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COMPENSATORY FEEDING FOLLOWING A PREDATOR REMOVAL PROGRAM DETECTION AND MECHANISMS

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Compensatory feeding following a predator removal program: detection and mechanisms

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1.0 Executive Summary

Northern pikeminnow *Ptychocheilus oregonensis* are a major source of predation mortality for juvenile salmonids migrating through the Columbia and Snake rivers (USA). In an effort to reduce salmon mortality, the Northern Pikeminnow Management Program (NPMP) was begun in 1990 to remove the largest northern pikeminnow from these large rivers. An important assumption behind this management program is that predation rate on salmonids by northern pikeminnow and other predators that remain in the rivers will not increase following removal (compensatory feeding), and thus reduce the expected benefits of removal. Of the possible compensatory processes (feeding rate, growth rate, reproduction, etc.) that might be occurring following predator removal, compensatory feeding may be especially important since it is a rapid behavioral response with sufficient scope to potentially diminish or negate the expected program benefits.

In this report, I examined field data and potential mechanisms of compensatory feeding that might be occurring within the northern pikeminnow populations that remains in the Columbia and Snake rivers. Field data from a pre-removal period (1983-1988) were compared with data from a post-removal period (1993-1996). Power analyses were conducted to estimate the number of samples necessary to detect changes in predation rate. Three mechanisms that might lead to compensatory feeding by northern pikeminnow were examined: changes in predator density, predator size distributions, and juvenile salmonid (prey) density.

Mechanistic analyses suggested that compensatory predation by northern pikeminnow is likely occurring in the Columbia River system, however, direct demonstration of compensation in a large, heterogeneous system may be statistically (and economically) infeasible since predation rates are highly variable and predators are dispersed. Detecting a change in the rate of predation in mid-reservoir zones, for example, would require a large sample size and there still appears to be a low likelihood of detecting changes of less than 50%.

Major findings were:

- Northern pikeminnow are currently feeding and growing below their maximum potential rates, thus increased, or compensatory, feeding is feasible.

- Compensatory feeding would occur as a behavioral response and thus would be observable on an individual or local level. Pooling samples over large areas or time periods would make it difficult to detect most increases in feeding.
- Few tests could be conducted on before-versus-after predator removal because of small sample sizes. Consumption indices (CI) on juvenile salmonids increased (compensation) in 4 of 5 comparisons and decreased in the other case; however, only 1 of 5 comparisons was significant with high power ($P < 0.01$, power = 0.99).
- Trends for CI's during 1990-1996 were generally decreasing, with 3 of 8 tests significant. Less than 40% of the variability was explained by these regressions.
- Predation rates (daily estimates or consumption indices, CI) were highly variable at specific locations and throughout the basin. Coefficients of variation ranged from ~75% to >140% at sites in John Day Reservoir sampled during 1983-1988. Data collected during a system-wide survey (1990-1993) had similar variability.
- Because of the high variability in predation rate estimates, the power to detect even large changes (2-4 times nominal = 1983-1986 rates) in predation rates is very low (power or $1-\beta < 0.5$). Directly detecting increases in predation rates that could completely compensate for predator removal benefits (e.g., 50%) appears to be unlikely with even 30 years of continuous sampling. Before-after and trend analysis methods were used to estimate power.
- The predation rate on salmonids was significantly higher at low predator density than at high predator density, suggesting compensation due to changes in predator density may be occurring. However, combining this model of predation rate with the change in frequency distributions of predator density before and after predator removal suggested that cumulative predation loss has declined in two of three habitats.
- Larger predators in a local area tended to capture more salmonids than smaller predators, suggesting compensation by this mechanism is possible. However, frequency changes in relative mass ratios before-versus-after predator removal

gave a mixed summary of predation loss, with increasing loss in two habitats (compensation) and decreasing loss in one habitat.

- Increasing the density of juvenile salmonid density through removal of predators may lead to an increase in predation rate that is roughly proportional to the percent increase in prey density.
- The mechanistic analyses suggested that compensatory feeding in response to predator removal may be occurring, possibly reducing or negating the estimated benefits estimated for the NPMP. The simple models used to estimate relative predation loss gave mixed results, however, some showing decreased relative mortality of salmonids due to predator removal and some showing compensatory feeding sufficient to negate removal benefits. Interactions between mechanisms, such as predator size and prey density, were not explored in this report.

Major recommendations were:

- Managers may want to re-evaluate the current monitoring program with respect to compensatory feeding. Results here suggested that the current field program will not be sufficient to detect increased feeding at levels that might compensate completely for the expected benefits of the program. If the current program is retained, managers will have to acknowledge the uncertainty related to possible compensatory feeding, perhaps throughout the duration of the NPMP.
- Some alternative evaluation(s) might be used to demonstrate the effectiveness of the NPMP with respect to compensatory feeding. Three approaches that might provide some resolution are briefly discussed:
    - Laboratory studies. Studies in large tanks or raceways might be used to better quantify predator-prey behaviors and the mechanisms that could lead to compensatory feeding. The major advantage of laboratory studies is that conditions are controlled and behavior could be directly observed. The major disadvantage of such studies is that results might not apply in a more complex field situation.
    - Field experiments. Although Before-After types of analyses are not likely to detect changes in feeding rates, field studies might be

designed to address compensatory feeding. For example, there may be locations or rivers where similar predator removals could be conducted and salmonid survival measured directly with available tag-recapture methodology (PIT tags or radio-tags, e.g.). The major advantage of this approach is that experiments might be conducted in a river environment that simulates the Columbia and Snake system; the biggest disadvantages might be finding appropriate reaches and the cost of the study.

  - Modeling. The models that have been used to date to predict the predation response and evaluate the NPMP do not have the spatial and individual detail necessary to fully evaluate compensatory feeding. There are modeling approaches that could implement the mechanisms described here, and others, and better test compensatory feeding hypotheses. The disadvantage of modeling is that it would be an indirect approach, while advantages would be lower cost and the option of including complex interactions.

- Managers and researchers should consider the importance of spatial scale in evaluating predation information. For example, the density of predators, characterized by the distributions of local predator catches, showed a considerable decline between a before (1983-1986) versus an after removal period (1993-1996). Such a change in predator density would not have been detected with pooled samples, but could have a considerable impact on loss estimates.
- Managers and researchers should consider sample size and power analyses in evaluating potential compensation in growth and reproduction. If field measures are highly variable in these parameters, detecting compensation will prove difficult.

2.0 Introduction

Predator removal is one of the oldest management tools in existence, with evidence that ancient Greeks used a bounty reward for wolves over 3,000 years ago (Anonymous 1964). Efforts to control predators on fish have been documented in scientific journals for at least 60 years (Eschmeyer 1937; Lagler 1939; Foerster and Ricker 1941; Smith and Swingle 1941; Jeppson and Platts 1959), and has likely been attempted for much longer. Complete eradication of a target species from a body of water has rarely been the objective of predator removal programs, which instead have attempted to eliminate predators from specific areas, to reduce the density or standing stock of predators, or to kill the largest individuals in the population (Meronek et al. 1996). In evaluating management programs that remove only part of a predator population, the compensatory response(s) of the remaining predators must be considered. Some potential compensatory responses by remaining individuals include increased reproductive output, increased growth rate, or increased consumption of certain prey species (Jude et al. 1987). If compensation by predators that remain in the system following a removal effort occurs, it may reduce the effectiveness of the predator control program.

Northern pikeminnow *Ptychocheilus oregonensis* (formerly called northern squawfish) consume juvenile salmon in rivers, lakes, and reservoirs in British Columbia, Washington, Idaho, Oregon, and California. Northern pikeminnow have been estimated to consume about 11% of all juvenile salmon that migrate through John Day Reservoir on the Columbia River (Rieman et al. 1991). Modeling studies suggested that removal of 20% of the northern pikeminnow population in John Day Reservoir would result in a 50% decrease in predation-related mortality of juvenile salmon migrating through this reach (Beamesderfer et al. 1991). Since the early 1940's, other programs have been implemented to remove northern pikeminnow, with hopes of improving the survival of juvenile salmon (Ricker 1941; Jeppson and Platts 1959).

In 1991, the Northern Pikeminnow Management Program (NPMP) was implemented in the Columbia and Snake rivers, which included establishing several fisheries for predator removal (Beamesderfer et al. 1996; Ward 1997; Friesen and Ward 1999). The goal of the NPMP has been to remove 10-20% of the largest northern pikeminnow in the system. Between 1991 and 1996, approximately 1.1 million northern pikeminnow were removed from the Snake and Columbia rivers (Friesen and Ward 1999), and total exploitation averaged 12% per year (Beamesderfer et al. 1996; Friesen and Ward 1999). Northern pikeminnow management consists of a sport-reward (bounty) fishery (87% of total catch), a dam-angling fishery (11% of catch), and a gill-net fishery (2% of catch). The NPMP has an annual cost of about $3.1 million (Friesen and Ward 1999).

The NPMP has been evaluated for its effects on the number and size structure of northern pikeminnow in the system, effects of removal on other predators such as smallmouth bass and walleye, and survival of juvenile salmon in the system (Beamesderfer et al. 1996; Friesen and Ward 1999; Knutsen and Ward 1999; Zimmerman 1999; Zimmerman and Ward 1999; Hankin and Richards 2000). Beamesderfer et al. (1996) concluded that exploitation goals were being met and that continued evaluation through indirect methods (predator population structure, consumption indexing, models, etc.) was necessary since a direct demonstration of a change in the rate of salmonid survival was not feasible. Friesen and Ward (1999) estimated a reduction in predation on juvenile salmonids of about 25% (median estimate) through the NPMP, equivalent to saving about 2% of the total downstream migration (3.8 million salmon saved of ~200 million migrants). The systemwide reduction in predation for 1992-2006 was updated to be 12-16% in a later analysis (D. Ward and H. Schaller memo to PATH, March 16, 1999). Hankin and Richards (2000) reviewed the biological and economic performance of the NPMP, although they did not consider the topic of compensatory feeding.

The general conclusion of other studies on the effects of the NPMP has been that there is little evidence for compensation in reproduction, growth, or feeding rate by northern pikeminnow and other piscivores in the system (Beamesderfer et al. 1996; Friesen and Ward 1999; Knutsen and Ward 1999; Ward and Zimmerman 1999; Zimmerman 1999; Zimmerman and Ward 1999). Knutsen and Ward (1999) found no trends in the relative weight, growth, or fecundity of northern pikeminnow sampled between 1990-1996, although there was considerable annual variation. The density, consumption of salmonids, mortality, and growth of smallmouth bass also showed few significant trends during this period (Ward and Zimmerman 1999). General food habits of northern pikeminnow, smallmouth bass, and walleye in the lower Columbia and Snake rivers have not shown dramatic shifts since the early 1990's that could be ascribed to implementation of the NPMP (Zimmerman 1999; Zimmerman and Ward 1999).

The studies cited above have generally examined field data pooled across reservoirs, or in some instances pooled into zones or habitats within reservoirs, for temporal trends between 1990, when predator removals began, and 1996. Data were examined for trends over this 7-year period, assuming that lack of an upward trend in predation rate would be evidence that compensation was not likely occurring in one of the predator populations. One weakness in this approach concerns the lack of a control site (Hurlbert 1984; Underwood 1994). Since 1990, northern pikeminnow have been removed throughout the lower Columbia and Snake river system so it is not possible to know whether observed trends might be caused by exploitation or some large-scale phenomenon affecting the whole region.

The objective of this report is to further examine the possibility of compensatory feeding by northern pikeminnow in the system following removal of a portion of the population. This work differs from the studies mentioned above in four ways: 1) I compare predation rates that were estimated prior (1983-1986) to implementation of the NPMP to predation rates measured after implementation of the program. Previous studies considered data collected primarily after implementation only; 2) I considered the variability of predation rates and the power of test procedures in drawing conclusions about rate changes and what changes might be detectable; 3) I examined specific mechanisms that might be theoretically expected to produce compensatory feeding; and, 4) I examined data at a different spatial scale than prior studies, emphasizing fine-scale sampling and individual responses rather that pooled data.

"Feeding compensation" in this report refers to the feeding response by individual predators of the target species (northern pikeminnow) that remain in the population following a removal effort and is thus an "intraspecific" compensation. "Interspecific" compensation may also occur, but was not considered in this study (see Ward and Zimmerman 1999 and Zimmerman 1999).

This report is broken down into three major parts:

1) **Analysis of direct evidence** (samples from 1983-1996) for changes in predation rate on juvenile salmon before versus after extensive predator removal. This includes estimates of the power of different sampling efforts needed to evaluate the compensatory feeding response of northern pikeminnow that remain in the system.
2) **Examination of specific mechanisms** by which compensatory feeding might occur. This section begins with a brief review of predator-prey theory relevant to evaluating compensatory feeding and includes a summary of northern pikeminnow feeding behavior and juvenile salmonid migration.
3) **Discussion of the analyses and recommendations** for management and future research.

Before beginning the major sections of the report, I discuss briefly three conditions that, if present, would make compensatory feeding unlikely. First, if predators are feeding at a maximum rate, then compensatory feeding following predator management would be unlikely. Pooling all prey types, the percent fullness of guts for northern pikeminnow was less than 20% of maximum gut capacity during spring and less than 10% of maximum during summer months (Figure 1), suggesting no physical limitation to increased feeding rates. Northern pikeminnow in mid-reservoir areas in particular would seem to be capable of greatly increasing their feeding rate on juvenile salmon. Field-measured rates of predation on salmonids in John Day mid-reservoir are often zero and range to about 0.4 prey per day (Petersen 1994; Ward et al. 1995; unpublished USGS data), whereas rates measured in forebays, tailraces, or following hatchery releases are often 5 prey per day or higher (Thompson and Tufts 1967; Vigg et al. 1991; Vigg and Burley 1991; Petersen and DeAngelis 1992; Petersen 1994; Shively et al. 1996). Individual northern pikeminnow have been observed with >15 juvenile salmonids in their gut (unpublished data; Vigg et al. 1991). Maximum observed ration in the field is ~9% (Petersen and DeAngelis 1992). Finally, bioenergetic modeling of northern pikeminnow feeding in John Day Reservoir suggested that their rate of consumption was, on average, only 46% of maximum (Petersen and Ward 1999).

Second, predators that are growing as fast as physiologically possible would be unlikely to increase their rate of food intake. The growth rates of northern pikeminnow are highly variable throughout their range. Rieman and Beamesderfer (1990) concluded that growth of northern pikeminnow in John Day Reservoir was high compared to rates of growth in lakes and reservoirs throughout Montana, Idaho, and Washington. Parker et al. (1995), however, noted considerable variation in growth rate parameters throughout the Columbia and Snake river system. Using von Bertalanffy growth models on females, ultimate fork length (L_∞) was greatest in Ice Harbor Reservoir (740 mm) and lowest in John Day Reservoir (510 mm). The growth coefficient (K) for females was highest in Lower Monumental Reservoir (0.196) and lowest in Ice Harbor Reservoir (0.070; Parker et al. 1995). These patterns would suggest that northern pikeminnow are unlikely to be feeding or growing at extreme rates that would preclude at least some increased predation on salmonids (compensatory feeding). A survey of 18 piscivorous fish species indicated that growth rates were <40% in 60% of the cases and the median growth rate was less than 30% of the maximum possible growth (Schindler and Eby 1997; D. W. Schindler, University of Washington, personal communication). Using the energetic approach of Shindler and Eby (1997), 20 of 21 growth rates of northern pikeminnow in John Day Reservoir were less than 40% of the physiological maximum and one estimate was about 60% of the maximum (Petersen and Ward 1999).

Third, the nutritional or energetic value of prey types could also limit or prevent compensatory feeding (Cruz-Rivera and Hay 2000). For example, if prey types available to northern pikeminnow had especially high caloric content compared to the energy value of juvenile salmon then predators may select this higher-energy prey and exclude salmonids. The energy content of juvenile salmon, however, is higher than most other prey types commonly eaten by northern pikeminnow, such as sculpins and crayfish (Petersen and Ward 1999). Also, the rapid switching behavior of northern pikeminnow in response to a local hatchery release (Thompson and Tufts 1967; Collis et al. 1995; Shively et al. 1996) and the common inclusion of juvenile salmonids in pikeminnow diet in many habitats (e.g., Poe et al. 1991; Ward et al. 1995; Zimmerman 1999; Petersen et al. 2000) suggests that there is little or no selection *against* juvenile salmon.

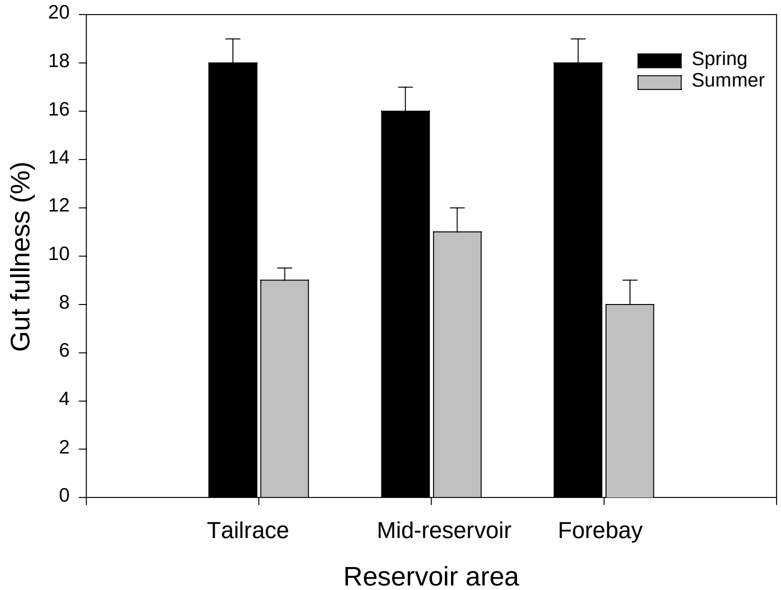

Figure 1. Average percent (± 1 SE) fullness for all northern pikeminnow collected in John Day Reservoir, 1983-1986. The percent fullness of a northern pikeminnow gut was estimated as the mass of food in the gut divided by the maximum volume of the gut x 100 (Burley and Vigg 1989). Analyses were divided by spring (April-June) and summer (July-August), and for three areas within the reservoir (forebay, mid-reservoir, and tailrace). Sample sizes for bars ranged from 267 to 1,702 predators.

3.0 Study areas and methods

Study areas

The Northern Pikeminnow Management Program has been conducted from the mouth of the Columbia River upriver to the tailrace of Priest Rapids Dam, and in the lower Snake River from its mouth to the tailrace of Hells Canyon Dam (Figure 2). Early studies (1983-1986) were conducted primarily in John Day Reservoir, which is the largest reservoir in the lower Columbia and Snake rivers (Figure 2). General results of the NPMP, such as exploitation rates, number of predators removed, potential benefits of removals, and analyses of compensatory responses were summarized by Beamesderfer et al. (1996) and Friesen and Ward (1999).

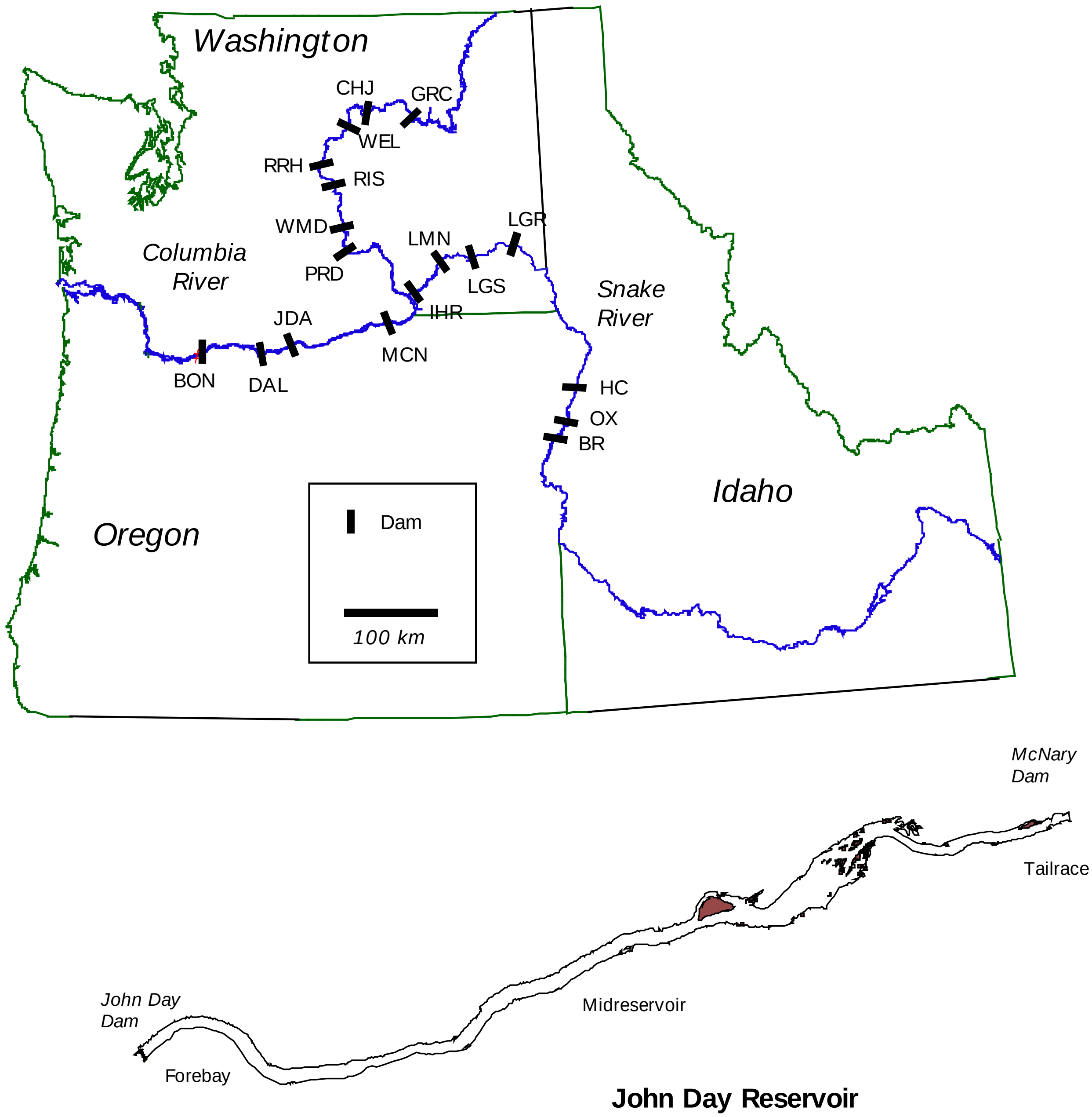

Figure 2. Location of dams on the Columbia and Snake rivers (top) and the reservoir zones (forebay, mid-reservoir, and tailrace) for John Day Reservoir. Dams on the Columbia River are Bonneville (BON), The Dalles (DAL), John Day (JDA), McNary (MCN), Priest Rapids (PRD), Wanupum (WMD), Rock Island (RIS), Rocky Reach RRH, Wells (WEL), Chief Joseph (CHJ), and Grand Coulee (GRC). Dams on the lower Snake River are Ice Harbor (IHR), Lower Monumental (LMN), Little Goose (LGS), Lower Granite (LGR), Hell's Canyon (HC), Oxbow (OX), and Brownlee (BR).

Primary datasets analyzed

Three primary datasets were used in the analyses below:

1) John Day Reservoir studies, 1983-1986, with some supplemental sampling in July 1988 (primary references: Beamesderfer and Rieman 1991; Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991).
2) System-wide survey of predation, 1989-1992 (primary references: Petersen et al. 1990; Shively et al. 1992; Petersen and Poe 1993; Burley and Poe 1994; Ward et al. 1995; unpublished USGS data).
3) System-wide evaluation of the NPMP (primary references: Beamesderfer et al. 1996; Ward and Friesen 1999; raw data for some analyses were provided by Dave Ward and Mark Zimmerman of the Oregon Department of Fish and Wildlife).

Seasons

The behavior and success of predators varies with different species and stocks of salmonids, depending on the migrational routes of prey, prey size, and other season-related phenomena (Poe et al. 1991; Vigg et al. 1991; Rieman et al. 1991). Analyses were divided into an early season (April-May), which corresponds to the major outmigration of spring chinook salmon, steelhead, and coho salmon, and a late season (June-August), which corresponds to outmigration of summer-fall chinook salmon (Vigg et al. 1991, e.g.).

Predator sampling methods

Sampling for northern pikeminnow and other predators was conducted using boat electrofishing. Sample locations within John Day Reservoir and in other reservoirs and reaches were generally divided into dam forebays, dam tailraces, and sites that were at least 5 km away from a dam, referred to as mid-reservoir or free-flowing sites. Within a location, the shoreline was divided into permanent "stations" along a shore, which ranged in length from about 0.5-2.0 km. A fishing run started at a haphazardly selected point within a station and ran parallel to the shore for 15 minutes. Northern pikeminnow are not commonly observed in water deeper than 5 m (Shively et al. 1996; Petersen et al. 2000) so no sampling was conducted away from shorelines. During the 15-min sampling period, all predators stunned by the electrical current were netted and placed in a live-well on the boat. Sampling was interrupted during a run only to allow adult salmonids to escape the electrical field; this was fairly uncommon. The distance along a shore covered on an individual sampling run varied considerably because of variable water velocity, obstacles, and the rate at which northern pikeminnow were being caught (higher catch rates usually slowed the boat speed to allow the netter time to retrieve all shocked fish). Sampling was conducted during day and night periods and on both sides of the river. Further details on field methods can be found in Poe et al. (1991) and Ward et al. (1995)

Northern pikeminnow were killed, weighed, and digestive tracts were removed and preserved. In the laboratory, gut contents were sorted into major taxa or groups and weighed. Many prey fish, including salmonids, can be identified to genus or species using diagnostic bones (Hansel et al. 1988). Specific methods on laboratory procedures were presented in Poe et al. (1991), and Vigg et al. (1991).

Consumption indices and individual predation rates

I used two slightly different measures of predation by northern pikeminnow on juvenile salmonids: consumption indices (CI), which are pooled for all individual predators collected during a month, and predation rates, which were computed for each individual predator. The CI's were used primarily in before-after and power analyses (section 4) since this index has been measured over a 14-year period (1983-1996). The individual rate estimates were used primarily in testing for mechanisms that might cause compensatory feeding (section 5). Justification for using individual rates, rather than pooled estimates such as CI's, is given in section 5.1.

Consumption indices. Prior to the start of the removal program (Before period = 1983-1986 and July 1988) intensive diet data were collected from predators in John Day Reservoir and predation rates were computed (salmonid prey per predator per d; Vigg et al. 1991; Petersen et al. 1990). During the period when predators have been removed (After period = 1991-96) data collection was streamlined and a "consumption index" was computed (Petersen et al. 1990; Ward et al. 1995). To make these two data sets comparable between the two periods, predation data from the Before period were used to compute consumption indices (CI) equivalent to the CI from the After period. The formula for consumption index (CI; Ward et al. 1995) is:

$$CI = 0.0209 \bullet T^{1.60} \bullet W^{0.27} \bullet (S \bullet GW^{-0.61}) \qquad (1)$$

where T is water temperature (^{o}C), W is the average weight in grams of northern pikeminnow, S is the average number of salmonids per predator, and GW is the average weight in grams of the gut contents. I applied this formula to compute CI's for the Before period (Appendix Table A1). Note that CI's were highly correlated to consumption rate R (smolts per predator per day), using predation rates estimated throughout the John Day Reservoir (R = exp(1.17 X ln(CI) - 0.41), $r^2 = 0.89$, P<0.001, n=86; Petersen et al. 1990).

During the After-removal period (1990-96), index data were collected only during May and July (M. Zimmerman, Oregon Department of Fish and Wildlife, personal communication), so the Before-removal data were also restricted to these months. After-removal data were collected during early morning hours, so Before data were standardized to a similar diel period. To increase the sample size, especially for the After period, I used a minimum sample of 10 predators collected during a month for estimating an index at any given year and location. Past studies have used 15 predators as the minimum sample (Petersen et al. 1990; Petersen 1994; Ward et al. 1995); however, reducing the minimum from 15 to 10 added 6 year-location estimates to the analysis for the After period. The quantitative and qualitative results were very similar if a sample of 15 was retained in the analyses (results not shown).

Individual consumption rates . Consumption rate estimates from the field (C) are often calculated by pooling data across many individuals to get one rate (e.g. Vigg et al. 1991; Petersen 1994), however, it is also possible to estimate predation rates for an individual fish. Per capita consumption rate (number of prey per predator per day) of salmonids was computed for each individual predator as:

$$C_i = n(24/DT). \qquad (2)$$

where C_i is the consumption rate for individual i, n is the number of smolts observed in the predator's gut, and DT is the average digestion time for a meal (hours) and 24 converts from hours to day (Windell 1978; Rieman et al. 1991). The time to 90%

digestion DT90 for northern pikeminnow feeding on juvenile salmon is (Beyer et al. 1988):

$$DT90 = 1147 \bullet M^{0.61} \bullet T^{-1.60} \bullet W^{-0.27} \quad (3)$$

where M is meal size (g), T is temperature (°C), and W is predator mass (g). Northern pikeminnow consume juvenile salmon during brief feeding bouts (Petersen and DeAngelis 1992; unpublished USGS analyses) and predators that have salmonids in their gut often have only salmon (Petersen, 2001). Thus I assumed that meal size was the number of salmon observed in a predator's gut times the average size of prey in the system during that month (Vigg et al. 1991). The number of salmon in a predator was the number of paired dentary bones, which are easily identifiable (Hansel et al. 1988).

To verify that this method for individual rates produced estimates similar to other consumption rate methods, I compared rate estimates made in Petersen (1994) for areas and months (McNary Dam tailrace, mid-reservoir, John Day Dam forebay; April through August) with an average predation rate across all individuals that occurred in the same area-month strata (Figure 3). The method used by Petersen (1994) is a modification of the Swenson and Smith (1973) approach as developed and applied by Vigg et al. (1991). The Swenson and Smith method pools ($N>15$) predators to estimate a rate. Rates from the two methods were similar, although the estimates based on averaging across individuals were slightly higher than those using the Swenson and Smith method (Figure 3). The regression coefficient was significantly different from 1.0 ($0.01 < P < 0.05$). The slight deviation from a 1:1 relationship may have been caused by my assumption that predators consumed meals of only salmon with the individual method (above), but inclusion of other diet items with the Swenson and Smith approach (see Vigg et al. 1991). Because of the similarity in estimates between these two approaches, I did not apply any correction to the computed individual rates.

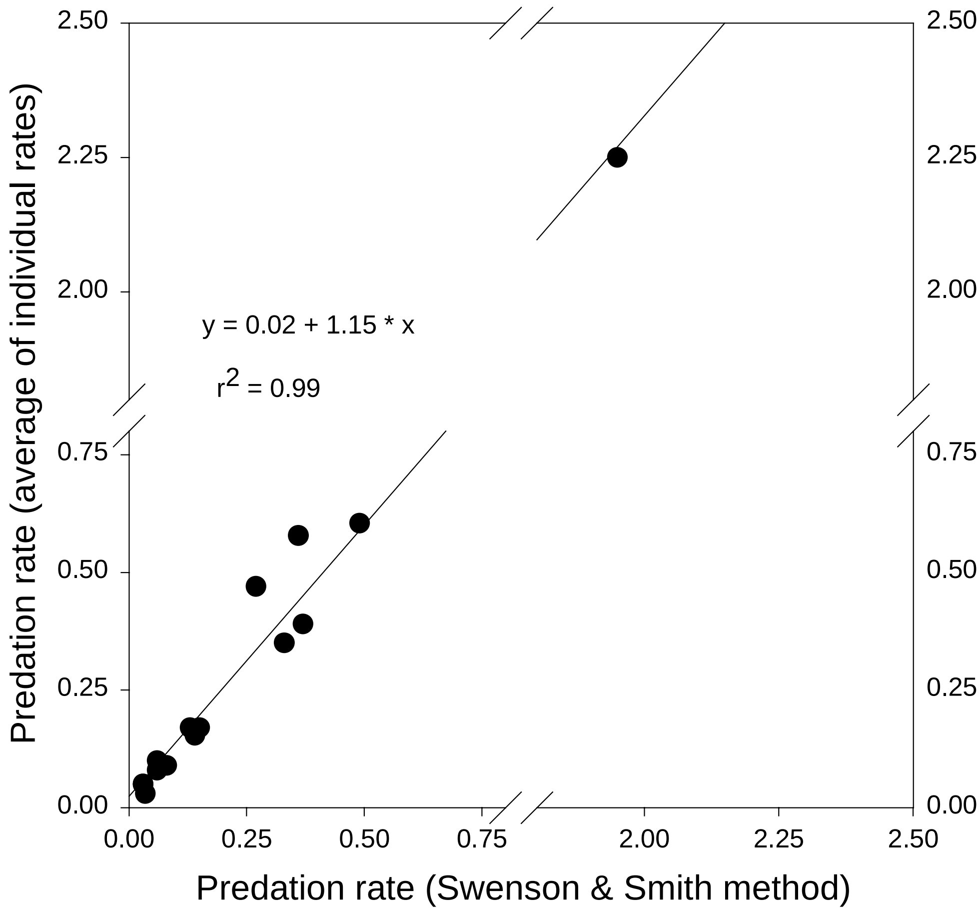

Figure 3. Comparison of predation rates (salmonids • northern pikeminnow^{-1} • d^{-1}) using the Swenson and Smith (1973) method, which pools predators in a sample (N≥15), and the individual method (see text), which estimates a rate for each individual predator. Each point is a location in John Day Reservoir (boat-restricted zone, mid-reservoir, forebay) by month (April through August) estimate. Values for the Swenson and Smith method are from Petersen (1994; his Table 1).

4.0 Predation rates before and after predator management

The purpose of this section is to examine predation rate data that were available to specifically test the null hypothesis: *Removal of northern pikeminnow during 1990-1996 did not influence the per capita rate of predation on salmonids for northern pikeminnow that remained in the system*. I used a before-after approach to examine absolute differences between periods (Before-After comparison; Underwood 1994), and a regression approach to examine trends in the predation rates since the start of the removal program (Trend analysis; Gerrodette 1987). If compensatory feeding has occurred on a large scale, then I would expect to see an increase in the rate of feeding during 1990-96 compared to 1983-1986.

4.1 Comparison of rates and trends

Before-After comparison. Before-after comparisons were only possible for sampling conducted within the John Day Reservoir, where data were collected in both periods (Appendix Table A1). Rate estimates were compared in three habitats within the reservoir, where predation rates on salmonids differ greatly (Vigg et al. 1991; Petersen 1994). In four of five comparisons, the average consumption index (CI) increased between 1983-1986 and 1990-96 (Table 1; Figure 4). Only in the John Day Dam forebay during July did the average CI decrease between these two periods. The percent change in average CI between the pre- and post-removal periods for a time/location stratum was quite large, ranging from –29% in the July/forebay case to +200% in the July/mid-reservoir comparison (Table 1). Sample sizes were, however, low in all comparisons (*N* from 1 to 7), standard errors were relatively large, and thus the power of comparisons was generally low (Table 1). In John Day Reservoir, and at other locations, consumption indices (CI's) showed considerable year-to-year variability (Figure 4). The average coefficient of variation across all years ranged from 50% in May at the forebay zone to 138% in July at the mid-reservoir. There was no control location that could be used to adjust for temporal trends that might be completely independent of the removals (Hurlbert 1984; Underwood 1994). These weaknesses and the small number of years available in both the Before and the After period make strong inferences impossible using the Before-After model.

Trends. Trends in the consumption indices measured annually were examined for the period 1990-96 only; there was a 3-year gap (1987-89) between the early sampling and the later sampling preventing a trend analysis for the complete period (1983-96). Consumption indices decreased significantly ($P<0.05$) in three of eight comparisons (Table 2); there was a marginally significant ($0.05 < P < 0.1$) decrease in one other case, Below Bonneville Dam during May. Trends in the other cases were not significantly different from zero. The explained variation from the linear regressions was relatively low, with a maximum of 37% (Table 2).

For the After Period, I used data from throughout the time when predator removals had been conducted (1990-1996) to compute average consumption indices. This assumes that a compensatory feeding effect was present even during the first few years when fewer predators had been removed. In the tailrace and forebay areas, the consumption indices appear to have been somewhat higher during 1990-92 than during later years, which seems less likely to have been caused by predator removal efforts.

Several of the trend analyses that showed a significant decline in consumption indices over the 1990-96 period were also driven by the high rates observed during the early years of the removal program (Figure 4). Excluding 1990-92, when relatively few predators had been removed from the system, there are few obvious trends in the consumption index data. Average daily temperature varied $\pm3.0\ ^{o}C$ during May and $\pm2.5\ ^{o}C$ during July (Figure 4), but average temperatures appear poorly correlated with the consumption index measured that year.

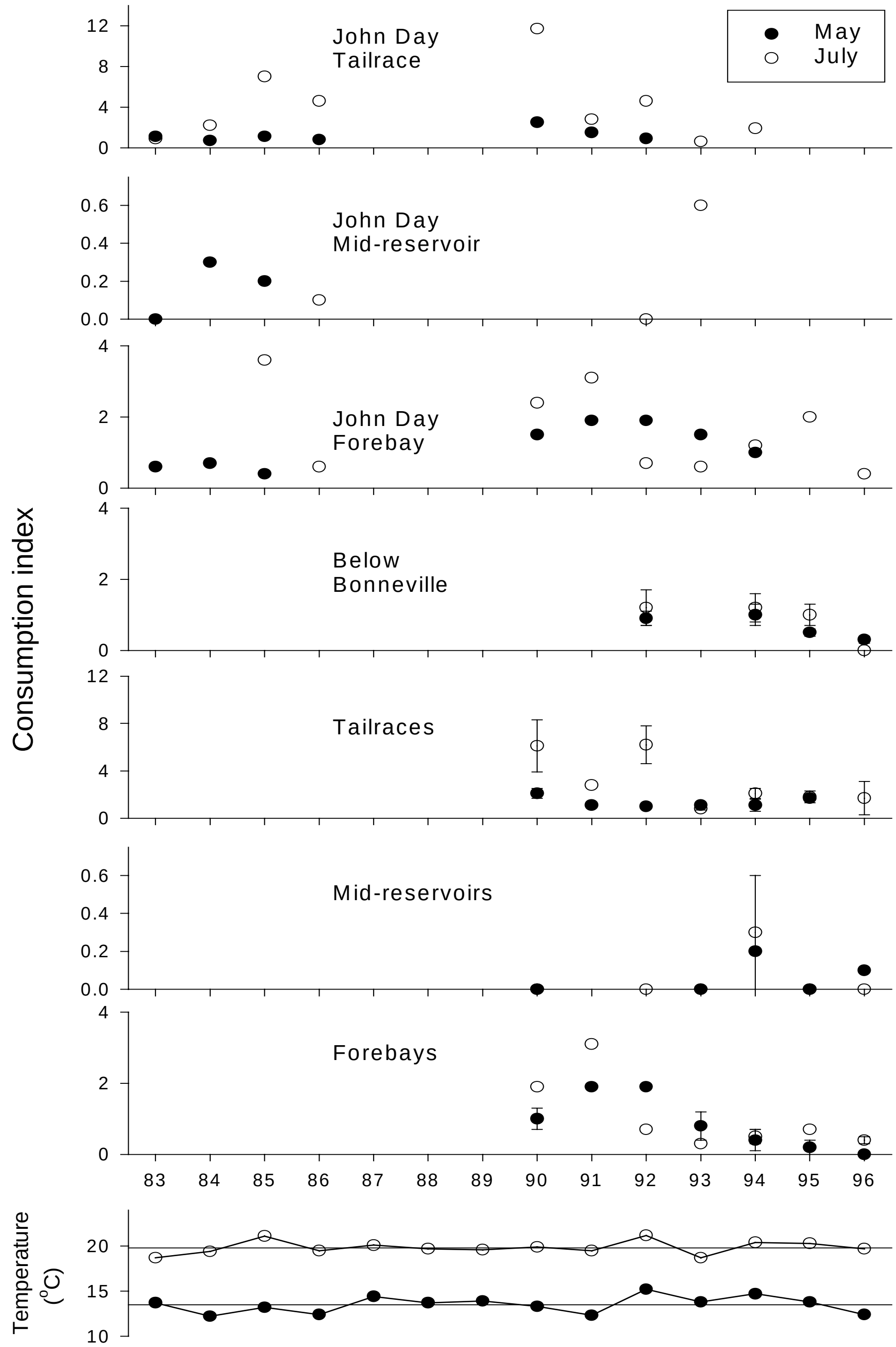

Figure 4. Predation on juvenile salmonids by northern pikeminnow over a 14-year period. The three panels for John Day reservoir and the panel for Below Bonneville Dam contain indices from specific reaches, while the panels labeled Forebays, Mid-reservoirs, Tailraces contain indices that were pooled across five reservoirs on the lower Snake and Columbia Rivers. Points are averages (±1 SE) of consumption indices where at least 10 predators were collected during a month. Note that scales differ between panels. The bottom panel is the average daily temperature during May (13.5 ^{o}C) and July (19.8 ^{o}C) measured at McNary Dam.

Table 1. Average consumption indices (CI's) of northern pikeminnow predation on juvenile salmonids in John Day Reservoir Before (1983-1986) and After (1990-1996) predator removal. Paired averages were compared by *t*-test. Both the probability of a difference (*P*, type I error) and the power of the test (1-β, power) to detect the observed difference at *P*=0.1 are given. Power was estimated with STPLAN (Brown et al. 1996), assuming equal variances (3 of 4 comparisons had equal variance).

Consumption Index						
Area / month	Before removal		After removal		t-test	
	Average (1 SE)	N	Average (1 SE)	N	P	Power
McNary Dam Tailrace						
May	0.9 (0.1)	4	1.6 (0.5)	3	0.27	0.43
July	3.7 (1.4)	4	4.3 (2.0)	5	0.81	0.07
Mid-reservoir						
May	0.2 (0.1)	3	-	-	-	-
July	0.1 (-)	1	0.3 (0.3)	2	-	-
John Day Dam Forebay						
May	0.6 (0.1)	3	1.6 (0.2)	5	<0.01	0.99
July	2.1 (1.5)	2	1.5 (0.4)	7	0.56	0.09

Table 2. Linear regressions for consumption indices versus year for data collected in the Columbia and lower Snake Rivers during 1990-1996. Data are from Friesen et al. (1997).

Period / Reach or reservoir area	Slope (SE)	P_{slope}	Intercept (SE)	$P_{intercept}$	r^2	N
May						
Below Bonneville	-0.15 (0.07)	0.06	15.0 (6.7)	0.05	0.24	11
Tailraces	-0.11 (0.10)	0.29	11.4 (8.9)	0.22	0.02	13
Mid-reservoirs	0.02 (0.02)	0.52	-1.4 (1.9)	0.53	0.01	4
Forebays	-0.22 (0.07)	0.01	20.9 (6.6)	0.01	0.37	14
July						
Below Bonneville	-0.16 (0.16)	0.34	15.8 (14.7)	0.31	0.00	9
Tailraces	-0.83 (0.30)	0.01	80.0 (28.0)	0.01	0.27	18
Mid-reservoirs	0.01 (0.05)	0.79	-1.3 (4.7)	0.80	0.01	6
Forebays	-0.30 (0.10)	0.01	28.8 (9.1)	0.01	0.35	16

4.2 Sample size and power analysis

In this section I examine the likelihood of detecting changes in predation rates under different sampling regimes and assumptions. In particular, I address two types of questions: 1) "How many years of post-removal sampling would be needed to detect an increase in predation rates?", and 2) "How many samples within one year at a particular location might be needed to detect an increase in predation rate?" . The importance of power considerations in fisheries management is well established (e.g., Peterman 1990; Osenberg et al. 1994).

Estimates of power and sample size were made using two approaches, trend analysis (Gerrodette 1987; Link and Hatfield 1990; Nickerson and Brunell 1998), and before-after sampling (Osenberg et al. 1994; Underwood 1994; and others).

As a first step in these analyses, the variability in consumption rates on juvenile salmonids was estimated. Variability estimates were made with data collected in John Day Reservoir during 1983-1988 (Vigg et al. 1991; Petersen et al. 1990) and data collected throughout the Columbia and Snake river system during 1989-93 (Ward et al. 1995). Ward et al. (1995) did not publish the raw consumption indices, which for this study were taken from Petersen et al. (1991), Shively et al. (1992), Petersen and Poe (1993), and Burley and Poe (1994).

Coefficients of variation (CV) for daily rates of predation in the forebay and tailrace areas of John Day Reservoir were fairly consistent, and averaged 79% and 72% across all months, respectively (Table 3). The mid-reservoir rates were more variable, and the CV averaged 140% (3). Rates from the system-wide survey (Table 4) were more variable than the rates estimated in John Day Reservoir alone, with CV's ranging from 93% to 197%. However, the variability among forebay, mid-reservoir, and tailrace locations in the system-wide survey showed a similar pattern to the data collected in John Day Reservoir – variation was about twice as high in the mid-reservoir areas as in the forebay and tailrace areas. The higher variability in the system-wide survey compared to John Day reservoir was likely the result of spatial differences between reservoirs. John Day Reservoir variability, on the other hand, was due largely to temporal variation both within a month and between years (see also Vigg et al. 1991; Petersen and DeAngelis 1992; Petersen 1994).

Trend analysis. Trend analysis is used when I expect a constant change in a parameter per time period (Gerrodette 1987). For the case here, trend analysis assumes that predation rate on salmonids changes at some constant rate per year, perhaps in response to annual, sustained removal of predators. This section addresses questions such as: What magnitude of change in a nominal predation rate can be detected with high power (type II error) with sampling over various periods of time?

I assumed that CV's were constant and used a linear model where the predation rate would increase by some constant absolute amount, so the predation rate C in some year i is :

$$C_i = C_1 (1 + r(I - 1)) \qquad (4)$$

where C_1 is the rate at the start of the trend and r is the annual rate of change (Gerrodette 1987; his eq. 1). I examined sampling scenarios for three levels of increased feeding (2 times nominal = 2x, 4x, or 6x; one-tailed test) that might occur over three periods (7, 14, or 30 years). These levels of increased feeding were arbitrarily selected, but such increases would have significant consequences and would compensate for some or all of the benefits of removal. The time periods examined represent the period of initial removal evaluation (7 yr), twice this period, and an arbitrarily long period (30 yr). Equation 4 above was solved for r when i = 7, 14, 30, and with $C_i = 2* C_1$, $C_i = 4* C_1$, or $C_i = 6* C_1$. Equation 10 from Gerrodette (1987; constant CVs, linear model) was iteratively solved to estimate the power of detecting changes during the sample periods.

Results of the trend analysis indicate there will be low power, at moderately high Type I error (0.1), to detect even large changes in rates of predation (Figure 5). In tailrace or forebay areas where the CV is about 75%, 30 years of sampling at a single site might detect a four-fold increase in the rate at a power >0.7 .

Table 3. Coefficients of variation (%) for predation rates by northern pikeminnow eating juvenile salmonids in the John Day Reservoir (1983-1986, and July, 1988). Rates were estimated in three areas of the reservoir and for all days with ≥15 predators. *N* is the number of daily samples.

Month	Reservoir area					
	John Day Dam forebay		Mid-reservoir		McNary Dam tailrace	
	CV (%)	*N*	CV (%)	*N*	CV (%)	*N*
April	71	3	-	-	87	8
May	51	7	90	4	55	12
June	96	3	122	4	62	12
July			173	3	84	18
August	96	5	173	3	74	9
Average	79		140		72	
Total number of predators		496		328		2,765

Table 4. Consumption index (CI) for northern pikeminnow predation on juvenile salmonids in the reach below Bonneville Dam and for three areas of reservoirs in the Columbia and Snake rivers. Data were collected during a 4-year study (1990-1993; Ward et al. 1995), and each sample had ≥15 predators.

Statistic for consumption index	Below Bonneville Dam	Forebays	Mid-reservoirs	Tailraces
Average	0.9	0.7	0.2	1.9
Median	0.8	0.4	0	1
Min	0	0	0	0
Max	3.2	3	1.6	7.8
CV (%)	93	115	197	105
N	18	20	28	33

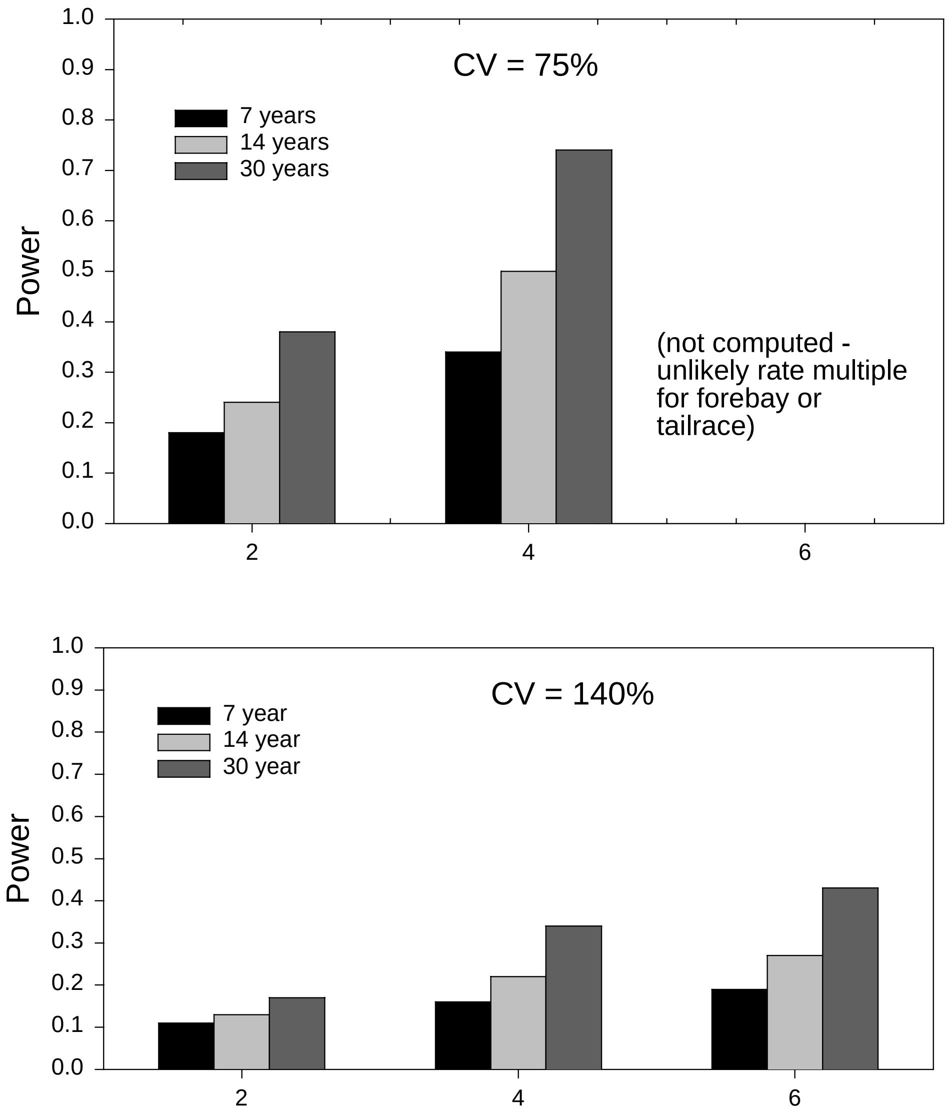

Figure 5. Power (type II error; 1- β) of detecting trends in the rate of predation on juvenile salmonids by northern pikeminnow. Power was estimated for three periods, three potential multiples of the nominal predation rate, and for two coefficients of variation (CV). Results are applicable to forebay and tailrace zones (top panel) and to the mid-reservoir areas (bottom panel). All calculations were for one-tailed tests and Type I error = 0.1 .

Before-after sampling. Before-after sampling can be used to test whether a parameter has changed between a before (control) period and an after (treatment) period (Underwood 1994). John Day Reservoir was the only area considered in this analysis, since this is the only reach where before-removal data were available. For all before-after analyses, I used a 2-sample design with a one-tailed test. Error assumptions were Type I error = Type II error = 0.1. Coefficients of variation were 140% for mid-reservoir and 75% for tailrace and forebay (see Tables 3 and 4). Coefficients of variation were assumed to be equal in Before and After periods. Software STPLAN was used to make power calculations (Brown et al. 1996).

I used two assumptions about the number of Before samples in exploring power. First, I assumed that the Before sample size was the number of **years** sampled in any month prior to removal (N=4; 1983-1986). In this case, all predators collected during a month were pooled for a CI estimate (Table 1, e.g.). Second, I used the maximum number of **days** sampled in May or July during the Before period (forebay N = 7; mid-reservoir N =4; Table 3; Appendix Table A2). The average CV was used for each habitat (Table 3). This approach treats each day as an independent sample, and samples are pooled across the 4-year Before period. Note that the currently-designed evaluation in the NPMP was not intended to estimate daily samples that would be directly comparable to the Before daily samples.

Frequency distributions of rate estimates from mid-reservoir areas were highly skewed to the left, with a high proportion of rates equal to zero (Figure 6). Strong skewness in a parameter distribution indicates that sample size and power analyses should not be computed assuming an underlying normal distribution. Thus, for the mid-reservoir areas I assumed a Poisson distribution. Frequency distributions for forebay and tailrace areas were not strongly skewed, so I used normal distribution assumptions.

For mid-reservoir area using yearly sampling, (Poisson distribution) it would be impossible to detect any rate increases less than 4 times the nominal rate (Figure 7). For the tailrace and forebay areas using yearly sampling (normal distribution assumption, CV=75%), a doubling (2 times) of the nominal rate might be detected within 10 years. Sample size requirements declined rapidly between rate multiples of 2x and 3x (Figure

7). Assuming daily sampling in the Before and After removal periods, a doubling of the nominal rate might be detected with <10 samples, but rate changes of 1.8 times the nominal rate, or less, would not be detectable with <500 samples (Figure 7).

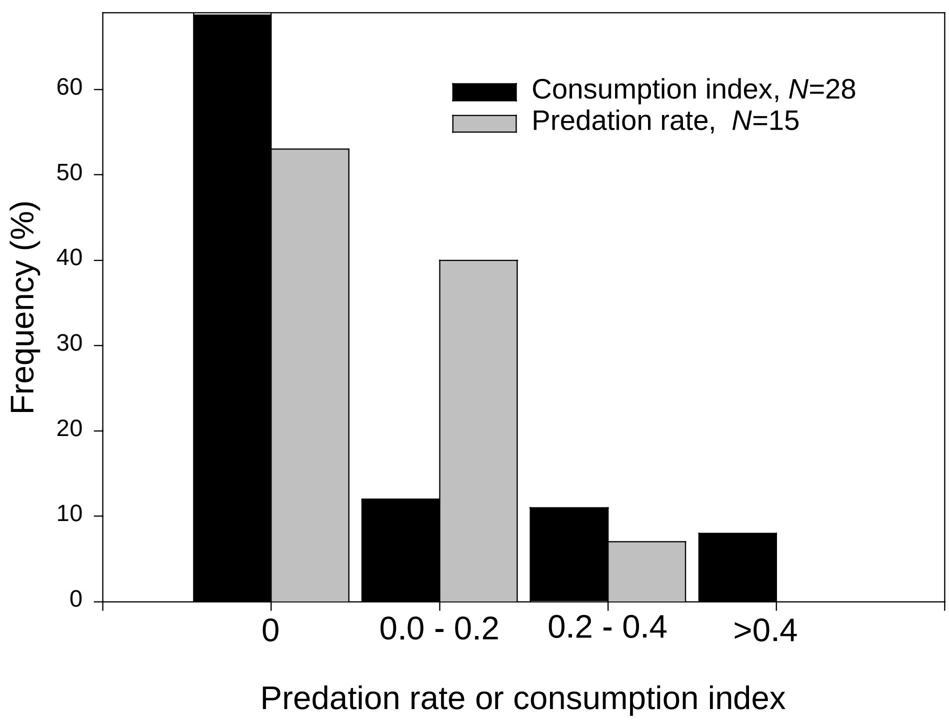

Figure 6. Frequency distributions of predation estimates on juvenile salmonids by northern pikeminnow in mid-reservoir locations. Predation rate estimates (gray) were from John Day Reservoir (1983-1986) and consumption index estimates (black) were from 13 reservoirs throughout the Columbia and lower Snake rivers (1990-93).

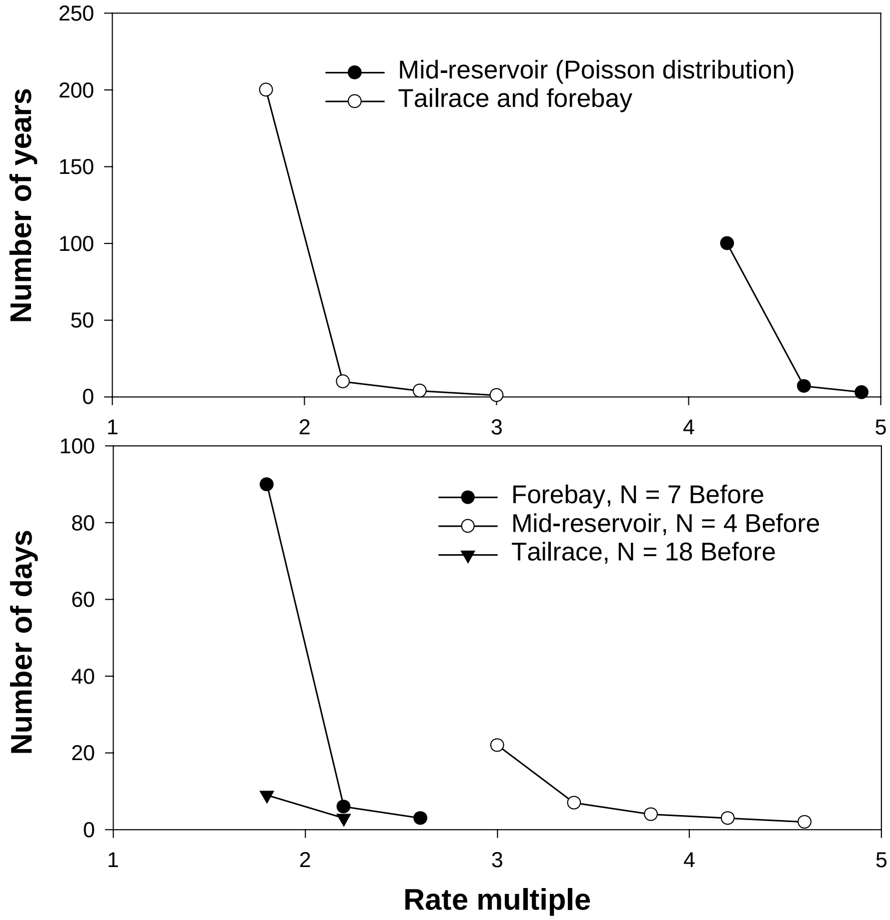

Figure 7. Number of samples needed to detect a change in predation rate using before-after testing. The upper panel assumed 4 years of Before sampling, and the mid-reservoir case assumes an underlying Poisson distribution. The lower panel assumed samples collected on individual days during the Before period for each habitat. The rate multiplier is the number of times a nominal rate would have to change to be detected. All cases assume that type I error = type II error = 0.1 .

5.0 Testing potential mechanisms of compensatory feeding

5.1 Background

5.1.1 Northern pikeminnow feeding behavior

Northern pikeminnow are omnivorous fishes, preying on fish, crustaceans, mollusks, insects, algae, and occasional items that don't normally occur in the aquatic environment such as berries, grains of wheat, and small rodents (Poe et al. 1991; unpublished USGS data). General descriptions of northern pikeminnow feeding have been given in numerous publications, including Ricker (1941), Buchanan et al. (1981), Poe et al. (1991), Vigg et al. (1991), and Ward et al. (1995). Northern pikeminnow prey on stocks of Pacific salmon and steelhead that migrate through the lower Columbia and Snake rivers in spring and summer.

Predation on juvenile salmon by northern pikeminnow occurs during all hours of the day and in all parts of the Columbia River (Vigg et al. 1991; Petersen et al. 1994; Ward et al. 1995). Predation on juvenile salmon appears to be a rapid response to changing prey density, which has been shown in a dam tailrace (Vigg 1988; Petersen and DeAngelis 1992), in lakes (Thompson and Tufts 1967), in small rivers (Collis et al. 1995; Shively et al. 1996), and in a large river (Columbia River) at a distance from dams (Collis et al. 1995). Release of salmonids from hatcheries has also been shown to cause movement of local pikeminnow and aggregation near the point of release (Thompson and Tufts 1967; Collis et al. 1995). In the laboratory, northern pikeminnow that have been starved for a brief period (>1 day) respond quickly to the introduction of salmonids in a tank, with rapid, chasing movements that often last for only a few minutes (USGS, unpublished observations). Juvenile salmon that have been introduced into a large raceway with northern pikeminnow formed tight groups at the water's surface, often in a corner of the raceway, following two or three attacks by predators. In general, northern pikeminnow are omnivores that likely respond to temporal changes in the local density of salmonids, capturing salmonids during brief feeding bouts after which they probably y return to consuming benthic-oriented organisms (Petersen, 2001).

5.1.2 Potential mechanisms of compensatory feeding

The NPMP in the Columbia and Snake rivers results in a reduced density of predators, and hopefully an increased density and number of juvenile salmonids that survive through the system. Selective removal of large predators also changes the size structure of the population. Changes in the density of predators, the density of juvenile salmonid prey, or the size structure of the predator population may be hypothesized to produce a compensatory feeding response.

At a small, local scale, competition and predation theory would predict that a decrease in predator density (northern pikeminnow) would lead to an increase in the rate of predation (Murdoch et al. 1975; Hassell 1978; Sutherland 1996; and many others). Predators often compete for food resources through complex direct and indirect mechanisms, and a reduction in predator density generally reduces the rate of interaction between predators, and increases the feeding rate on specific prey (e.g., Murdoch and Bence 1987; Diehl 1995). Diehl (1995), for example, showed how direct and indirect effects regulated prey density in a system with an omnivorous top predator, yellow perch *Perca flavescens*.

Similarly, the theory and evidence are strong for the effects of prey density on predation rate -- the functional response of predators. An increase in prey density, often over a large range of density, induces an increase in predation rate, which may be linear or non-linear (Holling 1959; Murdoch et al. 1975). Changes in prey density may not cause an increased rate of predation at very low prey densities, if switching between prey types must occur, or at high prey densities when predators are satiated or handling time is limiting (Murdoch et al. 1975). However, much of the data and theory on predator-prey relationships derived over the last 100 years has been based on single-prey systems and has not been tested in large, complex communities. When predators have multiple prey, for example, the functional response to changing prey density can become extremely complex (Abrams 1990, 1992). Direct tests of hypotheses about changes in predator or prey density in complex systems are rare (but see Diehl 1995).

Finally, the size of predators that are competing for limiting resources often governs the outcome of these interactions (Stephens and Krebs 1986; Lomnicki 1988).

Larger predators in laboratory or field situations often outcompete smaller predators through direct interference, by simply having better prey-capturing abilities (scramble competition), or by inducing behavioral responses in non-captured prey (Charnov et al. 1976; Werner and Hall 1977; Sih 1979; Mittelbach 1981). Larger northern pikeminnow have higher rates of capture of juvenile salmonids than smaller pikeminnow (Petersen 2001), suggesting this is a reasonable compensatory mechanism to explore.

5.1.3 Spatial scale of sampling and analysis

The spatial scale across which compensatory feeding might be occurring in the Columbia and Snake rivers, and is thus detectable, is an important consideration. The mechanisms briefly described above (predator density, prey density, predator size structure) would not necessarily function throughout the river system if predator-prey interactions are temporally and spatially patchy. Simulation and analytical models of spatially explicit systems of predators and prey have demonstrated how our observations and conclusions are scale-dependent (DeRoos et al. 1991; Pascual and Levin 1999; Donalson and Nisbet 1999; DeAngelis and Petersen 2001). Donalson and Nisbet (1999), for example, compared simulations of predator-prey systems across spatial scales using an ordinary differential equation (ODE) model and an individual-based spatially explicit model. One of their conclusions was to question the extrapolation of homogeneous ODE models across large spatial areas when there is reason to believe that predators or prey are patchily distributed. DeAngelis and Petersen (2001) used both an individual based simulation and an analytical model to show that estimating mortality on migrating prey is sensitive to the size of the “ecological neighborhood” around a predator. Their studies were developed with northern pikeminnow and juvenile salmonids as the model predator-prey system, but the results should apply to other predator-prey interactions.

Field studies have also demonstrated the importance of sampling scale in the detection of density effects. Jenkins et al. (1999) concluded that the growth rate of brown trout in streams was sensitive to trout density, but detection of this effect was difficult with purely observational data, at high fish densities, and when data were collected and analyzed at small spatial scales. Ray and Hastings (1996) examined 79 insect populations and found that the detection of a density effect depended on the mobility of the insects and the scale of sampling. In predator-prey systems, an appropriate sampling scale to detect density dependence depends on the mobility of the predator and the mobility of the prey, and the area over which densities are averaged (Hassell 1987; Stewart-Oaten et al. 1995; Ray and Hastings 1996). Rose and Leggett (1990) showed how the sign and magnitude of spatial correlation between predators and prey (cod and capelin) depend on the scale of data analysis and the presence of temperature refuges. Fauchald et al. (2000) found scale-dependence for murres (*Uria* spp.) feeding on capelin (*Mallotus villosus*) in the Barents Sea.

The appropriate scale for detecting whether changes in prey or predator density could influence the predation rate on salmonids by northern pikeminnow is not exactly known, but there are some relevant data. Northern pikeminnow that were radio-tagged in the Columbia River have shown long-distance (>10 km), migratory movements related to spawning and short-distance movements that are likely foraging-related, or representative of their ecological neighborhood. In two Columbia River reservoirs and in two free-flowing reaches (Columbia and Snake rivers), foraging-related movements were generally less than 2 km and in many instances the fish showed strong site fidelity (Martinelli and Shively 1997; J. H. Petersen, unpublished analyses). These observed movement patterns suggest an appropriate scale for future modeling efforts, and also correlate very well with the conclusion arrived at independently by DeAngelis and Petersen (2001). They used an individual-based model of predators and prey and found that juvenile salmonid mortality could only be predicted accurately when the ecological neighborhood (cell length) of the predator was relatively small (< 4 km). Larger cell sizes in their model overestimated salmonid mortality because the patchiness of the prey was not correctly captured.

Theory, laboratory, field, and model studies suggest that a predation response would more likely be detected at a small or intermediate scale, rather than a large spatial scale. Recent analyses of feeding by northern pikeminnow following predator removal have combined samples collected throughout a reservoir or over larger river reaches (Ward and Zimmerman 1999; Zimmerman 1999), and it seems less likely that these methods would detect density-dependent compensatory feeding. For these reasons, the analyses below concern primarily average rates of predation for samples collected over fairly short distances (transects). These analyses should have a higher probability of detecting compensatory feeding responses than analyses where data are pooled across many individuals and over large spatial areas such as reservoirs.

5.1.4 General methodology

In each of the analyses below, I conducted the following steps:

1. Derive and fit a simple model that describes the predation rate on salmonids (C, salmonids ingested • predator^{-1} • d^{-1}) as a function of predator density, predator size, or prey density. Models were fit to data collected in John Day Reservoir (1983-1988) prior to large-scale removals.
2. Summarize with frequency distributions the change in predator density, predator size, or prey density between the before removal period (1983-1986) with the after removal period (1993-1996). These frequency distributions are assumed to represent the percent occurrence (before and after) of predator or prey density or predator size where predator-prey interactions might occur.
3. Compute a "Loss" before and after removal due to each mechanism independently as: Loss = Σ Ci * Pi where Ci is the predicted rate of predation in class i and Pi is the proportion of class i measured either before or after removal (step 2 above). For example, if 20% of all predators occurred in samples having predator density of 2 predators per transect, then the loss for this density class would be the per capita predation rate predicted when density is 2 (C=f(2)) times 0.2 (20%).
4. Compare the before- and after- loss estimates as a *percentage* change; a positive percentage would be indication of increased predation loss and vice versa for a negative percentage. More complex modeling approaches are mentioned in the Discussion. Note that a percentage or relative approach, rather than estimating the total number of salmonids consumed by predators, was recommended by Hankin and Richards (2000; pp. 14-16)

5.2 Change in predator density

Reducing the density of a predator species could cause compensatory feeding through reduction in competitive interactions or through an indirect, prey response. It is also possible that reducing density could affect the predator-prey interaction in some manner that would cause a depensatory feeding response, or a reduced rate of predation.

About 1.1 million northern pikeminnow >250 mm FL were removed in the Columbia and Snake rivers by the NPMP between 1990-1996 (Friesen and Ward 1999). Catch-per-unit effort (CPUE) has been shown to be well correlated with mark-recapture population estimates (Ward et al. 1995), and thus CPUE has been used as an index of abundance (Ward et al. 1995; Zimmerman and Ward 1999). The abundance index has been the catch of predators during a 15-minute electroshock run expanded to the surface area of a reservoir (Ward et al. 1995). Comparing 1990-93 versus 1994-96, the abundance index declined by 19% in the reach below Bonneville Dam (compared to 1992 only), by 49% in Bonneville Reservoir, by 46% in John Day Reservoir, and by about 81% in the lower Snake River (Zimmerman and Ward 1999). Statistical tests were not conducted on these changes in abundance indices.

The pooled abundance indices above cover large reaches of the rivers, and hence local predator-predator interactions might not be detected. During April-May 1983-1986 in John Day Reservoir, the catch per 15-min transect of northern pikeminnow ranged from 0-17 at McNary tailrace, 0-5 at the mid-reservoir, and 0-13 at the John Day forebay (Figure 8). During June-July 1983-1986 in John Day Reservoir, catch distributions were similar to those from April-May (Figure 8). During 1993-1996, after the removal program had been in place, catch distributions had shifted to lower values and the mean catch was lower after predator removal in all paired comparisons (Figures 8 and 9). Zero catches per transect of northern pikeminnow were by far the most common, and catch distributions were strongly skewed to the left at all locations during both the 1980's and the 1990's (Figures 8 and 9). In each area and season, the major change appeared to be fewer samples in the high-catch categories and a higher percentage of zero catches. In the McNary Dam tailrace during April-May for example, the maximum catch decreased from

17 fish per 15-min during 1983-1986 to 5 fish per 15-min during 1993-1996, while zero catches increased from 56% in 1983-1986 to 76% in 1993-1996 (Figure 8).

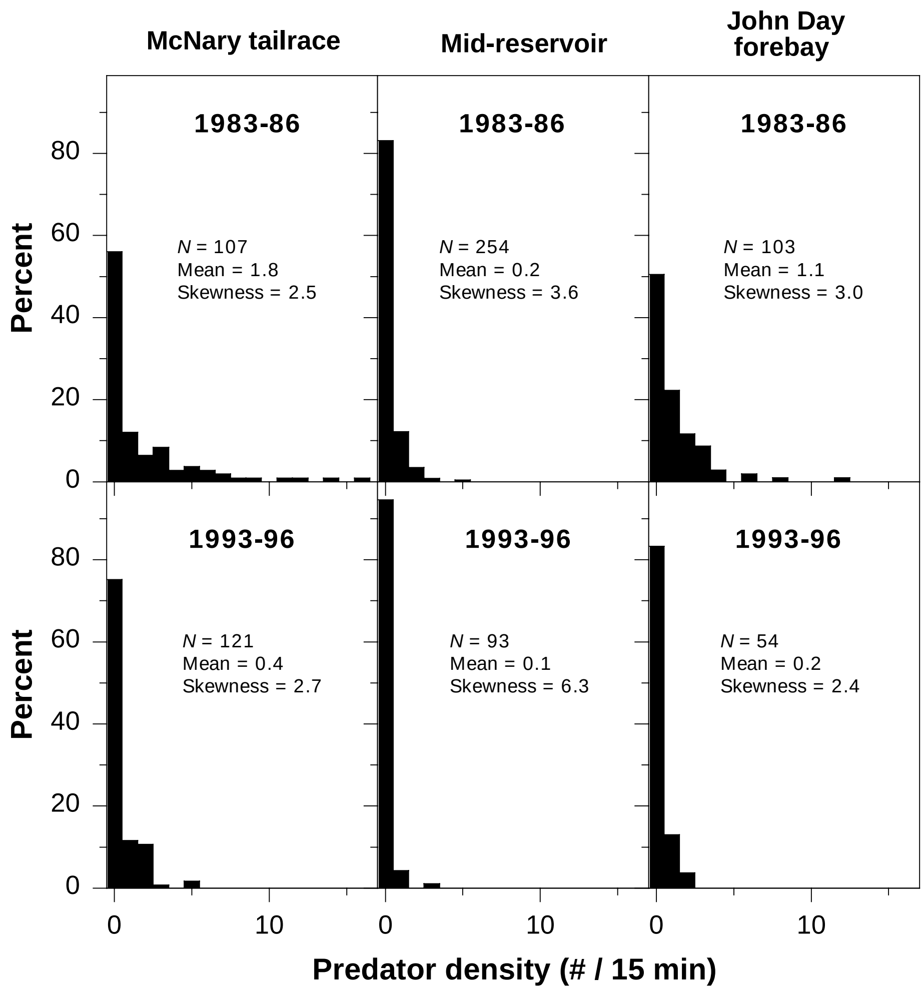

Figure 8. Frequency distributions of northern pikeminnow caught during April-May in three zones of John Day Reservoir for 1983-1986 (pre-removal period) and 1993-1996 (post-removal period). For consistency between periods, only samples collected between 0400 and 1000 were included.

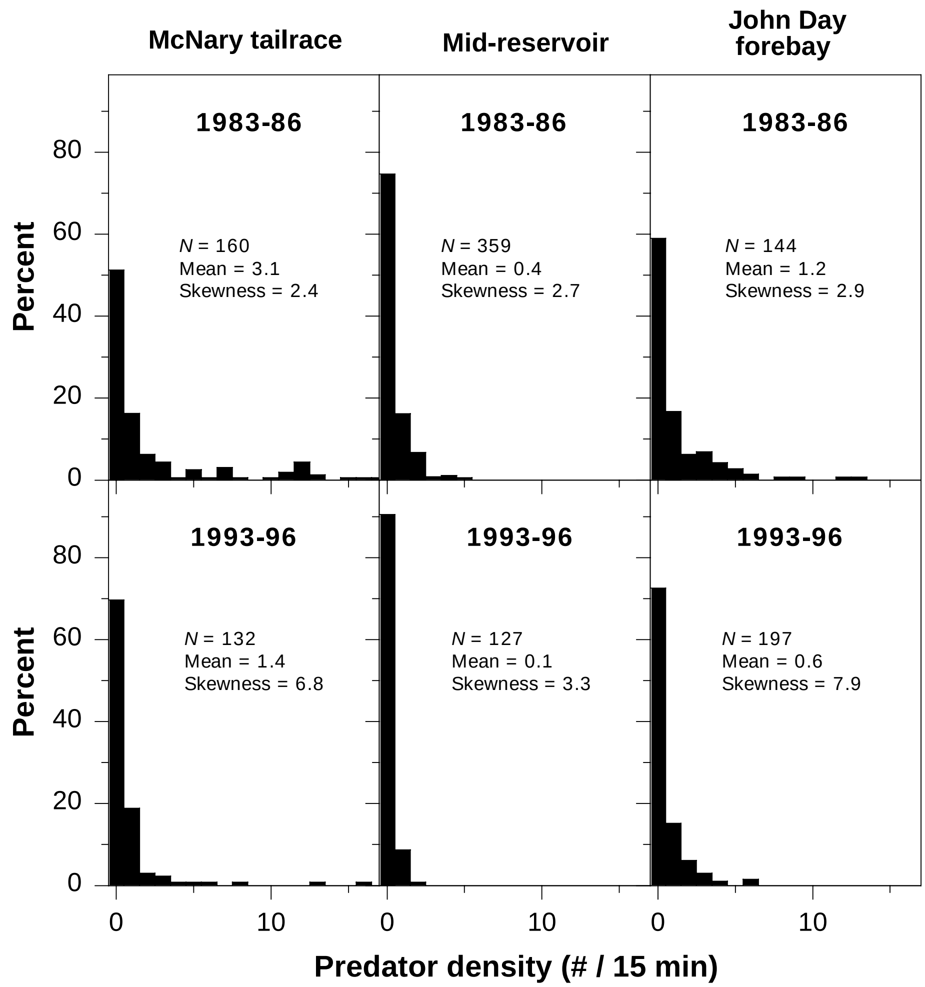

Figure 9. Frequency distributions of northern pikeminnow caught during June-August in three zones of John Day Reservoir for 1983-1986 (pre-removal period) and 1993-1996 (post-removal period). For consistency between periods, only samples collected between 0400 and 1000 were included.

Interference between predators has been modeled as the nonlinear decline in searching efficiency of predators with increasing predator density:

$$a = Q \bullet P^{-m} \qquad (5)$$

where a is searching efficiency in a patch, Q is the Quest constant, P is predator density in the patch, and m is the coefficient of interference (Hassell and Varley 1969). This model is a simplification of the classic Nicholson-Bailey model of predator density and searching efficiency (Nicholson 1933; Nicholson and Bailey 1935; Hassell 1978).
To estimate parameters of equation 1 using field data, a is often replaced by some measure of consumption rate C (prey per predator per unit of time) and an assumption is made that handling time is brief or negligible (Sutherland 1996):

$$C = Q \bullet P^{-m} \qquad (6).$$

If handling time is non-negligible then m will be underestimated.

I used equation 2 as an empirical model of potential interference in northern pikeminnow. Northern pikeminnow capture and swallow smolts rapidly and several smolts are often captured in rapid succession (Petersen and DeAngelis 1992; personal observation), so I have assumed that handling time can be ignored. Also, handling time for predators feeding on large prey is often negligible since prey are captured rapidly and physiological satiation is uncommon (Breck 1993; Essington et al. 2000). I regressed the average (all fish in a 15-min catch) consumption rates C against local predator density P using the logarithmic form of equation 2. Regressions did not include those transects where C was zero since I assumed that prey were likely unavailable to any of the predators when C was zero because of the patchy nature of migrating salmonids (Brege et al. 1988; Venditti et al. 2000; Petersen 2001; unpublished USGS data). This approach assumes that all predators in a local area would have approximately the same access to a patch of salmonids migrating through the river immediately prior to our sampling effort. Regression slopes (m) that were significantly ($P<0.05$) less than zero were an indication of potential interference, which could cause compensatory feeding as predator density decreases.

The interference coefficient m was significantly less than zero at each of the season/location strata when individual consumption rates were pooled within a catch

(Table 5). The interference coefficient was highest at the mid-reservoir location during April-May (m= -1.04) although only 17 samples were available for estimating this coefficient. Consumption rates and predator density were most variable at the McNary tailrace location where the amount of variation explained by the regression was 22% in April-May and 19% in June-August (Table 5). The Quest constant, Q, was similar at the three locations (range –0.07 to 0.43). Examination of individual bivariate plots (not shown) showed no evidence of decreased interference at lower predator densities, which has been observed in some studies (e.g. Hassell 1978).

Although there was a fairly strong indication that northern pikeminnow had higher feeding rates at lower predator densities (Table 5), extrapolating through the frequency distributions of before and after density (Figures 8 and 9) would suggest a decreased cumulative loss (Table 6). Dam forebay and mid-reservoir habitats showed decreased predation loss in each season, while the dam tailrace habitat was roughly equal in the two seasons (Table 6). The decrease in percent predation loss is caused by the shift in the frequency distributions of predator density to smaller values, and particularly the considerable increase in the number of catches with zero predators (Figures 8 and 9). This result emphasizes how frequency of “encounters” should be considered in loss analyses.

Table 5. Model fit results for individual consumption rate (salmon/predator/d) versus predator density for samples in three parts of the John Day Reservoir during two seasons. m is the parameter from the basic interference equation of Hassell and Varley (1969), fit using the linear form of their equation: $\log_{10}(\text{Consumption})=m*\log_{10}(\text{Density})+Q$. Pm is the probability that m is significantly less than zero and PQ is the probability that Q is not equal to zero. Data are from 1983-1986.

Location	Season	M	SE	P_m	Q	P_Q	r^2	N
Tailrace	Apr-May	-0.41	0.07	<0.01	-0.07	0.14	0.22	129
Tailrace	Jun-Aug	-0.43	0.07	<0.01	0.38	0.06	0.19	161
Mid-res	Apr-May	-1.04	0.16	<0.01	0.10	0.13	0.72	17
Mid-res	Jun-Aug	-0.92	0.22	<0.01	0.40	<0.01	0.64	11
Forebay	Apr-May	-0.57	0.13	<0.01	-0.01	0.89	0.25	57
Forebay	Jun-Aug	-0.82	0.10	<0.01	0.43	<0.01	0.63	40

Table 6. Predicted percent change in cumulative loss of juvenile salmonids to northern pikeminnow between before and after predator removal. Changes were computed using the frequency distributions of predator density and predicted predation rate at each predator density.

	Forebay	Mid-reservoir	Tailrace
April-May	-46%	-66%	-2%
June-August	-9%	-48%	+5%

The per capita rate of consumption of salmon for individual predators having at least one smolt in their gut ($C_i > 0$) varied widely but was not systematically influenced by predator density (Figure 10). The decline in the local predation rate on salmon with increasing predator density was caused by a decline in the proportion of predators that successfully captured salmon, rather than changes in the per capita rate of successful predators at different densities. The proportion of a catch that contained successful predators decreased with increasing predator density at all locations (Figure 11). When local predator density was 2 fish per transect, the average proportion of fish in the catch that had salmon in their gut was 0.63 to 0.81 (Figure 11). The proportion of catches with salmon declined with predator density at different rates in the three locations. At McNary tailrace the proportion decreased to 0.32 for predator densities of 9-16 pikeminnow and the proportion remained about the same as density increased. The proportion of successful pikeminnow per sample was about 0.2 for the highest densities encountered at the mid-reservoir and John Day forebay locations.

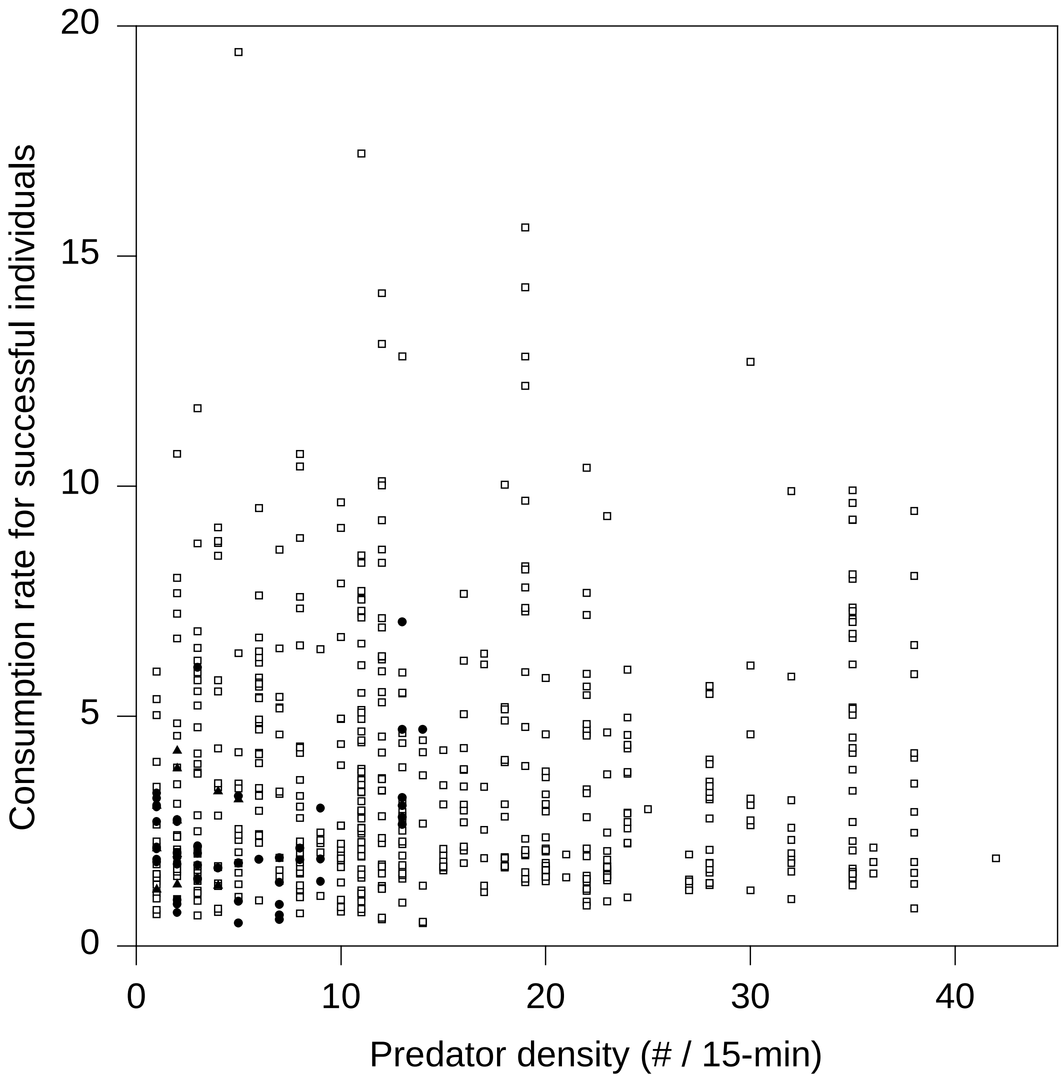

Figure 10. Rate of predation (salmonids predator day) for individual northern pikeminnow that had at least one salmonid in its gut plotted against predator density. Points are for fish collected in three zones of John Day Reservoir (1983-1986): McNary Dam tailrace (~), mid-reservoir (▲), and John Day Dam forebay (•).

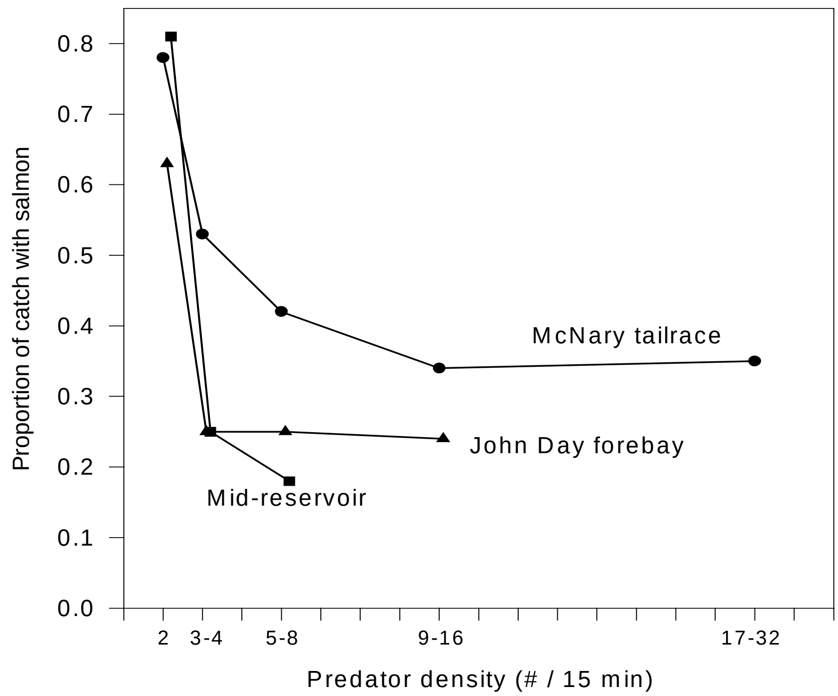

Figure 11. Average proportion of northern pikeminnow in a catch that have juvenile salmonids in their gut versus predator density. Different plots are for tailrace, forebay, and mid-reservoir sections of John Day Reservoir. Data from all months were pooled.

5.3 Change in predator size

Removing the largest northern pikeminnow in the Columbia and Snake rivers could cause a compensatory feeding response by the remaining, smaller fish through several potential mechanisms. If predators in a local area compete in some manner for passing salmonids, then larger northern pikeminnow might capture more salmonids based on better eyesight, faster swimming speed, or a higher capture success following an attack. Removing these large predators would enable the smaller fish to capture more salmonids, thus showing compensatory feeding. Predators can also limit the feeding success of nearby predators by influencing the behavior of prey, which has been called resource depression (Charnov et al. 1976) or mutual interference (Sih 1979). In this section I examine the change in the size frequency distribution in John Day Reservoir, test whether large fish in a local area tend to be more successful than small fish, derive a model of feeding success based on relative size, and compute before versus after effects with this model.

The annual exploitation rate of northern pikeminnow in John Day Reservoir averaged about 10% between 1991 and 1996, which is slightly lower than the systemwide exploitation average of 12.0% (Friesen and Ward 1999). The observed proportional stock density (PSD) of northern pikeminnow decreased from about 51% in 1990 to about 30% in 1996 (Friesen and Ward 1997), suggesting that there were fewer large predators compared to small predators in the reservoir. There has been no change in the relative weight of northern pikeminnow in John Day Reservoir or other parts of the system during predator removal (Friesen and Ward 1999).

The size structure of northern pikeminnow in John Day Reservoir appears to have changed between 1983-1986 and 1993-1996, at least in the McNary Dam tailrace and the John Day Dam forebay where tests could be conducted (Figure 13). In general, a smaller proportion of large predators was collected during 1993-1996 than during 1983-1986 especially in the McNary Dam tailrace. Frequency distributions from the mid-reservoir zone were not compared because of the small sample available for 1993-1996; the shift in size in this zone appears similar to the shift observed in the forebay zone (Figure 13).

In catches that had northern pikeminnow both with and without salmonids in their gut, the fish with salmonids were on average larger than predators without salmonids, except at the mid-reservoir location where only 19 total pikeminnow were collected in mixed catches (Figure 12). At McNary tailrace, the average mass of all successful predators was 995 g while the average mass of unsuccessful predators was 923 g ($P < 0.001$; t-test for equal means). At John Day forebay, successful versus unsuccessful predator sizes were 852 g and 642 g, respectively ($P < 0.001$; t-test for equal means).

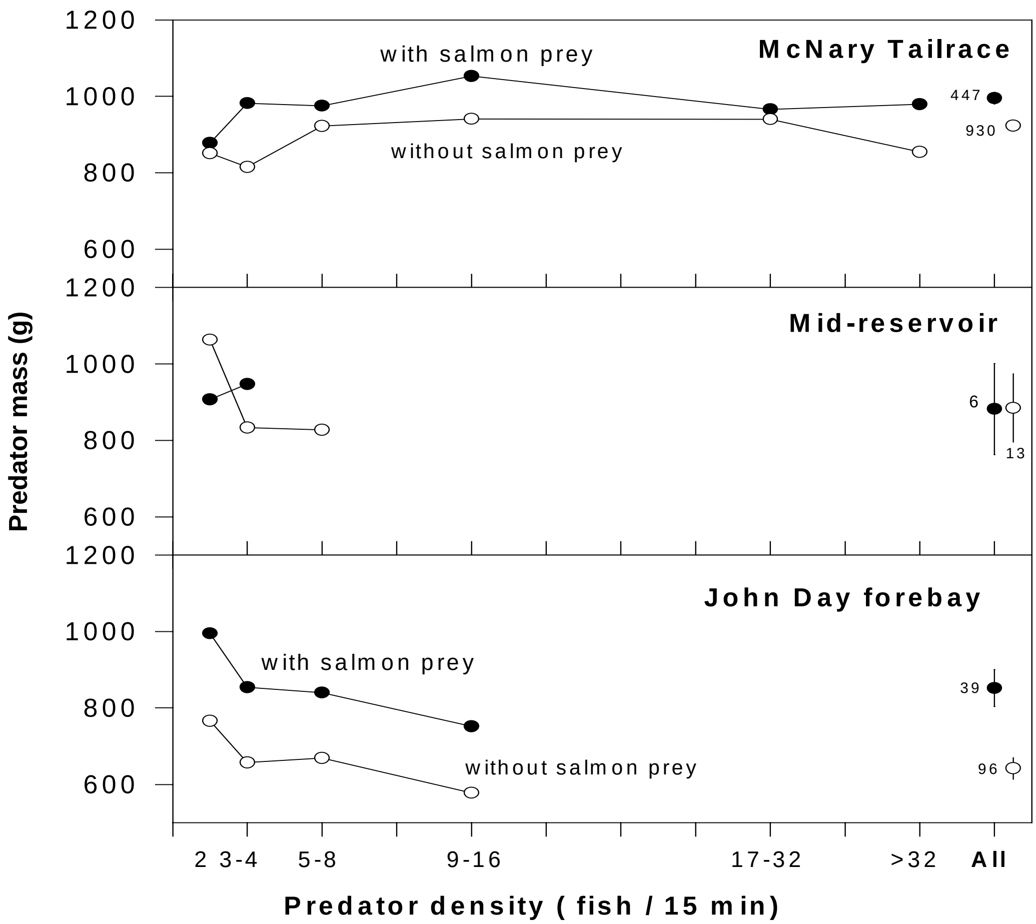

Figure 12. Average mass (±1 SE) of northern pikeminnow with (o) and without (•) juvenile salmonids in their gut as a function of local predator density. Results are shown for three zones within John Day Reservoir. All data were from catches where at least one pikeminnow in the catch had a salmon in its gut. Average mass across all predator densities (mean ± 1 SE; sample size adjacent to symbol) is shown on the far right (error bars for the McNary tailrace pooled average are smaller than the symbols).

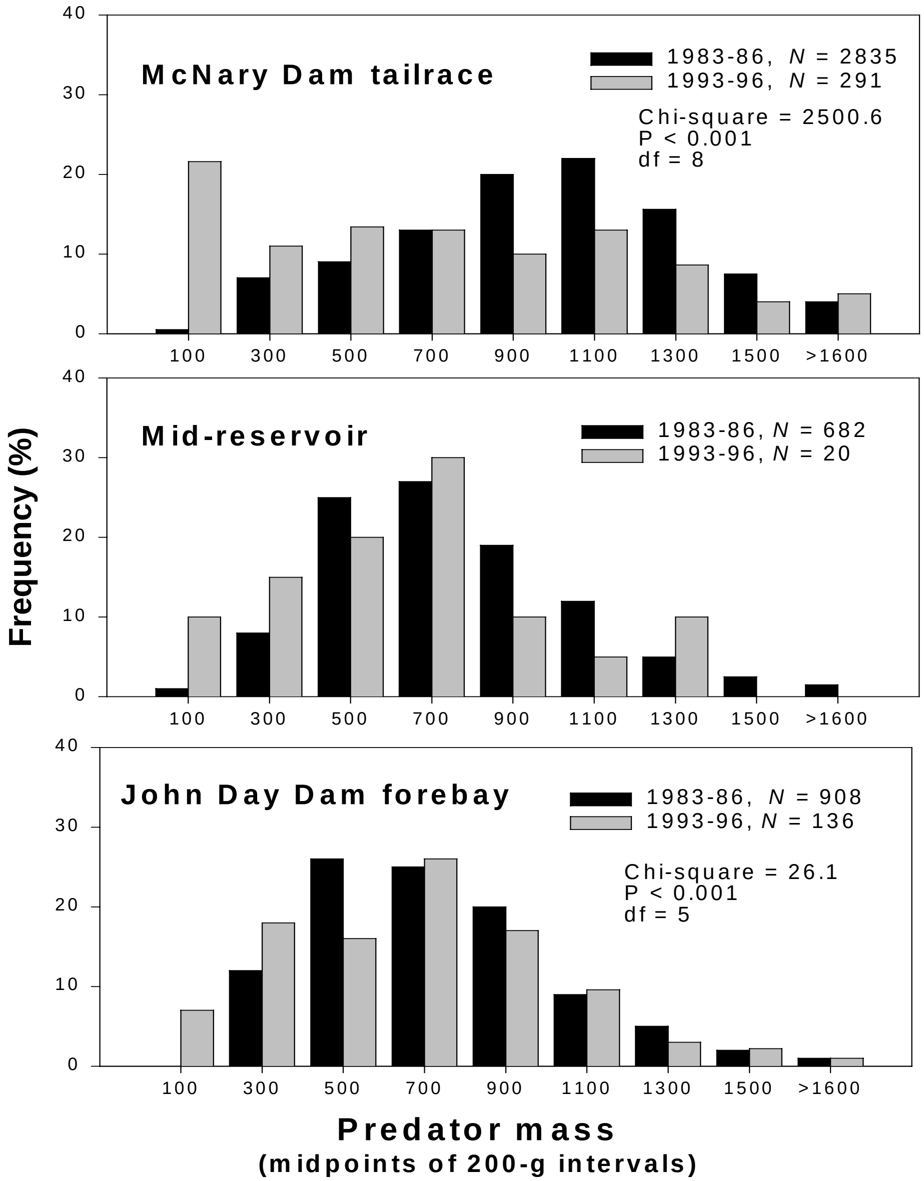

Figure 13. Frequency distributions of northern pikeminnow mass before (1983-1986) and after (1993-1996) a period of predator removal. Distributions are for three areas in John Day Reservoir. *N* is the number of predators. Distributions from the mid-reservoir were not statistically compared because of the small sample during 1993-1996.

Size or age is most often used as measures of an individual's competitive ability (Lomnicki 1988). However, the absolute size of an individual is often less important than an individual's size relative to others in the immediate area. A small competitor will often capture more prey when it is surrounded by competitors of similar size than if it is surrounded by an equal number of large competitors. I used the concept of relative competitive ability to test for possible changes following predator removal. Relative competitive ability (R_i) was first calculated for each individual fish i and was defined as the average mass of all individuals in a catch divided by an individual's mass (Sutherland and Parker 1985; Sutherland 1996). An R_i of 1.0 would indicate that a fish was surrounded by fish of similar size, an R_i greater than 1.0 would indicate that the fish was surrounded by relatively large fish, and an R_i less than 1.0 would be when a fish was surrounded by relatively small fish.

The average consumption rate C on juvenile salmon ($C > 0$) was fit to the model:

$$C = a\, R_{xi}^{\ b} \qquad (7)$$

where a and b are coefficients and R_{xi} was the average R_i within the catch (transect). Regressions were fit by least squares regression to $\log_{10}$ transformed version of the model. Regressions were fit for season and reservoir location, and only where two or more northern pikeminnow were collected in a catch.

The slopes of five of six regressions were negative, although only one of these coefficients was significantly different from zero ($P < 0.05$; Table 7). A low percent of variability was explained by the regressions using these averages across transects.

Table 7. Linear regression fit results for the average consumption rate (salmon/predator/d) versus relative competitive ability for samples in three parts of the John Day Reservoir during two seasons. Data are from 1983-1986.

Location	Season	Slope	SE	P_{slope}	Intercept	P_{int}	r^2 (%)	N
Tailrace	Apr-May	-1.12	0.87	0.20	-0.32	<0.01	2	97
Tailrace	Jun-Aug	-1.85	0.80	0.02	0.06	0.20	4	141
Mid-res	Apr-May	2.02	1.64	0.25	-0.48	<0.01	14	10
Mid-res	Jun-Aug	-2.51	3.73	0.53	0.09	0.68	7	7
Forebay	Apr-May	-4.20	2.20	0.06	-0.21	0.02	8	42
Forebay	Jun-Aug	-0.71	1.25	0.58	-0.05	0.51	1	31

If the data were pooled into classes according to relative mass ratio and average consumption rates computed, then there was a strong linear relationship between rate of predation on salmon and relative size (Figure 15).

Within a reservoir location the average R_i and the frequency distributions of Ri differed little between the 1983-1986 before period and the 1993-1996 after period (Figure 14). This suggests that removal of predators in the system has not greatly changed the local mixture of large versus small predators when two or more predators were captured in an area.

There was, however, an increase in the proportion of catches having only one northern pikeminnow between the before and after periods, where no competition or size effect would be expected. The proportion of transect catches with only one predator compared to all individuals collected in a habitat changed as: McNary dam tailrace: 8.6% before to 16.4% after; mid-reservoir: 47.4% before to 75.0% after; John Day dam forebay: 22.9% before to 32.4% after. This result suggests that juvenile salmonids might be encountering a higher frequency of isolated individual predators, where no size effect would be expected.

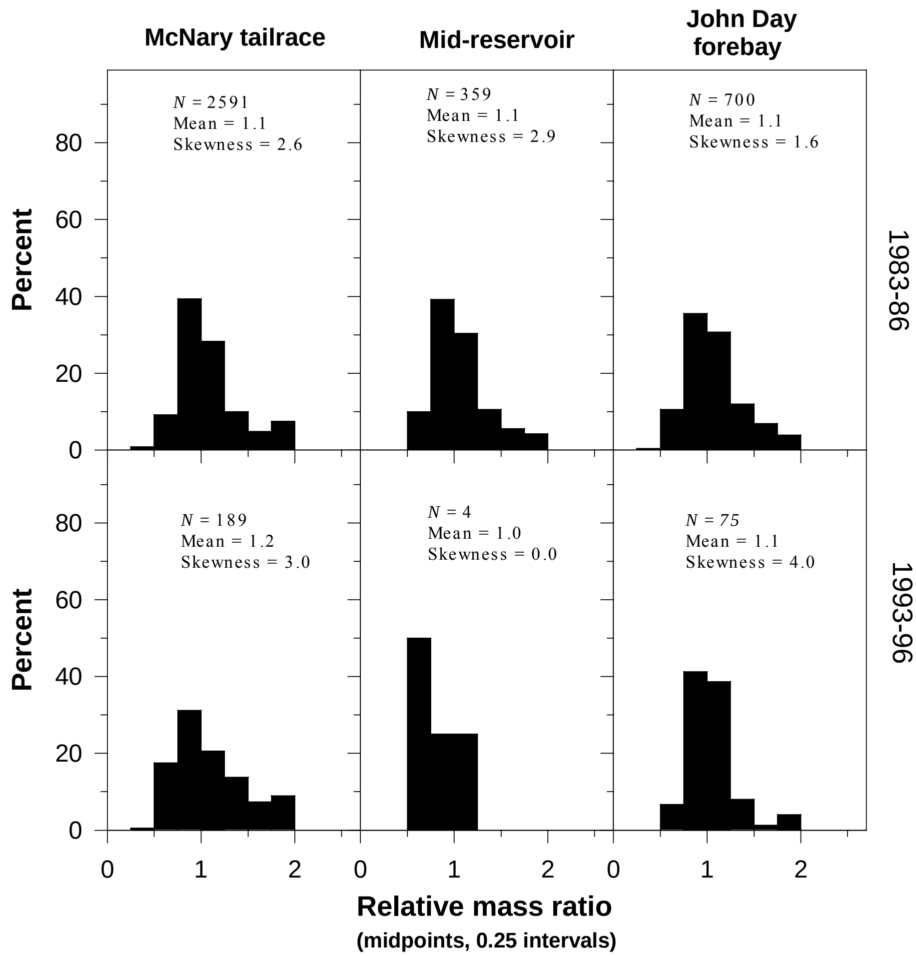

Figure 14. Frequency distribution of relative mass for individuals collected within John Day Reservoir before (1983-1986) and after (1993-1996) predator management. Relative mass is the ratio of a predator's mass to the average mass of all predators collected in that sample. Frequencies are only shown for samples where more than 1 northern pikeminnow was collected.

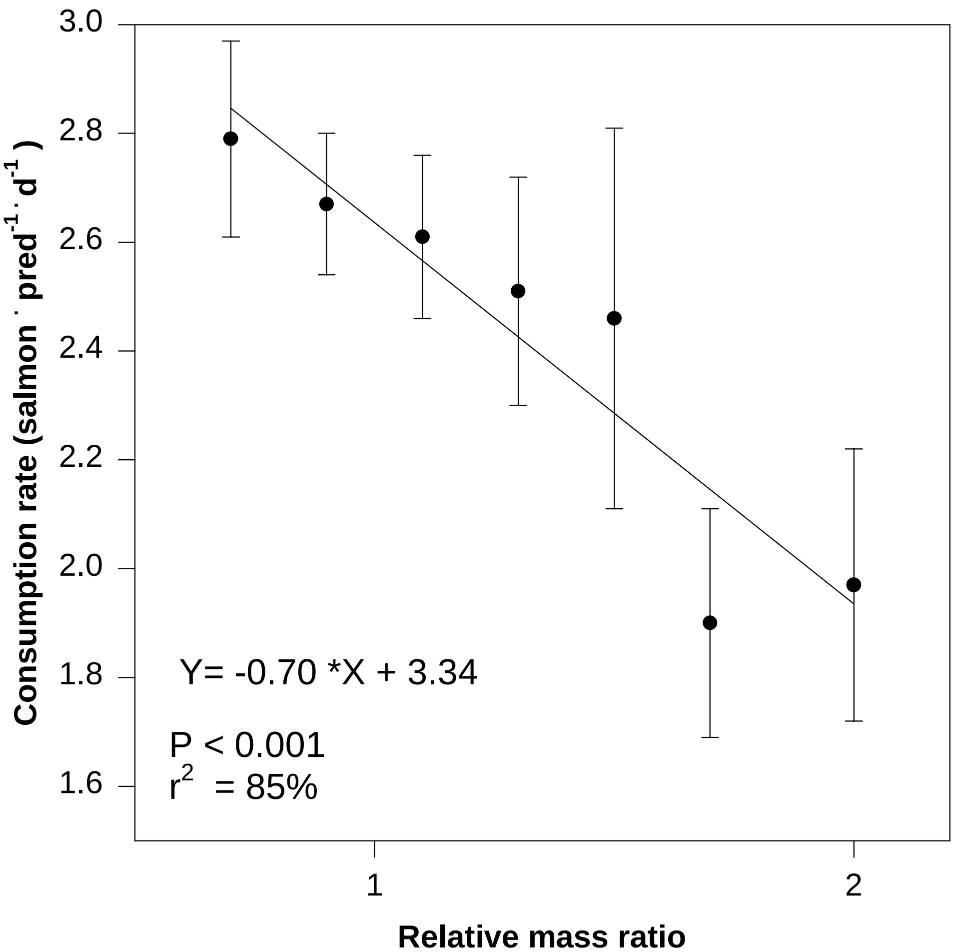

Figure 15. Average (1 SE) predation rate on juvenile salmonids by northern pikeminnow, pooled by the average relative mass ratio in a sample. All data from John Day Reservoir (1983-1986) were combined to make estimates. Samples sizes range from 17 to 405.

Applying the regressions in Table 7 with frequency distributions of relative mass (Figure 14) produced quite different predictions in the three reservoir areas (Table 8). Predicted predation rate expanded across all relative mass categories decreased in the tailrace, increased in the mid-reservoir, and showed different responses by season in the forebay (Table 8). The relatively large increases in predation rate in the mid-reservoir must be interpreted in light of the very small sample number ($N = 4$) of individuals collected during the after period in catches of more than 1 predator (Figure 14). The increased proportion of predators that were collected in catches equal to 1 in the after period (see page 54) is not included in the estimates made in Table 8.

Table 8. Percent change in cumulative loss of juvenile salmonids to northern pikeminnow between before and after predator removal. Changes were computed using the frequency distributions of relative mass ratios and predicted predation rate in each category of relative mass (see text).

Period	Forebay	Mid-reservoir	Tailrace
April-May	+23.8	+55.7	-6.7
June-August	-2.2	+36.0	-17.9

5.4 Change in juvenile salmonid (prey) density

The goal of predator removal is to increase the rate of survival of juvenile salmonids, and thus increase the total number of juvenile salmon passing down the river and entering the Pacific Ocean. If predator removal is successful, the average density of juvenile salmon per unit volume of water should increase above the pre-removal density levels, assuming that there is no concurrent increase in total water flow through the system in the before versus after removal periods. Northern pikeminnow and other predators are known to increase their rate of feeding as salmonid density rises, usually in a nonlinear manner (Thompson and Tufts 1967; Stephens and Krebs 1986; Petersen and DeAngelis 1992; Collis et al. 1995; Shively et al. 1996). Increases in prey density that accumulate through the system as a result of predator removal thus might stimulate a compensatory feeding response by remaining predators, especially by predators in the lower river. In this section, I describe two models of predation that include smolt density effects and discuss how average increases in smolt density might affect the overall mortality of juvenile salmonids. The two models are applicable to northern pikeminnow in distinctly different habitats – dam tailraces versus mid-reservoir sites – where the density, predation rates, and behavior of predators are assumed to differ greatly (Buchanan et al. 1981; Poe et al. 1991; Vigg et al. 1991; Ward et al. 1991; Petersen and Ward 1999; Petersen, unpublished manuscript; and others).

The response of northern pikeminnow to daily changes in density of salmonids (their "functional response") has been studied primarily with data collected in the McNary Dam tailrace (Vigg 1988; Bledsoe et al. 1990; Vigg et al. 1991; Petersen and DeAngelis 1992). Models of the functional response have been developed, parameterized, and compared (Vigg 1988; Petersen and DeAngelis 1992). Within the tailrace of McNary Dam, northern pikeminnow predation on juvenile salmonids was fit (Figure 16) to a "type II" or a "type III" functional response model (Petersen and DeAngelis 1992), using the terminology of Holling (1959). Northern pikeminnow feeding on salmonids in McNary Dam tailrace was fit to a type II model by Petersen and DeAngelis (1992) as:

$$C = \beta N / [1 + \beta N \alpha S/(wT)] \qquad (8)$$

where N is smolt density, S is smolt size (g), w is predator size (g), T is temperature (^oC), and α and β were fit parameter equal to 156.7 and 0.8, respectively. An important characteristic of this model is that predation rate increases across the whole range of prey densities, even at the lowest prey densities (Figure 16).

A "modified type II" functional response (Murdoch 1973) may be more appropriate for mid-reservoir areas where predators consume primarily benthic types of prey and only occasionally consume a meal of juvenile salmonids (Poe et al. 1991; Petersen and Ward 1999; Petersen 2001). In the modified type II formulation, the rate of predation is zero across a range of low prey densities and then rises rapidly when some threshold density of prey is reached (Figure 16). Benthic-feeding predators may ignore low-density patches of juvenile salmonids (a "density refuge") that pass nearby, particularly since pursuing these pelagic prey could involve a significant energy expenditure (see for example, Stephens and Krebs 1986). The modified type II functional response as applied here is analogous to "switching" between prey types (Murdoch 1973; Abrams 1990).

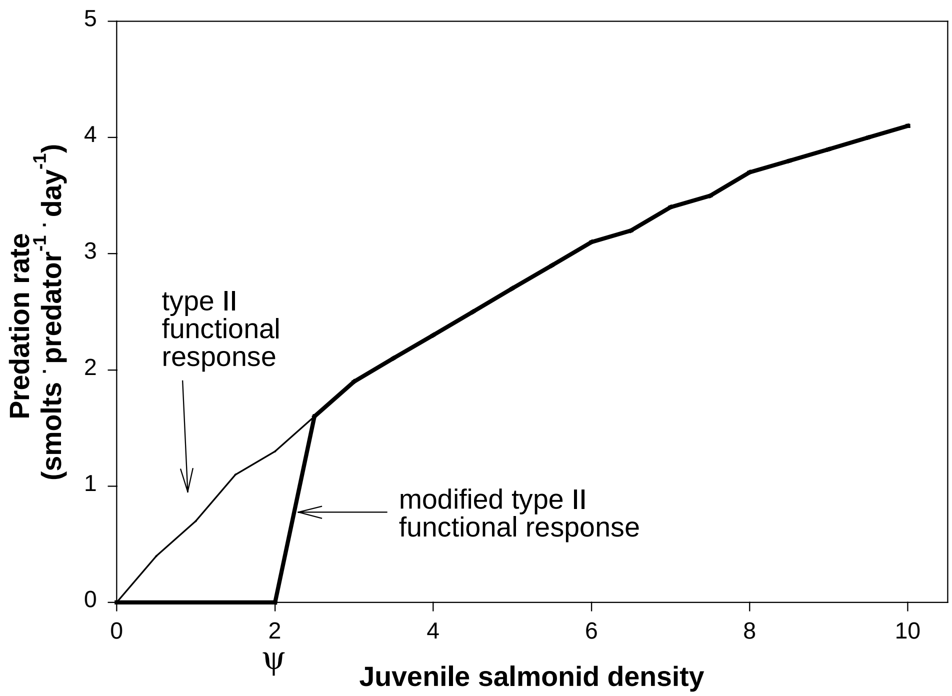

Figure 16. Example of type II and modified type II functional responses for northern pikeminnow, using equations 8 and 9 in the text. Parameter values are from Petersen and DeAngelis (1992), assuming threshold prey density (ψ) in the modified type II form is 2.0. Juvenile salmonid density has units of MI • km^{-2} • d^{1-} • 1000, where MI is an index of juvenile salmonids adjusted to daily flow.

For the modified type II functional response, I assumed that predators did not feed on smolts until the local smolt density reached a threshold density ψ. At ψ, the predator switched from a benthic foraging mode to a pelagic foraging mode (smolts) and preyed upon salmonids according to the type II equation above. Predation on salmonids in mid-reservoir areas can thus be modeled as:

$$C = [\beta(N-\psi)] / [1 + \beta(N-\psi)\alpha S/(wT)] \qquad (9a),$$

which can also be written as:

$$C = 0 \qquad N \leq \psi \qquad (9b)$$

$$C = \beta N / [1 + \beta N\alpha S/(wT)] \qquad N > \psi \qquad (9c).$$

The models for individual predation on juvenile salmon described above (equations 8 and 9) were used to estimate the magnitude of compensatory feeding that might be expected from increased smolt density. Simulations were done for two areas, a dam tailrace and a mid-reservoir, since predators in these areas have different responses to smolt density and different functional response models. Juvenile salmonid density changes daily in the river so during a smolt migration season individual predators at a particular location encounter a frequency distribution of daily smolt densities. If predator management increases the total number of smolts migrating through the system, the frequency distribution of prey density will change and the daily predation rate per predator will change. Total consumption of salmonids per predator was computed for a nominal distribution of smolt densities (1985 distribution, arbitrarily chosen) and compared to test distributions of density, which described an increase (+10%, + 20%, …, +60%) in total passage for the season. Per capita predation rate C (smolts/predator/d) was computed for each density category i and total consumption per predator L was equal to (C * number of days at density i) summed across all density categories. Predation rate C was computed for a 1000-g predator eating 15-g smolts at 20 ^{o}C. For both equations, smolt density was the migrational index (MI; Fish Passage Center) of juvenile salmon passing the dam adjusted for the daily flow, and has units MI km^{-2} d^{-1} *1000 (see Vigg 1988 and Petersen and DeAngelis 1992). [Note that type II and type III functional response models fit the available field data equally well, and for the analyses below applying the fitted type III model in the tailrace does not significantly affect the conclusions.]

To use equation 9, an estimate of the prey density threshold was necessary. I used equation 9 and field data to back-calculate the smolt density when smolts were consumed and then to estimate the threshold prey density ψ. Individual predators from John Day Reservoir (1983-1986) that had smolts in their gut (and thus had a non-zero predation rate on juvenile salmon) were assumed to have recently encountered a density of smolts equal to or greater than the threshold density, and this encounter had stimulated a feeding bout. Given the observed predation rate C for an individual predator (see section 5.2), and known values for predator size, smolt size, and temperature, equation 9c can be used to compute the prey density N, after solving equation 9c for N. Smolt size S was the average size of juvenile salmonids for a given month passing McNary Dam (Vigg et al. 1991). The threshold smolt density ψ was approximated from these estimates of N. Note that this approach does not rely on direct field measurement of prey density.

Back-calculated estimates of smolt density N ranged from 0.8 to 15.0 MI km^{-2} d^{-1} *1000 (Figure 17). The median of the N estimates was 3.8 MI km^{-2} d^{-1} *1000 in the McNary Dam tailrace, 3.8 MI km^{-2} d^{-1} *1000 in the mid-reservoir, and 4.1 MI km^{-2} d^{-1} *1000 in the John Day Dam forebay. The threshold smolt density ψ would be toward the lower end of these distributions of density since predators could be stimulated to feed on juvenile salmon across a range of smolt densities, from ψ up to a high density. The 10^{th} percentile of the distributions were: tailrace=1.3, mid-reservoir=1.9, and forebay=1.4. For discussion purposes, and especially because of the apparent truncation of the density distribution in the mid-reservoir (Figure 17), I used a smolt density of 2.0 MI km^{-2} d^{-1} *1000 as an estimate of ψ in the mid-reservoir area.

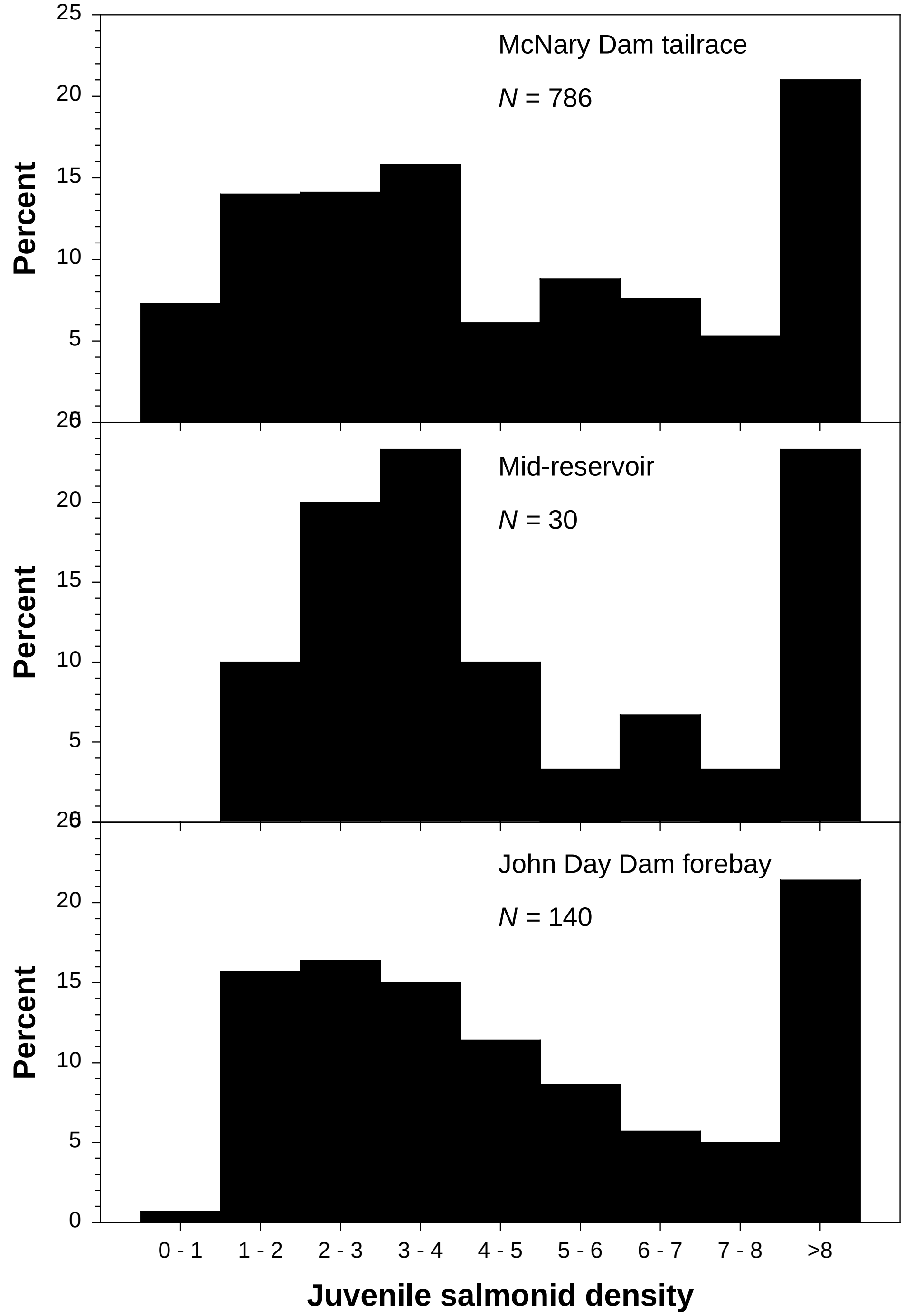

Figure 17. Back-calculated density of juvenile salmonids for individual northern pikeminnow that had recently consumed salmonids (non-zero predation rate) in three areas of John Day Reservoir. Density estimates are based on the type II functional response (see text).

For 1985 and 1986, the percent of all smolts that passed McNary Dam on days when smolt density was less than the threshold density (ψ = 2.0) in the mid-reservoir model was 21% and 43%, respectively (Figure 18). For 1994-96, this percentage was 18%, 26%, and 40%, respectively. In other words, roughly one third of all smolts from the whole seasonal migration appeared to pass the dam on days when density was below the level that would stimulate feeding by predators in the mid-reservoir. Most smolt passage (>57% in years plotted in Figure 18) occurred on days when density appeared to be high enough to stimulate a feeding response. Although the total passage on low-density days was only 18-40%, the proportion of the season where density was below ψ was considerable ranging from 62 to 95 days out of 118 total days (Figure 18).

An increase in total passage of juvenile salmonids, and thus increased daily densities, would likely cause some compensatory feeding by predators (Figure 19). A 10% increase in total passage of smolts (a 10% increase per smolt density category) would cause a 7% increase in predation by northern pikeminnow in the tailrace area and a 17% increase in the mid-reservoir area (Figure 19). If the total smolt passage increased by 50%, per capita predation rate is predicted to increase by ~35% in the tailrace and by ~67% in the mid-reservoir area (Figure 19).

In the mid-reservoir area, changes in predation rates were greater than in the tailrace because the increased density across all categories caused a higher proportion of the smolt population to pass at densities above the threshold for predation. In the tailrace area, changes in predation rates were less than the change in total passage because the rate of increase in predation rate declines at higher smolt densities. Unlike passage through the mid-reservoir where I assume a modified type II functional response, there is no density refuge for passage through the tailrace.

The modified type II functional response model allows a proportion of the salmonid population to escape predation as long as they migrate past predators on days (or in patches) when the smolt density is below the threshold density. Assuming the modified type II model for northern pikeminnow, smolts saved from predation could escape compensatory feeding as long as they migrate only on days when density is below ψ (a density "refuge"). The total number of salmonids that can escape predation by migrating at low density is, however, limited as total passage increases. During 1985 for example, if smolt density on all 118 days was just below (1.9) the threshold density (2.0) so all smolts were within the density refuge, the total passage would have been only 73% of the passage observed for this year (Figure 18). Assuming that saved smolts migrated only on low-density days and they increased the density of these 62 days (Figure 18) to 1.9, the increase in total passage is 17%. Such selective behavior of the saved smolts for specific days or patches seems unlikely.

Large predators that remain in the system would have a somewhat higher compensatory response than smaller predators. Using the tailrace model for example, a 30% increase in total passage caused a 1000-g predator to increase feeding by about 21% whereas a 2000-g predator would increase feeding rate by about 43%. Petersen and DeAngelis (1992) conducted a sensitivity analysis of the type II functional response model for predator size, temperature, smolt size, and parameter uncertainty.

The values in Figure 19 are approximate and do not, for example, take into account the change in smolt size and temperature during the season. Such considerations would require a more sophisticated modeling analysis (see Discussion; Petersen and DeAngelis 2000; DeAngelis and Petersen 2001). The approach described above assumed that "saved" salmon would be randomly distributed in time and space and would migrate down the river with the local patch, i.e., there would be no active selection for low- or high-density patches of salmonids. This assumption could be modified.

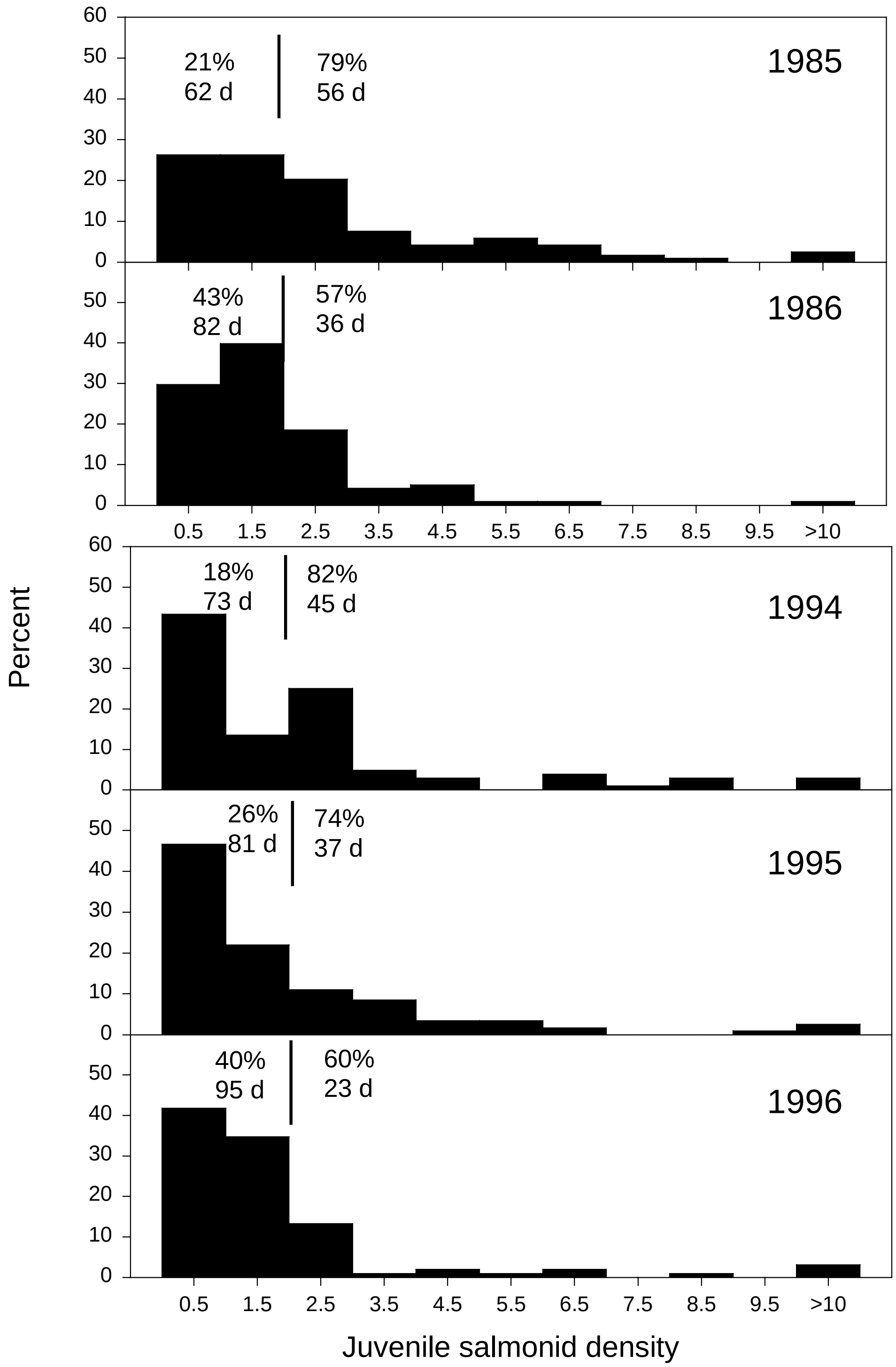

Figure 18. Frequency distributions of smolt density (migrational index) at McNary Dam for two years before predator removal and three years after a period of predator removal. For comparative purposes, these frequency distributions were limited to the period each year when 95% of all juvenile salmonids pass McNary Dam (April 9 - August 4; Fish Passage Center, personal communication). Numbers left and right of the vertical line are the percent of all smolts that passed McNary Dam on days that were below and above the threshold prey density (2.0), and the total number of days when smolt density was below and above the threshold.

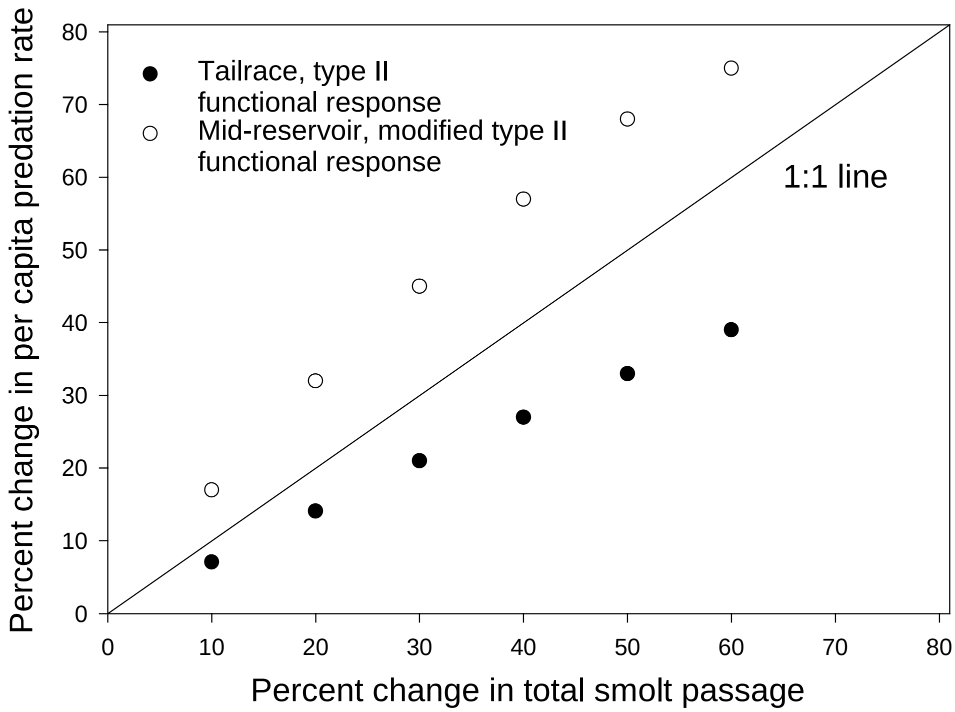

Figure 19. Changes in per capita consumption of juvenile salmonids by northern pikeminnow in response to increasing density of smolts over a migration season. Two different functional response models were used, one applicable to a dam tailrace and one applicable to a mid-reservoir area (see text). Estimates were made for a 1000-g predator eating 15-g smolt prey at 20 ^{o}C.

6.0 Discussion

6.1 General conclusions

These analyses suggest that compensatory predation by northern pikeminnow is likely occurring in the Columbia River system, however, direct demonstration of compensation in a large, heterogeneous system may be statistically (and economically) infeasible since predation rates are highly variable and predators are dispersed. The rate of predation in the middle of John Day reservoir is on the order of 0.1 salmon per predator per day with relatively high variability around the estimate (see section above on Predation Rates; Petersen 1994). Detecting a change in this rate would require a large sample size and there still appears to be a low likelihood of detecting changes of less than 50%.

The possibility of compensatory predation has been recognized since the start of the NPMP and during its evaluation (Rieman and Beamesderfer 1990; Beamesderfer et al. 1990, 1996). The seminal study of Beamesderfer et al. (1990) on northern pikeminnow management concluded that salmonid survival was most sensitive to changes in the numbers of predators, prey density, maximum consumption rate, search efficiency of predators, and water temperature. The sensitivity of their model results to predator search efficiency, in particular, suggests that compensatory predation could be on the same scale as the response to predator removal. A 10% reduction in predator numbers caused a savings of 175,336 salmonids, while a 10% increase in searching efficiency throughout the reservoir resulted in an additional 150,213 salmonids eaten. There is no direct way of measuring such parameters as “search efficiency”, but the analyses here suggest that increased search or capture success may be occurring via the mechanisms examined. Beamesderfer et al. (1990) acknowledged that their ability to estimate predator search efficiency was “very weak”.

My conclusions concerning compensatory predation differ from some recent analyses of the NPMP (Zimmerman 1999; Zimmerman and Ward 1999). Zimmerman (1999) examined the diets of northern pikeminnow, walleye, and smallmouth bass in the lower Columbia and Snake rivers during 1990-1996. He concluded that the weight of salmonids consumed per predator did not increase during this period, thus compensatory predation was not likely occurring. Zimmerman and Ward (1999) compared northern pikeminnow consumption indices between 1990-93 versus 1994-96 and found no increase in the later period. All of these analyses, and those herein, used the same data for 1990-1996, so the dissimilar results are caused by different assumptions and approaches. A major difference concerns pooling of data across reservoirs or larger reaches. I did not pool as extensively as Zimmerman (1999) and Zimmerman and Ward (1999), arguing that compensatory responses are likely to be local phenomena if they occur. Secondly, the power analyses suggested that detecting even quite large increases in salmonid consumption will be difficult with the recent level of sampling.

I used John Day Reservoir in most of the analyses above because abundant data were available both before and after implementation of the NPMP. The NPMP exploitation rate in John Day Reservoir averaged 9.4% during 1991-1996, while the system-wide exploitation rate averaged 12.0% (confidence bounds 8.1% to 15.5%; Friesen and Ward 1999). During 1993-1996, which I used for several analyses, the exploitation rate in John Day Reservoir ranged from 6 to 11%, slightly lower than the system-wide average. My general conclusion about the effect of changing predator density on predation rate should still hold, however, since compensatory feeding was predicted across a broad range of predator densities.

To my knowledge, compensatory feeding in response to predator removal has not been examined in a system as large as the Columbia River. Some predator removal studies and their results were reviewed by Beamesderfer et al. (1996). Meronek et al. (1996) reviewed 250 fish control projects, although their search did not include any of the northern pikeminnow control efforts (e.g., Foerster and Ricker 1941; Jeppson and Platts 1959; Beamesderfer et al. 1996). Meronek et al. (1996) concluded that 43% of all projects were successful, 29% were unsuccessful, and 28% had insufficient data. Goodrich and Buskirk (1995) cite some examples where native vertebrate populations may require control to conserve rare species, although they note control measures may be costly and create unexpected ecological problems including compensatory feeding by non-target species. Goodrich and Buskirk (1995) conclude that control of abundant native populations should be undertaken as a last resort in managing endangered species.

The magnitude of the compensatory feeding response predicted in these analyses (Tables 6 and 8; Figure 19) may be sufficient to compensate for the benefit of direct predator removals. I did not attempt to combine the changes in feeding rates into an overall estimate, but the increases predicted from predator size and prey density effects are similar in magnitude to the expected decrease in predation due to removal (Beamesderfer et al. 1996; Friesen and Ward 1999). Combining the different mechanisms was beyond the scope of this study but might be possible using a more complex modeling approach (see Recommendations).

A compensatory feeding response by other piscivore species is possible, but a response by northern pikeminnow would be the most critical because of its broad distribution, high abundance, and rank as a salmonid predator (e.g., Poe et al. 1991; Rieman et al. 1991; Ward et al. 1995). Smallmouth bass, walleye, and channel catfish are less abundant predators than northern pikeminnow and their overall effect is assumed to be lower (Vigg et al. 1991; Rieman et al. 1991). Nonetheless, these predators may have significant local effects on salmonid survival (e.g., Tabor et al. 1993; Petersen et al. 2000). Slight differences in habitat preferences among northern pikeminnow, smallmouth bass, or walleye (e.g., Petersen et al. 2000) would separate species and reduce the chance that a change in northern pikeminnow density or size distribution would stimulate increased predation by the other piscivorous species. Rieman and Beamesderfer (1990), however, noted that "Interactions among members of the native and introduced community are not predictable", and responses by these other predators seem possible, especially a response to increased prey (salmonid) density.

6.2 Detecting changes in predation rates

The power analyses in this report imply that detection of even large changes in predation rates (e.g., +100%; one-tailed assumption) is unlikely because of the high annual and daily variation in measured rates. Other studies have not considered the inherent variation in predation rates or diets in their analyses on compensatory feeding (Beamesderfer et al. 1996; Zimmerman 1999; Zimmerman and Ward 1999). Zimmerman (1999) compared the mean weight of consumed salmonids by northern pikeminnow and other predators during the first 7 years of predator removal (1990-96) and concluded that there was no evidence for compensatory feeding. He also observed high variation among years, making the power of any tests low. Zimmerman pooled all data across reservoir zones, rather than separating out tailrace, mid-reservoir, and forebay locations, which would increase total sample size, but would decrease the chances of detecting local responses.

Overall, the empirical data available to compare predation rates is not sufficient to make strong statements on compensatory feeding, and the likelihood of detecting even a major increase in predation rate on salmonids is low unless sampling effort is greatly increased. These conclusions suggest that inferences about compensatory feeding by northern pikeminnow may depend more on indirect measures or the examination of mechanisms.

The equation used for trend analysis is adequate for general estimates of power and sample size, although other formulations and assumptions might provide some improvement (Link and Hatfield 1990; Gerrodette 1991). Link and Hatfield (1990) found that the method of Gerrodette (1987) may have overestimated power, so my estimates of power may be somewhat high. The approach of Nickerson and Brunell (1998) could also be applied to estimate power when considering concomitant variables such as temperature. Before-after control-impact (BACI) designs are generally thought to be superior to simple before-after analysis because they control for possible location effects (Underwood 1994; Stewart-Oaten et al. 1995), however, these designs must be implemented prior to a treatment and cannot be applied in this case.

Maximum rates of predation on juvenile salmonids by northern pikeminnow can potentially be >10 salmonids per predator per day (Figure 10; unpublished USGS data). It is therefore biologically possible for the rates observed during 1983-1986 (range <0.1 to 2.0 prey/d; Petersen 1994) to increase by several multiples, especially in the mid-reservoir area which had the lowest nominal rate. It appears very unlikely that any reasonable level of sampling effort in the mid-reservoir areas will detect even changes as great as 4 or 6 times the nominal rate. This is unfortunate since mid-reservoir areas are probably where the highest loss of salmonids occurs, because most of the predator population resides in these large areas (Rieman et al. 1991; Petersen 1994). In dam forebay or tailrace areas, long-term sampling or intensive, within-year sampling might detect changes in the predation rate on the order of >3 times nominal. Even in these areas, however, the rapid increase in sample number as the rate multiplier decreases (Figures 5 and 7) means that rate changes of less than 2 times the nominal rate are unlikely to be detected without major efforts: >30 samples for a before-after analysis or >30 years of data for trend analysis.

6.3 Compensatory mechanisms

To test for predator density and predator size effects, I divided samples into those "with" versus "without" salmon present, which assumes a patchy distribution of salmonid prey. Little direct evidence is available to characterize juvenile salmonid distributions at fine spatial and temporal scales in these large rivers, but several types of data suggest patchy distributions. Key et al. (1994) observed juvenile fall chinook salmon in Columbia River reservoirs "moving freely as loose aggregates". Most salmon were collected in water that was less than 3 m deep, although older fish may have moved offshore beyond the range of the beach seine. Juvenile salmonids often delay in the forebay of hydroelectric projects (Ruggles and Watt 1975; Venditti et al. 2000), generally passing dams during night hours (e.g. Brege et al. 1988), which likely creates diel pulses of prey in reservoirs. Passage indices at dams may vary ±50% between consecutive days (Fish Passage Center, Portland, Oregon), creating temporal patches of salmon. Hydroacoustic surveys for juvenile salmonids in the Columbia River also suggest non-random distributions (D. Feil, U.S. Geological Survey, unpublished data). Finally, hatcheries often release several million juvenile salmonids during a few days, creating large patches that are known to stimulate feeding by northern pikeminnow and other predators (Thompson and Tufts 1967; Collis et al. 1995; Shively et al. 1996).

The movement of prey and some analyses of predator feeding patterns suggest that predator-prey encounters occur during relatively brief intervals over limited distances, which makes compensatory predation more likely. Petersen and DeAngelis (1992) showed that captures of salmonids occurred during brief "feeding bouts" in

McNary Dam tailrace. Northern pikeminnow that have salmonids in their gut generally have few other prey present (Petersen 2001), also suggesting discrete feeding periods.

The "interference" that is inferred from the models of predation rate versus predator density or predator size would seem to be occurring through a prey response rather than via direct predator-to-predator interaction. In circular tanks and large raceways where pikeminnow-salmonid interactions have been observed (e.g., Gadomski and Hall-Griswold 1992; Petersen and Gadomski 1994; Mesa 1994), pikeminnow are fairly inactive when juvenile salmonids are not present. Soon after salmonids were introduced into a tank, often within minutes, predators began chasing and attacking prey. Predator activity was highest for a brief period, numerous attacks occurred, and then the rate of predator-prey encounters decreased. Initially smolts were widely dispersed throughout the tank but after a few attacks by pikeminnow the smolts formed schools or aggregated along tank walls or in corners. These observations are consistent with the bout feeding behavior in the field mentioned above (Petersen and DeAngelis 1992; Petersen, 2001). Thus, when a local group of predators encounters a patch of smolts, a few predators, likely the largest individuals, attack and capture a meal but these attacks stimulate some type of response (e.g. schooling or aggregation behavior) by the remaining smolts. This altered behavior in some manner reduces the rate of predator-prey encounters or prey attacks by remaining predators so only a small portion of the local predator population captures smolts. This phenomenon has been called behavioral depression (Charnov et al. 1976) or mutual interference (Sih 1979).

Other studies have shown how prey behavior can influence predation rates and loss. Several studies have shown how aggregation behavior by prey can reduce risk through predator confusion and risk dilution (see citations in Rangeley and Kramer 1998). These same types of prey behaviors could cause the predation rate in a local area to decline. Rangeley and Kramer (1998) observed an increase in the size of shoals of juvenile pollock *Pollachius virens,* and in the proportion of fish shoaling, when pollock were exposed to a model predator. These results occurred in open water where pollock could not retreat into a protective algal habitat. Johannes (1993) found that aggregation of golden shiners *Notemigonus crysoleucas* was correlated with increased predation pressure by several predator species. Golden shiners were more aggregated during day than night and younger shiners were more aggregated than older. Higher densities of predators caused higher variance in prey density, or greater aggregation. Parrish (1992) described how predators may "shape" fish schools.

With both of the functional response models used to examine prey density effects (tailrace and non-tailrace), compensatory predation would seem to be roughly proportional to the increase in prey density (Figure 19). An increase in density below the threshold level in the modified type-II model would not stimulate feeding, however it appears that relatively few prey can escape predation mortality by migrating in this low-density "refuge". Alternatively, salmonids could escape predation by migrating in high-density patches and satiating predators. Feeding to satiation by northern pikeminnow in the system does not appear to occur very often, except perhaps following large hatchery releases of juvenile salmonids. Average gut fullness during June-August, for example, was higher for predators that had recently consumed salmonids (fullness ~24% of maximum gut capacity; N =619) compared to predators with non-salmonid prey only (fullness ~5%; N =2225), but this level was still far below maximum. Satiation by other piscivores also appears to be rare (Essington et al. 2000). Increasing prey density might also not stimulate higher predation rates if the behavior of prey changes at higher densities or longitudinally in the river. Spring chinook salmon ("stream-type") and steelhead, for example, tend to migrate along the thalweg of the mainstem rivers, often away from shore-oriented predators (Healey 1991; Petersen et al. 2000). Fall ("ocean-type") chinook salmon, on the other hand, are shoreline oriented while they rear in mainstem rivers (Mains and Smith 1964), making them available to predators. As fall chinook salmon get larger and start to migrate, they may move offshore also and become less available to predators (Healey 1991), which might reduce encounters and the possibility of compensatory predation.

7.0 Recommendations

1. **Field sampling of consumption indices.** The analyses in this report would suggest that compensatory feeding is possible or likely, but they do not demonstrate the actual occurrence of such feeding. Managers may want to re-evaluate the current monitoring program with respect to compensatory feeding. Results here suggest that the current field program will not be sufficient to detect increased feeding at levels that might compensate completely for the expected benefits of the program. If the current program is retained, managers will have to acknowledge the uncertainty related to possible compensatory feeding, perhaps throughout the duration of the NPMP.
2. **Alternative evaluations of compensatory feeding.** Some alternatives to directly sampling predation rates or indices in the Columbia and Snake rivers should be considered. Rieman and Beamesderfer (1990) also recognized this need: "Any such effort [predator control program] should include research to document compensation in predator populations and the fish community". Three types of analyses and studies might be possible to test the compensation hypothesis:
   - <u>Laboratory tests of mechanisms</u>. The mechanisms described here might be examined with laboratory studies using variable predator density, predator size, and prey density. Results of such studies would help to confirm or refute specific hypotheses about behavior and compensatory feeding. Studies in large tanks or raceways would have to be carefully devised and interpreted with caution due to potential container effects and restrictions of predators and prey in a confined space.
   - <u>Reach survival studies</u>. Although direct measurement of changes in the feeding rate of northern pikeminnow would appear difficult, and no true controls are available, it might be possible to devise a "reach" survival study in another system and infer results to the Columbia and Snake rivers. For example, a BACI-type experimental design might be used in several paired

reaches with migrating salmonids and northern pikeminnow populations. Radio- or PIT-tagged juvenile salmonids could be used to estimate survival before and after predator removal in both control and impact reaches. Techniques are becoming available to design such studies with a high level of power (Leberton et al. 1992; Pollock et al. 1995; Skalski 1999). Finding a stream or river with suitable control-impact reaches could be difficult, and the cost of the study would likely be high. The high annual costs of the NPMP ($3.1 million), and the potential importance of the program, however, may make a reach survival study worth the cost and effort.

- Mechanistic modeling. Predator-prey or predator-predator interactions, which could lead to compensatory feeding, would occur over relatively local areas where changes in predator density, predator size, or prey density might influence nearby predators. A spatially-explicit model could be constructed to account for local behaviors and possible interactions between various mechanisms. Such a model could be used to explore, for example, whether changes in salmonid migration behavior might offset compensatory feeding. Other researchers have used individual-based, spatially-explicit models of predators and migrating salmonid prey to examine complex interactions (Jager et al. 1995; Petersen and DeAngelis 2000; DeAngelis and Petersen 2001). Rose (2000) recently argued that individual-based models are a valuable tool for fisheries management.

3. **Spatial scale of sampling.** Managers and researchers should consider the importance of spatial scale in evaluating predation information. For example, the density of predators, characterized here by the distributions of local predator catches, showed a considerable decline between a before (1983-1986) versus an after removal period (1993-1996). Such a large change in predator density would not have been detected with samples pooled across reservoir habitats. Spatial scale consideration becomes especially important when evaluating behavioral

interactions of predators or prey, such as feeding rates, spawning aggregations of predators, or schooling behavior of salmonid prey.

4. **Power analyses and sampling needs in other studies of the NPMP.** Evaluation of compensation in growth and fecundity following predator removal should also consider the variability in data and our ability to detect changes. Small compensatory changes in feeding, growth, and fecundity (e.g., 10% in each) may be very difficult to detect, but their cumulative impact could significantly reduce the effectiveness of the management program.

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10.0 Appendices

Table A1. Consumption indices (CI) from John Day Reservoir used in the before-after analyses. These indices are from individuals collected during May and July only. Locations: McN RZ =McNary Dam tailrace, Mid-res =mid-reservoir, JD Fore = John Day Dam forebay. Periods: Before removal = 1983-1988, After removal = 1990-1996. Npred is the number of predators in the sample (Npred ≥ 10).

Period	Location	Month	Year	Npred	CI
Before	McN RZ	May	83	83	1.1
Before	McN RZ	July	83	94	0.9
Before	Mid-res	May	83	18	0.0
Before	JD Fore	May	83	251	0.6
Before	McN RZ	May	84	121	0.7
Before	McN RZ	July	84	114	2.2
Before	Mid-res	May	84	128	0.3
Before	JD Fore	May	84	87	0.7
Before	McN RZ	May	85	146	1.1
Before	McN RZ	July	85	122	7.0
Before	Mid-res	May	85	122	0.2
Before	JD Fore	May	85	83	0.4
Before	JD Fore	July	85	32	3.6
Before	McN RZ	May	86	318	0.8
Before	McN RZ	July	86	723	4.6
Before	Mid-res	July	86	111	0.1
Before	JD Fore	July	86	77	0.6
After	McN RZ	May	90	60	2.5
After	McN RZ	July	90	50	11.7
After	JD Fore	May	90	38	1.5
After	JD Fore	July	90	16	2.4
After	McN RZ	May	91	55	1.5
After	McN RZ	July	91	77	2.8
After	JD Fore	May	91	23	1.9
After	JD Fore	July	91	17	3.1
After	McN RZ	May	92	35	0.9
After	McN RZ	July	92	67	4.6
After	Mid-res	July	92	13	0.0
After	JD Fore	May	92	38	1.9
After	JD Fore	July	92	27	0.7
After	McN RZ	July	93	119	0.6
After	Mid-res	July	93	10	0.6
After	JD Fore	May	93	11	1.5
After	JD Fore	July	93	40	0.6
After	McN RZ	July	94	31	1.9
After	JD Fore	May	94	11	1.0
After	JD Fore	July	94	57	1.2
After	JD Fore	July	95	13	2.0
After	JD Fore	July	96	13	0.4

Table A2. Consumption rates (salmonids consumed • predator^{-1} • d^{-1}) from daily samples collected in John Day Reservoir during 1983-1986. Locations are 1=McNary Dam tailrace, 2=mid-reservoir, 3=John Day Dam forebay. Npred is the number of predators in the sample (Npred ≥ 15), and Rate is the consumption rate.

Obs	Location	Year	Month	Day	Npred	Rate
1	1	83	5	11	33	0.43
2	1	83	5	12	21	0.38
3	1	83	5	19	23	0.55
4	1	83	6	21	51	0.66
5	1	83	8	1	52	0.30
6	1	83	8	2	39	0.06
7	1	84	4	10	22	0.05
8	1	84	4	13	16	0.02
9	1	84	4	14	19	0.10
10	1	84	5	8	40	0.52
11	1	84	5	9	24	0.39
12	1	84	6	5	70	0.16
13	1	84	6	6	24	0.07
14	1	84	8	7	85	0.52
15	1	84	8	8	29	0.74
16	1	85	4	9	52	0.34
17	1	85	4	10	17	0.20
18	1	85	5	7	30	0.30
19	1	85	5	8	47	1.00
20	1	85	6	4	42	0.50
21	1	85	6	5	49	0.50
22	1	85	7	18	62	3.79
23	1	85	8	6	47	0.48
24	1	85	8	14	26	0.06
25	1	86	4	14	37	0.02
26	1	86	4	28	26	0.13
27	1	86	4	29	25	0.12
28	1	86	5	12	35	0.47
29	1	86	5	14	20	1.00
30	1	86	5	27	32	0.28
31	1	86	5	28	65	0.25
32	1	86	5	29	17	0.21
33	1	86	6	9	72	0.64
34	1	86	6	10	98	0.39
35	1	86	6	11	21	0.86
36	1	86	6	23	49	0.12
37	1	86	6	24	55	0.42
38	1	86	6	25	31	0.13
39	1	86	6	26	27	0.34
40	1	86	7	7	65	0.23
41	1	86	7	8	80	1.07
42	1	86	7	9	67	2.08
43	1	86	7	10	25	0.67
44	1	86	7	14	107	4.14
45	1	86	7	15	91	1.51
46	1	86	7	16	59	1.39

47	1	86	7	17	21	0.19
48	1	86	8	4	70	0.09
49	1	86	8	5	79	0.24
50	1	86	8	6	41	0.61
51	3	84	4	17	15	0.00
52	3	84	5	21	19	0.15
53	3	84	5	22	44	0.04
54	3	84	6	12	15	0.00
55	3	84	6	19	28	0.11
56	3	84	8	21	34	0.00
57	3	85	5	16	21	0.00
58	3	85	5	23	22	0.11
59	3	85	6	17	16	0.18
60	3	85	6	19	15	0.00
61	3	85	8	21	19	0.00
62	3	85	8	22	19	0.21
63	3	86	7	7	15	0.13
64	3	86	7	9	20	0.00
65	3	86	7	31	26	0.00
66	4	83	4	19	32	0.05
67	4	83	4	20	58	0.03
68	4	83	4	25	15	0.12
69	4	83	5	25	64	0.37
70	4	83	5	26	39	0.49
71	4	83	5	27	16	0.33
72	4	83	6	27	19	0.04
73	4	83	8	26	24	0.16
74	4	84	5	4	16	0.52
75	4	84	5	11	22	0.55
76	4	84	5	29	19	0.03
77	4	84	8	27	17	0.56
78	4	84	8	28	21	0.16
79	4	84	8	29	20	0.12
80	4	85	5	31	22	0.24
81	4	85	6	25	15	0.07
82	4	85	6	26	20	0.00
83	4	85	7	18	28	0.87
84	4	85	8	27	29	0.05
85	1	88	7	14	94	1.27
86	1	88	7	15	50	1.84
87	1	88	7	16	21	0.40
88	1	88	7	18	53	4.39
89	1	88	7	19	98	4.20
90	1	88	7	20	47	2.24
91	1	88	7	22	52	0.55
92	1	88	7	23	95	0.42
93	1	88	7	24	20	0.69