Section 3

EFFECT OF LIVE FOOD DIETS ON THE FORAGING BEHAVIOR OF CULTURED FALL CHINOOK SALMON

by

Desmond J. Maynard, Gail C. McDowell, Glen A. Snell, Anita L. LaRae, Thomas A. Flagg, and Conrad V.W. Mahnken

Resource Enhancement and Utilization Technologies Division
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Manchester Research Station
P.O. Box 130
Manchester, Washington 98353

Introduction

Hatchery-reared salmonids may experience a low postrelease survival because they lack experience in foraging on natural prey (Miller 1952, Hochachka 1961, Reimers 1963). Typically, during the first few weeks after release, cultured salmonids eat less and forage on more indigestible material than wild-reared fish (Sosiak et al. 1979, Myers 1980, O'Grady 1983, Johnsen and Ugedal 1986, Hvidsten 1994, Fjellheim et al. 1995).

Several hypotheses may explain reduced foraging success and starvation; for example:

(i) newly released fish delay feeding until they are fully acclimated to their new surroundings;

(ii) pellet-reared fish are unable to recognize natural prey or find natural prey unpalatable as they could not develop a taste preference for it earlier in life;

(iii) pellet-reared fish must first develop experience in recognizing, capturing, and handling live prey which is considerably more cryptic and evasive than pellets before they can forage efficiently in their natural environment;

(iv) hatchery-reared fish may remain in denser aggregations than the prey base they encounter during their seaward migration can support.

However, it is probable that some combination of all these factors working together is the real reason why hatchery-reared fish appear to be starving when they are recaptured shortly after release.

This section describes experiments to determine if the use of live food diets improves the postrelease foraging ability of hatchery-reared salmon. The hypothesis is that live food diets will provide juvenile salmon with the experience they require to recognize, capture, handle, and ingest the natural live prey on which they will depend after release. Previous work (Maynard et al. 1996a) demonstrated that supplementing pellet diets with live feeds improved the laboratory foraging ability of fall chinook salmon. Using this information, the current study examines how a total live food diet affects both the laboratory and in situ foraging ability of fall chinook salmon.

Methods

In February 1996, six clear acrylic tanks (400-L capacity) were set up in an indoor fish culture laboratory at the Manchester Research Station. Each rectangular tank (152 × 46 × 46 cm) was supplied with a low flow (0.1-0.5 L/min) of city well water. The water in each tank was reprocessed by an aquarium filter (25 L/min) equipped with activated carbon, polyester fiber filter material, and a rotational wheel biofilter. Three sides of each tank were screened with gray PVC plastic sheet to prevent each group of fish observing the feeding behavior of others.

In March 1996, 300 fall chinook salmon swim-up fry were obtained from the WDFW Bingham Creek Hatchery. The fish were transported to Manchester Research Station and systematically divided into six equal lots of 50 fish. Each lot was ponded into one of the six

tanks. The fish in three tanks were designated as controls and were reared exclusively on a commercial diet of semi-moist pellets. The fish in the other three tanks were fed the experimental live food diet of blackworms (*Lumbricules* spp.), brine shrimp (*Artemia salina*), bloodworms (*Chironomid* spp.), glassworms (*Coretrum* spp.), amphipod (*Gammarus* spp.) and shrimp (*Caridea* spp.). On rare occasions, when the required quantity of live food was unavailable, the diet was supplemented with whole frozen brine shrimp and krill (*Euphausiid* spp.). At first, the control ration was restricted so that the fish grew at a rate in parallel with the experimental fish. However, by October the control fish were visibly larger than those fed the live food diet.

The six groups were maintained in the tanks for six months. At the end of October 1996, they were transferred outdoors to six green circular fiberglass tanks (1.47-m diameter). Each tank was supplied with unfiltered well water (3.8 L/min). The subsequent handling and husbandry of fish in all tanks was similar and, apart from diets, followed standard salmon culture protocols.

The foraging behavior of fish from the two treatments was compared in rectangular tanks (400 L) identical to those described above. Three sides of each tank were totally covered and a black polyethylene curtain hung across the front, which could be opened to enable the behavior to be observed during each test. A layer of pea gravel (4 cm) covered the bottom of each arena to create a more natural foraging environment in which prey could hide.

Thirty-six laboratory foraging trials (eighteen per treatment) were conducted in the laboratory test arenas in September 1996. In each trial, a single fish was acclimated to the test arena for 48 hours before any prey were added. During acclimation the entire tank was covered, leaving the fish in total darkness. Two hours before each trial, the top cover was removed and a light turned on to allow the fish to adjust to the visual environment in which they would be observed. Fifteen minutes before the trail, prey was introduced into the tank through a gray PVC feeding tube (10-cm diameter). This gave the prey time to settle into the gravel so that fish were challenged both to recognize their prey and to seek it actively among the small stones.

The prey in each trial consisted of 20 amphipods, 20 blackworms, and 5 glassworms. The amphipods and blackworms were obtained commercially. The glassworms were collected from a small pond near the Manchester Research Station.

The treatments were alternated between trials until eighteen fish from each treatment were tested. Each trial was initiated by uncovering the front of the tank and removing the feeding tube. The frequency and time relationship for each prey the fish approached, attacked, captured, ingested, lost, or rejected, were recorded by an observer with the help of event-recorder software on a computer. The trial period lasted 60 minutes, after which the light was turned down, leaving the fish to forage overnight.

The prey handling time, which is a measure of the time taken by a fish to manipulate each item it ingests, was determined by observing an ingestion and tracing back through the record to

find the original attack on that particular prey item. With this approach a fish capturing, rejecting, recapturing, and then ingesting a prey item was considered a complete string of events. Frequency of behaviors (approach, attack, capture, reject, and ingest) were analyzed with nonparametric Mann-Whitney U-tests. The prey handling time data were analyzed with *t*-tests.

In May 1997, after an additional 8 months of rearing, the foraging tests were initiated in situ. The fish were trucked in tanks, still separating each rearing group, from the Manchester Research Station to a location on Bingham Creek near the Bingham Creek Hatchery. They were placed in Bingham Creek, upstream of the hatchery, in twelve nylon net cages ($1 \times 1 \times 0.3$ m deep).

A single fish was placed in each cage, with six cages randomly receiving fish from one treatment and six from the other treatment. The cages were then submerged in the creek at least 2 m away from each other to prevent any interaction between fish. The only food available to these fish was natural prey in the creek that drifted, swam, or crawled into the cage. Both aquatic insects and salmonid fry were known to enter these cages.

After seven days the fish were retrieved and sacrificed. Their stomachs and intestines were then removed and preserved separately in formaldehyde solution (10%). The contents were weighed to the nearest 0.001 g. As it was difficult to distinguish reliably between digestible and indigestible material, only the weight of the total gut contents was used for data analysis. The gut contents are expressed as a percentage of overall body weight to compensate for differences in fish length. These foraging bioassays in situ were repeated over a five-week period until at least 25 fish from each treatment had been tested in the cages.

Results

Laboratory Trials

Prey behavior was the principal factor affecting fish foraging success. The blackworms immediately disappeared into the substrate. Consequently, the fish were never observed to approach, attack, capture, or ingest blackworms. Like blackworms, amphipods spent most of their time in the gravel where they were unavailable to the fish. Fish only detected and captured amphipods during the infrequent times they emerged and swam over the gravel surface for a short distance before burrowing again. During these movements six fish saw and ingested a total of 9 amphipods.

Glassworms, by contrast, stayed in the water column and were highly visible to the fish. This resulted in fish approaching, attacking, capturing, and ingesting glassworms more than any other live prey (Fig. 1). Thirteen fish from each treatment ate a total of 80 glassworms during the observation period. Fish spent most of their effort in approaching, attacking, and capturing non-food items, such as air bubbles and woody debris (Fig. 1). Nine fish actually ingested 12 non-food items.

No statistically significant difference was detected between treatments in the number of approaches, attacks, captures, or ingestions made towards any food item (Fig. 1). Fish from both treatments displayed similar behavior to live prey (Fig. 1a and b). However, pellet-fed fish were observed to approach, attack, and capture non-food items more often than fish reared on live food (Fig. 1c).

Although fish from both treatments attacked non-food items more often than anything else, pellet-reared fish directed a significantly ($P = 0.016$) larger percentage of their attacks at non-food items (Fig. 2). Similarly, fish fed live food directed a significantly ($P = 0.006$) greater percentage of their attacks at glassworms. The percentage of attacks directed at amphipods and blackworms was similar for both groups.

Foraging efficiency (ingests/attacks) was high for glassworms, followed by amphipods, and lowest for non-food items (Fig. 3). There was no statistically significant difference between treatments in their foraging efficiency on amphipods or non-food items. However, pellet-fed fish foraged significantly ($P = 0.014$) more efficiently on glassworms than live food fed fish.

In general, prey handling time was longest for amphipods, intermediate for glassworms, and shortest for non-food items (Fig. 4). With the relatively small sample sizes ($n = 3$-13) and large variance associated with behavior, it was not possible to detect any statistically significant differences between treatments in average prey handling time. Based on the actual data, the live food fed fish spent slightly more time handling live food and the pellet-reared fish slightly more time handling non-food items. This is in contrast to foraging theory that would predict that prey handling time should decrease with experience (Hughes 1979, Hughes et al. 1992). However in an earlier study we also saw a greater, although not statistically different, handling time of live prey for chinook salmon that had previous experience handling live food (Maynard et al. 1996a). Therefore, this may be more an indication of interest in these food types rather than the time needed to handle them.

Although they had not fed for two days and some of the prey were easy and attractive targets, 6% of fish fed live diets and 22% of pellet-fed fish did not attack anything in the test arenas (prey or non-food items). Seventeen percent of live food fed fish and 28% of pellet-fed fish failed to attack any live prey items and ingested nothing during observation

The In Situ Trials

The guts of many of the fish in the cages were near empty, with roughly 38.5% of the fish having a gut content that weighed less than 0.1 g (Fig. 5). Only 26.9% of the study fish (6 live food and 8 pellet-fed) had a gut content that weighed between 1 and 4% of their body weight. Only two fish had more than 1 g of material in their gut. While the guts of all of the live food treatment fish had some material inside, the guts of 3 of the pellet-fed fish contained nothing.

On average, the live food fed fish placed in cages were smaller than the pellet-fed fish (Fig. 6). The gut content weight of fish reared on a live food diet was greater than fish reared on

a pellet-only diet (Fig. 7). However, with the high variance and small sample size, it was not possible to detect a statistically significant (P = 0.606) difference between the two treatments.

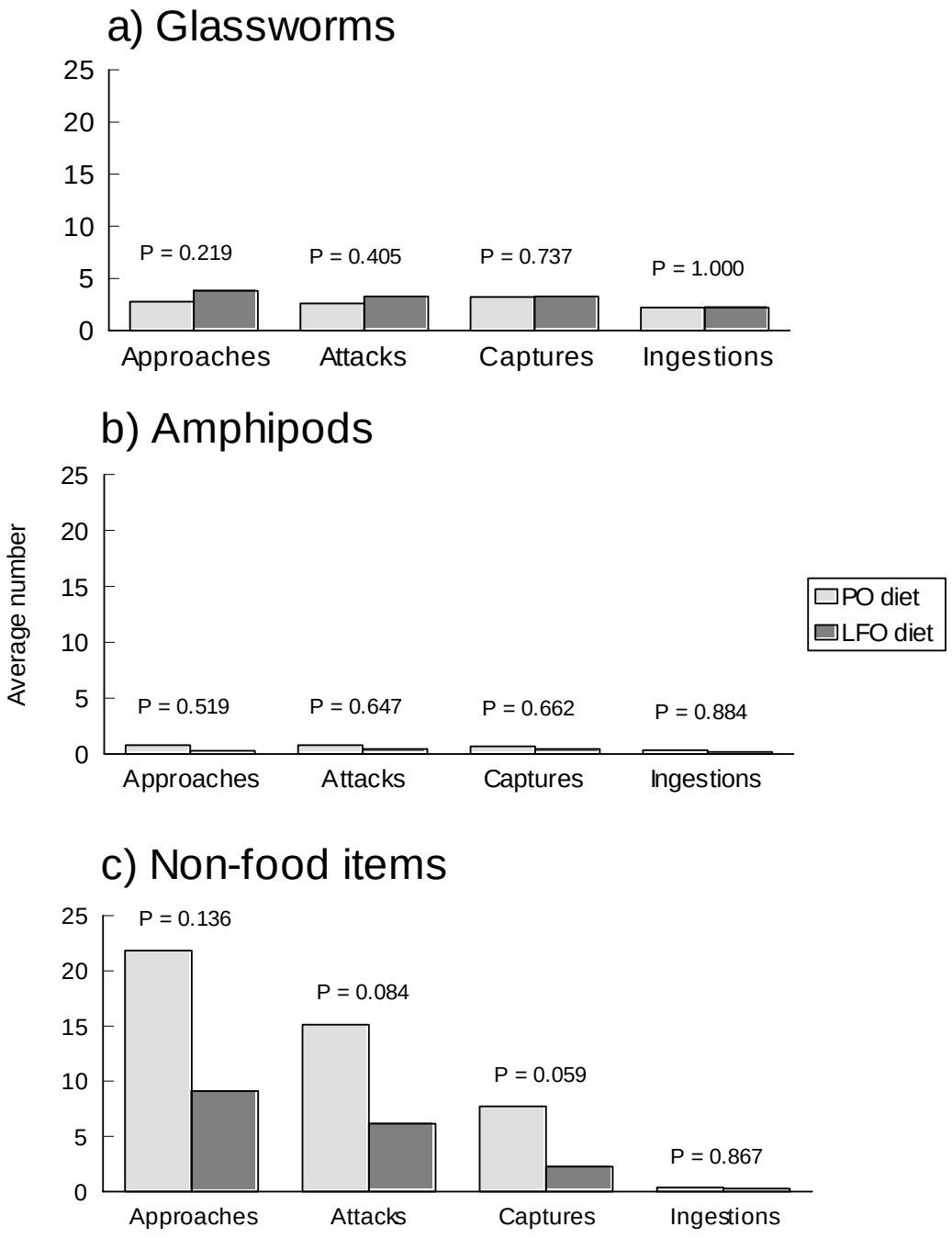

Figure 1. Foraging behavior of fall chinook salmon observed with (a) glassworms, (b) amphipods, and (c) non-food items. Salmon were reared on a pellet-only diet (PO; N = 18) or a live food-only diet (LFO; N = 18). The probability values (P) are based on Mann-Whitney U-tests.

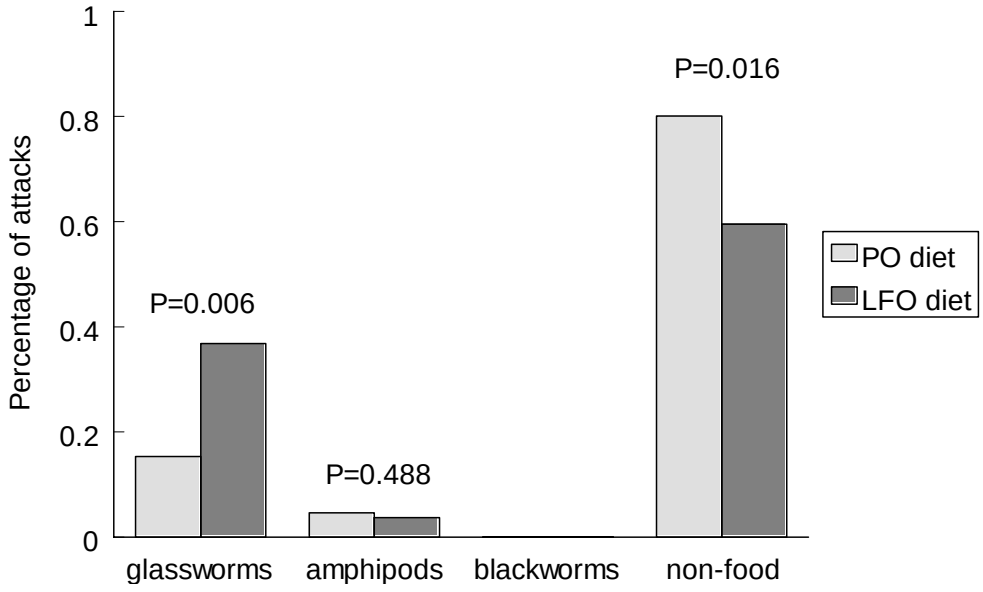

Figure 2. Percentage of attacks by fall chinook salmon on each prey item. Salmon were reared on a pellet-only diet (PO; N = 18) or a live food-only diet (LFO; N = 18). The probability values (P) are based on Mann-Whitney U-tests.

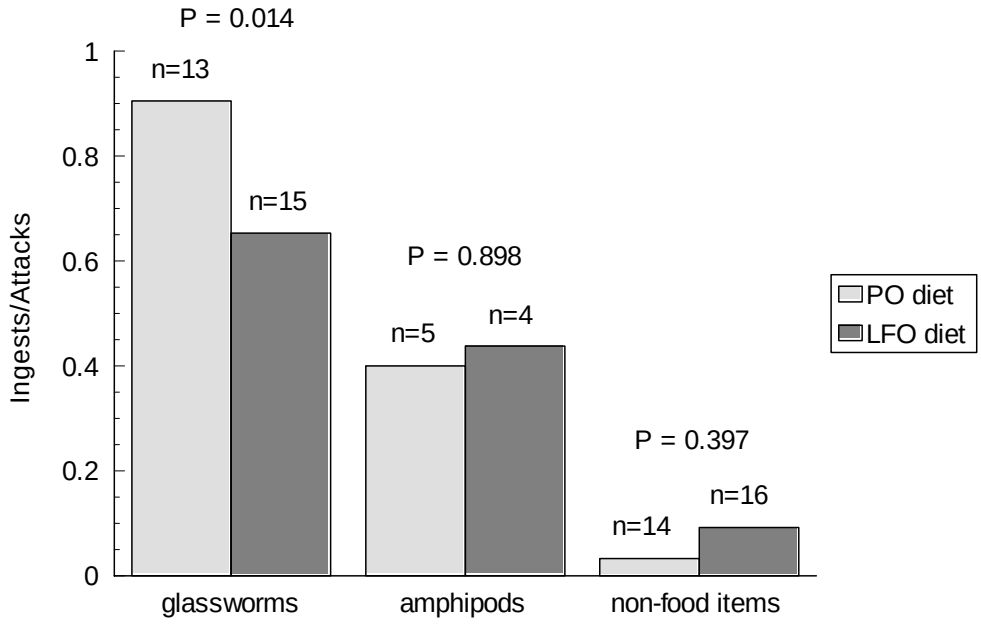

Figure 3. Foraging efficiency (ingests/attacks) of fall chinook salmon on each prey item. Salmon were reared on a pellet-only diet (PO) or a live food-only diet (LFO). Probability values are based on *t*-tests.

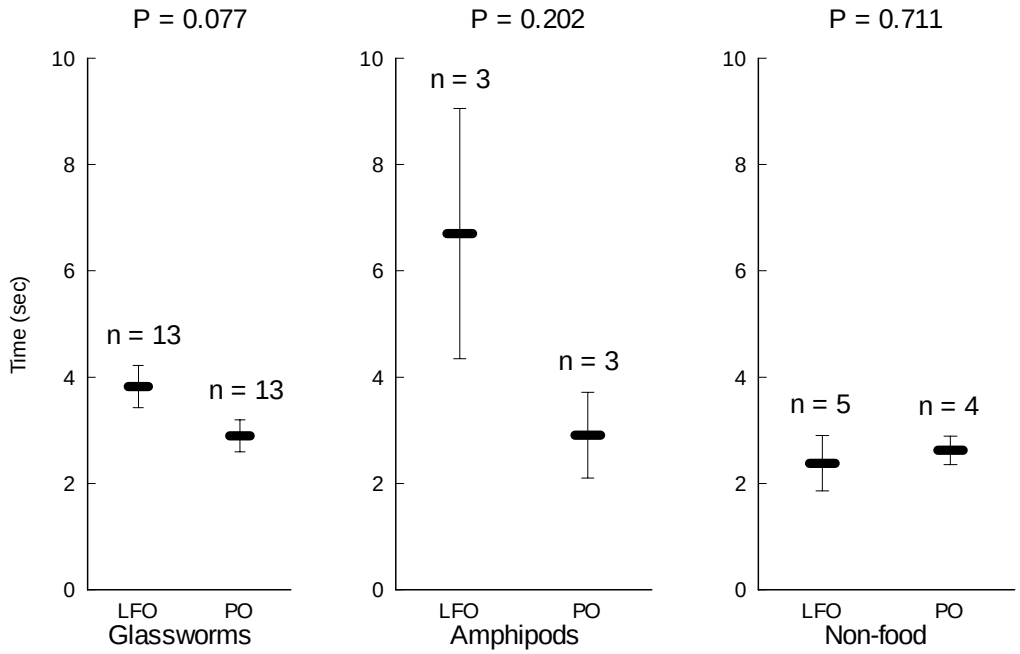

Figure 4. Average prey handling time of fall chinook salmon. Salmon were reared on a pellet-only diet (PO) or a live food-only diet (LFO). Probability values are based on *t*-tests.

Discussion

In the freshwater and estuarine environments juvenile fall chinook salmon feed primarily on insects, amphipods, shrimp (*Neomysis* and *Mysis* spp.), and zooplankton (Sasaki 1966, Busby and Barnhart 1995, Rondorf et al. 1990). Some time after they enter the ocean they switch over to primarily feeding on fishes (Brodeur 1991). In all three environments the prey are taken as they are observed drifting or swimming in the water column. As with most other predators, the prey of chinook salmon have evolved successful strategies to avoid being preyed on. Thus, in the laboratory, we observed that the antipredator characteristics of the prey had the strongest effect on salmon foraging success. As with other predators (Irvine and Northcote 1983, Sih and Moore 1990, Sih 1993), prey activity and movement were key factors in determining the prey chinook salmon selected to attack.

Blackworms successfully avoided predation by burrowing into the substrate. For the most part, the amphipods also successfully hid in the substrate and only became vulnerable to chinook salmon predation when they occasionally emerged and swam in the open water column. The glassworms were from a population lacking fish and appeared to not have evolved an effective strategy for avoiding fish predation. Their high visibility and swimming about in open water made them attractive targets for chinook salmon. This resulted in their being the most frequently consumed prey item in the test arenas.

Interestingly, fish from neither rearing treatment searched for blackworms or amphipods by rooting around in the gravel as if following a scent trail. As the fish in the live food diet treatment had extensive opportunity to learn blackworm scent prior to testing, it appears that chinook salmon do not search for prey based on chemical cues. This supports the concept that chinook salmon, like other salmonids, are primarily visual hunters that are initially attracted to prey based on their visual cues (Chapman and Bjornn 1969, Fausch 1991). Specifically, movement of the proper size and shape object within the visual field stimulates the initial approach, attack and capture of a potential prey item. Once the prey is captured, taste and texture then become the primary cues involved in making the decision to ingest or reject the captured prey item (Bres 1989, Willers 1991).

In the laboratory tests, the live food diet failed to improve chinook salmon foraging ability on both evasive (blackworm and amphipod) or easy to capture (glassworm) prey. Equally important, being reared on a pellet diet did not seem to preclude fish from being able to switch over to live food when it was readily available. However, the pellet diet did increase fish interest in attacking non-food items. In this regard, the greatest distinction between the two rearing types was the percentage of attacks salmon directed at each type of prey. The pellet diet fish directed a greater percentage of their attacks at non-food items than fish reared on live feed, while live diet fish directed a greater percentage of their attacks at glassworms than pellet-reared fish did. Although the results are not significantly different, the pellet-only fish actually performed more than twice as many attacks and captures on non-food items as live food diet salmon. Field studies have also observed that salmon reared on prepared pelletized diets initially tend to ingest more non-food plant material after release than fish reared on natural feeds (Johnsen and Ugedal 1986, Myers 1980). In combination, this laboratory and field evidence suggests that fish reared on pellets spend more of their activity budget in pursuing non-food items than salmonids reared on natural animal feeds.

The semi-moist diet the pellet diet fish were reared on in this study contains processed grain byproducts, lecithin, and guar gum from plants. In addition, the proximate composition of this artificial feed (43% protein, 14% crude fat, 2% crude fiber, 10.5 % ash, 22% moisture, and 1% phosphorous) markedly differs from the proximate composition of live animals, like chironomids (9.1% crude protein, 13.6% crude fat, 0% crude fiber, 0.9% ash, 83.9% moisture, 0% phosphorous), fed to the live diet fish (Cresswell 1993). These chemical and water content differences must result in pelleted feeds having a markedly different flavor and texture than the live animals that salmonids naturally consume. When salmonids are reared on artificial diets they must become conditioned to accept plant materials that they would otherwise reject. As a result of this deconditioning of the rejection response to vegetable material, pellet-reared salmonids must relearn to reject the vegetable debris they encounter in our test tanks, or the streams, rivers, or estuaries they initially reside in after release. In the learning process they will tend to spend more energy and time in pursuing this energetically unprofitable material. As natural prey are hard to find and estuaries retain large amounts of drifting vegetative debris, pellet-reared chinook salmon may starve to death before they learn which items to invest their time in attacking and capturing. Fortunately, the current trend in developing artificial diets is to remove plant fillers from feeds and replace them with ingredients derived from aquatic animals.

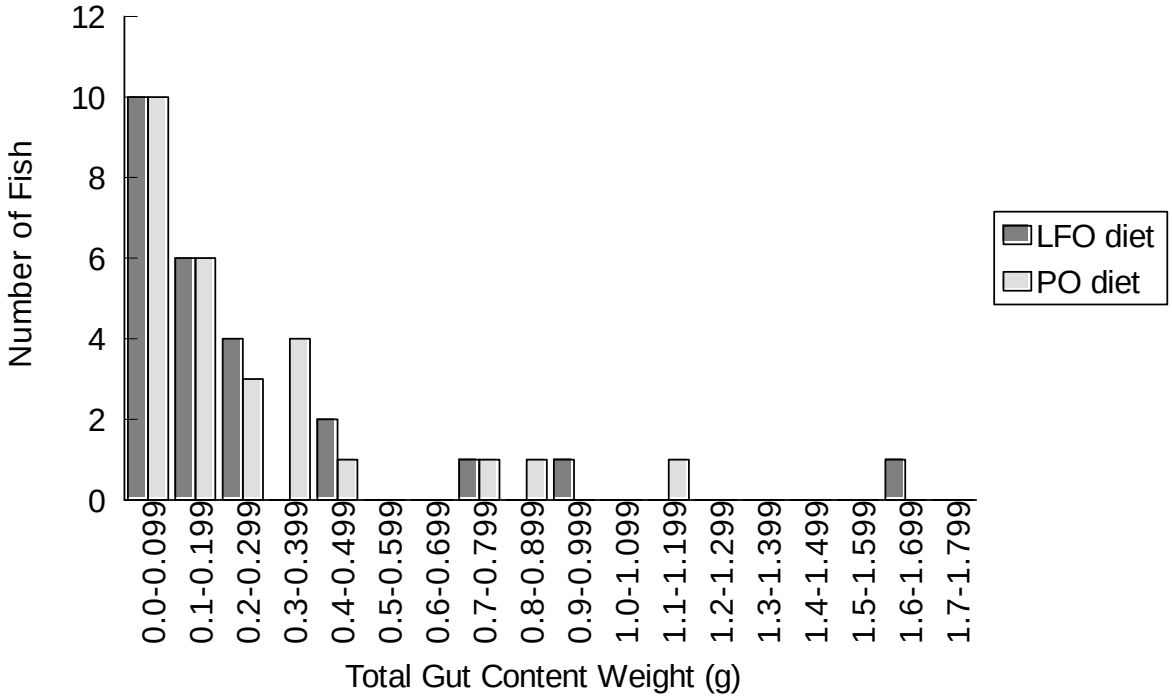

Figure 5. Histogram of total gut contents of fall chinook salmon placed in Bingham Creek cages. Salmon were reared on a pellet-only diet (PO) or a live food-only diet (LFO). Probability values are based on a Student *t*-test.

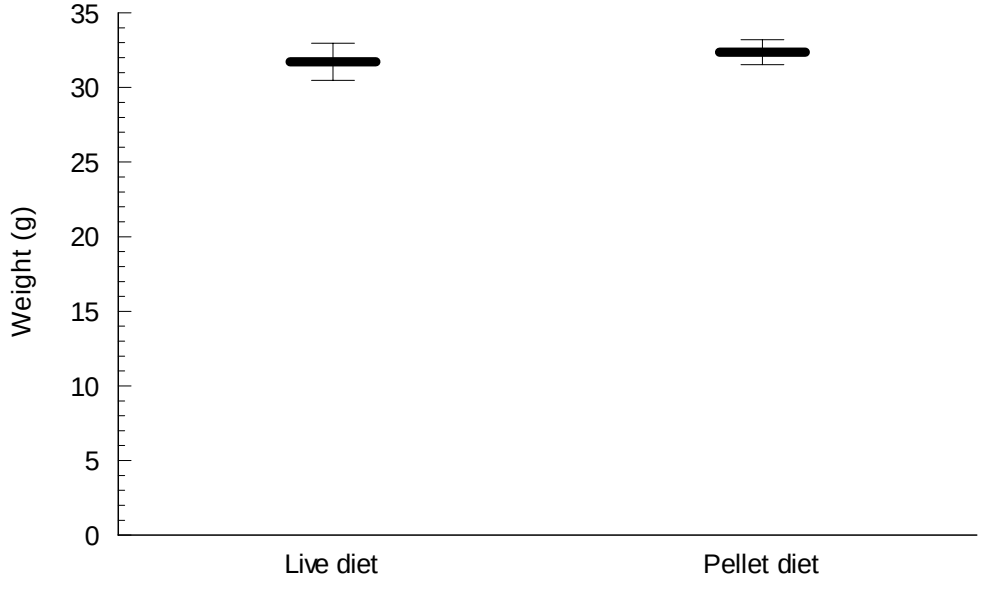

Figure 6. Average weight of fall chinook salmon placed in Bingham Creek cages.

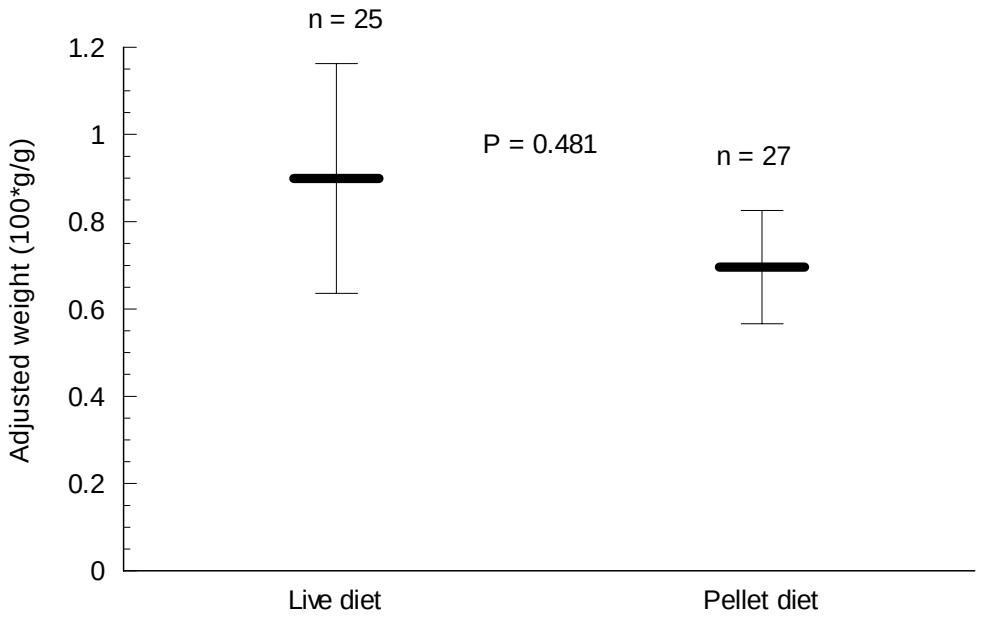

Figure 7. Percent body weight of material in gut of fall chinook salmon after residing in Bingham Creek cages for one week. Probability values are based on a Student *t*-test.

The stomach fullness of the fish from the in situ trials (cages) was considerably less than expected of fish feeding in the wild. The stomach contents of wild chinook salmon usually weigh more than 2% of their total body weight (Healey 1979). However, only 27% of the fish in this study even reached a 1% total gut (stomach and intestine) content. By the time the fish were tested in the enclosures, they averaged 32.06 g in weight, which would anticipate material in their gut to weigh over 0.321 g. However, 38.5% of the fish in the cages had less than 0.100 g in their gut. This lower than expected gut fullness of hatchery fish has been observed in an earlier study as well (Maynard et al. 1996b). In the earlier study it was suggested that social interaction may have precluded most of the fish in the cages from feeding. However that is clearly not the case in the current study where there was only one fish per cage. This lower than expected stomach fullness may be representative of a hatchery (rather than wild) fish model since other studies also indicate that it is common for hatchery fish released into the wild to initially have less material in their digestive system than expected (Sosiak et al. 1979, Myers 1980, O'Grady 1983, Johnsen and Ugedal 1986, Hvidsten 1994, Fjellheim et al. 1995).

Although not statistically significant, the increased amount of material in the guts of live food compared to pellet-reared fish suggests that live food diets might improve postrelease foraging ability. The presence of material in the guts of all live food diet fish, and only 88% of the pellet-reared fish, also suggests live food diets may improve postrelease foraging ability. These findings agree with other observations that the stomachs of hatchery-reared salmonids released into the wild often contain less food than naturally-reared fish (Sosiak et al. 1979, Johnson et al. 1996). It also agrees with an earlier finding with fall chinook salmon that

supplementing artificial diets with live feeds can improve foraging behavior in a laboratory setting (Maynard et al. 1996a). However, at this time, the strength of these findings does not justify the expenses associated with rearing hatchery-produced salmon on a total live food diet.

The laboratory findings indicate that chinook salmon can learn to forage on new prey, like glassworms, when given the opportunity. This has been observed with other salmonid species as well. When initially exposed to three different prey types, hatchery-reared Atlantic salmon exhibited different prey preferences than wild-reared fish, however within a short time they switched over to match the prey preference of their wild-reared counterparts (Reiriz et al. 1998). In other studies, pellet-reared Atlantic salmon have also demonstrated their capability to learn to use new food types by switching over to wild prey (Stradmeyer and Thorpe 1987). It has also been shown that sockeye salmon can readily learn to forage more effectively on prey with repeated exposure to it. However, not all salmonids show this high level of prey switching flexibility. Hatchery-reared brook trout had difficulty in switching to alternate food items when they were made available (Ersbak and Haase 1983). Rainbow trout required four days of exposure to novel prey before they would even approach it, and another eight days before they demonstrated good prey capture responses (Ware 1971). Given fall chinook salmon seem to have the flexibility to switch over to new prey types, the question now becomes why don't they show better foraging success when they are challenged to forage naturally in field studies.

There may be explanations for the reason so many fish had little material in their guts. One possible explanation is that the fish, which like most salmonids are dusk and dawn feeders, simply digested most of the material before they were sampled at 1400 hours. This is unlikely as at 10^0 C the time to 50% evacuation of material in the stomach is 6 to 15 hours for salmonids (Brett and Higgs 1970, Windell et al. 1976). This would mean that even if fish had eaten the usual 2% of their body weight in the morning they should have at least 0.3g in their stomachs in the afternoon, rather than having a total gut content that usually weighed less than 0.2 g. Another explanation is that sufficient quantities of the right type of prey did not enter the cages. This appears unlikely, as various types of insect larvae were observed crawling on the inside of the cages when the fish were retrieved, but if they were noxious or otherwise predator resistant they may not have been useful food sources.

Possibly many fish were stressed by the new environment and not composed enough to forage for food. Other laboratory studies (Maynard et al. 1996a, Paszkowski and Olla 1985), and many field studies (Ersbak and Haase 1983, Maynard et al. 1996b, Miller 1952, Hochachka 1961, Reimers 1963, Sosiak et al. 1979, Myers 1980, O'Grady 1983, Johnsen and Ugedal 1986) have found that hatchery fish starve for several weeks after release. In the natural environment the fish are experiencing very different water sources, physical conditions (gravel, vegetation, overhead cover, temperature, sounds, and light levels), predators, and many other animals they never previously encountered. If this is true, then the problem might be overcome by acclimating the fish to natural environments prior to release, and using a good feeding response as the cue for adaptation to their new surroundings.

References

Bres, M. 1989. The effects of prey relative abundance and chemical cues on prey selection in rainbow trout. J. Fish Biol. 35:439-445.

Brett, J.R. and D.A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 27:1767-1779.

Brodeur, R.D. 1991. Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ. Biol. Fishes 30:303-315.

Busby, M.S. and R.A. Barnhart. 1995. Potential food sources and feeding ecology of juvenile fall chinook salmon in California's Mattole River Lagoon. Calif. Fish Game 81(4):133-146.

Chapman, D.W. and T.C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. *In* T.B. Northcote (editor), Symposium on salmon and trout in streams, p. 153-176. H.R. McMillan lectures in fisheries, University of British Columbia, Vancouver.

Cresswell, R.L. 1993. Aquaculture desk reference. Van Nostrand Reinhold, New York, 206 p.

Ersbak, K. and B.L. Haase. 1983. Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. N. Am. J. Fish. Manage. 3(2):142-151.

Fausch, K.D. 1991. Trout as predator. *In* J. Stolz and J. Schnell (editors), Trout, p. 65-80. Stackpole Books, Harrisburg.

Fjellheim, A., G.G. Raddum, and B.T. Barlaup. 1995. Dispersal, growth, and mortality of brown trout (*Salmo trutta* L.) stocked in a regulated West Norwegian river. Regul. Rivers Res. & Manage. 10(3-4):137-145.

Healey, M.C. 1979. Utilization of the Nanaimo River estuary by juvenile chinook salmon *Oncorhynchus tshawytscha*. Fish. Bull., U.S. 77(3):653-668.

Hochachka, P.W. 1961. Liver glycogen reserves of interacting resident and introduced trout populations. J. Fish. Res. Board Can. 18:125-135.

Hughes, R.N. 1979. Optimal diets under the energy maximizing premise: the effects of recognition time and learning. Am. Nat. 113:209-221.

Hughes, R.M., M.J. Kaiser, P.A. Mackney, and K. Warburton. 1992. Optimizing foraging behaviour through learning. J. Fish Biol. 41(Suppl. B):77-91.

Hvidsten, N.A. 1994. Migration and nutrition in wild and hatchery reared salmon postsmolt. Nord. J. Freshwat. Res. 69:100.

Irvine, J.R. and T.G. Northcote. 1983. Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. Aquat. Sci. 40(10):1745-1749.

Johnsen, B.O. and O. Ugedal. 1986. Feeding by hatchery-reared and wild brown trout, *Salmo trutta* L., in a Norwegian stream. Aquacult. Fish. Manage. 17:281-287.

Johnson, J.H., J.F. McKeon, and D.S. Dropkin. 1996. Comparative diets of hatchery and wild Atlantic salmon smolts in the Merrimack River. N. Am. J. Fish. Manage. 16(2):440-444.

Maynard, D.J., G.C. McDowell, E.P. Tezak, and T.A. Flagg. 1996a. Effect of diets supplemented with live food on the foraging behavior of cultured fall chinook salmon. Prog. Fish-Cult. 58:187-191.

Maynard, D.J., E.P. Tezak, B.A. Berejikian, and T.A. Flagg. 1996b. The effect of feeding spring chinook salmon a live food supplemented diet during acclimation, 1995. *In* D.J. Maynard, T.A. Flagg, and C.V.W. Mahnken (editors), Development of a natural rearing system to improve supplemental fish quality, 1991-1995. Report to Bonneville Power Administration, Contract DE-AI79-91BP20651, p. 98-112.

Miller, R.B. 1952. Survival of hatchery-reared cutthroat trout in an Alberta stream. Trans. Am. Fish. Soc. 81:35-42.

Myers, K.W. 1980. An investigation of the utilization of four study areas in Yaquina Bay, Oregon, by hatchery and wild juvenile salmonids. Master's thesis, Oregon State University, Corvallis, 234 p.

O'Grady, M.F. 1983. Observations on the dietary habits of wild and stocked brown trout, *Salmo trutta* L., in Irish lakes. J. Fish Biol. 22:593-601.

Paszkowski, C.A. and B.L. Olla. 1985. Foraging behavior of hatchery-produced coho salmon (*Oncorhynchus kisutch*) smolts on live prey. Can. J. Fish. Aquat. Sci. 42:1915-1921.

Reimers, N. 1963. Body condition, water temperature, and over-winter survival of hatchery reared trout in Convict Creek, California. Trans. Am. Fish. Soc. 92:39-46.

Reiriz, L, A.G. Nicieza, and F. Brana. 1998. Prey selection by experienced and naïve juvenile Atlantic salmon. J. Fish Biol. 53(1):100-114.

Rondorf, D.W., G.A. Gray, and R.B. Fairley. 1990. Feeding ecology of subyearling chinook salmon in riverine and reservoir habitats of the Columbia River. Trans. Am. Fish. Soc. 119(1):16-24.

Sasaki, S. 1966. Distribution and food habits of king salmon *Oncorhynchus tshawytscha*, and steelhead trout, *Salmo gairdnerii*, in the Sacromento-San Joaquin Delta. Calif. Dep. Fish Game Fish Bull. 136:108-114.

Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behavior. *In* R.N. Hughes (editor), Diet selection: an interdisciplinary approach to foraging behavior, p. 182-211. Blackwell Scientific Publications, London.

Sih, A. and R.D. Moore. 1990. Interacting effects of predator and prey behavior in determining diets. *In* R.N. Hughes (editor), Behavioral Mechnaisms of Food Selection, NATO ASI series, vol. G 20, p. 771-796. Springer Verlag, Berlin.

Sosiak, A.J., R.G. Randall, and J.A. McKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. J. Fish. Res. Board Can. 36:1408-1412.

Stradmeyer, L. and J.E. Thorpe. 1987. The responses of hatchery-reared Atlantic salmon, *Salmo salar* L., parr to pelleted and wild prey. Aquacult. Fish. Manage. 18(1):51-61.

Ware, D.M. 1971. Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J. Fish. Res. Board Can. 28:1847-1852.

Willers, B. 1991. Trout Biology. Lyons and Burford Publishers, New York, 273 p.

Windell, J.T., J.F. Kitchell, D.O. Norris, J.S. Norris, and J.W. Foltz. 1976. Temperature and rate of gastric evacuation by rainbow trout, *Salmo gairdneri*. Trans. Am. Fish. Soc. 105(6):712-717.