboratory, it has been shown that coho salmon rapidly learn to recognize and avoid a predator after observing it attack conspecifics (Olla and Davis 1989). This approach to predator-avoidance training could be implemented by briefly exposing each lot of production fish to the main predators they will encounter after release. The loss of a few fish sacrificed in these training sessions should be outweighed by the larger number of trained fish that will survive later.

Swimming Performance

Swimming ability, which is critical to a fish's ability to escape from a predator, can be improved by implementing exercise programs. The swimming performance of coho salmon, Atlantic salmon and brook trout significantly improved after they were forced to swim at higher velocities for 6 weeks or more (Besner and Smith 1983; Leon 1986; Schurov et al. 1986a). This exercise regime also enhanced their growth. The postrelease survival of exercised fish has generally (Burrows 1969; Wendt and Saunders 1972; Cresswell and Williams 1983; Leon 1986; Schurov et al. 1986b), but not always (Lagasse et al. 1980; Evenson and Ewing 1993), been higher than that of unexercised fish. The survival benefit of exercise was only realized in programs that forced salmonids to swim at high velocities for some time each day for at least 2 weeks. This exercise training may be implemented with current technology by rearing fish in either high-velocity circular or rectangular circulating ponds or by creating high velocities in conventional raceways by temporarily drawing them down or recirculating water within them.

Foraging Training

Foraging theory suggests that supplementing standard pelletized diets with live foods will profoundly increase postrelease foraging ability of cultured fish. Gillen et al. (1981) found that previous experience in capturing live prey enhanced the foraging behavior of tiger muskellunge (F_1 hybrid of female muskellunge, Esox masquinongy, x male northern pike, E. lucius) by decreasing the time and number of strikes required to capture natural live prey.

In our laboratory, fall chinook salmon reared on a pellet diet supplemented with live prey fed on twice as many familiar (e.g., chironmid larvae) and novel prey (e.g., mayfly larvae) as their counterparts reared on a pellet-only diet (Figure 2). Even though food was abundantly supplied to both treatment groups, the growth and natural coloration of fish reared on the live-food supplemented diet was better than that of fish fed only pellets.

Field trials generally confirm that live-food supplemented diets improve the postrelease foraging ability and survival of cultured fish. Tiger muskellunge reared in the hatchery on a live fish diet had higher postrelease survival than their cohorts reared only on pellets (Johnson 1978). Similarly, brown trout reared in earthen-bottom ponds with natural food supplementation had a higher postrelease survival than control trout reared in non-earthen-bottom tanks and fed only pellets (Hesthagen and Johnsen 1989). Live foods for salmonids can be produced by adopting techniques used in the culture of many warmwater fish species. Besides the beneficial effects to fish, live food diets have the potential to both reduce feed costs and produce less undigested waste than standard diets.

Supplemental Dissolved Oxygen

The level of dissolved oxygen in the rearing environment is critical for salmonids. At rest, a fish uses up to 10% of its metabolic energy to support gill ventilation (Wooten 1990). If the oxygen content of water declines, available energy must be directed from other life functions to increase respiratory ventilation. The difference between the energy required for respiration and the total available energy is the metabolic scope for activity.

At 15°C, salmonids require 10 ppm of dissolved oxygen to be fully active (McCauley 1991). A brook trout living in water with 7 ppm dissolved oxygen has only three-fourths of the metabolic scope of a trout living in water with 10 ppm dissolved oxygen (Fry 1971). Thus, although salmonids can survive and grow in a 7-ppm dissolved oxygen environment, their metabolic scope is sharply curtailed.

As the metabolic scope for activity is reduced by lower levels of available dissolved oxygen, there is a commensurate decrease in activities such as sustained swimming performance. Growth and food conversion are also limited by available dissolved oxygen. In a study using coho salmon, Herman et al. (1962) showed that growth and food-conversion efficiency increased with a rise in environmental dissolved oxygen up to the highest level tested (8.3 ppm). Theoretically, both learning ability and disease resistance of fish may similarly be limited by dissolved oxygen.

Fish culture textbooks suggest that a 7-ppm dissolved oxygen environment is satisfactory for rearing salmonids and that the dissolved oxygen level should never fall below 5 ppm (Leitritz and Lewis 1980; Piper et al. 1982; Mclarney 1984). However, these texts also indicate that higher dissolved oxygen levels are preferred for improving fish quality and reducing stress. Piper et al. (1982) indicate inflow water to ponds should be at 100% oxygen saturation and never drop below 80% oxygen saturation anywhere in the pond. Leitriz and Lewis (1980) indicate that a 10 to 11 ppm dissolved oxygen environment is best for culturing trout which may show discomfort at a level of 7.8 ppm. The recommended 10 to 11 ppm dissolved oxygen level should provide salmonids with a full metabolic scope of activity.

A 10 ppm dissolved oxygen environment can be achieved in the fish culture environment with supplementation oxygen technology. Most research on this technology has been used to increase the weight of fish that can be produced per unit volume (Dwyer et al. 1991). However, it has also been observed that in hatcheries utilizing oxygen injection and supplemental aeration systems, disease incidence decreased and fin quality, feed conversion, and fish survival improved (Marking 1987). The cost and inconvenience of retrofitting these systems to production hatcheries is relatively low compared to the benefits in fish quality that can be achieved.

Rearing Density

Rearing density is one of the most important and well studied factors affecting fish quality. In rainbow trout (O. mykiss), both growth and condition factor are inversely related to rearing density (Refstie 1977). Westers and Copeland (1973) and Maheshkumar (1985) found that the fin condition of

Atlantic salmon deteriorated with increasing rearing densities. However, in a study in which another strain of Atlantic salmon was reared in a different type of vessel at rearing densities of 8.5 to 68.7 kg/m^3 (0.53 to 4.29 lbs/ft^3) no relationship between rearing density and fin condition, growth, or in-culture survival was found (Soderberg and Meade 1987).

Inverse relationships between rearing density and growth, condition factor, and food conversion efficiency have been observed in coho salmon (Fagerlund et al. 1981). In addition, coho salmon reared at high densities suffered greater physiological stress as measured by body water content, fat and protein contents, interrenal cell nuclear diameter, and mortality rates. For coho salmon smolts, rearing densities as low as 16 kg/m^3 (1 lb/ft^3) can induce physiological stress (Wedemeyer 1976), and increased rearing density reduces both gill ATPase levels (Banks 1992) and plasma thyroid hormones (Pitano et al. 1986).

In a survey of 85 variables related to strain and culture conditions, only the five associated with either water flow, amount of living space, or relative water level in rivers explained the postrelease survival of Atlantic salmon (Homer et al. 1979). The adult return of coho salmon also appears to be inversely related to rearing-pond density in some (Sandercock and Stone, unpublished, as reported in Fagerlund et al. 1981; Banks 1992), but not all, studies (Hopley et al. 1993).

Martin and Wertheimer (1989) examined the effect of one low, two intermediate, and one high rearing densities on the postrelease survival of chinook salmon. In the hatchery, all four rearing densities showed similar high survival (99.5% or greater), but fish reared at higher densities were smaller at release. The low-density group showed the highest adult return (1.0%), followed by the two intermediate-density groups (0.9 and 0.7%) and the high-density group (0.6%). However, the increased number of smolts produced at the two higher densities compensated for their reduced return rate and yielded a higher number of adult returns per unit volume of rearing space.

Most other chinook salmon studies have shown a consistent inverse relationship between rearing density and percentage of fish surviving to recruit to the fishery and spawning area (Hopley 1980, Fagerlund et al. 1987, Denton 1988, Downey et al. 1988, Banks 1990). However, as adult return is a function of both the number of fish released and the percentage of that number surviving to adulthood, the greatest number of fall chinook adults can be produced by rearing fish at intermediate densities (Martin and Wertheimer 1989).

The relationship between rearing density and adult returns for all salmonid species indicates that a larger percentage of fish recruit to the fishery and spawning population when they are reared at a lower density. Thus, for any given number of cultured juveniles, the total adult yield will be greatest when they are reared in a large (low density) rather than a small (high density) volume vessel. Since water, not land, is the primary constraint at most fish-culture facilities, postrelease survival and total adult returns can be increased by installing larger vessels that reduce density by increasing rearing volume.

Conclusions

As demonstrated in our review, there are many culture strategies for increasing the postrelease survival of hatchery-reared salmonids. Strategies that involve rearing salmonids at low densities with naturalistic substrate, in-stream structure, and cover will reduce chronic stress and disease, and increase survival. They will also minimize potential risks from the shifts in selection pressures associated with the conventional culture environment. Strategies such as foraging training, swimming exercise, and antipredator conditioning will also behaviorally and morphologically prepare fish for survival in the postrelease environment.

Traditionally, these strategies have been rejected by hatcheries because it has been presumed that they will increase costs, maintenance, or disease. These concerns are either unfounded or can be eliminated with alternative technology. For example, salmonids can be reared at a lower density over natural substrates in large dirt-bottom raceways or ponds without increasing water consumption or incurring the higher construction costs associated with concrete ponds. Similarly, the harvest of natural feeds from on-site production facilities will enhance foraging ability and overall fish quality. Natural feeds may also reduce overall feed costs and enhance effluent water quality by reducing the generation of undigested settleable solids.

Culture strategies that increase postrelease survival can significantly reduce salmon enhancement costs. Based on several sources, we estimated the traditional cost per smolt at publicly operated facilities at about $0.15 for coho salmon, $0.25 for spring chinook salmon, and $0.34 for steelhead (Mayo 1988; Heen 1993; R. Hager, Hatchery Consultants, Inc., personal communication). The quantity of smolts an enhancement program must produce to yield a given number of recruits is dependent on the smolt-to-adult survival. Thus, culture strategies that increase smolt-to-adult survival reduce both the total number of smolts a program must release and the cost/recruit. For example, for a spring chinook salmon smolt costing $0.25 to produce, doubling postrelease survival from 0.5 to 1.0% reduces production costs for each recruit from $50 to $25 for a net saving of $25 per recruit. With enhancement programs designed to produce half a million recruits, implementation of these culture strategies could save up to $12 million in smolt production costs each year.

There are also significant benefits to the natural spawning population that arise from increasing the postrelease survival of cultured fish. For instance, doubling postrelease survival from 0.5 to 1.0% reduces the number of adults that culture programs must remove from wild-spawning populations by half. This reduction in the number of broodstock required is crucial with conservation and supplementation programs designed to build naturally spawning populations, as well as with enhancement facilities that are mining naturally spawning populations for broodstock. This increase in postrelease survival also halves the number of hatchery fish that must be released to produce a given number of recruits. This should reduce the postrelease competition for resources that occurs between wild and hatchery fish, thus potentially improving wild fish survival. These culture strategies may also minimize the genetic impact of cultured fish spawning with the natural population by inhibiting the development of domestic strains that are distinct from the wild strains from which they were derived. Finally, by producing fewer smolts, enhancement facilities will produce less biowaste and use less natural resources than with traditional fish culture practices. In summary, the reviewed innovative culture strategies will benefit wild stocks as well as target cultured salmonids by reducing broodstock collection and smolt release numbers and by lessening domestication and environmental impacts.

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Figure 1. Comparative in-stream survival of fall chinook salmon released from conventional (barren; n = 83) and seminatural (substrate, structure, and cover; n = 203) raceways.

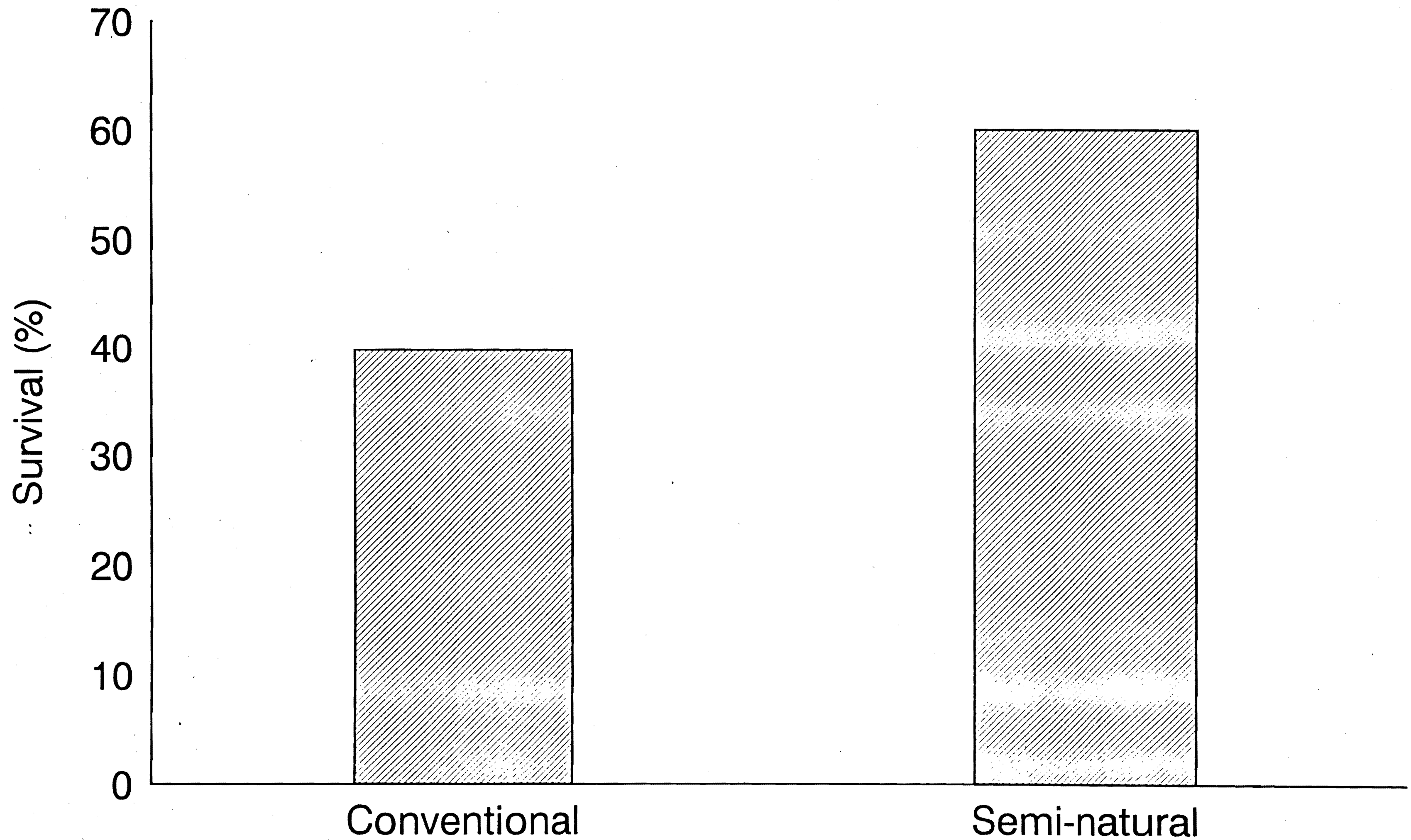
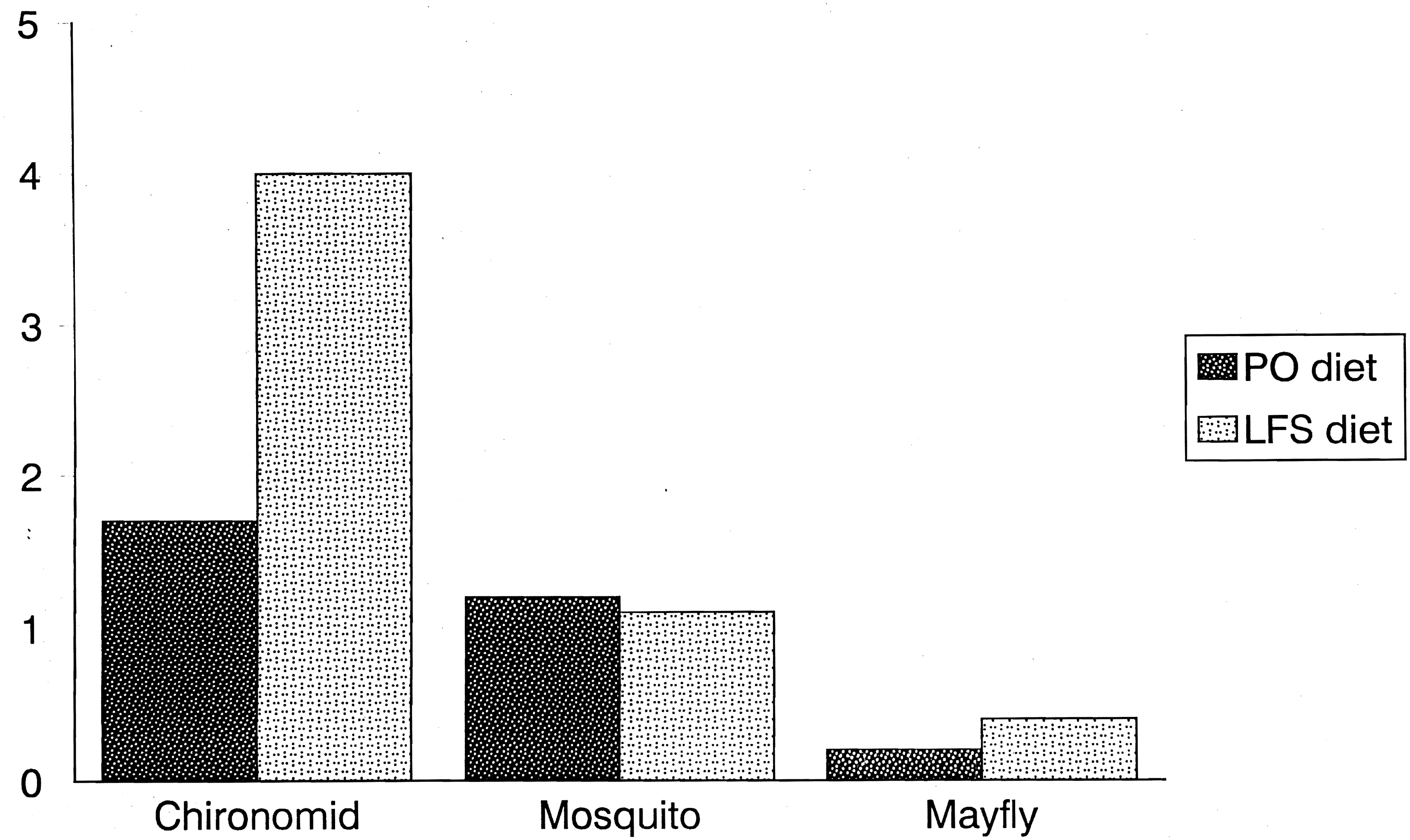

Survival (%)
70
60
50
40
30
20
10
0
Conventional
Semi-natural

Figure 2. Average number of test prey ingested by fall chinook salmon reared on pellet only (PO; n = 20) or live-food supplemented (LFS; n = 20) diets.


5
4
3
2
1
0
Chironomid
Mosquito
Mayfly
PO diet
LFS diet