CONSUMPTION RATES AND ESTIMATED TOTAL LOSS
OF
JUVENILE SALMONIDS BY NORTHERN SQUAWFISH
IN
LOWER GRANITE RESERVOIR, WASHINGTON

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Abstract

Food habits and importance of prey were assessed for two length groups of northern squawfish *Ptychocheilus oregonensis* (250-349 mm and > 349 mm total length) collected from Lower Granite Reservoir, Washington, during 1987-1991. Salmonids were the most important prey item by weight for both length groups of squawfish during April, May, and June for all 5 years pooled, accounting for 50.2% and 72.3% by weight of all food items. Also, salmonids were the most important food item in the index of relative importance (IRI; 54.4% of the total score)for squawfish > 349 mm, whereas insects were the dominant food item in the IRI (74.8% of the total score) for the smaller length group of squawfish. Crayfish and suckers (*Catostomus* spp.) were the most important prey items by weight during the summer, fall, and winter months from seasonal sampling during 1987.

Mean daily consumption rates and daily ration of salmonid (Pacific salmon and steelhead *Oncorhynchus* spp.) and non-salmonid fish prey were estimated for both length groups of northern squawfish during the smolt outmigration periods (April through June) of 1987-1991. Consumption of salmonids was highest for both length groups during April, and declined during May and June. Northern squawfish > 349 mm were the dominant predators of salmonids. Incidence of predation increased linearly with squawfish size. Importance of non-salmonid fishes increased from April to June for both length groups of squawfish. Mean daily ration of fish prey increased from May to June, peaking near 26 mg of fish/g of predator in June (pooled data). Mean daily ration of salmonids was relatively stable during the 3 months, approaching 11 mg of salmonid per g of predator. Diel feeding patterns show feeding peaks during late morning and evening hours. An annual loss of salmonids to squawfish predation during the April through June outmigration in Lower Granite Reservoir (Rkm 175 to Rkm 216) was estimated at 128,641 salmonids or 35.7 salmonids per hectare. Lengths of salmonids consumed did not differ significantly from lengths available in Lower Granite Reservoir during the three month period. Because of the population size structure of northern squawfish, a larger portion of northern squawfish are physically capable of ingesting chinook than steelhead. These physical limitations of ingestible prey size may cause size selective predation pressures to be greater on the population of steelhead than on the population of chinook migrating through the reservoir.

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Table of Contents

Title Page i

Authorization to Submit ii

Abstract iii

Acknowledgments v

Table of Contents vi

List of Tables viii

List of Figures ix

  Introduction 1

  Study Area 4

    Lower Granite Smolt Outmigration 6

  Methods 8

    Predator collections 8

    General food habits 10

    Consumption 11

    Size Selectivity 15

    Population characteristics 15

    Estimated Loss of Salmonids 16

  Results 18

    Dietary Analysis 18

      Spring 18

      Summer 26

      Fall 26

      Winter 29

    Consumption 29

    Daily Ration 34

Diel consumption 36

Salmonid Size Selectivity 48

Population parameters 52

Estimated loss 52

Discussion 58

Dietary analysis 58

Consumption and Daily Ration 59

Diel consumption 62

Size Selectivity 63

Population parameters 65

Estimated Loss 70

Summary 73

References 75

List of Tables

Table 1. Sampling periods for collection of northern squawfish during 1987-1991, Lower Granite Reservoir. A + symbol indicates a time period sampled 9

Table 2. Sample size, incidence of salmonid predation, and percent empty stomachs for all northern squawfish length groups sampled by season during the years 1987-1991 and all years combined in Lower Granite Reservoir 19

Table 3. Relative importance of prey items of northern squawfish pooled based on percent number, weight, frequency of occurrence, and the IRI score collected during April, May, and June, 1987-1991 and all years combined, Lower Granite Reservoir, Washington. 21

Table 4. Relative importance of prey items of northern squawfish pooled (n=25, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the summer of 1987, Lower Granite Reservoir, Washington 27

Table 5. Relative importance of prey items of northern squawfish pooled (n=49, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the fall of 1987, Lower Granite Reservoir, Washington 28

Table 6. Relative importance of prey items of northern squawfish pooled (n=5, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the winter of 1987, Lower Granite Reservoir, Washington 30

Table 7. Consumption (prey/predator) of salmonids and non-salmonids for northern squawfish for the months of April, May and June and all months combined Lower Grantite Reservoir, Washington. Consumption statistics are: sample size (N), mean predator weight (W), mean consumption (prey/predator;n), and mean prey weight (w). 31

Table 8. Summary of loss of juvenile anadromous salmonids by northern squawfish > 250 mm by predator length group, salmonid species, and month in Lower Granite Reservoir, Washington.57

Table 9. Comparison of selected gill net catch per unit effort (CPUE) values between John Day Reservoir and Lower Granite Reservoir (CPUE = catch/hour). 67

List of Figures

Figure 1. Map of Lower Granite Reservoir, southeastern Washington, with inset of the proximity of study area to the Columbia River basin and John Day Reservoir. 5

Figure 2. A) Timing and magnitude of outmigration for yearling chinook salmon and steelhead based on 1987 counts at Lower Granite dam (Koski et al. 1988). B) Timing and magnitude of outmigration for sub-yearling chinook salmon based on 1986 counts at Lower Granite dam (Koski et al. 1987) 7

Figure 3. Flow chart of steps involved in estimating mean daily consumption of juvenile salmonids by northern squawfish (from Vigg et al. 1991). 12

Figure 4. Flow diagram of algorithm used to calculate total loss of juvenile anadromous salmonids from northern squawfish predation in Lower Granite Reservoir, Washington, 1987-1991. 17

Figure 5. Length frequencies of northern squawfish sampled (solid bars) and of northern squawfish that contained salmonids (clear bars) in the digestive tract. Percent incidence of salmonid predation by 25 mm length groups (solid line) of northern squawfish. 20

Figure 6. Importance of prey items (based on the Index of Relative Importance) ingested by two length groups of northern squawfish (250-349 mm and >349 mm) during the spring months of 1987-1991, Lower Granite Reservoir. 25

Figure 7. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) from pooled data during April, May, and June, and all three months combined from 1987-1991, Lower Granite Reservoir. 35

Figure 8. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1991, Lower Granite Reservoir. 37

Figure 9. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1990, Lower Granite Reservoir. 38

Figure 10. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non=salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1989, Lower Granite Reservoir. 39

Figure 11. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1988, Lower Granite Reservoir. 40

Figure 12. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined from 1987, Lower Granite Reservoir. 41

Figure 13. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1987, Lower Granite Reservoir. 42

Figure 14. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1988, Lower Granite Reservoir. 43

Figure 15. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1989, Lower Granite Reservoir. 44

Figure 16. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1990, Lower Granite Reservoir. 45

Figure 17. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1991, Lower Granite Reservoir. 46

Figure 18. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1987-1991 (pooled), Lower Granite Reservoir. 47

Figure 19. Maximum ingested fork length of salmonids by northern squawfish in 25 mm length increments (solid squares) in Lower Granite Reservoir, 1987-1991. Line A represents regression equation for northern squawfish lengths < 400 mm ($Y=(0.945*X)-126.5$; $r^2=0.89$). Line B represents regression equation for northern squawfish > 250 mm ($Y=(0.252*X)+91.8$; $r^2=0.34$). Line C represents regression equation developed by Poe et al. (1991) for the relationship of maximum ingested salmonid length to northern squawfish length ($Y=(0.716*X)-84.435$; $r^2=0.96$) from John Day Reservoir . . 49

Figure 20. Length distributions(25 mm increments) of chinook salmon and steelhead collected from Lower Granite Reservoir during the juvenile anadromous salmonid outmigration, 1987-1991 (Bennett et al. 1988, 1990, 1991, unpublished data). . . 50

Figure 21. Length distributions (25 mm increments) of chinook, steelhead, unknown salmonids, and all salmonids combined ingested by northern squawfish in Lower Granite Reservoir, 1987-1991. 51

Figure 22. Age distribution of northern squawfish collected with gill nets from Lower Granite reservoir, 1985-1990, overlaid with Von Bertalanffy growth models developed for squawfish from John Day Reservoir and Lower Granite Reservoir. 53

Figure 23. Catch curve from gill net catches of northern squawfish collected during 1985-1990 with regressionline of ages 6-14 used for survival estimate. 54

Figure 24. Length distributions (25 mm increments) of chinook, steelhead, and unknown salmonids ingested by northern squawfish in Lower Granite Reservoir during April through June, 1987-1991. 55

Introduction

Most research on northern squawfish *Pytchocheilus oregonensis* has generally been related to ecological interactions with salmonid populations, either through predation and losses of juvenile salmonids or competition with juvenile salmonids (Brown and Moyle 1981). Evidence supporting significant competitive interactions is weak (Brown and Moyle 1981), however, significant losses of juvenile salmonids due to predation have been documented throughout the range of northern squawfish (Ricker 1941; Eggers et al. 1978; Thompson and Tufts 1967; Rieman et al. 1991), especially in lake populations or altered habitat such as reservoirs, water diversions, and areas near hydroelectric dams (Brown and Moyle 1981). Several control measures have been implemented at various locations to reduce squawfish populations (Poe et al. 1988). In more riverine habitats, impacts of predation by squawfish appear to be less substantial (Buchanan et al. 1980; Falter 1969; Kirn et al. 1986).

Between 1933 and 1975, a total of 28 hydroelectric dams were constructed in the Columbia River drainage which comprise the Federal Columbia River Power System (Northwest Power Planning Council (NPPC) 1984). In addition, several other federal and nonfederal dams were constructed throughout the states of Washington, Oregon, and Idaho (NPPC 1987). Construction of the dams and creation of reservoirs dramatically changed the physical habitat by altering river flows, velocities, and temperatures.

Severe negative impacts on the indigenous runs of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* resulted from creation of complete barriers, inundation of spawning and rearing habitat, delays in migrations, and direct and indirect mortality from turbines and reservoir passage (Ebel 1977, Raymond 1979, 1988). A large portion of the anadromous runs consist of hatchery reared stocks, and depleted wild runs of anadromous stocks continue to decline (Raymond 1988).

Abundance of northern squawfish has increased with the creation of reservoir environments (Poe et al. 1991). Large areas of slack water have created more favorable rearing environments (Hjort et al. 1981), and increases in abundance of other native fishes and introduced predators have dramatically changed the complexity and trophic dynamics of the river system. Gray and Dauble (1977) reported up to 43 species of fish representing 9 families of fish found in the Hanford reach of the Columbia River. Bennett et al. (1983) reported up to 30 species representing 9 families in the lower Snake River reservoirs.

The magnitude and dynamics of predation on juvenile anadromous salmonids by northern squawfish and other predators were clearly demonstrated for John Day Reservoir, Columbia River (Poe et al. 1991; Vigg et al. 1991; Beamesderfer and Rieman 1991; and Rieman et al. 1991). Northern squawfish is the major predator of salmonids in John Day Reservoir (Rieman et al. 1991) and probably throughout the Columbia River drainage. Significant losses were attributed to squawfish predation in John Day directly associated with the area in the tailrace of McNary Dam, although the majority of the predation occurred within the reservoir environment (Rieman et al. 1991). While other research is ongoing (Petersen et al. 1990) to index salmonid losses in other Columbia and Snake River reservoirs, consumption estimates as outlined in Vigg et al. (1991) have not been made for any other Columbia and Snake River reservoirs.

The purpose of my research was to describe seasonal importance of prey items of northern squawfish, and to estimate the importance, mean daily consumption and total loss of juvenile anadromous salmonids in Lower Granite Reservoir, Snake River.

Study Area

Lower Granite Reservoir is the first in a series of four impoundments on the lower Snake River (Figure 1). Lower Granite Lock and Dam is located at river kilometer (Rkm) 173.1. Construction was completed in 1975. Surface area at full pool (225 m msl) is 3,602 hectares with 146.5 km of shoreline. Mean depth of the reservoir is 16.6 m with a mean width of 643.3 m. Mean annual discharge from Lower Granite Dam is 1,400 m^3/s. At this discharge, mean water travel time is 4.9 days (Funk et al. 1985). The reservoir is located primarily in southeastern Washington, and west central Idaho near the cities of Clarkston Washington, and Lewiston, Idaho. The project provides hydroelectric power, barge navigation to the cities of Clarkston and Lewiston, flood control, and some irrigation supply benefits.

Water temperatures range from 4°C to 23°C, peaking in late summer. Vertical temperature gradients are rare, and occur only during low flow (Funk et al. 1985).

The physical habitat of the reservoir is characterized by steep talus shorelines with frequent basalt outcroppings. A large portion of the shoreline consists of large boulder rip rap placed as part of the levee system at time of dam construction. Littoral habitat is limited, with the majority located in the upper portion of the reservoir. Of the total surface area, 15% is < 6 m depth, 78% of which is located upstream of Rkm 194 (Myers and Sather-Blair 1989).

Sampling locations

Sampling locations have ranged from Rkm 215.8 to 175.5 during the five years of study (Figure 1). Sampling has occurred in shallow (<6

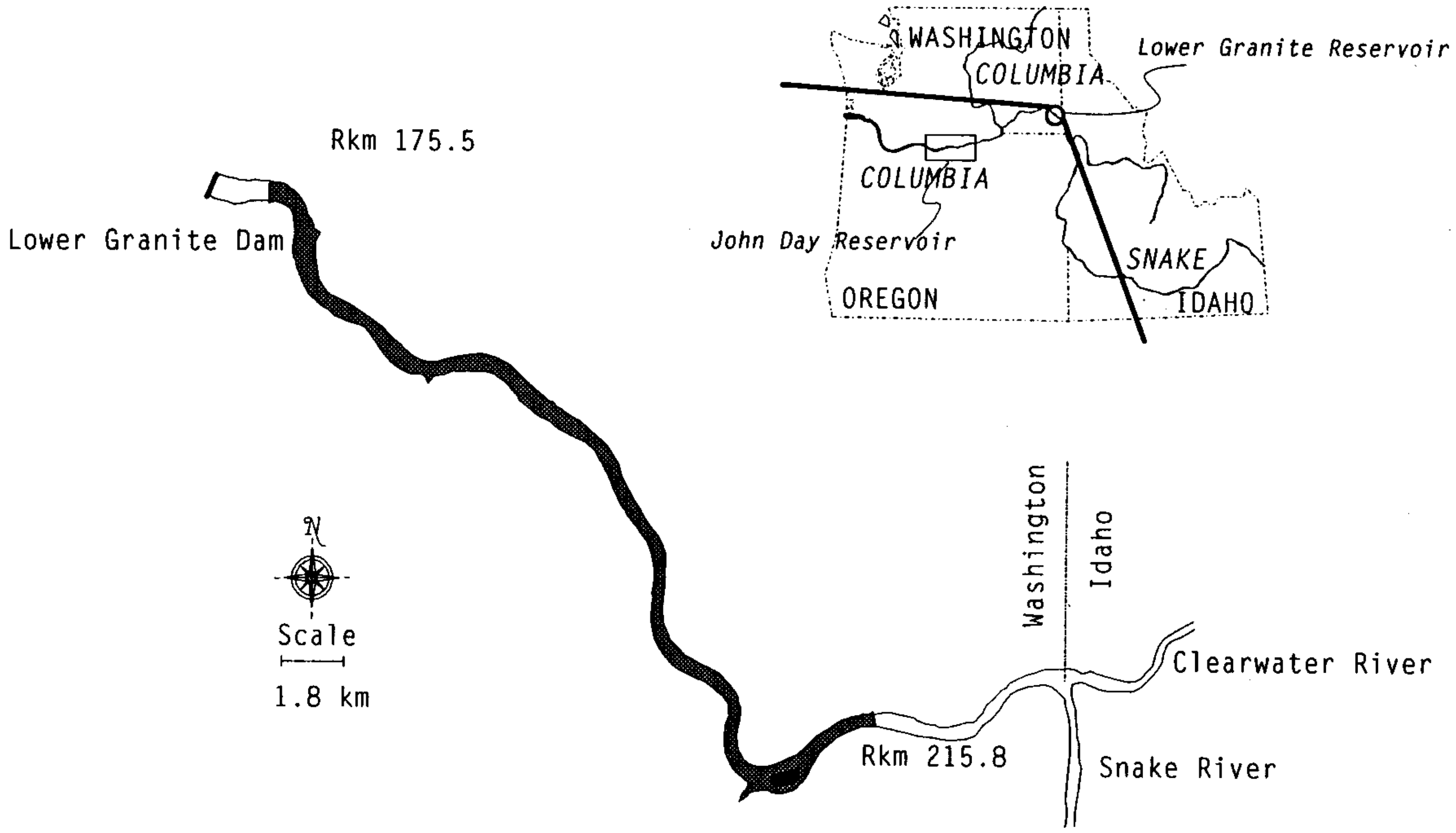

Figure 1. Map of Lower Granite Reservoir, southeastern Washington, with inset of the proximity of study area to the Columbia River basin and John Day Reservoir.

m), mid-depth (6 m - 18.3 m) and deep waters. The fish community upstream of Rkm 215.8 was sampled intensely during 1985 and 1986 (Bennett and Shrier 1986, 1987), but not for consumption estimation purposes.

Lower Granite Smolt Outmigration

The migration of juvenile salmonids in the Snake River consists primarily of yearling spring and summer chinook salmon *Oncorhynchus tshawytscha* and steelhead, and to a much lesser extent, fall (sub-yearling) chinook salmon, and sockeye salmon *O. nerka*. Hatchery releases during 1989 totaled 20,229,774 juvenile anadromous salmonids (Buettner and Nelson 1990). Based on counts at the Lower Granite Dam collection facility for the outmigration, spring and summer chinook usually begin early April and reach a maximum peak (numbers per day over Lower Granite) during the third or fourth week of April (Koski et al. 1988). Numbers of chinook steadily decline through May, whereas steelhead reach maximum peaks usually during the first two weeks in May (Figure 2). The sub-yearling chinook outmigration typically peaks in mid July (Koski et al. 1987; Figure 2).

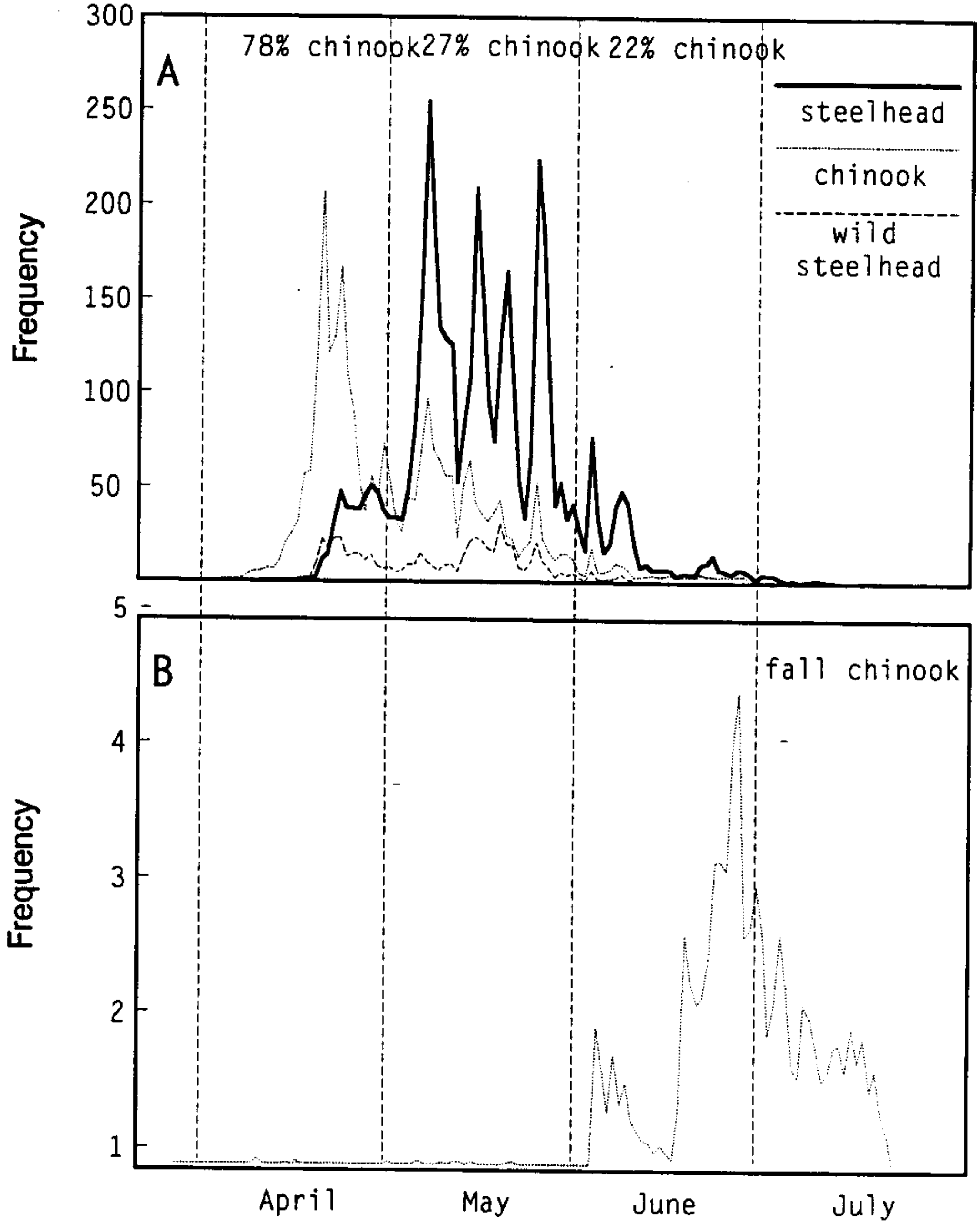

Figure 2. A) Timing and magnitude of outmigration for yearling chinook salmon and steelhead based on 1987 counts at Lower Granite Dam (Koski et al. 1988). B) Timing and magnitude of outmigration for sub-yearling chinook salmon based on 1986 counts at Lower Granite Dam (Koski et al. 1987).

Methods

Predator collections

Sampling gear used for collecting northern squawfish during this study included: horizontal bottom, mid-water, and surface gill nets (both monofilament and multifilament), vertical multifilament gill nets, shoreline boat electrofishing, beach seining, open water purse seining, bottom trawling, and surface trawling. Horizontal bottom gill nets 69 m long x 1.8 m deep, with 3.2, 4.4, and 5.1 cm bar mesh, proved to be the most effective sampling technique for predator sized northern squawfish (> 250 mm)(Arthaud 1992). Eight nets were fished during day and night hours at each station for 7 to 8 hours (1987) or nets were fished starting 3 hours before dark for 6 to 8 hours (1988-1991).

Squawfish digestive tracts were collected seasonally during 1987 (Table 1). Following 1987, only the spring season was sampled (April-June) during the major smolt outmigration.

All northern squawfish captured were measured (total length; TL) to the nearest millimeter. Weights of individual squawfish were estimated using a length-weight regression equation previously developed (Bennett et al. 1983). Digestive tracts of all squawfish > 250 mm were removed whole in the field, and preserved in a 10% formalin solution (1987) or placed on ice, and frozen from 2 to 10 hours after being removed (1988-1991).

Food items were identified to the lowest possible taxon, and enumerated. Estimated live weights and digested weights of each food item were recorded. All insects and amphipods that were visibly alike and in good condition were grouped, and an average wet weight was used

Table 1. Sampling periods for collection of northern squawfish during 1987-1991, Lower Granite Reservoir. A + symbol indicates the time period sampled.

Month	Week	Year				
		1987	1988	1989	1990	1991
April	1			+	+	+
	2			+	+	+
	3	+		+	+	+
	4	+		+	+	+
May	1	+	+	+	+	+
	2	+	+	+	+	+
	3	+	+	+	+	+
	4	+	+	+	+	+
June	1		+	+	+	+
	2		+	+	+	+
	3			+	+	+
	4			+	+	+
July	1					
	2					
	3	+				
	4	+				
August	1					
	2					
	3	+				
	4	+				
October	1	+				
	2	+				
	3	+				
	4	+				
December	1	+				
	2	+				
	3	+				
	4	+				

to estimate live weight for that group. Organisms were blotted dry for a standard 1 minute drying time.

Live weights of Cladocerans (*Leptodora kindtii*, and *Daphnia* spp.) were estimated for the first 10 individuals encountered. Live weights of decapods were estimated by rostrum length (mm) to total length (mm) and total length to weight (g) regression equations developed by Dunsmoor (1990).

Live weights for fish in the digestive tracts were estimated when possible by fork length (FL)-weight regression equations developed by Vigg et al. (1991) for species found in John Day Reservoir on the Columbia River. Standard, nape to tail, or diagnostic bone lengths were measured for fish too digested to obtain fork lengths. Fork lengths were estimated from regression equations developed by Hansel et al. (1988). In instances when no length was able to be obtained, an average weight of all fish of the same genus was assigned.

Digested weights were obtained by blotting prey items and weighing to the nearest mg. Insects and amphipods were weighed as a group. Cladocerans were weighed as a group if enough were present in the stomach, otherwise estimated live weights were used in lieu of digested weights. Individual prey fish and crayfish were weighed separately, unless they were too digested to separate individuals. In such cases, the items were weighed as a group, and weight was apportioned evenly by the number of each prey item.

General Food Habits

Northern squawfish were divided into two length groups (250-349 mm and > 349 mm) for purposes of comparing size related differences in food habits and incidence of salmonid predation. Percent incidence of predation was calculated for northern squawfish in 25 mm groupings. Yearly and seasonal relative importance of prey items in the diet was determined for northern squawfish by comparing percentages of number (N), weight (W), and frequency of occurrence (F) of each prey item, as well as an index of relative importance (IRI; Pinkas et al. 1971). The IRI, as reviewed by Hyslop (1980) combines the values of N, W and F in the formula:

$$IRI = (\%N + \%V) \times \%F$$

Groupings of prey items were determined before calculating the components of the IRI, as %F is not additive (Dunsmoor 1990). Estimated live weight was used in the analysis.

Consumption

Daily consumption and daily ration of salmonids (salmon and steelhead combined) and non-salmonids (all fish other than salmonids) were estimated for the two length groups of northern squawfish (250-349 mm and > 349 mm). Consumption estimates were made for each of the five years independently, and all five years pooled. Temporal trends in consumption were estimated by calculating consumption estimates for April, May, and June separately from pooled data.

Daily consumption rates were estimated as described by Vigg et al. (1991) who modified the original method developed by Swenson (1972) and Swenson and Smith (1973). The eight major steps involved in the calculation are outlined by Vigg et al. (1991; Figure 3). 1) Digestive tract contents of squawfish were evaluated on a diel time schedule throughout the period of juvenile salmonid migration. The diel time

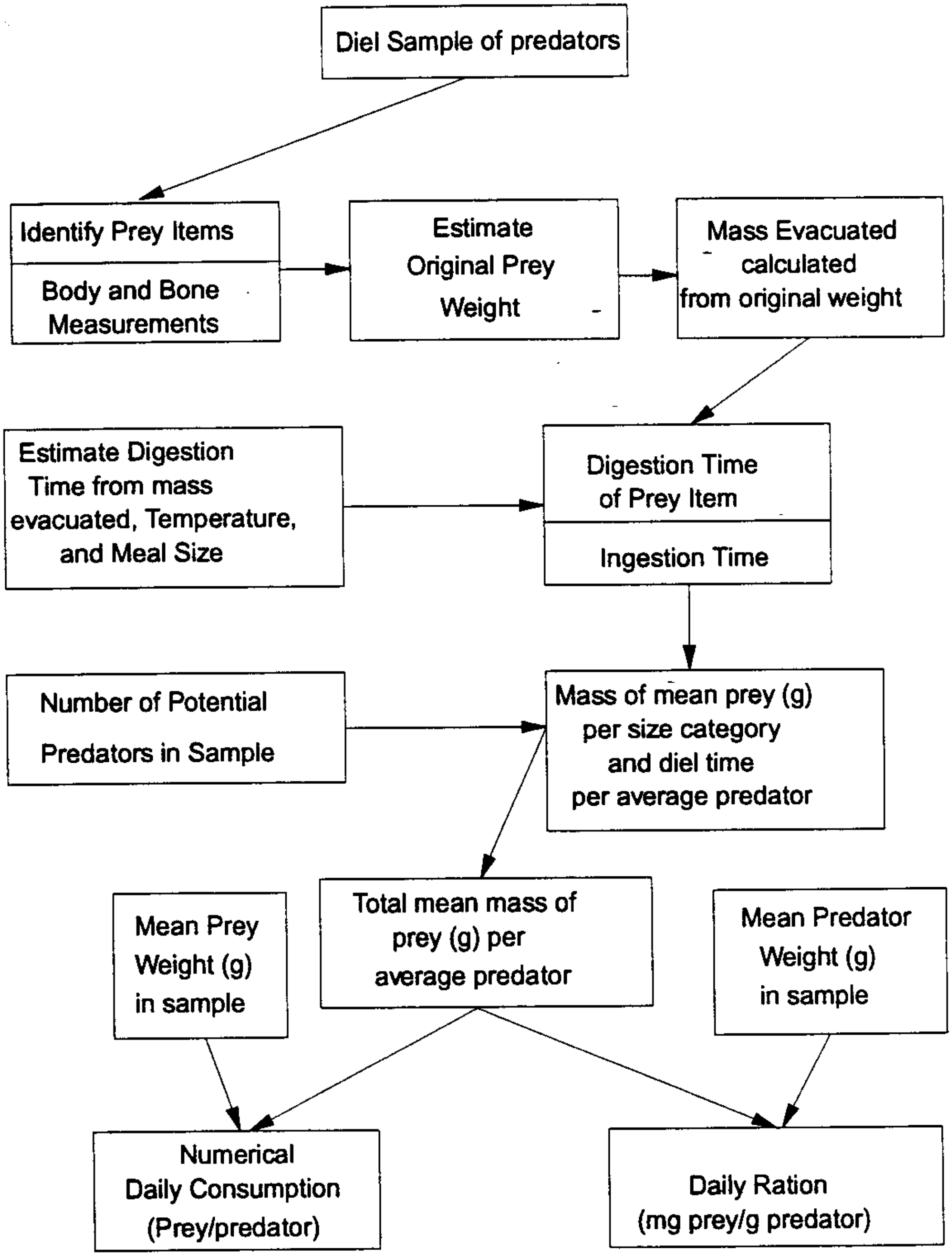

Figure 3. Flow chart of steps involved in estimating mean daily consumption of juvenile salmonids by northern squawfish (from Vigg et al. 1991).

strata used in the calculations were 6, four hour time intervals. 2) The original prey weight was back calculated from regressions of weight against body length and diagnostic bone measurements as developed by Hansel et al. (1988). 3) Percent digestion (mass evacuated) was calculated as the difference between sample (digested) weight and the estimated original prey weight. 4) Evacuation rate (digestion time in hours) as a function of water temperature (°C), squawfish weight (g), meal size (g), and mass evacuated (g) were estimated from regression equations developed from Beyer et al. (1988). Daily water temperatures were obtained for each sampling day from records at Lower Granite Dam (Corps of Engineers, unpublished data). The algorithm for estimating digestion time as presented in Vigg et al. (1991) is derived from solving for t (time) in equation 1 of Beyer et al. (1988). The equation is the following:

$$1{,}330.753E^{1.081}S^{-0.469}T^{-1.606}P^{-0.175}$$

where E is the prey mass evacuated (g), S is prey meal weight (g), T is temperature (C°), and P is predator weight (g). Meal size (g) was calculated as described by Vigg et al. (1991) using the following equation:

$$S = O_i + O_j + D_k \;;$$

where O_i is the sum of the original weight of the specified prey fish item; O_j is the original weights of any other prey fish items in the stomach that were within 10% of the original weight and 20% of the percent digestion of the specified prey item; and, D_k is the digested weight of all other food items in the stomach. 5) Time of prey ingestion (fish only) was calculated from data derived from steps 3) and

4) as: time at capture - digestion time. 6) The mass of prey consumed per diel time period per prey size category per day was calculated. 7) The data from step 6) were divided by the number of potential predators in the sample for each diel time and prey stratum to estimate average mass consumed per average predator. Consumption can be summarized by the following equation presented in Vigg et al. (1991):

$$C=\sum_{i=1}^{t}\sum_{j=1}^{s}\frac{\sum_{k=1}^{p}W_{ij}}{F_{ij}};$$

where C is the daily consumption (g) by an average predator; W_{ij} is the undigested weight of prey fish of a given size category (*j*) during a given diel time interval (*i*), and F_{ij} is the number of potential predators from the sample that could have contained prey fish of size *j* that were no more than 90% digested during time period *i* (i.e. a squawfish was considered part of the sample for all time intervals from the time of capture back to the limits of time when ingested food would have been detectable; Wahl and Nielsen 1985). Prey size categories were in 10 g increments up to 100 g, every item greater than 100 g was the last grouping. 8) Daily ration (mg prey/g predator) and numerical consumption (prey/predator) were derived from dividing C by mean predator and prey weights for the sample as follows:

Daily Ration (mg prey / g predator) = C * 1000 / Mean Predator Weight (g);
Numerical Consumption (prey/predator) = C / Mean Prey Weight (g)

Vigg et al. (1991) report that an important limitation of the method is that because the method is based on pooled stomachs rather than individual predators, variances cannot be directly calculated for the consumption estimate.

Size Selectivity

Linear regression was used to relate maximum length of ingested salmonid to length of predator (Poe et al. 1991). Length frequency distributions of juvenile salmonids ingested by northern squawfish from all years combined were compared to length frequency distributions available in the environment using a Chi-square goodness of fit (Zar 1984). Length data from all juvenile salmonids captured in Lower Granite Reservoir by all gear types during the five year study period (Bennett et al. 1988, 1990, 1991, unpublished data) were pooled and used to represent lengths of juvenile salmonids in the environment.

Population characteristics

A von Bertalanffy growth model for northern squawfish for the lower Snake reservoirs (Bennett et al. 1983) was used to describe growth in Lower Granite. Total annual mortality estimates were calculated by pooling age frequencies from 1985 through 1990 from gill net catches in Lower Granite, and constructing a single catch curve (Ricker 1975). A catch curve for each individual year was also constructed, and mortality estimates were averaged over the five years. Relative catches of the 1978 and 1979 year classes were also used to estimate total annual mortality using cohort specific catch curves (Ricker 1975).

Abundance of squawfish > 250 mm FL was estimated using the density estimate of 4.4 squawfish/ha for John Day Reservoir on the Columbia River (Beamesderfer and Rieman 1991). The density was multiplied by total surface area of Lower Granite (3602 ha). The proportion of squawfish > 349 mm in the population of squawfish > 250 mm was estimated from pooled length frequencies of squawfish from 1985-1990.

Estimated Loss of Salmonids

Estimated loss of salmonids was calculated similar to Rieman et al. (1991), and can be described by the following equation:

$$L_{hij} = PS_i C_{ij} D_j G_{hij};$$

where L_{hij} is the loss of salmonids species *h* lost to squawfish in size group *i* during month *j*, P is the population of squawfish > 250 mm, S_i is the proportion of the predator population in size group *i*, C_{ij} is consumption of predator size group *i* during month *j*, D_j is the number of days in month *j*, and G_{hij} is the proportion of salmonid species *h* in squawfish size group *i* during month *j* (Figure 4). Mean daily consumption per average predator per day estimates for each month and each predator size group from the pooled data (1987-1991) were used for C_{ij}. Because of limited sample size, relative proportions of ingested chinook and steelhead were calculated using only the identifiable chinook and steelhead from pooling both size groups of predators for each month.

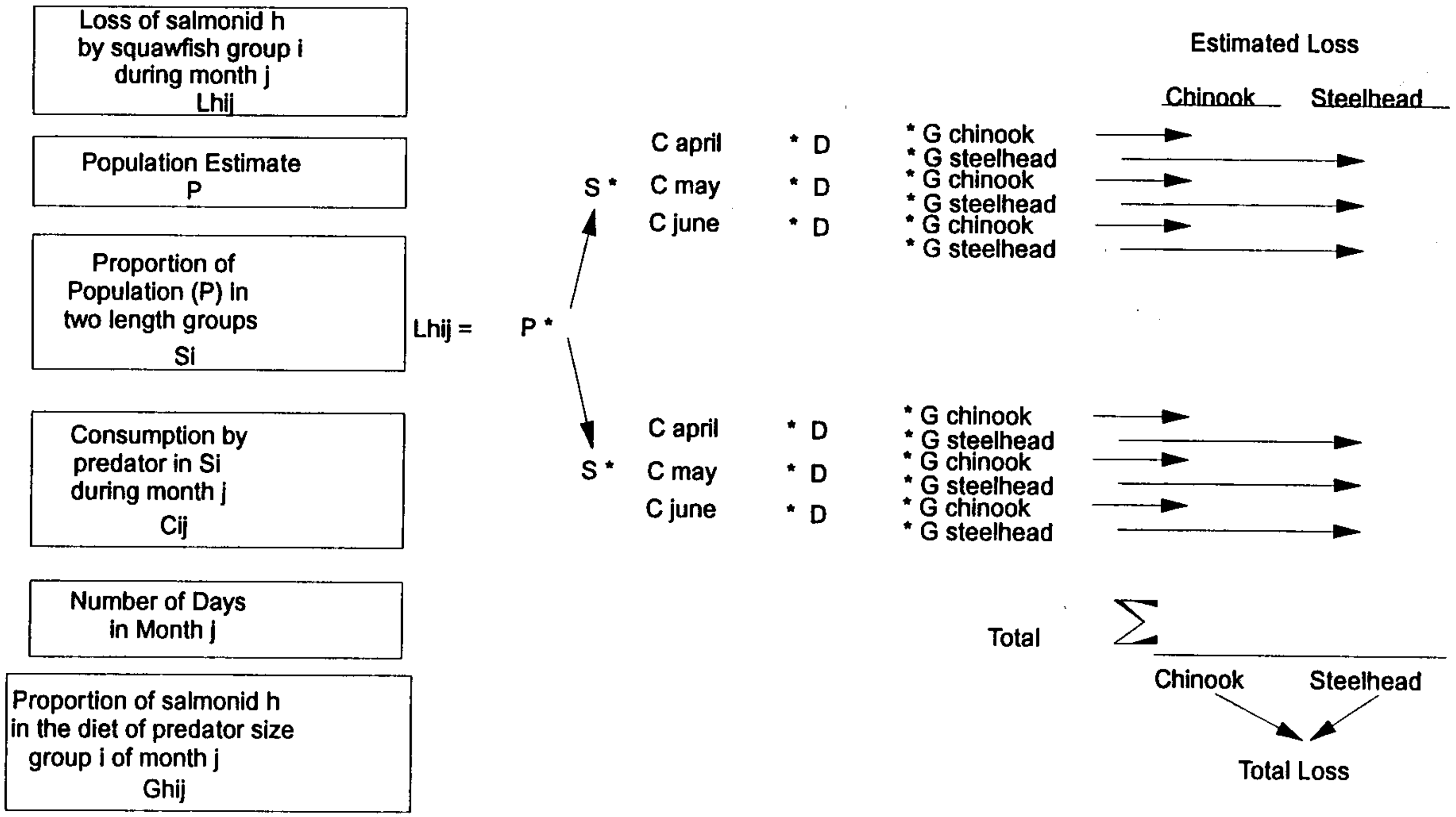

Figure 4. Flow diagram of algorithm used to calculate total loss of juvenile anadromous salmonids from northern squawfish predation in Lower Granite Reservoir, Washington, 1987-1991.

Results

Dietary Analysis

A total of 998 squawfish (> 250 mm) digestive tracts were examined during the 5 years of study, 427 (48.4%) were empty. The percentage of empty stomachs during the spring months ranged from 19% in 1987 to 51% in 1989. During the spring months, squawfish in the > 349 mm length group generally had a lower percentage of empty stomachs than the 250-349 mm length group (Table 2). Incidence of salmonid predation (%) increased linearly with squawfish length (Figure 5).

Spring. - Salmonids were generally the most important prey item by weight of squawfish in the 250-349 mm length group accounting for 50.2% of the total weight of all food items for all five years pooled (Table 3). Salmonids were totally absent from the diet during 1987 and 1988, and crayfish were the dominant prey item by weight (52.8% and 57.9%, respectively). Crayfish were second in importance by weight for the years 1989-1991 (Table 3). Non-salmonid prey fish also accounted for a large percentage of the total weight of prey items during 1987 and 1988.

Insects were important based on total number and percent frequency of occurrence throughout all years (Table 3). Insects occurred in 51% of all squawish examined in the 250-349 mm length group.

With the exception of 1991, where salmonids were the most important prey (46.0%), insects dominated the IRI scores ranging from 59.5% (1988) to 89.5% (1987). Insects were the most important prey during all five years pooled, accounting for 74.8% of the total IRI score (Figure 6).

Table 2. Sample size, incidence of salmonid predation, and percent empty stomachs for all northern squawfish length groups sampled by season during the years 1987-1991 and all years combined in Lower Granite Reservoir.

Year	Season	Size Group (mm)	Sample Size	Incidence of Predation (%)	Percent Empty
1987	Spring	250 - 349	21	0.0	19.0
		>349	37	35.1	18.9
	Summer	>250	34	0.0	26.5
	Fall	>250	68	0.0	27.9
	Winter	>250	15	0.0	66.7
1988	Spring	250 - 349	34	0.0	41.1
		>349	58	32.7	31.0
1989	Spring	250 - 349	142	9.8	64.1
		>349	172	26.7	39.5
1990	Spring	250 - 349	52	7.7	50.0
		>349	147	17.7	36.7
1991	Spring	250 - 349	58	13.8	48.3
		>349	160	19.3	49.3
All Years	Spring	250 - 349	307	8.5	53.1
		>349	574	23.5	39.3
		>250	881	18.2	44.1

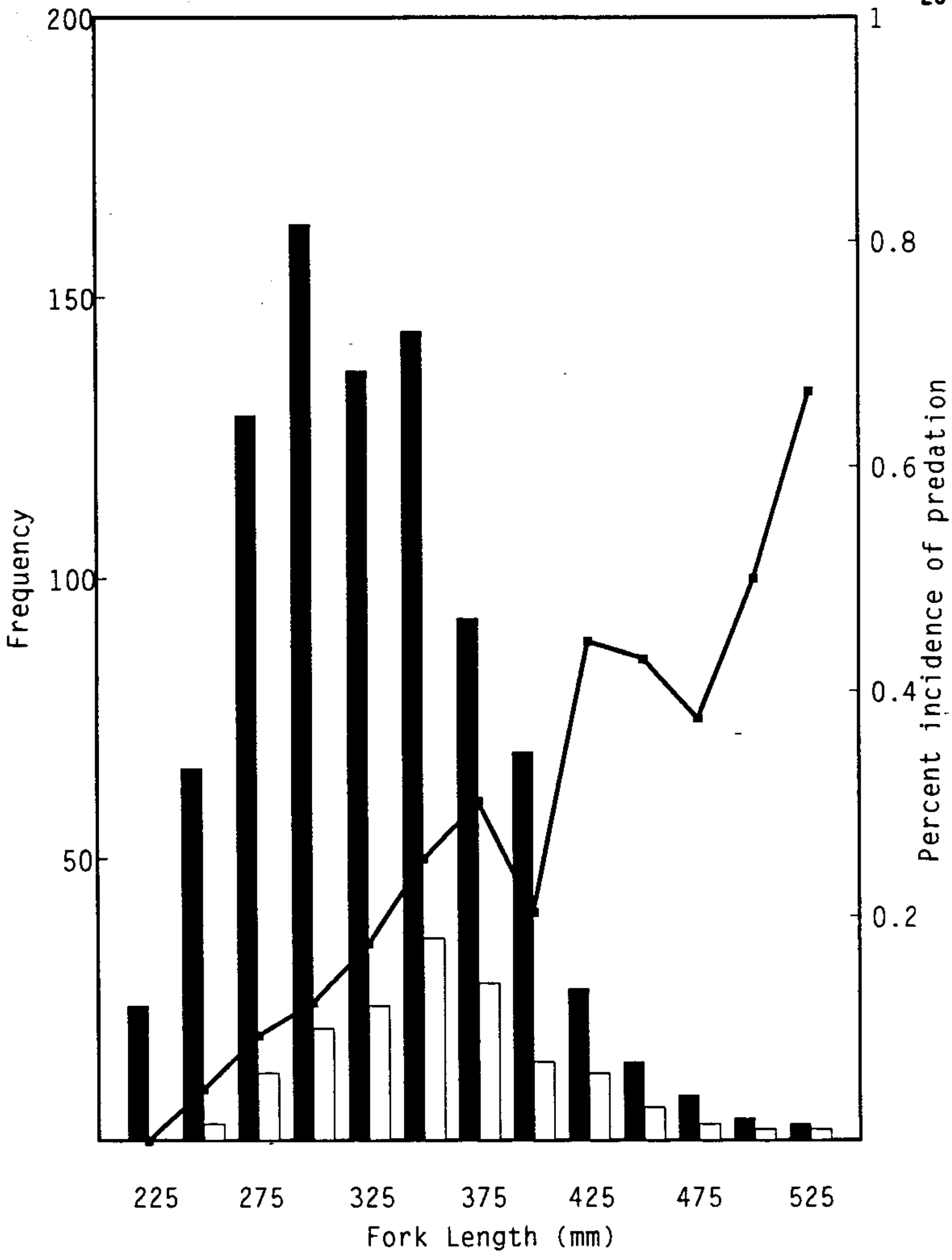

Figure 5. Length frequencies of northern squawfish sampled (solid bars) and of northern squawfish that contained salmonids (clear bars) in the digestive tract. Percent incidence of salmonid predation by 25 mm length groups (solid line) of northern squawfish.

Table 3. Relative importance of prey items of two length groups of northern squawfish based on percent number, weight, frequency of occurrence, and the IRI score collected during April, May, and June, 1987-1991 and all years combined, Lower Granite Reservoir, Washington.

Year	Predator Length Group (mm)	Stomachs with Food	Stomachs Empty	Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
1987	250 - 349	17	4	OSTEICHTHYES							
				Salmonidae	0	0.00	0	0.0	0.0	0.0	0.0
				Non-salmonidae	4	7.74	3	2.0	31.1	17.6	5.0
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	2	13.14	2	1.0	52.8	11.8	5.4
				INSECTA	190	3.99	16	95.5	16.0	94.1	89.5
				MISCELLANEOUS FOOD	3	0.01	2	1.5	0.0	11.8	0.1
	> 349	30	7	OSTEICHTHYES							
				Salmonidae	15	452.31	13	3.3	71.5	43.3	36.9
				Non-salmonidae	1	7.03	1	0.2	1.1	3.3	0.1
				Unknown Fish	2	49.60	2	0.4	7.8	6.7	0.6
				CRUSTACEA							
				Decapoda	16	115.54	11	3.5	18.3	36.7	9.1
				INSECTA	426	8.28	15	92.4	1.3	50.0	53.4
				MISCELLANEOUS FOOD	1	0.00	1	0.2	0.0	3.3	0.0
1988	250 - 349	20	14	OSTEICHTHYES							
				Salmonidae	0	0.00	0	0.0	0.0	0.0	0.0
				Non-salmonidae	9	45.90	5	2.6	37.5	25.0	10.1
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	10	70.85	10	2.9	57.9	50.0	30.5
				INSECTA	328	5.59	12	94.3	4.6	60.0	59.5
				MISCELLANEOUS FOOD	1	0.00	1	0.3	0.0	5.0	0.0

Table 3. continued.

Year	Predator Length Group (mm)	Stomachs with Food	Stomachs Empty	Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
1988	> 349	40	18	OSTEICHTHYES							
				Salmonidae	27	1185.46	19	37.0	83.2	47.5	65.7
				Non-salmonidae	2	14.62	2	2.7	1.0	5.0	0.2
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	30	222.03	18	41.1	15.6	45.0	29.4
				INSECTA	13	2.40	9	17.8	0.2	22.5	4.7
				MISCELLANEOUS FOOD	1	0.00	1	1.4	0.0	2.5	0.0
1989	250 - 349	51	91	OSTEICHTHYES							
				Salmonidae	15	307.20	14	3.9	76.2	26.9	32.4
				Non-salmonidae	2	27.61	2	0.5	6.9	3.8	0.4
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	10	47.09	10	2.6	11.7	19.2	4.1
				INSECTA	347	11.13	23	90.8	2.8	44.2	62.2
				MISCELLANEOUS FOOD	8	10.06	6	2.1	2.5	11.5	0.8
	> 349	104	67	OSTEICHTHYES							
				Salmonidae	61	1408.12	46	22.2	72.0	44.7	65.4
				Non-salmonidae	5	62.46	5	1.8	3.2	4.9	0.4
				Unknown Fish	3	74.40	3	1.1	3.8	2.9	0.2
				CRUSTACEA							
				Decapoda	58	394.62	39	21.1	20.2	37.9	24.3
				INSECTA	145	4.75	12	52.7	0.2	11.7	9.6
				MISCELLANEOUS FOOD	3	10.90	3	1.1	0.6	2.9	0.1

Table 3. continued.

Year	Predator Length Group (mm)	Stomachs with Food	Stomachs Empty	Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
1990	250 - 349	26	26	OSTEICHTHYES							
				Salmonidae	4	81.92	4	5.3	15.4	15.4	7.2
				Non-salmonidae	0	0.00	0	0.0	0.0	0.0	0.0
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	6	35.69	5	7.9	12.5	19.2	5.4
				INSECTA	65	64.30	15	85.5	22.5	57.7	85.5
				MISCELLANEOUS FOOD	1	104.00	1	1.3	36.4	3.8	1.9
	>349	93	54	OSTEICHTHYES							
				Salmonidae	29	1358.80	26	15.1	67.2	28.0	33.7
				Non-salmonidae	6	130.20	6	3.1	6.4	6.4	0.9
				Unknown Fish	0	0.00	0	0.0	0.0	0.0	0.0
				CRUSTACEA							
				Decapoda	63	503.63	55	32.8	24.9	59.1	50.0
				INSECTA	91	26.30	20	47.4	1.3	21.5	15.3
				MISCELLANEOUS FOOD	3	4.30	3	1.6	0.2	3.2	0.1
1991	250 - 349	30	28	OSTEICHTHYES							
				Salmonidae	10	194.40	8	21.3	59.8	25.8	46.0
				Non-salmonidae	2	3.50	2	4.2	1.1	6.4	0.8
				Unknown Fish	4	68.10	4	8.5	20.9	12.9	8.4
				CRUSTACEA							
				Decapoda	7	47.95	7	14.9	14.7	22.6	14.7
				INSECTA	15	0.85	9	31.9	0.3	29.0	20.6
				MISCELLANEOUS FOOD	9	10.46	6	19.1	3.2	19.4	9.5

Table 3. continued.

Year	Predator Length Group (mm)	Stomachs with Food	Stomachs Empty	Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
1991	> 349	81	79	OSTEICHTHYES							
				Salmonidae	37	1039.60	31	17.6	69.8	38.8	65.1
				Non-salmonidae	12	38.90	11	5.7	2.6	13.8	2.2
				Unknown Fish	6	150.00	6	2.8	10.1	7.5	1.9
				CRUSTACEA							
				Decapoda	30	250.85	24	14.3	16.8	30.0	18.0
				INSECTA	51	4.41	13	24.3	0.3	16.2	7.7
				MISCELLANEOUS FOOD	74	6.28	6	35.2	0.4	7.5	5.1
All Years	250 - 349	144	163	OSTEICHTHYES							
				Salmonidae	29	583.52	26	2.8	50.2	17.9	14.1
				Non-salmonidae	17	84.75	12	1.6	7.3	8.3	1.1
				Unknown Fish	4	68.10	4	0.4	5.9	2.8	0.2
				CRUSTACEA							
				Decapoda	35	214.72	34	3.3	18.5	23.4	7.6
				INSECTA	945	85.86	75	89.8	7.4	51.7	74.8
				MISCELLANEOUS FOOD	22	124.53	16	2.1	10.7	11.0	2.1
	> 349	348	226	OSTEICHTHYES							
				Salmonidae	169	5444.29	135	14.0	72.3	38.9	54.4
				Non-salmonidae	26	253.21	25	2.1	3.4	7.2	0.6
				Unknown Fish	11	274.00	11	0.9	3.6	3.2	0.2
				CRUSTACEA							
				Decapoda	197	1486.67	147	16.3	19.7	42.4	24.7
				INSECTA	726	46.14	69	60.0	0.6	19.9	19.5
				MISCELLANEOUS FOOD	82	21.49	14	6.8	0.3	4.0	0.5

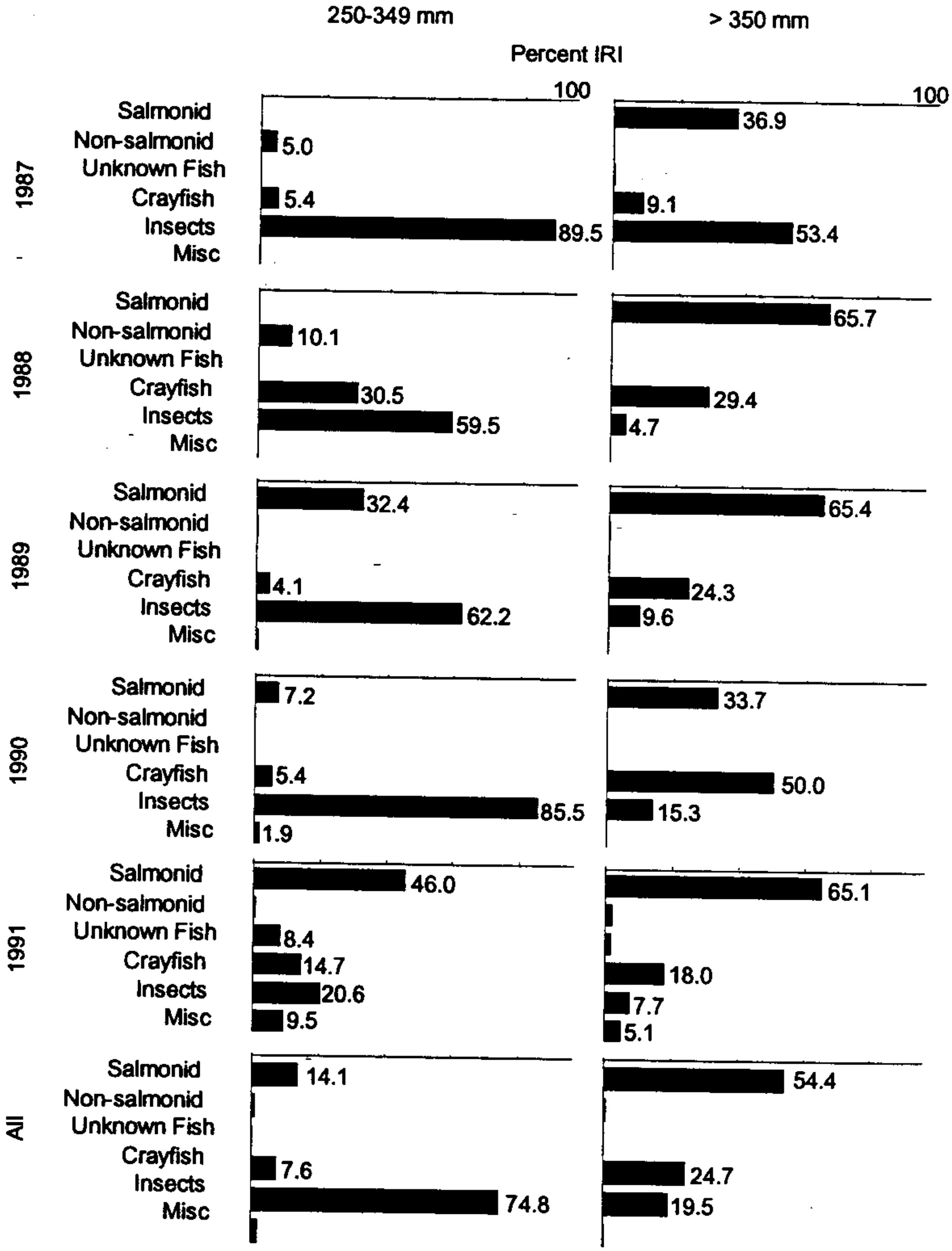

Figure 6. Importance of prey items (based on the Index of Relative Importance) ingested by two length groups of northern squawfish (250-349 mm and >349 mm) during the spring months of 1987-1991, Lower Granite Reservoir.

Salmonids were the most important prey item by weight for the >349 mm length group of squawfish, accounting for 67.1% (1990) to 83.2% (1988) of the total weight of all food items (Table 3). Crayfish were of secondary importance during all five years ranging from 15.6% to 24.8% of the total weight of prey items.

Salmonids were the most important prey item for all 5 years pooled, accounting for 54.4% of the total IRI score. Salmonids were second in importance during the years 1987 and 1990 when insects and crayfish had the highest ranking. Insects and crayfish were similar in importance for all 5 years pooled, accounting for 24.7% and 19.5% of the IRI (Figure 6).

Summer. - Diets of northern squawfish changed seasonally. Of the 25 tracts that contained food, no salmonids were observed. Fish remained an important component in the diet, accounting for 30.2% of the weight of prey items. However, catostomids dominated the fish component. Crayfish were the dominant prey item by weight (45.7%). Cladocerans (primarily *Leptodora kindtii*) were the most important prey item in the IRI, accounting for 73.5% of the total IRI. Cladocerans were the most important prey item based on percent number, frequency of occurrence, and the IRI (Table 4).

Fall. - Diets of northern squawfish during the fall months were similar to those of the summer (Table 5). Fish were the most important component of the diet (49.6% by weight), dominated by catostomids. No salmonids were observed in the digestive tracts of northern squawfish. Crayfish continued to be an important food item by weight (34.7%). However, cladocerans were replaced in importance by insects, primarily

Table 4. Relative importance of prey items of northern squawfish pooled (n=25, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the summer of 1987, Lower Granite Reservoir, Washington.

Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
OSTEICHTHYES							
Catostomidae	11	10.82	2	0.19	12.44	8.00	2.1
Centrarchidae	1	10.00	1	0.02	11.50	4.00	0.9
Unknown Fish	5	5.41	3	0.09	6.22	12.00	1.6
CRUSTACEA							
Decapoda	5	39.69	4	0.09	45.65	16.00	15.1
Amphipoda	236	2.48	2	4.18	2.85	8.00	1.2
Cladocera	5248	16.20	8	92.85	18.63	32.00	73.5
INSECTA	146	2.35	13	2.58	2.70	52.00	5.7

Table 5. Relative importance of prey items of northern squawfish pooled (n=49, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the fall of 1987, Lower Granite Reservoir, Washington.

Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
OSTEICHTHYES							
Catostomidae	9	86.01	8	0.11	39.16	16.33	16.2
Centrarchidae	14	10.32	2	0.18	4.70	4.08	0.5
Unknown Fish	3	12.54	1	0.04	5.71	2.04	0.3
CRUSTACEA							
Decapoda	14	76.11	10	0.18	34.65	20.41	18.0
Amphipoda	68	0.25	6	0.86	0.11	12.24	0.3
Cladocera	4584	9.73	2	58.06	4.43	4.08	6.5
INSECTA							
Unknown Insect	35	0.25	8	0.44	0.11	16.33	0.2
Coleoptera	71	0.39	11	0.90	0.18	22.45	0.6
Diptera	1206	19.95	31	15.28	9.08	63.27	39.0
Hemiptera	67	0.09	11	0.85	0.04	22.45	0.5
Homoptera	1618	2.12	15	20.49	0.97	30.61	16.6
Hymenoptera	172	0.22	8	2.18	0.10	16.33	0.9
MISCELLANEOUS	34	1.67	4	0.43	0.76	8.16	0.2

dipterans. Dipterans were the most important component, accounting for 39% of the total IRI.

Winter. - Fish were the most important component by weight and the IRI in the winter (n=15). Centrarchids and catostomids comprised the fish in the diet (Table 6).

Consumption

Numerical consumption (prey/predator/day) of salmonids by northern squawfish > 250 mm ranged from 0.09 (1990) to 0.18 salmonids/predator/day (1987; Table 7). Numerical consumption differed notably between the two length groups of northern squawfish. Squawfish in the 250-349 mm length group had relatively low consumption of salmonids with an overall estimate of 0.06 salmonids/predator/day (Table 7). Salmonid consumption ranged from 0.11 (1990; Table 7) to 0.28 salmonids/predator/day (1987; Table 7) for squawfish in the larger length group, with an overall estimate of 0.17 salmonids/predator/day (Table 7).

The non-salmonid component of daily consumption was several times higher during 1987 (0.43 non-salmonids/predator/day) and 1988 (0.33 nonsalmonid/predator/day) than during 1989-1991 for all predators (> 250 mm) pooled together. The majority of the non-salmonid consumption was in the smaller length group (250-349 mm; Table 7). Consumption of nonsalmonids over all 5 years pooled for the smaller length group was 0.08 nonsalmonids/squawfish compared to 0.02 nonsalmonids/squawfish for the larger length group (Table 7).

Pooled data showed temporal trends in numerical consumption from month to month in both length groups and all length groups pooled (Table

Table 6. Relative importance of prey items of northern squawfish (n=5, digestive tracts containing food items) based on percent number, weight, frequency of occurrence, and the IRI score collected during the winter of 1987, Lower Granite Reservoir, Washington.

Prey Items	Number of Prey	Weight of Prey (g)	Frequency of Prey	Percent Number	Percent Weight	Percent Frequency	Percent IRI
OSTEICHTHYES							
Catostomidae	2	5.89	2	16.67	13.48	40.00	16.1
Centrarchidae	3	17.89	2	25.00	40.95	40.00	35.2
Unknown Fish	2	11.89	2	16.67	27.21	40.00	23.4
CRUSTACEA							
Decapoda	2	7.97	2	16.67	18.24	40.00	18.6
INSECTA	3	0.05	1	25.00	0.11	20.00	6.7

Table 7. Consumption (prey/predator) of salmonids and non-salmonids for northern squawfish for the months of April, May and June and all months combined Lower Grantite Reservoir, Washington. Consumption statistics are: sample size (N), mean predator weight (W), mean consumption (prey/predator:n), and mean prey weight (w).

Year	Predator Size Group	Prey Group	Consumption Statistic	Months			Total
				April	May	June	
1987	> 250 mm		N	-	46	-	58
			W	-	526	-	508
		Salmonid	n	-	0.164	-	0.178
			w	-	34.9	-	30.5
		Non-salmo	n	-	0.507	-	0.4311
			w	-	1.911	-	1.94
	250 - 349 mm		N	-	-	-	21
			W	-	-	-	269
		Salmonid	n	-	-	-	0
			w	-	-	-	0
		Non-salmo	n	-	-	-	1.34
			w	-	-	-	1.9
	>349 mm		N	8	29	-	37
			W	522	678	-	644
		Salmonid	n	0.69	0.2614	-	0.282
			w	15.7	34.9	-	30.5
		Non-salmo	n	0	0	-	0
			w	0	0	-	0
1988	> 250 mm		N	-	37	55	92
			W	-	619	508	554
		Salmonid	n	-	0.245	0.116	0.168
			w	-	44.7	49.6	46.8
		Non-salmo	n	-	0.358	0.336	0.332
			w	-	5.7	5.3	5.5
	250 - 349 mm		N	-	11	23	34
			W	-	253	285	275
		Salmonid	n	-	0	0	0
			w	-	0	0	0
		Non-salmo	n	-	0.548	0.471	0.504
			w	-	4.8	5.3	5.1
	> 349 mm		N	-	26	32	58
			W	-	774	669	716
		Salmonid	n	-	0.35	0.202	0.269
			w	-	44.8	49.6	46.8
		Non-salmo	n	-	0.182	0	0.1161
			w	-	7.3	0	7.3

Table 7. continued.

Year	Predator Size Group	Prey Group	Consumption Statistic	Months			Total
				April	May	June	
1989	> 250 mm		N	149	135	30	314
			W	423	498	451	458
		Salmonid	n	0.186	0.06	0.018	0.12
			w	18.2	35.1	90.2	22.3
		Non-salmo	n	0.008	0.023	0	0.011
			w	2.11	14.1	0	11.1
	250 - 349 mm		N	80	50	12	142
			W	278	277	275	277
		Salmonid	n	0.065	0.031	0	0.051
			w	11.6	10.7	0	11.4
		Non-salmo	n	0	0.044	0	0.011
			w	0	2.6	0	2.6
	> 349 mm		N	69	85	18	172
			W	592	627	569	607
		Salmonid	n	0.332	0.085	0.03	0.186
			w	19.6	39.5	90.2	24.6
		Non-salmo	n	0.02	0.024	0	0.0156
			w	2.1	19.8	0	13.9
1990	> 250 mm		N	48	56	90	199
			W	450	502	598	538
		Salmonid	n	0.168	0.11	0.027	0.09
			w	26.3	50.8	45.3	38.7
		Non-salmo	n	0	0	0.28	0.031
			w	0	0	24.2	24.2
	250 - 349 mm		N	22	14	16	52
			W	271	276	325	290
		Salmonid	n	0.071	0.048	0	0.046
			w	15.8	12.2	0	14.6
		Non-salmo	n	0	0	0	0
			w	0	0	0	0
	> 349 mm		N	26	42	79	147
			W	601	578	654	625
		Salmonid	n	0.345	0.134	0.03	0.112
			w	28.2	54.7	45.3	41.5
		Non-salmo	n	0	0	0.69	0.0652
			w	0	0	24.2	24.2

Table 7. continued.

Year	Predator Size Group	Prey Group	Consumption Statistic	April	May	June	Total
1991	> 250 mm		N	145	50	23	218
			W	500	562	730	539
		Salmonid	n	0.169	0.11	0.021	0.14
			w	16.3	37.7	61.9	21.7
		Non-salmo	n	0.012	0.024	0.12	0.013
			w	62.1	2.11	11.1	46.2
	250 - 349 mm		N	46	8	4	58
			W	273	254	305	272
		Salmonid	n	0.159	0	0	0.124
			w	13.6	0	0	13.6
		Non-salmo	n	0.03	0.125	0	0.04
			w	1.3	2.1	0	1.7
	> 349 mm		N	99	42	19	160
			W	606	621	820	635
		Salmonid	n	0.156	0.137	0.03	0.142
			w	17.2	37.7	61.9	23.7
		Non-salmo	n	0.017	0	0.17	0.015
			w	77.3	0	11.1	64.1
1987-1991	> 250 mm		N	353	324	199	881
			W	450	526	565	509
		Salmonid	n	0.173	0.11	0.056	0.127
			w	18.5	41.0	51.7	28.8
		Non-salmo	n	0.005	0.06	0.193	0.024
			w	52.1	6.1	14.4	17.9
	250 - 349 mm		N	151	100	56	307
			W	276	271	294	278
		Salmonid	n	0.09	0.023	0	0.057
			w	12.8	11.2	0	12.6
		Non-salmo	n	0.007	0.15	0.289	0.076
			w	1.4	3.2	5.3	3.7
	> 349 mm		N	202	224	148	574
			W	597	641	668	633
		Salmonid	n	0.24	0.152	0.073	0.172
			w	19.9	42.7	52	31.4
		Non-salmo	n	0.008	0.02	0.634	0.016
			w	62.3	13.6	22.0	33.2

7). Both length groups showed a decrease in consumption of salmonids from April to June. No salmonids were consumed during themonth of June by squawfish in the smaller length group. Numerical consumption of salmonids was 3.2 times greater during April than during June for squawfish > 349 mm (Table 7).

Mean weight of ingested salmonids was similar during April and May for squawfish 250-349 mm (12.8 g and 11.2 g, respectively). However, mean weight of ingested salmonids for squawfish > 349 mm more than doubled from April to May and stayed high through June (Table 7).

Nonsalmonid consumption increased sharply from May to June for both length groups of squawfish (Table 7). Mean weight of ingested nonsalmonids was relatively high in April, then decreased nearly three fold during May and June for squawfish > 349 mm. Mean prey weight of nonsalmonids gradually increased from May to June for the smaller length group of squawfish.

Daily Ration

Total daily ration (mg prey/g predator/day) of fish in the diet of squawfish in the 250-349 mm length group (pooled data) was relatively constant (Figure 7). Total daily ration of fish during April was exclusively attributed to salmonids in the diet. However, the salmonid component in the daily ration of fish showed a steady decline from April (4.2 mg of salmonid/g of squawfish/day) to May (0.9 mg of salmonid/g of predator/day). Daily ration of fish in the diet during May was mixed with salmonids and non-salmonids. Daily ration increased slightly during June; non-salmonids entirely composed the diet (Figure 7). Total daily ration of fish in the diet declined from April to May in the years

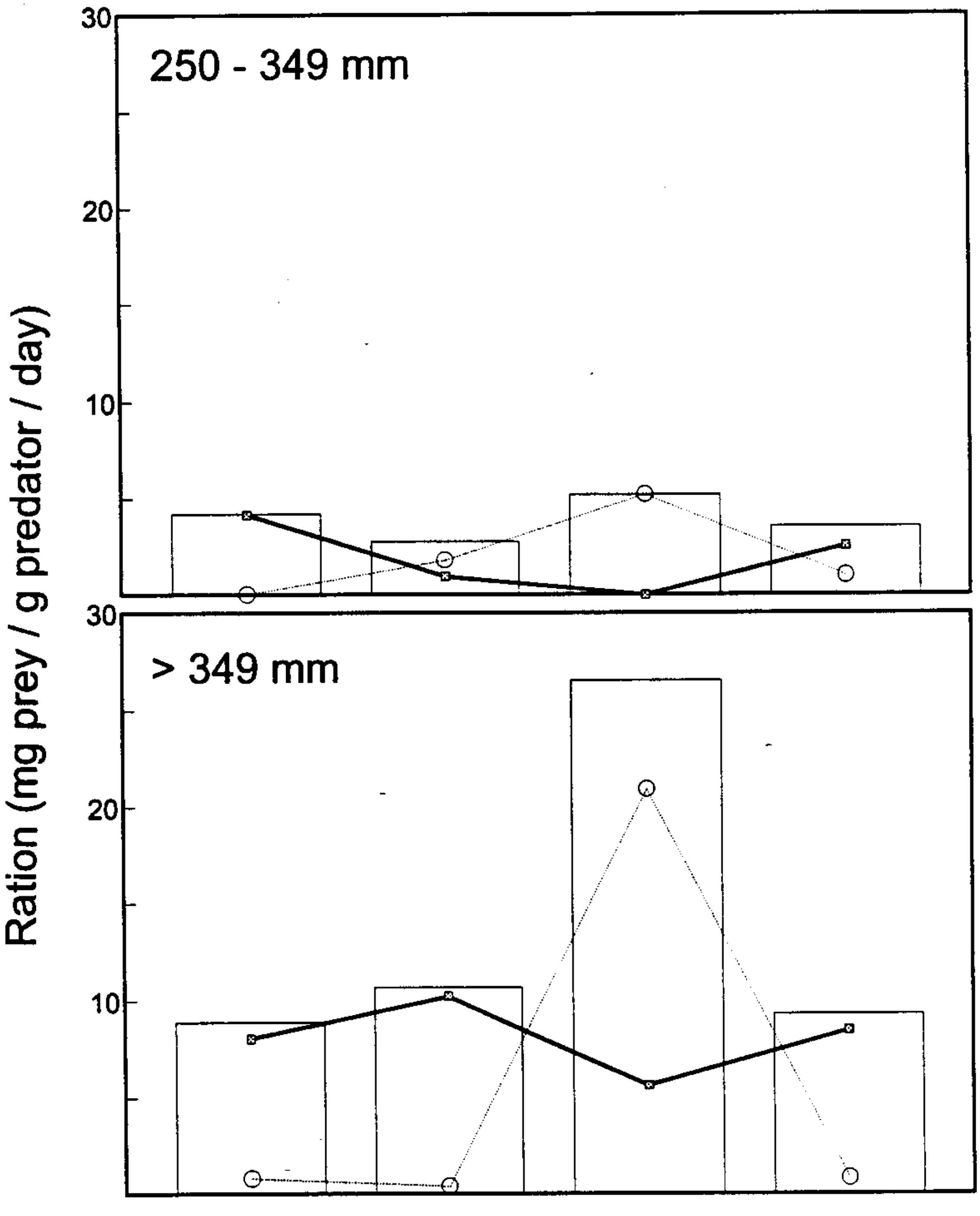

Figure 7. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) from pooled data during April, May, and June, and all three months combined from 1987-1991, Lower Granite Reservoir.

1988-1991, individually (Figures 8-12).

Total daily ration of fish in the diet of squawfish > 349 mm differed quite notably from the smaller length group (Figure 7). Daily ration of fish increased sharply throughout the 3 month time period, reaching a high in June of 26.6 mg of fish/g squawfish/day. Total daily ration was almost exclusively made up of salmonids during April and May. Non-salmonids were the main contributor to total daily ration during June. Data from 1990 heavily influences this pattern (Figure 9). The total daily ration of fish declined notably during June of 1988, 1989 and 1991 (Figures 8, 10, and 11). No stomachs were collected during June 1987 (Figure 12).

Diel Consumption

The pattern of diel consumption of prey fish (g prey/predator/4 hr) generally was consistent over the 5 years sampled separately and pooled (Figures 13-18). Diel feeding patterns of large squawfish (> 349 mm) generally showed late morning and evening peaks in consumption, with the exception of 1989 which showed peaks at the 0200 and 2200 hour intervals (Figure 15). Consumption was generally at the lowest point during the 1400 hour interval all 5 years. Peak consumption of non-salmonids generally occurred during the morning hours by squawfish > 349 mm (Figures 13-18).

Diel feeding patterns of prey fish by smaller squawfish (250 -349 mm) were at low levels throughout the day. A stronger peak consistently occurred either in the 1800 or 2200 hour intervals on both salmonid and non-salmonid prey fishes during all 5 years sampled (Figures 12-17).

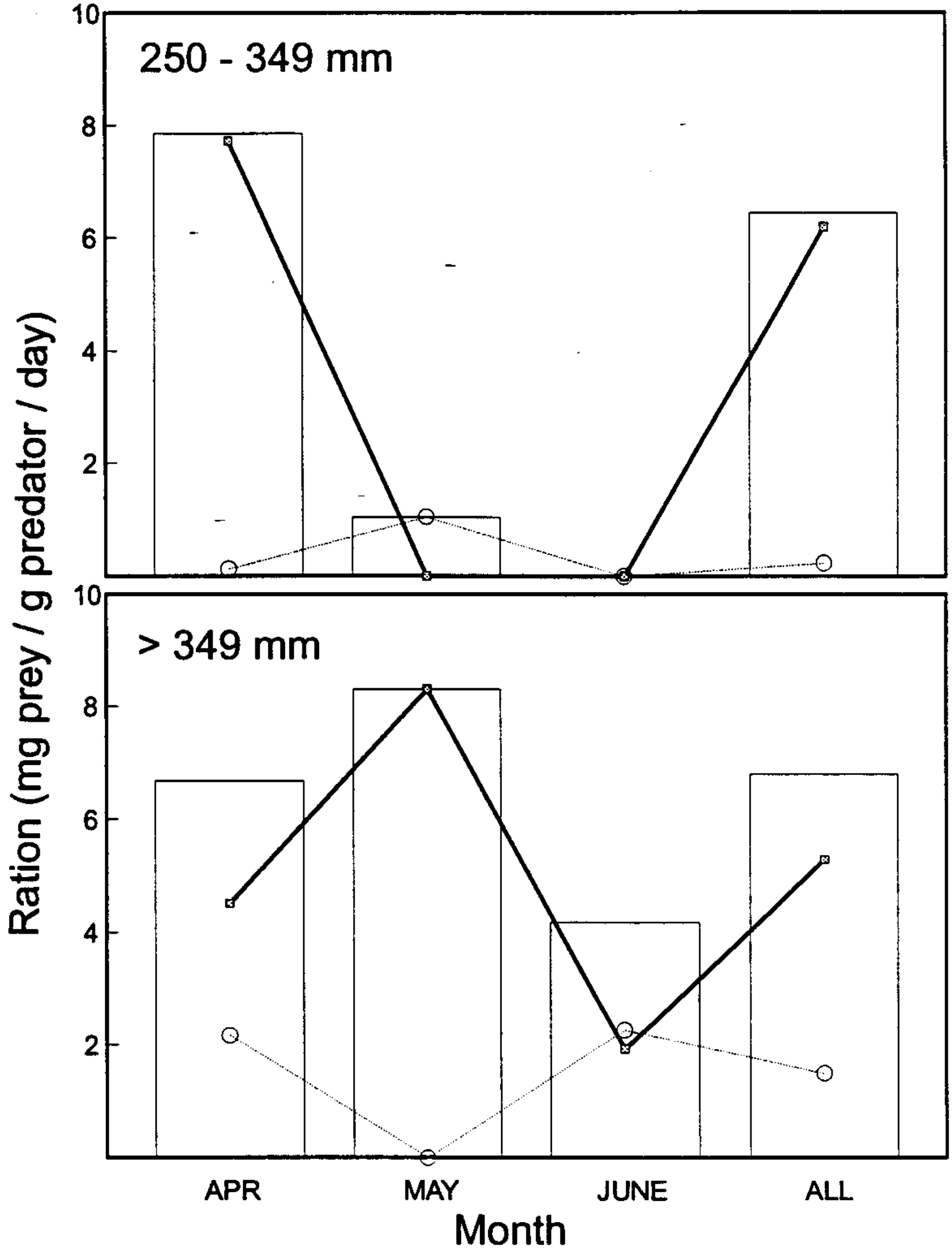

Figure 8. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1991, Lower Granite Reservoir.

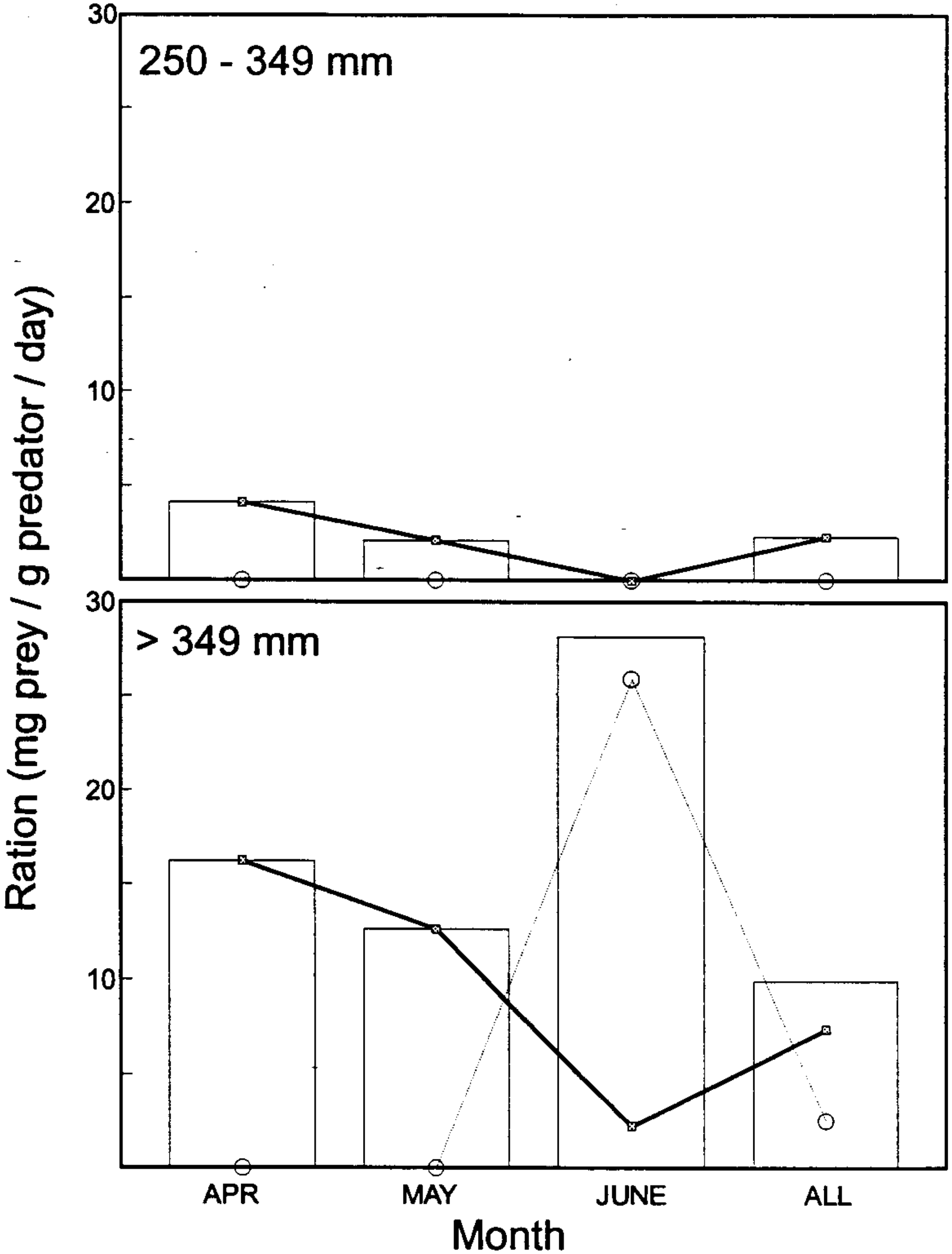

Figure 9. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1990, Lower Granite Reservoir.

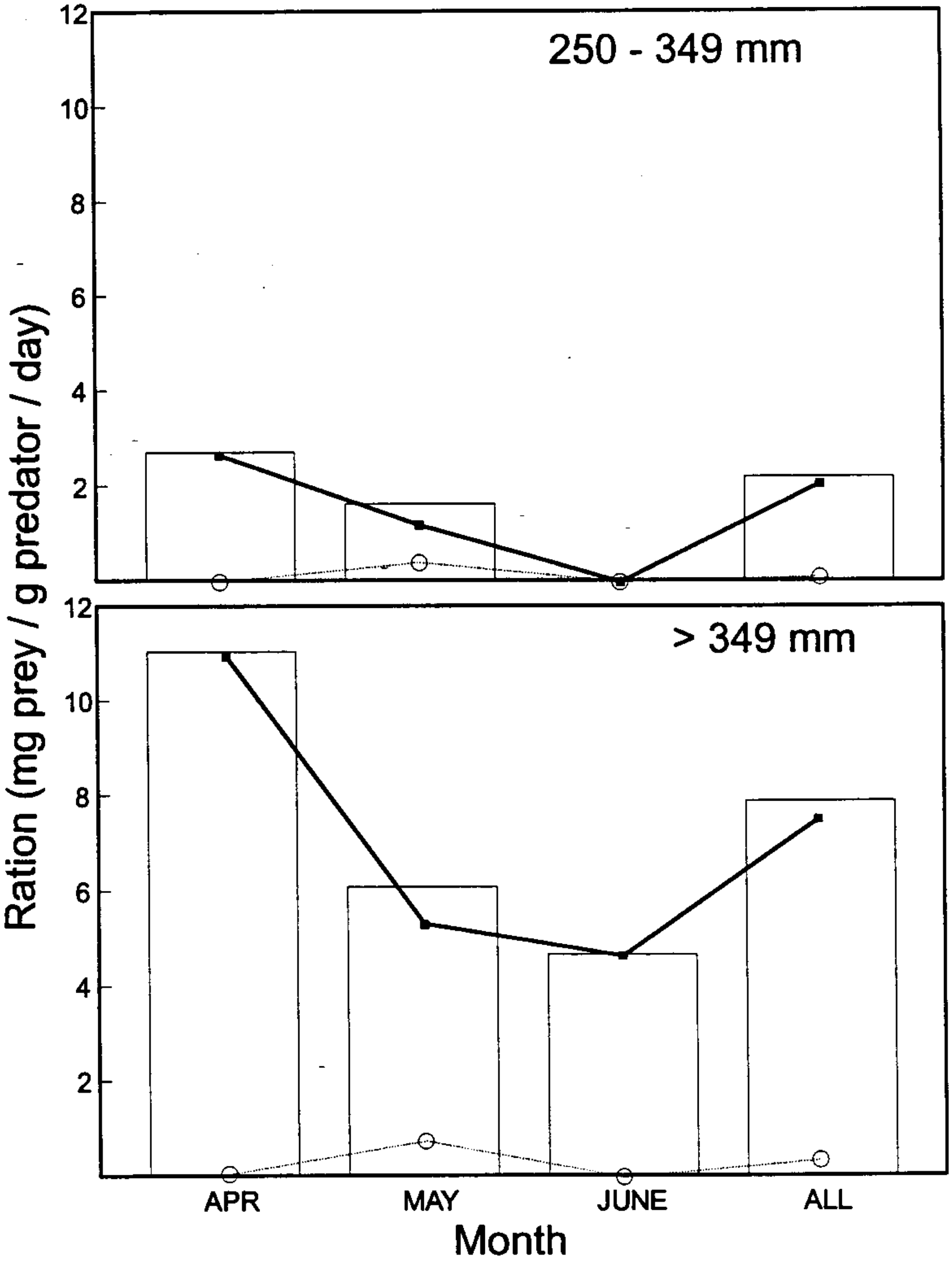

Figure 10. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1989, Lower Granite Reservoir.

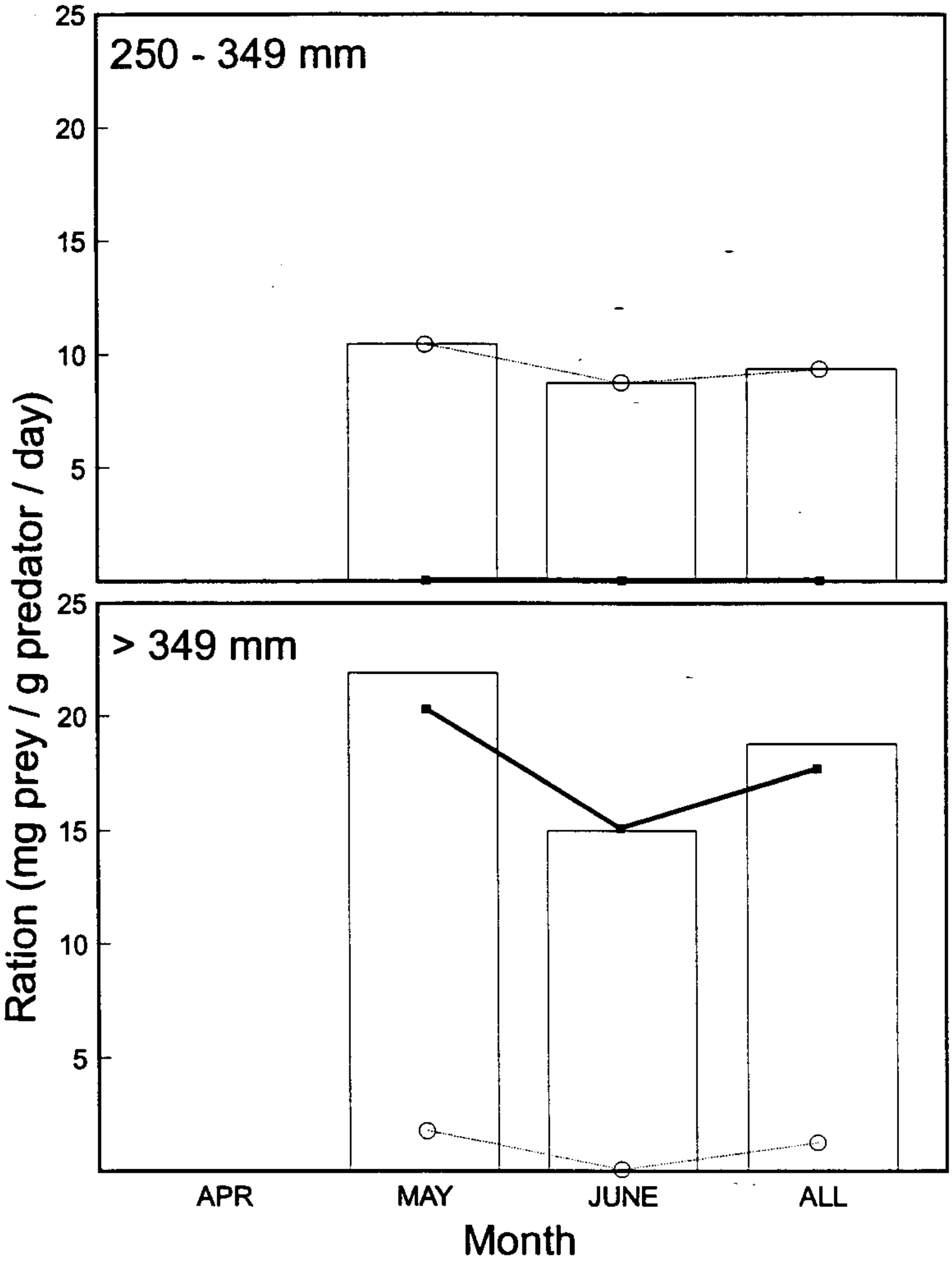

Figure 11. Mean daily ration (mg prey/g predator/day) of all fish prey (bars), salmonid prey (solid line), and non-salmonid fish prey (broken line) for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined during 1988, Lower Granite Reservoir.

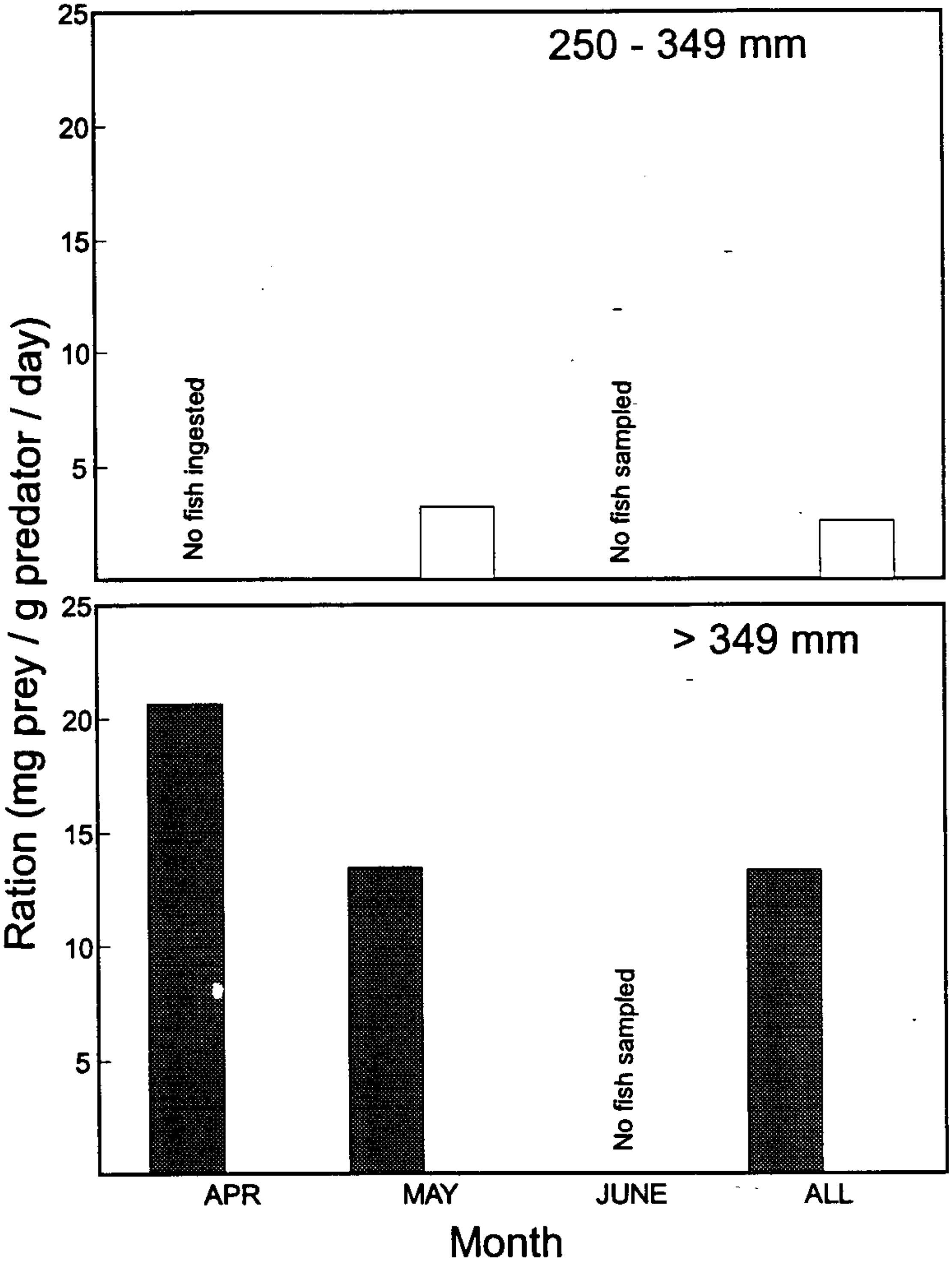

Figure 12. Mean daily ration (mg prey/g predator/day) of salmonid (shaded bars) and non-salmonid (open bars) fish prey, for two length groups of northern squawfish (250-349 mm and > 349 mm) during April, May, and June, and all three months combined from 1987, Lower Granite Reservoir.

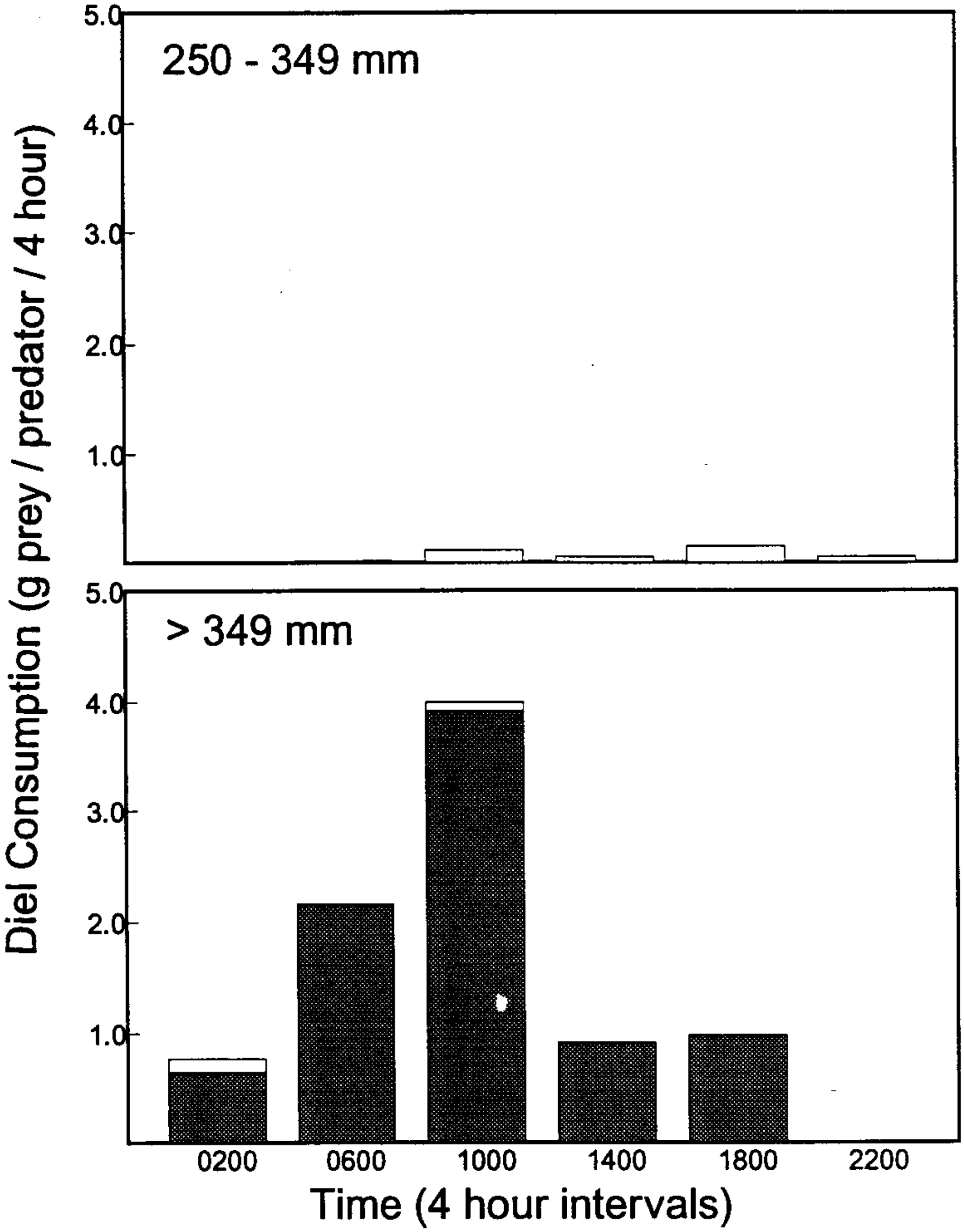

Figure 13. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1987, Lower Granite Reservoir.

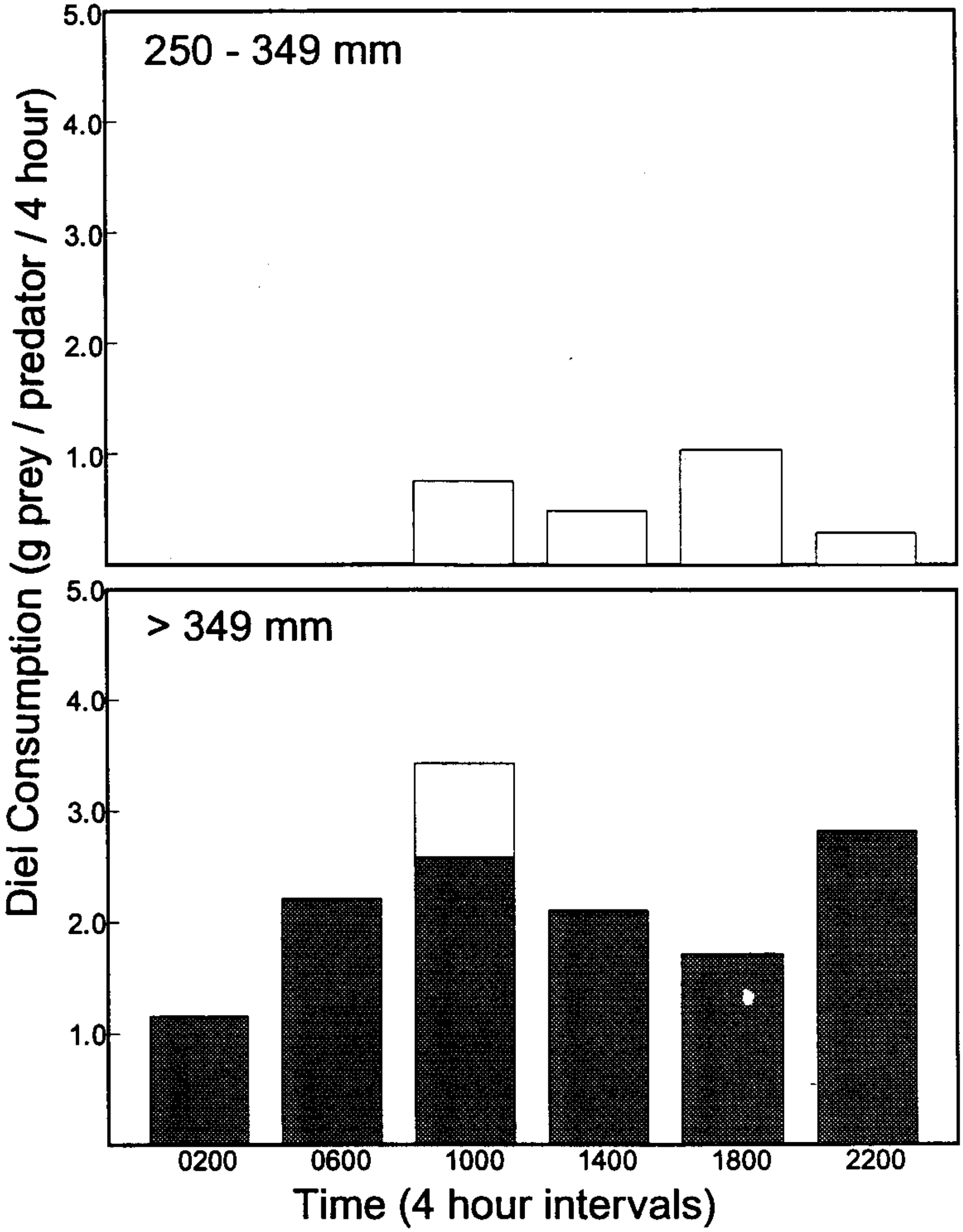

Figure 14. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1988, Lower Granite Reservoir.

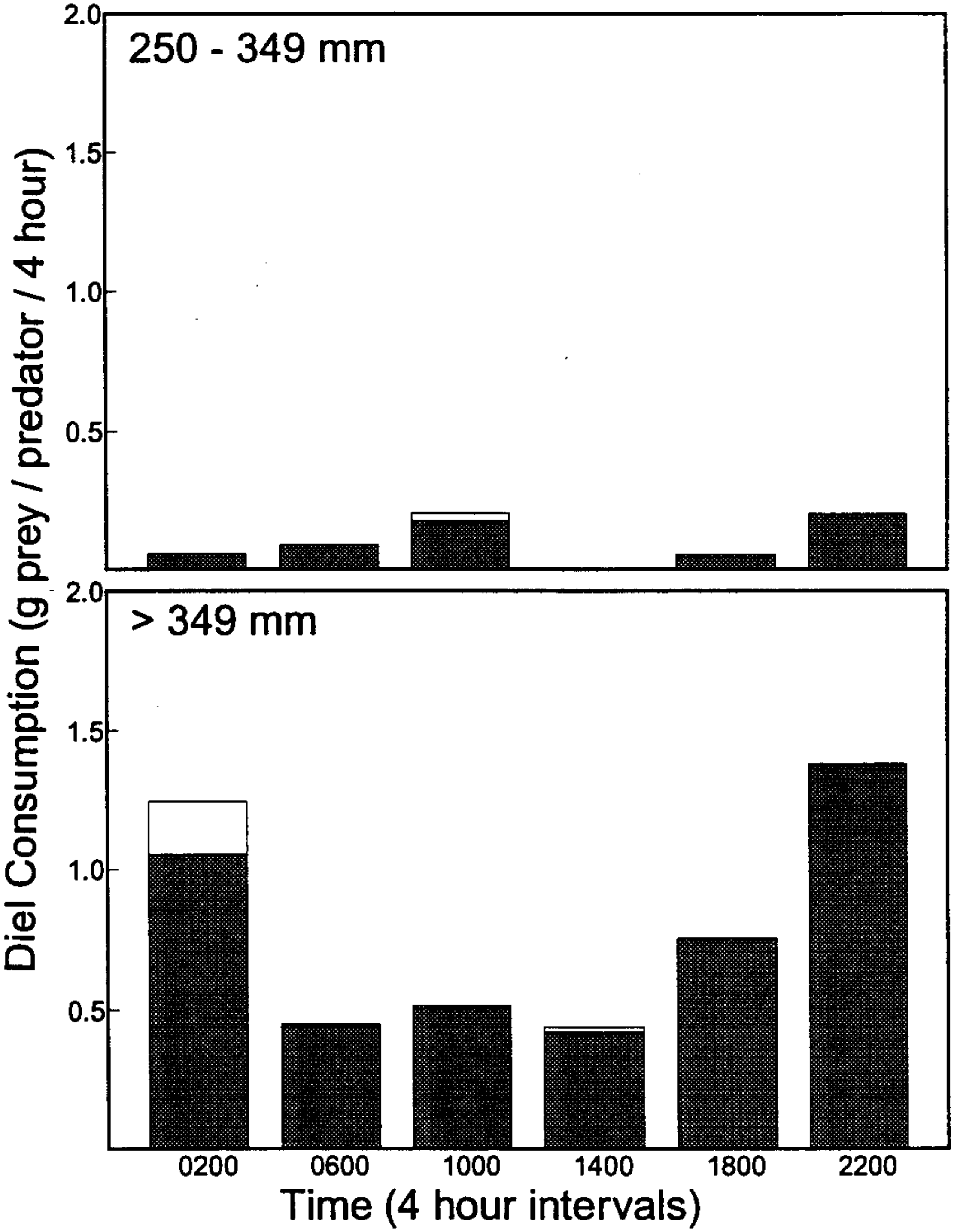

Figure 15. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1989, Lower Granite Reservoir.

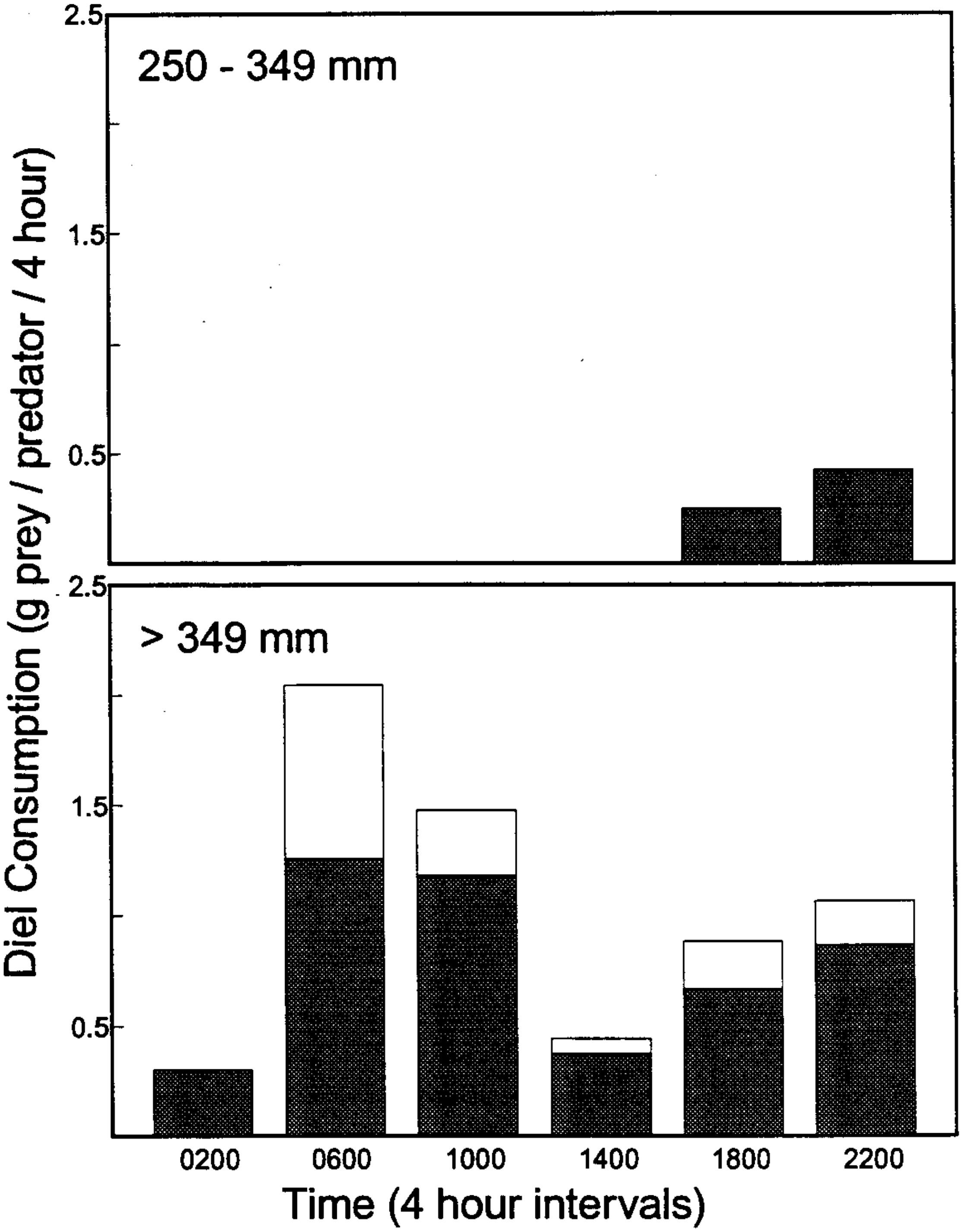

Figure 16. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1990, Lower Granite Reservoir.

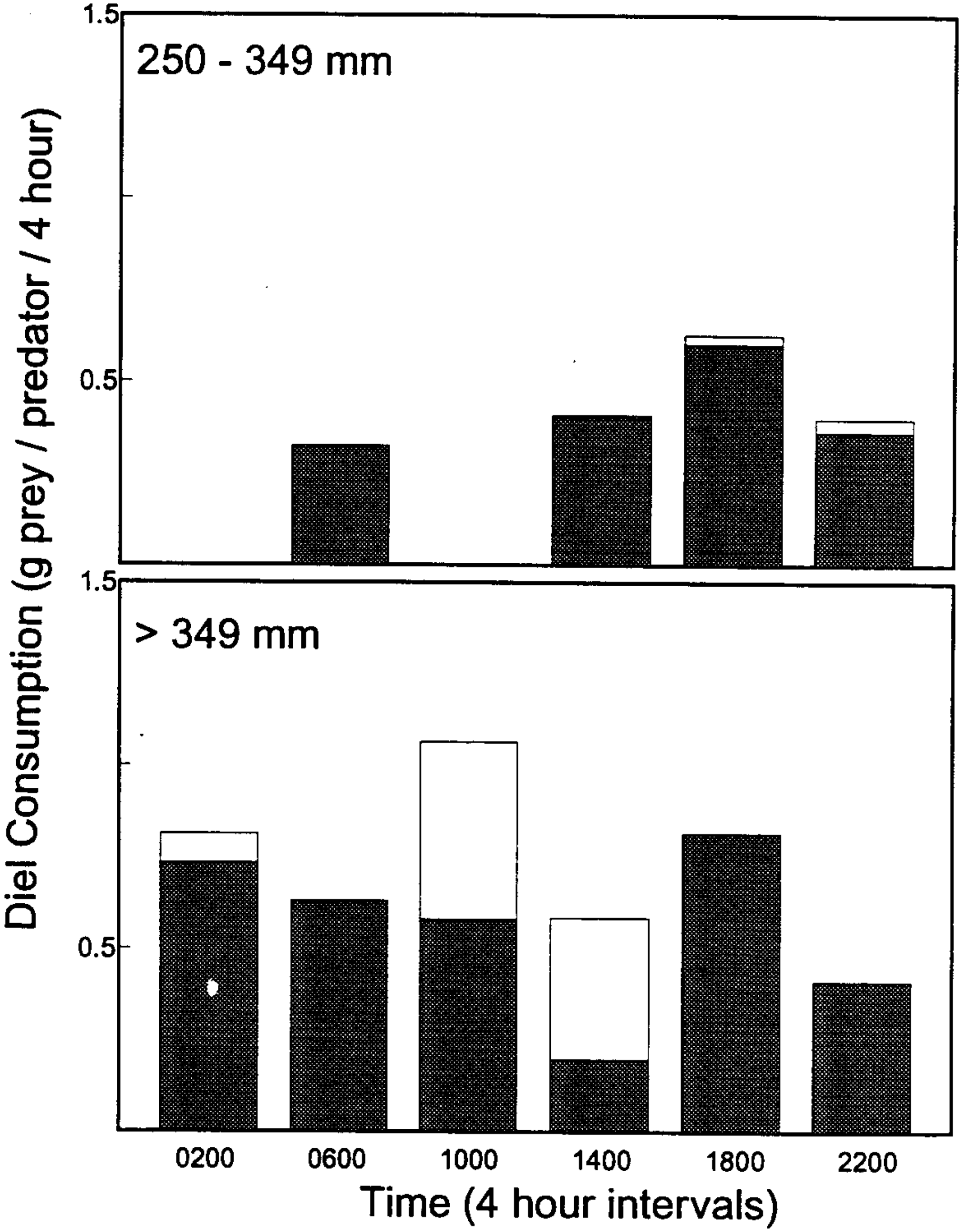

Figure 17. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1991, Lower Granite Reservoir.

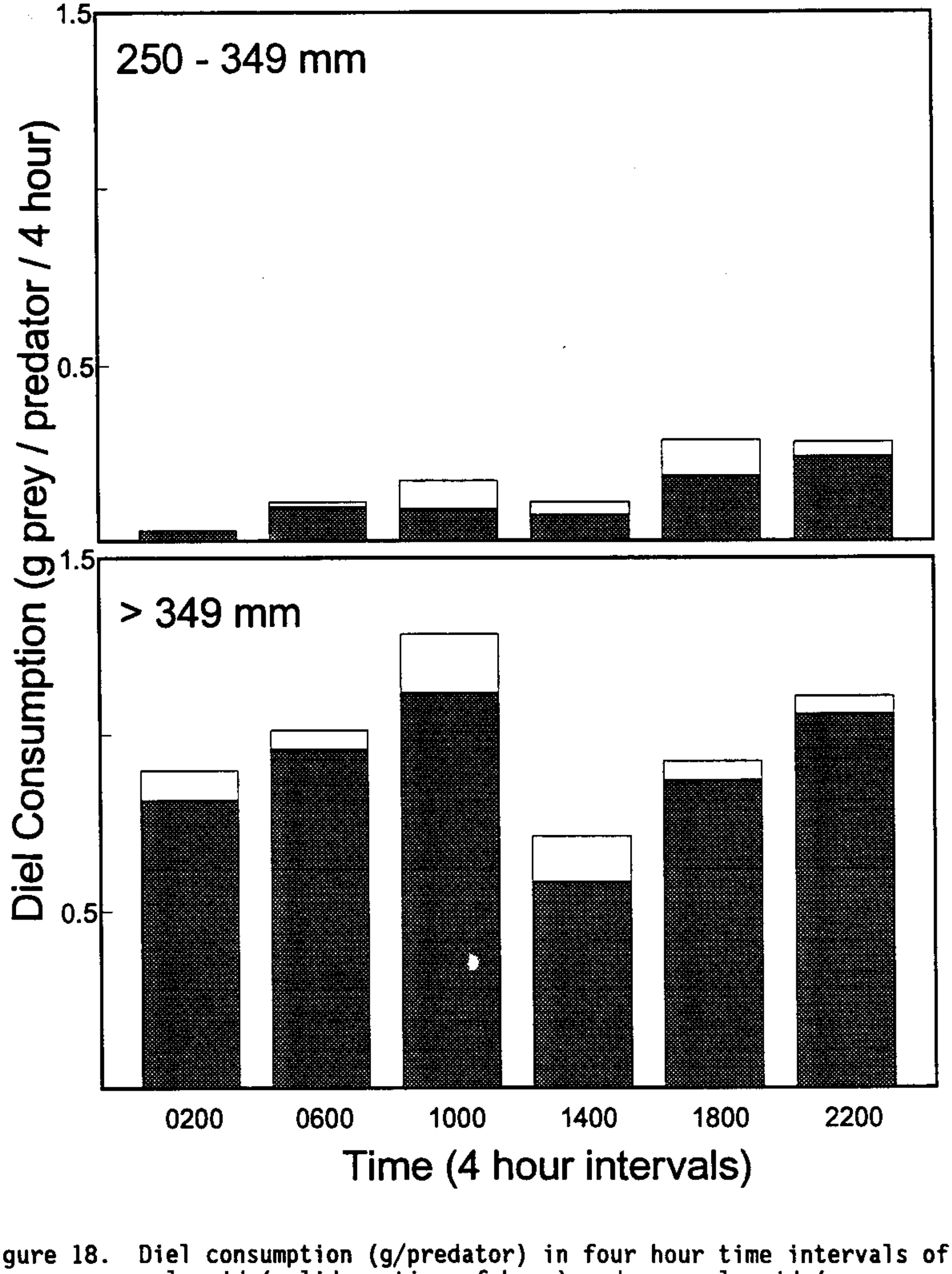

Figure 18. Diel consumption (g/predator) in four hour time intervals of salmonid (solid portion of bars) and non-salmonid (open portion of bars) fish prey items for two lengths of northern squawfish (250-349 mm and > 349 mm) during the juvenile anadromous salmonid outmigration, 1987-1991 (pooled), Lower Granite Reservoir.

Salmonid Size Selectivity

A linear model (r^2=0.34) did not describe the relationship between the ingested salmonid length and squawfish length in Lower Granite as reported for John Day Reservoir by Poe et al. (1991; Figure 19). Maximum ingested salmonid length fell below that predicted by Poe et al. (1991) for squawfish > 400 mm in Lower Granite, which flattened the slope of the line (Figure 19). The relationship of maximum ingested salmonid and squawfish length was linear (r^2=0.89) for squawfish < 400 mm, however, ingested salmonids were longer than those predicted by Poe et al. (1991), which steepened the slope of the line relative to Poe et al. (1991; Figure 19).

Salmonid length distributions in Lower Granite Reservoir, as represented by the length frequencies of chinook and steelhead collected by all sampling gears during the years 1987 - 1991 (Bennett et al. 1988, 1990, 1991, unpublished data), show peaks at 125-150 mm and 200-250 mm for chinook and steelhead, respectively (Figure 20). The length distribution of ingested chinook salmon (Figure 21) did not differ significantly from the length distribution of chinook in Lower Granite Reservoir (P=0.20). Also, no difference was found between the length distribution of ingested steelhead (Figure 21) and steelhead collected in Lower Granite Reservoir (P=0.225). However, the length distribution of unidentifiable salmonids (Figure 21) did differ significantly from both the distributions of chinook (P<0.001) and steelhead (P<0.001) available, indicating a mixture of both chinook and steelhead in the unidentifiable salmonids. When all ingested salmonids were pooled, the mode of ingested salmonids was between 100-125 mm FL (Figure 21).

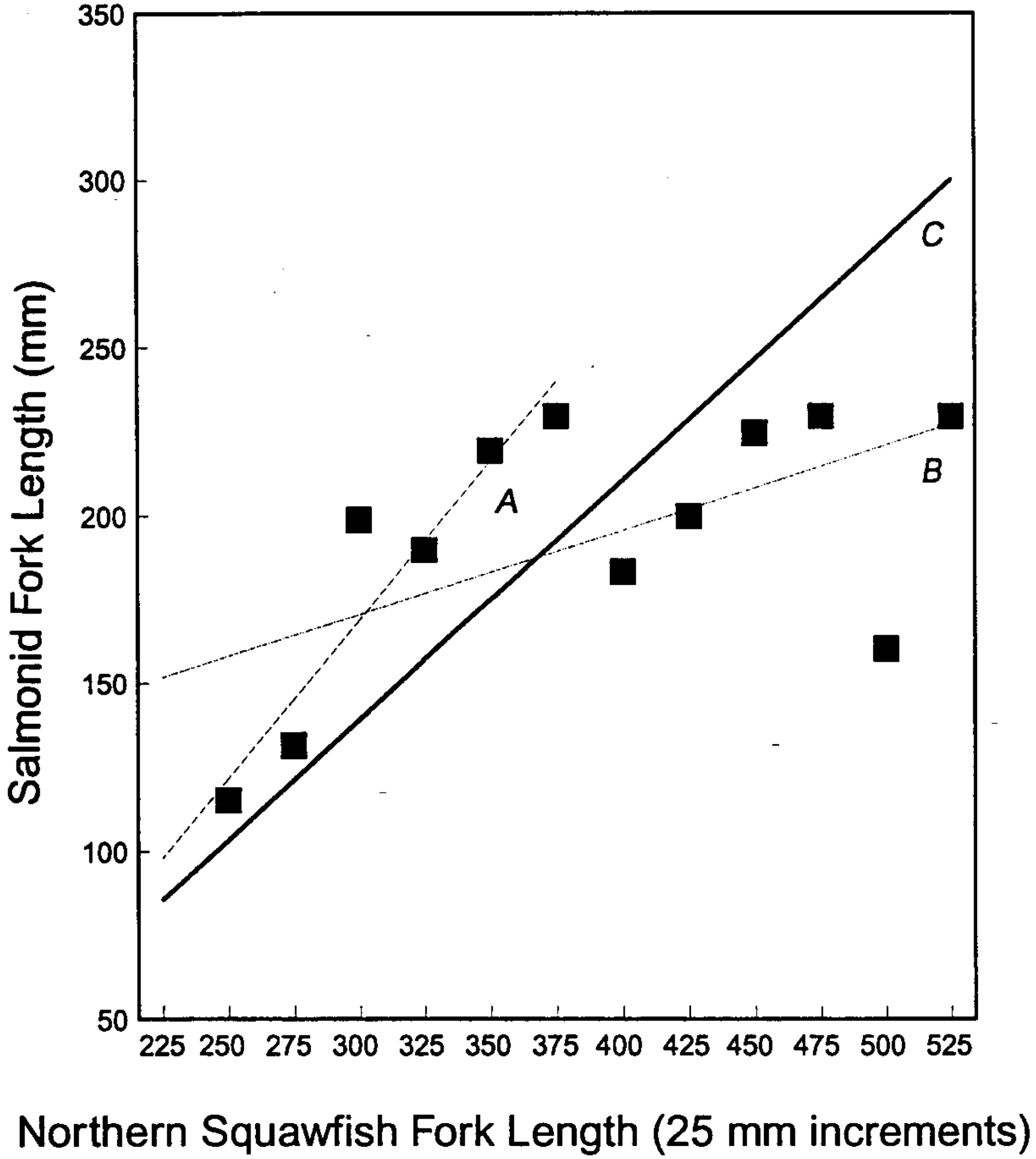

Figure 19. Maximum ingested fork length of salmonids by northern squawfish in 25 mm length increments (solid triangles) in Lower Granite Reservoir, 1987-1991. Line A represents regression equation for northern squawfish lengths < 400 mm ($Y=(0.945*X)-126.5$; $r^2=0.89$). Line B represents regression equation for northern squawfish > 250 mm ($Y=(0.252*X)+91.8$; $r^2=0.34$). Line C represents regression equation developed by Poe et al. (1991) for the relationship of maximum ingested salmonid length to northern squawfish length ($Y=(0.716*X)-84.435$; $r^2=0.96$) from John Day Reservoir.

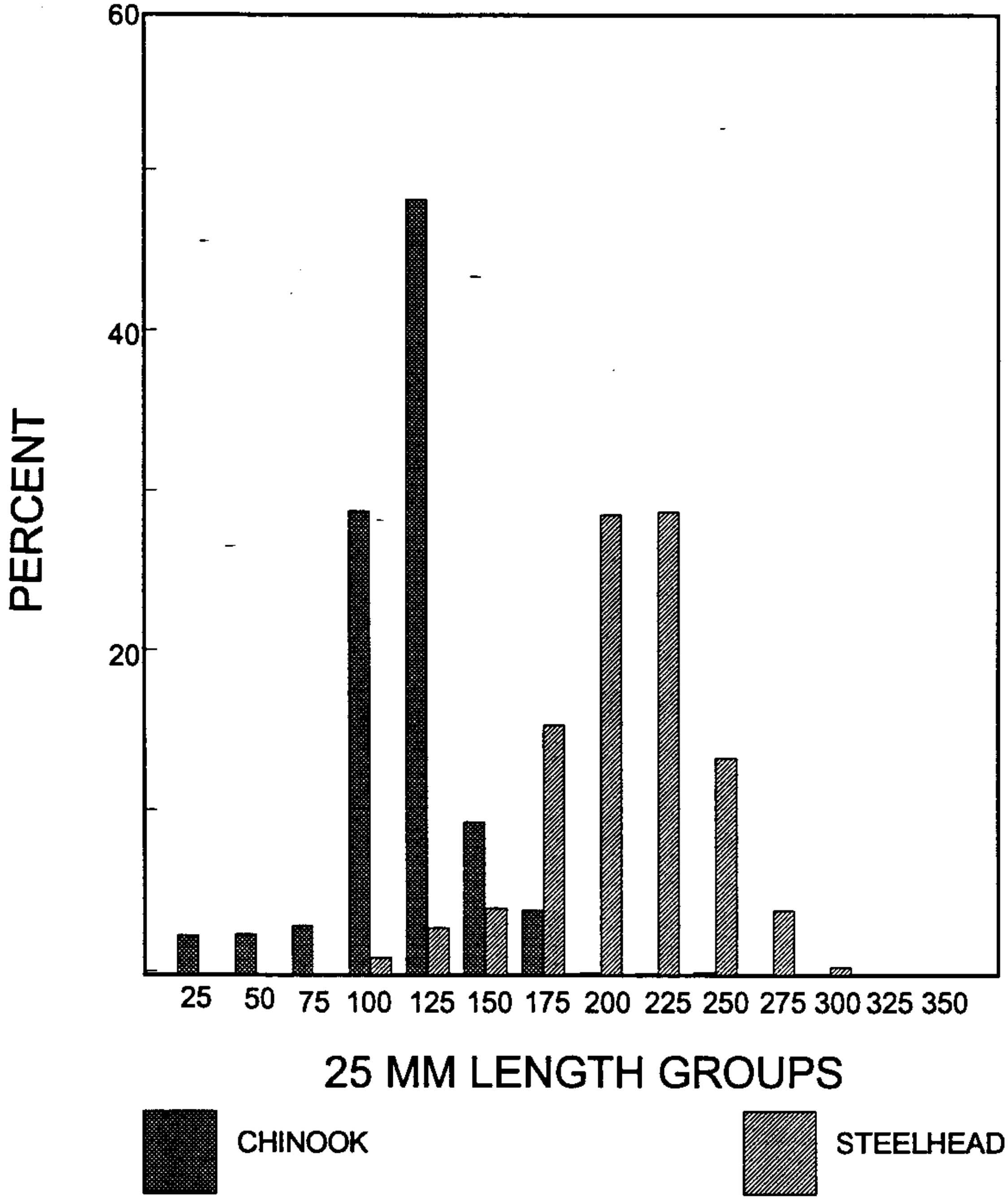

Figure 20. Length distributions(25 mm increments) of chinook salmon and steelhead collected from Lower Granite Reservoir during the juvenile anadromous salmonid outmigration, 1987-1991 (Bennett et al. 1988, 1990, 1991, unpublished data).

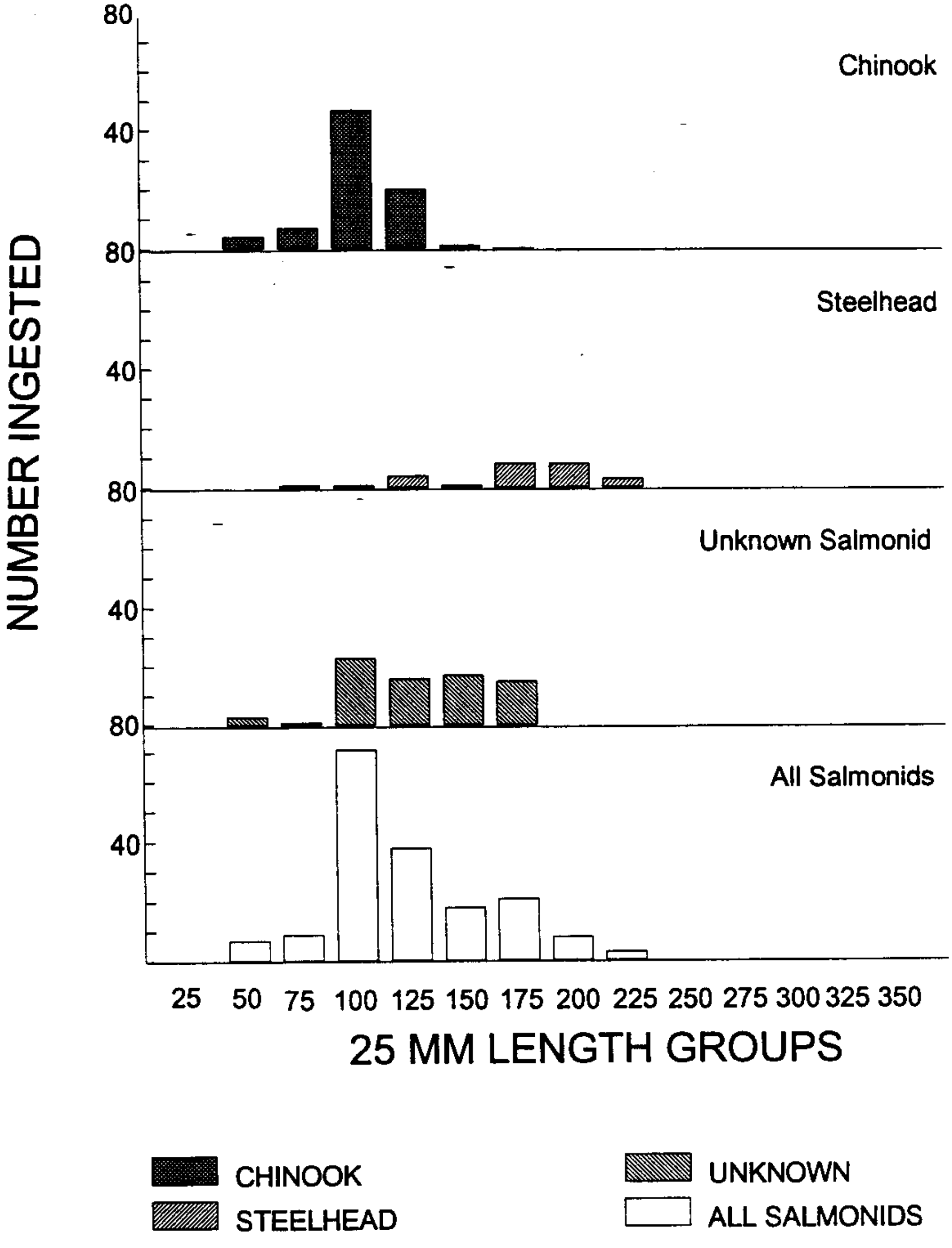

Figure 21. Length distributions (25 mm increments) of chinook, steelhead, unknown salmonids, and all salmonids combined ingested by northern squawfish in Lower Granite Reservoir, 1987-1991.

Population parameters

A von Bertalanffy growth model developed for the lower Snake reservoirs (Bennett et al. 1983) described growth of northern squawfish similar to that reported for John Day Reservoir (Rieman and Beamesderfer 1990; Figure 22) although differences in growth were apparent toward the upper age classes (Figure 22).

The right limb of the catch curve from the pooled age data was linear. Squawfish > age 6 were assumed to be fully recruited to the gear (Figure 23). A regression (r^2 = 0.98) for ages 6-14 resulted in an estimate of total instantaneous mortality of 0.37. Instantaneous mortality for each individual year ranged from 0.28 (1988; r^2=0.82) to 0.47 (1989; r^2=0.92). The mean of the 5 years was 0.38. The 1978 and 1979 cohort specific total instantaneous mortality were 0.41 (r^2=0.72) and 0.40 (r^2=0.82), respectively.

The maximum estimated population for squawfish in Lower Granite reservoir for fish > 250 mm is 15,850 (3,602 ha x 4.4 squawfish/hectare). The proportion of squawfish > 349 mm from the population of all squawfish > 250 mm was estimated to be 44%.

Estimated loss

The ratio of chinook to steelhead in the diet varied from April through June, for all 5 years pooled (Figure 24). April had the highest percentage of chinook among all months, accounting for 98% (n=60) of the identifiable salmonids. During May, steelhead were most frequent, accounting for 58% (n=34) of the identifiable salmonids. The ratio of identifiable chinook to steelhead was nearly 1:1 during June, with chinook slightly higher at 54% (n=11). Using these proportions, loss

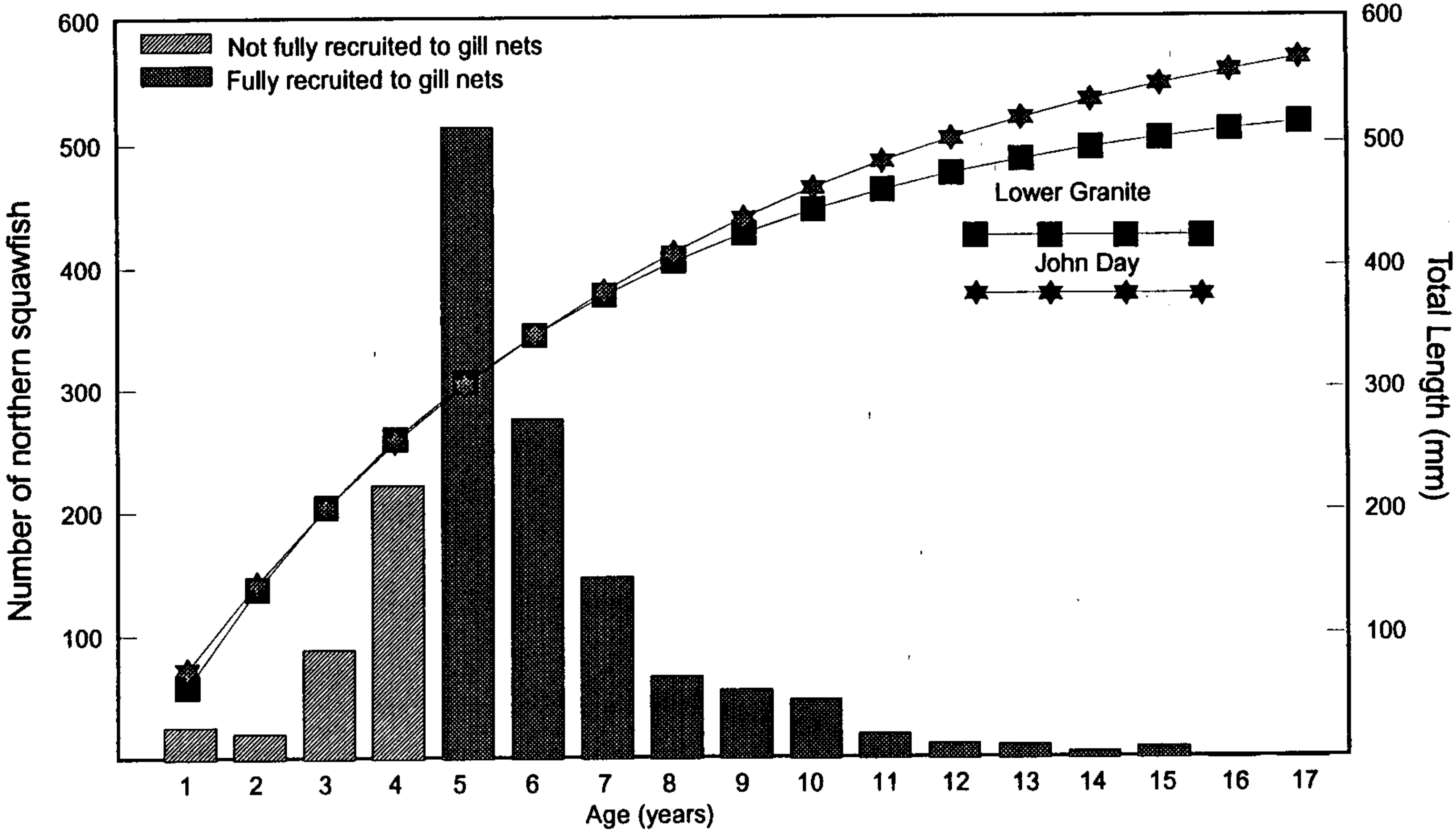

Figure 22. Age distribution of northern squawfish collected with gill nets from Lower Granite Reservoir, 1985-1990, overlaid with Von Bertalanffy growth models developed for squawfish from John Day Reservoir and Lower Granite Reservoir.

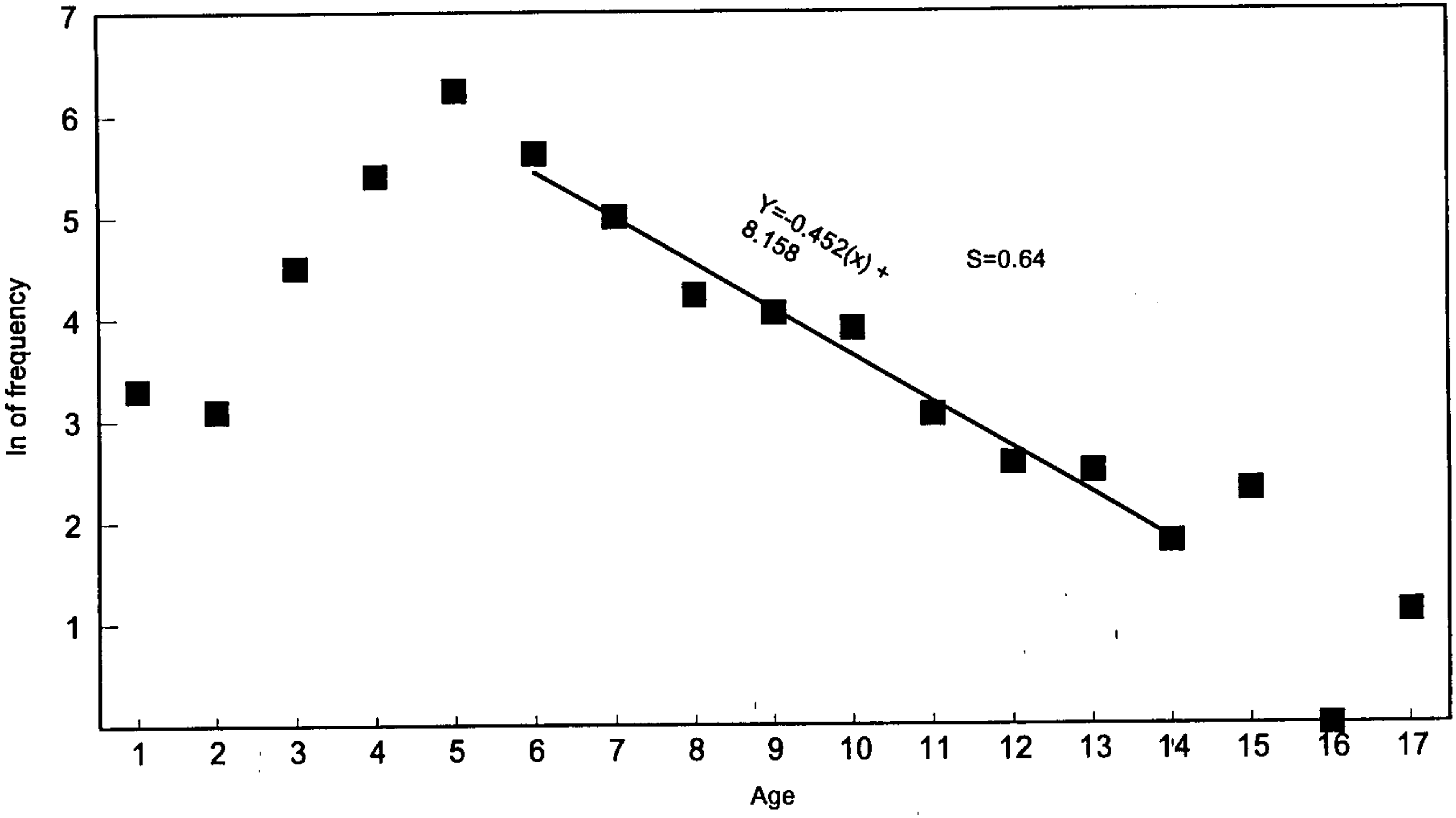

Figure 23. Catch curve from gill net catches of northern squawfish collected during 1985-1990 with regression line of ages 6-14 used for survival estimate.

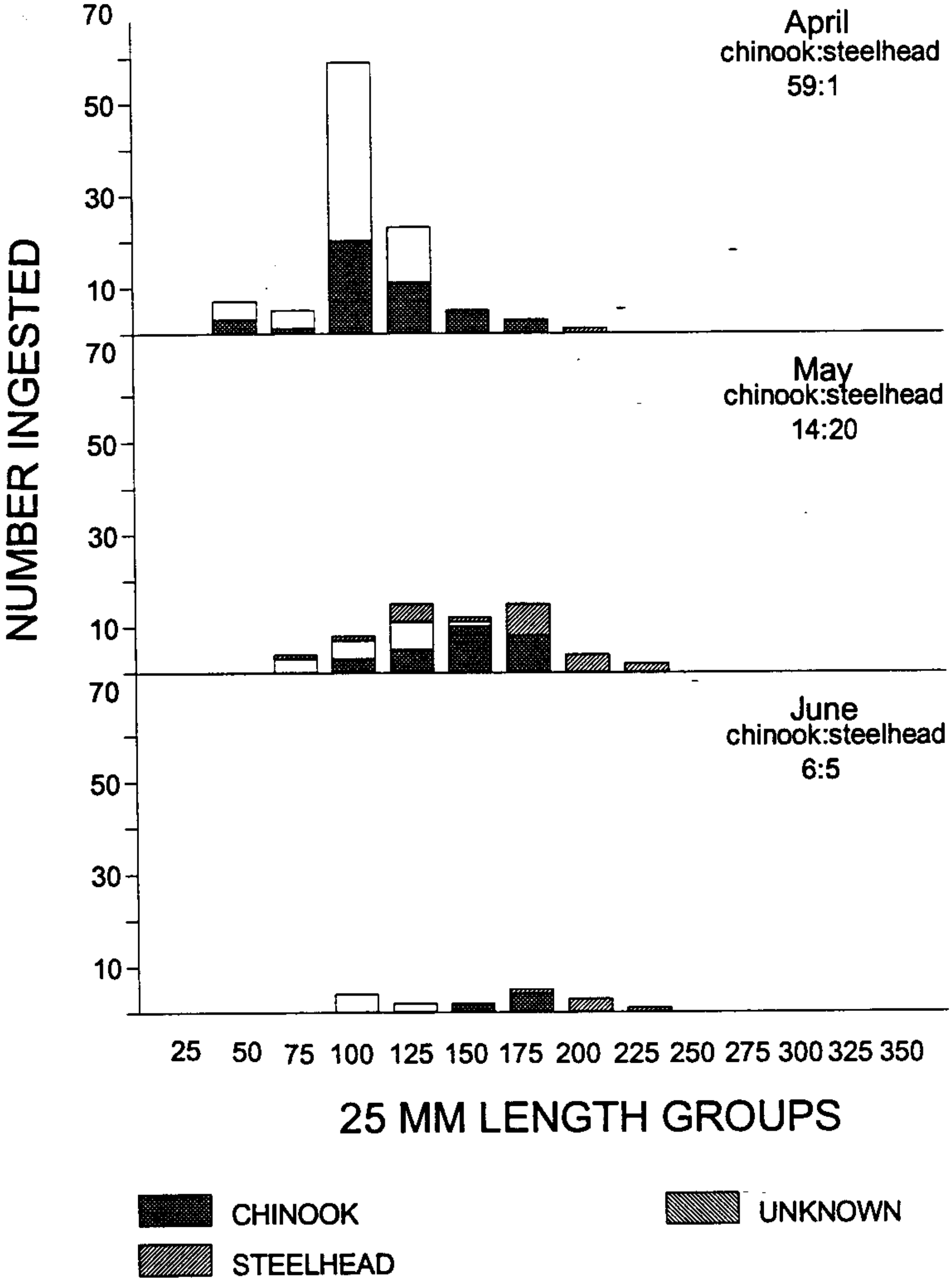

Figure 24. Length distributions (25 mm increments) of chinook, steelhead, and unknown salmonids ingested by northern squawfish in Lower Granite Reservoir during April through June, 1987-1991.

estimates for the Lower Granite Reservoir are summarized in Table 8. Loss estimates ranged from 200,500 salmonids (1987) to 110,700 (1991), with a 5 year mean of 137,739. Using the pooled data, losses were estimated at 128,642 salmonids, of which 76% were chinook salmon. Losses were highest during April, comprising 58% of the total. Squawfish > 349 mm accounted for 76% of the total loss.

Table 8. Summary of loss of juvenile anadromous salmonids by northern squawfish > 250 mm by predator length group, salmonid species, and month in Lower Granite Reservoir, Washington.

	Year					
Loss Categories	1987	1988	1989	1990	1991	All
Number of Predators	15,850	15,850	15,850	15,850	15,850	15,850
Number < 349 mm	8,876	8,876	8,876	8,876	8,876	8,876
Number > 349 mm	6,974	6,974	6,974	6,974	6,974	6,794
Number consumed in April						
(250-349 mm)	-	-	17,308	18,906	41,540	23,965
(> 349 mm)	144,362	-	69,461	72,181	33,265	50,213
Total loss for April	144,362	-	86,769	91,087	74,805	74,178
Percent of Total	80	-	72	65	68	58
Number consumed in May						
(250-349 mm)	-	-	8,530	13,207	0	6,329
(> 349 mm)	56,210	75,668	18,376	28,970	29,619	32,862
Total loss for May	56,210	75,668	26,906	42,177	29,619	39,191
Percent of Total	20	64	22	30	27	31
Number consumed in June						
(250-349 mm)	-	-	0	0	0	0
(> 349 mm)	-	42,262	6,277	6,277	6,277	15,273
Total loss for June	-	42,262	6,277	6,277	6,277	15,273
Percent of Total	-	36	6	5	5	11
Total loss April, May and June	200,572	117,930	119,952	139,541	110,701	128,641
Loss of chinook (April)	141,908	-	85,294	89,539	73,534	72,917
Loss of chinook (May)	23,046	31,024	11,032	17,293	12,144	16,068
Loss of chinook (June)	-	23,033	3,420	3,421	3,421	8,324
Loss of steelhead (April)	2,454	-	1,475	1,548	1,272	1,261
Loss of steelhead (May)	33,164	44,644	15,875	24,885	17,475	23,122
Loss of steelhead (June)	-	19,229	2,856	2,856	2,856	6,949
Total chinook loss	164,954	54,057	99,746	110,253	89,099	97,309
Percent of Total	82	46	83	79	80	76
Total steelhead loss	35,618	63,873	20,206	29,289	21,603	31,332
Percent of Total	18	54	17	21	20	24
Loss per hectare	55.7	32.7	33.3	38.7	30.7	35.7

Discussion

The presence of salmonids in the diet of squawfish is common throughout Pacific drainage (Ricker 1941; Thompson and Tufts 1959; Eggers et al. 1978; Poe et al. 1991). Other investigations have found squawfish not to be major predators of salmonids (Falter 1969; Kirn et al. 1986; Buchanan et al. 1980). However, most research showing high importance of salmonids in the diet is associated with unnatural or altered environments (Brown and Moyle 1981), such as near hatchery release points (Thompson and Tufts 1959), or in hydroelectric dam forebays and tailraces (Uremovich et al. 1980; Bentley and Dawley 1981; Poe et al. 1991). The high importance of salmonids in the diet of northern squawfish in Lower Granite Reservoir, the first large impounded, altered habitat encountered by downstream migrants, is consistent with these other reported findings.

Dietary Analysis

Occurrence of salmonids in the diet of northern squawfish > 250 mm was less in Lower Granite (18.2%) than reported for John Day Reservoir (33.5%). Over all years combined, during the spring outmigration, salmonids accounted for 50.2% and 72.3% by weight of all food items for squawfish in the 250-349 mm and the > 349 mm length group, respectively. Poe et al. (1991) report 8% and 19% near Irrigon and Arlington, within the main pool of John Day Reservoir. Percent weight of salmonids in the diet in Lower Granite was closer to those reported for squawfish collected from the McNary Dam tailrace (78%) and the John Day Dam forebay (66%)(Poe et al. 1991). The tailrace and forebay areas of Lower Granite were not sampled during the five year study. Recent work on indexing consumption of salmonids by northern squawfish in lower Snake River reservoirs (Shively et al. 1992) computed higher consumption indices in these areas than in mid-reservoir locations, suggesting a higher importance of salmonids in the diet of squawfish in areas associated with the dams.

Insects were the most important prey group in the smaller length group of squawfish during four of the 5 years sampled, which is consistent with an apparent trend from insects to fish and crayfish from smaller squawfish to larger squawfish (Falter 1969; Eggers et al. 1978; Poe et al. 1991). Crayfish were important components of the diet among all sizes of squawfish and all seasons. During the summer and fall seasons, crayfish increased in relative importance, and along with non-salmonid fishes, replaced the importance of salmonids in the diet. Poe et al. (1991) report a similar switch to crayfish and prickly sculpin *Cottus asper* in June near the end of yearling outmigration in John Day Reservoir.

Consumption and Daily Ration

Consumption estimates from pooling the 5 years of data are probably the best representation of salmonid consumption for Lower Granite Reservoir. Mean daily numerical consumption for April and May (prey/predator) of salmonids by squawfish (> 250 mm) in the Lower Granite pool were less in general than those reported for the John Day pool and the McNary restricted zone (Vigg et al. 1991). Consumption estimates for Lower Granite were highest during the month of April (0.173 salmonids / squawfish) when the majority of the smolt outmigration is yearling chinook (Figure 2). Consumption estimates during May were slightly lower at 0.11 salmonids/squawfish. The majority of the salmonid outmigration during May in Lower Granite is dominated by steelhead (Figure 2). My consumption estimates would most closely compare to the May daily consumption estimate of Vigg et al. (1991) of 0.251 salmonids/squawfish for the John Day pool for squawfish > 250 mm. Yearling chinook and steelhead peak in abundance at the McNary Dam on the Columbia River during May (Poe et al. 1991). My consumption estimate for squawfish > 349 mm from Lower Granite are closer to the John Day pool values for squawfish > 250 mm of 0.24 and 0.15 salmonids/squawfish during April and May, respectively. Estimates of salmonid consumption during June are similar for squawfish > 250 mm in Lower Granite and John Day pools (Vigg et al. 1991), at 0.06 and 0.09, respectively. The number of prey per predator dropped from April to June in Lower Granite, whereas mean prey weight increased nearly three fold, indicating the majority of the salmonids being ingested were probably steelhead. Primarily hatchery steelhead smolts are migrating through the reservoir during June (Buettner and Nelson 1990; Koski et al. 1988). Decreased numbers and large body size of steelhead smolts probably explain the drop in the salmonid component of the diet.

The non-salmonid fish component of the diet from the pooled data increased notably during June for both length groups of salmonids. During 1988 and 1989, non-salmonid and salmonid consumption declined from April to June. However, consumption increased for non-salmonids in June during 1990 and 1991 and overall 5 years combined. Non-salmonid consumption was notably higher during June of 1990 (0.63 non-salmonids/predator). Of all digestive tracts collected in June during the 5 years (n=199), 45% were collected during 1990, which heavily influenced the pooled data. No June samples were obtained during 1987.

Mean daily ration (mg prey/g of predator) of salmonid and non-salmonid prey fish from the pooled data followed the same pattern as mean daily consumption. For squawfish > 349 mm, the peak in non-salmonid consumption during June was also evident in daily ration (mg/prey/g of predator), which suggests that the increase in consumption (prey/predator) observed was not merely due to smaller prey size. However, with the exception of 1990, total daily ration of fish prey declines. Vigg et al. (1991) report a decline in total consumption during June, and attributed a possible explanation to peak spawning. Temperature greatly influences digestion rates and thereby regulates daily ration (Vigg and Burley 1991; Vigg et al. 1991; Beyer et al. 1988). Total daily ration (all prey items) for northern squawfish would be expected to follow patterns similar to changes in water temperature, and increase during June as observed during 1992.

Temperatures during June of 1990 were not notably different from June of other years to suggest a higher metabolic demand for that year. The downward trend observed in daily ration of prey fish during the other 4 years probably represents a switch to other non-fish prey items such as crayfish, which is evident in the IRI scores. The trend observed in daily ration of fish prey during 1990 is probably closer to the trend for daily ration of all prey items. Catostomids dominated the non-salmonid component of the diet during all years, and may have been in greater abundance during 1990 than in other years. The lower daily ration of salmonids during June in all years suggests lower availability of favorable sized salmonids to squawfish, when fewer chinook remain in the system.

Daily ration was nearly two times higher during May and June of 1987 and 1988 than other years. The peak daily ration observed was approaching 21 mg/g for both April 1987, and May 1988. These peaks may be an anomaly of smaller sample sizes during 1987 and 1988 (n=58 and 92, respectively), and the 1989-1991 data may be the most representative.

The magnitude of daily ration observed for squawfish > 349 mm during 1989 is very similar to values reported for John Day Reservoir (squawfish > 250 mm). Total daily ration of prey fish in the diet of squawfish in Lower Granite was highest in April (11 mg/g), corresponding to the peak outmigration of yearling chinook. Vigg et al. (1991) found daily ration to level off at about 12 mg/g for squawfish > 400 mm. Peak daily ration of fish occurred during the month of July, approaching 30 mg/g in the boat restricted zone of McNary Dam during the peak of the sub-yearling smolt migration (Vigg et al. 1991). The only daily ration observed that approached 30 mg/g in Lower Granite was consumption of non-salmonids during June 1990 of 26 mg/g. Consumption was not followed during the other summer months.

Diel consumption

Diel feeding patterns on salmonids were similar among years. Feeding occurred throughout the entire day and night, with peaks indicating higher feeding activity in the late morning and late evening hours. Steigenberger and Larkin (1974) found peak activity and feeding to occur in twilight and dark hours in two British Columbia Lakes. Vigg et al. (1991) report peak feeding in the pool area of John Day to occur at dawn, and feeding remained strong throughout the day. Feeding patterns reported for the McNary Dam boat restricted zone showed strong feeding throughout nighttime hours and into the early morning (Vigg et al. 1991).

Vigg et al. (1991) hypothesize that differences observed in feeding activities between the two areas in John Day Reservoir are related to prey availability and coincide with peaks of prey activity. Bennett et al. (1988) found differential use between day and night by juvenile salmonids in shallow water areas of Lower Granite. Shallow water areas near Lower Granite Dam that had relatively high numbers of chinook and steelhead during day time hours had relatively low catches of salmonids during nighttime hours. Bennett et al. (1988) hypothesized that the differences observed indicated holding and possible foraging areas during the day, and migration further downstream during nighttime hours. Peaks in feeding patterns observed in Lower Granite may reflect higher activity of juvenile salmonids (feeding or migrating; or moving into and out of littoral areas) making them more available as suggested by Vigg et al. (1991).

Size Selectivity

The linear relationship of maximum ingested salmonid length and northern squawfish length described by Poe et al. (1991) could not be duplicated in this study. Maximum ingested salmonid lengths by larger northern squawfish (> 400 mm) were less than those found in John Day (Figure 19), which may indicate a size preference, or smaller prey being more vulnerable to capture, or higher densities of smaller fish available. The fact that the smaller northern squawfish ingested larger salmonids than predicted by the relationship of Poe et al. (1991) was confounding. Steelhead migrating through Lower Granite are considerably larger than salmonids migrating through John Day. Modal sizes of steelhead are between 200 and 250 mm FL in Lower Granite (Figure 20), greater than any of the peak salmonid sizes represented in Poe et al. (1991). Larger salmonids in the squawfish < 400 mm may be due to a greater availability of larger sizes, increasing the opportunity of ingesting weaker or moribund individuals of larger sizes than they would otherwise consume.

Similarities in sizes between ingested and available salmonids indicates an absence of size selective predation on salmonids by the population of squawfish in Lower Granite Reservoir. The chinook population is receiving higher predation pressure than steelhead due to their small size, although size ranges being ingested do not differ from sizes available. According to the relationship developed by Poe et al. (1991), the majority of chinook salmon (< 150 mm; Figure 19) are vulnerable to predation by squawfish > 330 mm. Using my relationship for squawfish < 400 mm, chinook salmon are vulnerable to predation by squawfish > 292 mm. The majority of steelhead (< 250 mm) in John Day Reservoir are vulnerable to squawfish > 470 mm (Poe et al. 1991) or > 400 mm in Lower Granite. Because of the population size structure, a larger portion of the squawfish population are physically capable of ingesting chinook than steelhead. Because of these physical limitations of ingestible prey size, size selective predation pressures may be greater on the population of steelhead migrating through the reservoir. Clearly, smaller juvenile steelhead should be more vulnerable to predation than are the larger steelhead, although, this was not evident from our sample of identifiable steelhead.

Poe et al. (1991) report evidence of size selective predation for smaller size groups of salmonids. Their evidence suggests size selective predation on the population of salmonids by squawfish, rather than individual prey size preference. Two other studies cited in Poe et al. (Uremovich et al. 1980; Olney 1975) found ingested salmonid lengths to be similar to environmental availability, similar to my findings for Lower Granite.

Population Parameters

To relate mean daily consumption to total loss of salmonids, estimates of predator abundance are mandatory (Rieman et al. 1991). Recent work by Thorne (1992) estimated the population size of predators in Lower Granite Reservoir to be 33,600 based hydroacoustic surveys accompanied with gill net surveys. The gill net surveys were to estimate proportions of various fish species. The estimate included northern squawfish, channel catfish *Ictalurus punctatus*, and smallmouth bass *Micropterus dolomieu* combined. However, given high variability of the catch, and strong size and species selectivity of the sampling gear, the population estimate of predators is crude at best. An attempt to further derive a population estimate of predator sized northern squawfish from this estimate would not be meaningful. The abundance estimate used for Lower Granite for my analysis was based on the density of northern squawfish reported for John Day.

A comparison of squawfish population structure using growth, mortality, catch per unit effort (CPUE) data, and recruitment factors of

Lower Granite Reservoir provided a means of relative comparison with John Day (Beamesderfer et al. 1990; Rieman et al. 1991) as to probable densities of predator size squawfish in Lower Granite Reservoir.

Growth of northern squawfish is similar in Lower Granite to that reported for John Day (Figure 22). Rieman and Beamesderfer (1990) report mortalities ranging from 0.14 to 0.44, depending on the method used. However, they chose 0.25 as a best approximation, similar to that reported for Lake Washington (0.27) (Bartoo 1977). Annual mortality might be higher for squawfish in Lower Granite Reservoir than reported for John Day, but is within the range of uncertainty reported for John Day.

A comparison of catch per unit of effort (CPUE; effort = 1 hour) using bottom gill nets between Lower Granite and John Day indicates lower densities of predator sized fish in Lower Granite than found in John Day (Table 9). Season wide CPUE for squawfish > 250 mm FL (March - August) of bottom gill nets ranged from 1.15 to 2.66 during 1985 and 1986 for John Day Reservoir, depending on area sampled (Nigro et al. 1985). Monthly CPUE from April through June of 1986 ranged from 0.7 to 1.96 depending on area sampled (Beamesderfer et al. 1987). Catch per unit of effort in Lower Granite for bottom gill nets during 1988 and 1989 (Bennett et al. 1990, 1991) was approximately two to ten times lower than those ranges reported for John Day ranging from zero to 0.7 squawfish per hour depending on area sampled (Table 9). Bottom gill nets used during 1988-1991 are similar to those used in John Day. Mesh size of the nets were equal, however, dimensions of the nets were different. Nets used in the comparison of John Day were monofilament,

Table 9. Comparison of selected gill net catch per unit effort (CPUE) values between John Day Reservoir and Lower Granite Reservoir (CPUE = catch/hour).

Reservoir Location	1985[c]	1986[d]	1987	1988	1989
John Day Reservoir[a]	1.34	1.29			
Forebay	1.66	1.46			
Arlington	1.20	1.17			
Irrigon-Patterson	1.53	1.25			
McNary Tailrace	2.22	1.15			
Boat Restricted Zone	1.57	2.66			
John Day Reservoir[b]					
Forebay					
April		1.67			
May		1.75			
June		1.05			
Arlington					
April		1.96			
May		1.12			
June		0.70			
Irrigon					
April		0.95			
May		1.69			
June		2.04			
McNary					
April		0.85			
May		1.59			
June		1.78			
Lower Granite Reservoir (Rkm)					
224	0.48	0.29			
223		0.09			
217		0.73			
216	0.24	0.15			
214		0.19			
213		0.20			
207		0.32			
205	0.31		0.14	0.14	0.25
194	-			0.04	0.04
193			0.04	0.07	0.09
192	0.08		0.00	0.01	
184	0.00		0.05		
183			0.01		
180			0.09	0.03	0.14
179	0.13				

[a] Means for March - August (Nigro et al. 1985)

[b] Monthly means (Beamesderfer et al. 1987)

[c] All seasons combined - Lower Granite 1985 (Bennett and Shrier 1986)

[d] Spring months only - Lower Granite (Bennett and Shrier 1987; Bennett et al. 1988, 1990, 1991)

46 m long by 2.4 m deep (110.4 m^2)(Beamesderfer and Rieman 1991), whereas nets used in Lower Granite were multifilament, 69 m long x 1.8 m deep (124.2 m^2). I believe that densities of squawfish > 250 mm are less in the Lower Granite pool than in the John Day pool. Petersen et al. (1991) report a general decrease in catch from Bonneville Reservoir up-river which may continue up into the Snake River reservoirs. Other factors may explain an apparent lower density of squawfish evident by our sampling.

During the 5 years of study, no sampling was conducted in the Lower Granite forebay or tailrace, which probably had higher densities of predator sized squawfish than observed in the pool. Relative densities of squawfish were 12-18 times higher in the restricted zone of McNary Dam tailrace than other areas in John Day Reservoir (Beamesderfer and Rieman 1991). Bentley and Dawley (1981) captured 1442 adult squawfish in 10 purse seine sets and 260 adult squawfish in eight drift net sets in the tailrace of Lower Granite Dam, indicating relatively high concentrations. Bennett et al. (1983) reported higher densities of adult squawfish in the tailrace of Lower Granite Dam during the spring months than were observed during the summer and fall months, suggesting a seasonal migration to the tailrace area.

Higher densities of squawfish probably occur near the upstream boundaries and into the free flowing reaches of the Snake River above the Lower Granite pool which were not sampled. As part of the predator control program in the Columbia and Snake rivers, Burley et al. (1991) reported notably higher catches of predator sized squawfish at the extreme upper end of the reservoir near Rkm 223. The nearest upstream dam is Hells Canyon Dam, approximately 225 km above Lower Granite Dam. The Hells Canyon reach of the Snake River is a relatively high gradient river, with abundant areas of high velocity water, possibly preferred by squawfish. Faler et al. (1988) found squawfish to concentrate at flow shears in the tailrace of McNary dam. This type of habitat is only present in the free flowing section above Lower-Granite. I believe that during spring months, many larger northern squawfish migrate to areas in the upper reservoir and the free flowing sections of the river for spawning.

Limited rearing areas for young of the year (YOY) squawfish may further reduce densities of northern squawfish relative to John Day. The upper portion of Lower Granite may serve as a rearing area for squawfish that will eventually move upstream and reside above the reservoir. Extremely high densities of YOY northern squawfish have been observed in shallow, sandy, low gradient littoral areas associated with the upper section of the reservoir, along with high densities of YOY largescale suckers *Catostomus macrocheilus*, peamouth *Mylocheilus caurinus*, redside shiners *Richardsonius balteatus*, and smallmouth bass. (Bennett et al. 1985, 1987, unpublished data). LaBolle (1984) found a similar distribution of juvenile larval squawfish and other native cypriniforms in John Day Reservoir. These areas may be more preferred due to differences in temperature or food abundance (Hjort et al. 1981, LaBolle 1984). Lower Granite has relatively few backwater and shallow littoral areas. Competition for space and food resources may force YOY squawfish into less suitable habitat, reducing survival (Hjort et al. 1981; LaBolle 1984). Shallow littoral areas in Lower Granite Reservoir are especially vulnerable to frequent 1.5 m water level fluctuations which may further limit habitat availability. Factors determining year class strength and recruitment of northern squawfish are not well understood (Rieman and Beamesderfer 1990).

Estimated Loss

In Lower Granite Reservoir, squawfish in the 250-349 mm length group are not significant predators of salmonids. Only a small percentage of fish in this length group contained salmonids. Clearly, squawfish > 349 mm are the major predators of salmonids, consistent with the findings of Poe et al. (1991) and Vigg et al. (1991).

On an absolute scale, the magnitude of loss relative to John Day appears considerably lower. If all 22.5 million smolts outmigrating reach Lower Granite reservoir, only 0.6% of the total outmigration from April to June is lost to squawfish predation, compared to approximately 11% of the salmon and steelhead that entered John Day (Rieman et al. 1991).

However, some important considerations need to be made in comparing these absolute losses. This loss estimate is based on probable density of squawfish in the main Lower Granite pool. Higher densities of squawfish probably occur in the forebay area of Lower Granite Dam,as well as the extreme upper end of the reservoir, which would notably increase estimated losses. An estimated 1,100,320 salmon and steelhead were lost to predation by northern squawfish during April to June in John Day Reservoir, of which 26% was in the restricted zone (Rieman et al. 1991). If 26% were subtracted from the April, May, June time period, a total loss from the pool is 814,237 or 38.7

salmonids/hectare The estimated loss in the Lower Granite pool is 35.7 salmonids/hectare. Therefore, on a relative scale, loss observed in the reach of Lower Granite Reservoir that I sampled is approximately 92% of what was observed in John Day.

The total surface area of all four lower Snake River reservoirs (13,720 hectares) is only 65% the size of John Day Reservoir (Bennett et al. 1983). If losses throughout all of the Lower Snake reservoir pools are similar to what I observed in Lower Granite (35.7 smolts/hectare), total estimated loss would be 490,000 smolts. In addition to these losses, there are three dams in addition to Lower Granite Dam in this reach of the Snake River: Little Goose Dam (Rkm 113.2), Lower Monumental Dam (Rkm 67.0), and Ice Harbor Dam (Rkm 15.6). During the April through June time period, an estimated 286,000 smolts were lost in the boat restricted zone in John Day Reservoir. If losses at each dam are of the magnitude reported by Rieman et al. (1991), then losses associated with the dams could be as high as 4x that of all of the lower Snake River reservoir habitat combined. Although, with a large portion of smolts transported at Lower Granite Dam and Little Goose Dam (Koski et al. 1988), densities of smolts may be much less in Little Goose and Lower Monumental reservoirs, and losses associated with predation may differ from Lower Granite and John Day. This emphasizes the need to evaluate predation and predator control programs on a system wide basis to identify greatest areas of loss, and to better evaluate the potential of predator control programs system wide.

Consumption and loss estimates for Lower Granite Reservoir did not include the July time period, when a large proportion of sub-yearling fall chinook are still in Lower Granite (Figure 2; David Bennett, University of Idaho, unpublished data). The size, water temperature and speed of migration may make sub-yearling chinook especially vulnerable to predation (Rieman et al. 1991; Poe et al. 1991; Bennett et al. 1987). Bennett et al. (1987) reported relatively high densities of sub-yearling chinook rearing in low gradient upper littoral areas of Lower Granite. This type of habitat may offer a refugium from predation (Hjort et al. 1981). However, little is known about the migration characteristics of fall chinook through Lower Granite.

Snake River stocks of fall chinook have declined significantly in abundance from historic times (Irving and Bjornn 1981; Waples et al. 1991), primarily due to loss of historic spawning areas and high dam related mortalities. Any losses attributed to predation may be substantial at such low population levels (Rieman and Beamesderfer 1990).

Summary

1). Northern squawfish were major predators of juvenile anadromous salmonids during the spring outmigrations of 1987-1991 in Lower Granite Reservoir. Salmonids were more important by percent weight, frequency of occurrence, and the IRI for larger northern squawfish (>349 mm).

2). Consumption estimates of salmonids by northern squawfish were highest in Lower Granite Reservoir during April (0.173 salmonids/squawfish). Consumption of salmonids declined during May (0.11) and June (0.06). The non-salmonid prey fish component of the diet increased notably during June.

3). Daily ration (mg prey / g predator) of salmonid and non-salmonid prey fish followed similar patterns of daily consumption. Highest daily ration observed was 26 mg prey / g predator on non-salmonid prey fish during June.

4). Diel feeding patterns on salmonids by northern squawfish were similar among years with peaks in feeding activity occurring during late morning and evening hours.

5). Similarities in sizes between ingested and available salmonids indicates an absence of size preference of salmonids by northern squawfish. However, due to the size structure of the northern squawfish population, size selective predation pressures are probably occurring on the steelhead population migrating through Lower Granite Reservoir.

6.) Growth of squawfish in Lower Granite Reservoir is comparable to John Day Reservoir on the Columbia River. Mortality estimates were generally higher, but within the range of uncertainty reported for John Day Reservoir. Catch per unit of effort of gill net catches of northern squawfish > 250 mm was generally lower than reported for John Day Reservoir.

7.) The total loss estimate of juvenile anadromous salmonids due to predation in the Lower Granite pool, on a relative scale, is comparable to John Day pool (35.7 salmonids per hectare and 38.7 salmonids per hectare, respectively). Losses may be substantially higher in areas with higher densities of squawfish, such as the forebay and tailrace of Lower Granite Dam, and the upper portions of the reservoir.

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