POPULATION ESTIMATES, FOOD HABITS AND ESTIMATES OF CONSUMPTION OF SELECTED PREDATORY FISHES IN LAKE PEND OREILLE, IDAHO

A Thesis

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ABSTRACT

In Lake Pend Oreille, Idaho from April 1997 through April 1999, 449 kamloops (rainbow trout) *Oncorhynchus mykiss*, 348 bull trout *Salvelinus confluentus*, and 165 lake trout *Salvelinus namaycush* $\geq$ 406 mm fork length were tagged by volunteer anglers and 39 kamloops, 42 bull trout, and 19 lake trout were recaptured. Movement of recaptured fish varied from less than 1 km to approximately 30 km, and time between tagging and recapture varied from 3 days to 667 days. A Chapman's mark-recapture model estimated 14,607 kamloops, 12,134 bull trout, and 1,792 lake trout $\geq$ 406 mm fork length. Kamloops $\geq$ 406 mm averaged 597 mm and ranged from age 4 to 9. Bull trout $\geq$ 406 mm averaged 524 mm and ranged from age 6 to 12, and lake trout $\geq$ 406 mm averaged 605 mm and ranged from age 6 to 11.

Stomach samples were collected from kamloops (n = 180), bull trout (n = 11), lake trout (n = 242), northern pikeminnow *Ptychocheilus oregonensis* (n = 3,322), and other predatory fishes (n = 782) sampled by electrofishing and angling. Stomach samples were taken from harvested fish and non-lethally from non-harvested fishes using lavage techniques. Dietary analysis indicated that kamloops (77%), bull trout (66%), and lake trout (87%) fed primarily on kokanee *O. nerka*, whereas northern pikeminnow and other predatory fishes sampled fed primarily on insects, other fishes, and miscellaneous prey items.

Bioenergetic modeling indicated that in Lake Pend Oreille kamloops, bull trout, and lake trout collectively consumed more than 153.5 metric tons-mt (65%) of the 235.2 mt of kokanee produced (e.g. biomass gained/yr) 95% CI: [105.4 mt, 286.3 mt] in 1998 explaining 73% of the kokanee biomass lost. Kamloops constitute 82% of the pelagic predator biomass and consumed 53% of the annual kokanee production, whereas bull trout (14% of the biomass) consumed 10%, and lake trout (4% of the

biomass) consumed 2%. Kamloops, bull trout, and lake trout constituted a major source of mortality to subadult/adult kokanee in Lake Pend Oreille in 1997-1998.

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INTRODUCTION

Lake Pend Oreille, Idaho, has produced the world record rainbow trout (kamloops) *Oncorhynchus mykiss* (16.8 kg) and bull trout *Salvelinus confluentus* (14.5 kg), supported commercial harvests of kokanee *O. nerka* and opossum shrimp *Mysis relicta*, and provided a variety of fishing opportunities for a wide spectrum of angler interests. However, in the last 40 years, fisheries for kokanee, rainbow trout, and bull trout have declined and presently provide limited angler opportunities. The sport fishery for lake trout *S. namaycush,* however, has increased.

Presently, Lake Pend Oreille provides fisheries for trophy kamloops and bull trout and a consumptive fishery for kokanee (Maiolie and Elam 1992). The Gerrard strain of rainbow trout (kamloops) *O. m. gairdneri* was introduced into Lake Pend Oreille in 1941. Kokanee were first observed in the early 1930's after presumably migrating downstream from Flathead Lake, Montana (Stross 1954). In addition, sport fisheries exist for brown trout *Salmo trutta*, lake whitefish *Coregonus clupeaformis*, cutthroat trout *O. clarki*, and in recent years lake trout, which were introduced in the early 1920's. Creel surveys conducted by Idaho Department of Fish and Game (IDFG) in 1990 showed approximately 38% of anglers fished for kokanee while 60% fished for trout and char species (Paragamian et al. 1991).

The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). In Lake Pend Oreille, kokanee, an important component of the food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981). One of the lake recovery goals established by IDFG is to sustain an annual harvest of 750,000 kokanee.

Understanding the flow of energy between trophic levels is imperative to effectively manage fisheries in a lentic ecosystem (Ney 1981). The bioenergetic demands of fish predators and the effect of these demands on the Lake Pend Oreille ecosystem are not fully understood. However, recently initiated research projects are examining many factors thought to be contributing to the decline of kokanee, including: kokanee/opossum shrimp interactions (Chipps and Bennett 2000), zooplankton abundance and availability (Chipps 1997; Clarke 1999), quality and quantity of spawning habitat (Idaho Department of Fish and Game, unpublished), and the influence of predation on kokanee abundance.

Predatory salmonids (kamloops, bull trout, and lake trout) in Lake Pend Oreille reportedly rely heavily on kokanee as a prey item (Anderson 1978; Pratt 1985; Rieman and Falter 1981). Finding a balance between forage fish and predators requires a detailed look at both the environment and species relationships (Wydoski and Bennett 1981). This project was conducted because no known research has quantified predation by these salmonid fishes or assessed effects of predation upon the kokanee population by these fishes in Lake Pend Oreille.

The overall objectives of the project were:

OBJECTIVES

1. Estimate the population abundance of kamloops, bull trout, and lake trout ≥ 406 mm in Lake Pend Oreille, Idaho;
2. Identify food items in the stomachs of kamloops, bull trout, lake trout ≥ 406 mm and northern pikeminnow ≥ 100 mm from Lake Pend Oreille, Idaho; and
3. Estimate kokanee consumed by kamloops, bull trout, lake trout ≥ 406 mm and relative consumption by kamloops, bull trout, lake trout and northern pikeminnow in Lake Pend Oreille, Idaho.This thesis will treat each objective as a separate chapter.

STUDY AREA

Lake Pend Oreille is a meso-oligotrophic body of water located in the Panhandle region of northern Idaho (Rieman and Falter 1981; Figure 1.1). Lake Pend Oreille is fed by streams originating in the Selkirk Mountains to the Northwest, the Cabinet Mountains to the Northeast and the Coeur d'Alene Mountains to the East. The lake is contained in the glacially formed Purcell Trench. It is the largest natural lake in Idaho and the fifth deepest lake in the nation with a mean depth of 164 m and a maximum depth of 351 m. The lake's major inlet, the Clark Fork River, is regulated by Cabinet Gorge Hydroelectric Development (circa 1952) and the outlet, the Pend Oreille River, is regulated by Albeni Falls Hydroelectric Development (circa 1952). Lake Pend Oreille has a surface area of about 38,300 ha, 59% of which is considered to be deep water habitat (>15m) suitable throughout the year for kokanee (Paragamian et al. 1991).

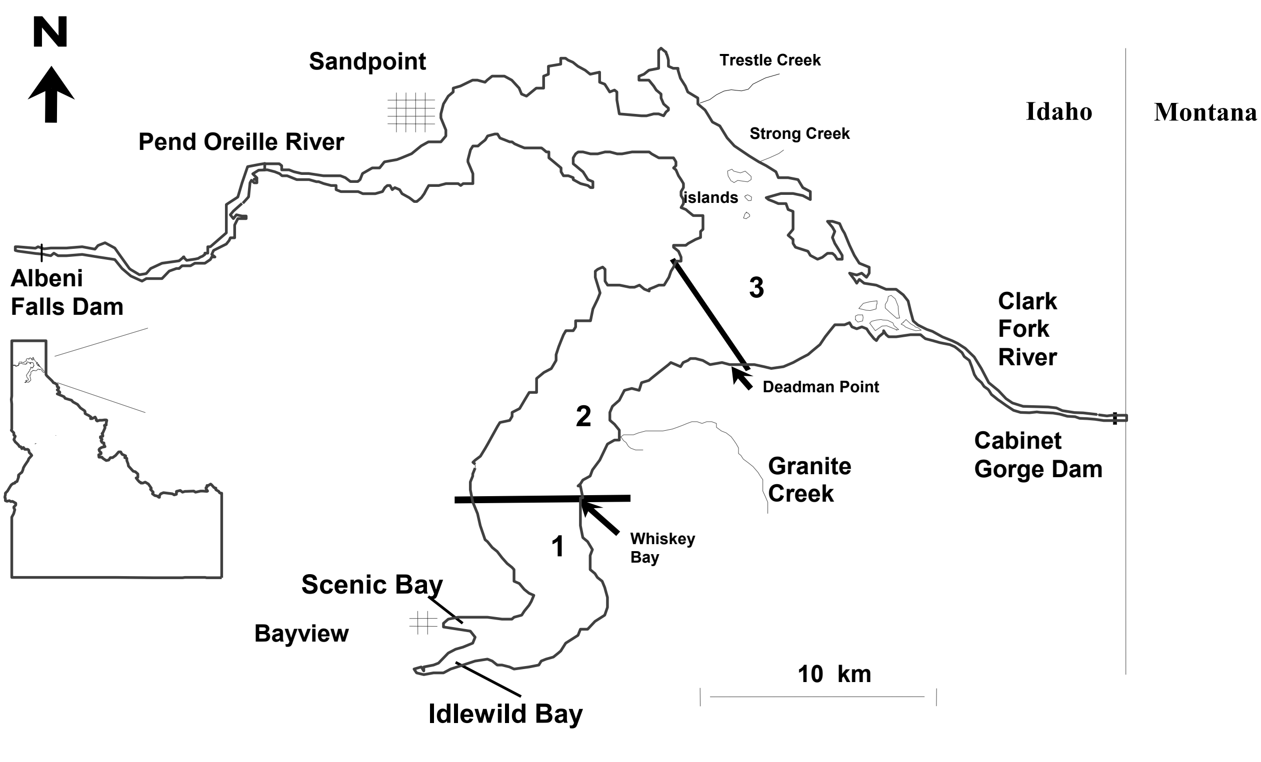

Figure 1.1. The Lake Pend Oreille study area in northern Idaho, showing samplng sections (1-3)

Objective One

POPULATION DYNAMICS

INTRODUCTION

Understanding the influence of a particular fish species upon its ecosystem involves examining each of the component parts. Multiple species must be addressed in ecosystem approaches to fisheries management; otherwise assessing individual populations can be unrealistic and misleading. Growth characteristics of each species, including length at age, weight at age, and mortality, in addition to population estimates are essential components to a thorough understanding of population dynamics. Based on sampling concerns expressed by Everhart and Youngs (1981) four major constraints are apparent in pelagic waters: 1) sampling fishes using traditional methods (electrofishing, gillnetting, trap nets, or set lines) is not always effective. Angling, in some cases, may be the only feasible sampling technique within the constraints of the project. However, without proper planning, angling may not be efficient. 2) Standardizing a mark-recapture study that can be used on multiple species is only possible if the same tag (methods) can be safely applied and retained by each species through the recapture effort. 3) Special considerations must be made when dealing directly or indirectly with threatened or endangered species. 4) Often, research involves or requires the cooperation of anglers, the media, and a variety of other constituents which demands special social, political, and economic organization. All of these constraints were factored into my assessment of the population abundance of large salmonid predators in Lake Pend Oreille.

Objective 1. Estimate population abundance of kamloops, bull trout, and lake trout ≥ 406 mm in Lake Pend Oreille, Idaho.

METHODS

To tag sufficient numbers of fish, I relied on an extensive recruitment and training program of volunteer anglers. I trained anglers and charter boat captains to apply spaghetti tags to kamloops, bull trout, and lake trout ≥ 406 mm fork length between April 1997 and April 1999. Spaghetti tags were used because of their potential ease of application, high retention, and high detectability by anglers who may recapture them. Anglers were instructed to tag only kamloops, bull trout, and lake trout ≥ 406 mm fork length because this is believed the minimum size above which all three species regularly consume kokanee (Anderson 1978; Pratt 1984; Rieman and Falter 1981). Training sessions and fishery technicians accompanying fishing boats have been effectively used to tag large predatory fishes and assure minimal tag loss in other Idaho lakes using similar methods (P. Janssen and J. Fredericks, Idaho Department of Fish and Game, pers. comm.). Once netted, fish were placed in an aerated live well, examined for previous tags, and tagged through the muscle under the dorsal surface of the back posterior to the dorsal fin. Fatigue from capture proved sufficient to immobilize fish without the need for anesthetic. One person was able to safely and accurately follow the tagging protocol, following a detailed training session. Tag number, fork length, species, approximate location of catch, depth of catch, date of catch, and name of angler were recorded. Fish were allowed to recover and then gently released. Fish that appeared injured or in poor condition were not tagged.

Anglers fished all portions of Lake Pend Oreille (Figure 1.1) throughout the study and used a variety of angling techniques depending on weather conditions and time of the year. To assure quality data collection and to keep participants motivated, regular contact was made with each of the volunteers including: frequent phone calls, visits to marinas, and accompanying volunteers on tagging trips.

In addition to relying on anglers to mark and recapture lake trout, a gillnetting effort was conducted during daylight hours November 1-4, 1998. Nets were fished for 30 minute durations on the lake bottom in 10 to 30 m of water. Monofilament nets were approximately 16 m long by 3 m deep, and mesh sizes started at 50 mm and increased by 12 mm increments every 3 m of net length to a maximum of 100 mm diameter. Locations were chosen in areas of traditionally high lake trout catch rates: the islands along the northern side of the lake, the mouth of the Clark Fork River west to Deadman Point, and Whiskey Bay (Figure 1.1).

Population abundance was not estimated for northern pikeminnow *Ptychocheilus oregonensis* because of a lack of willingness among anglers to release fish, however other data were collected to assess population structure. Length at age, weight at age, catch rates, and stomach samples (Objective 2) were collected from northern pikeminnow ≥ 100 mm using electrofishing in areas of known kokanee spawning along the lake shore (Maiolie and Elam 1993), and with angling through the 'Summa Fun' Squawfish Derby hosted by the Lake Pend Oreille Idaho Club (LPOIC) from May 23 to August 23, 1998. Electrofishing surveys were performed weekly in June shortly after the peak kokanee emergence in Lake Pend Oreille (Mallet 1968), at monthly intervals until October prior to adult kokanee spawning, then weekly through November. One site was located along the northern portion of the lake (Trestle Creek to Strong Creek) and two in the southern portion (Scenic Bay and Idlewilde Bay; Figure 1.1). Electrofishing surveys began after dark and lasted until approximately 8 km of the shoreline were sampled (4-5 hours). All fish captured were identified, measured, and stomach samples collected. Incidental kamloops and bull trout captured were tagged and/or stomach samples collected (Objective 2).

A recapture effort for kamloops was performed during November 1998 because of traditionally high catch rates during this time and included several techniques. Catch information was collected by angler surveys and voluntarily returned survey cards. Angler surveys were performed by trained technicians at main marinas, boat launches, and the IDFG Chilco check station on U.S. Highway 95. Additional catch information was acquired from the annual LPOIC Thanksgiving Challenge Derby November 21 through 29, 1998. Survey cards were distributed with each derby entry ticket and cash drawings after the derby encouraged survey card returns. Catch information included number of hours fished, number of kamloops, bull trout, and lake trout caught and length of each fish, location of catch, date of catch, and tag number from marked fish that were caught. Angler surveys were conducted throughout the derby by trained technicians at marinas and boat launches along the north, middle, and south portions of the lake. Fish collected in November were pooled and treated as a single recapture effort.

A Chapman's estimator was used to estimate population abundance (Ricker 1975):

$$\hat{N} = \frac{(m+1)(c+1)}{r+1} - 1$$

where: $\hat{N}$ = Estimated population abundance

m = Marked fish in the population at time of population estimate

c = Captured fish during recapture effort

r = Recaptured fish during the recapture effort

Approximate 95% confidence intervals:

$$\left[\frac{\hat{N}}{1+\hat{N}\,(1.96SE)} \, , \, \frac{\hat{N}}{1-\hat{N}\,(1.96SE)} \right]$$

where: $\hat{N}$ = Estimated population abundance

SE = Standard Error

$$SE = \sqrt{\text{Variance } 1/\hat{N}}$$

$$\text{Variance } 1/\hat{N} = (\hat{N} - c / \hat{N} - 1) * c*p*q/(c*m)^2$$

where: $\hat{N}$ = Estimated population abundance
c = Captured fish during recapture effort
p = r/c
q = 1-p
m = Marked fish in the population at time of population estimate

Main assumptions of this model are:

1. No mark is lost
2. Homogeneity of capture probability for all animals
3. Homogeneity of survival for all animals in the population
4. Random distribution or sampling
5. All marks are recognized and reported
6. Negligible amount of recruitment during the time the recoveries are being made

A recapture effort for bull trout was performed from August 20 – November 4, 1998 using weirs, operated on bull trout spawning tributaries, and gillnet sampling. Weirs located on Trestle Creek and East Fork of Lighting Creek (8-20-98 to 10-29-98) were monitored by U.S. Forest Service personnel. Only fish passing the weirs on their downstream migration were used for the recapture effort. Data from a gill net effort (11-1-98 to 11-4-98) provided additional recapture information for bull trout. Methods used for this effort were identical to those previously described for lake trout.

Results from weirs and gillnetting efforts in the fall of 1998 were pooled and treated as a single recapture effort, and abundance estimates were calculated similar to kamloops.

A recapture effort for lake trout was performed during the annual LPOIC Annual Spring Challenge Derby April 25 – May 1, 1999, because of traditionally high catch rates during this time. Catch information was collected by voluntarily returned survey cards and angler surveys, and included number of hours fished, number of kamloops, bull trout, and lake trout caught and length of each fish, location of catch, date of catch, and tag number from recaptured fish. Survey cards were distributed with each derby entry ticket and cash drawings after the derby encouraged survey card returns. Angler surveys were conducted throughout the derby by trained technicians at marinas and boat launches along the north, middle, and south portions of the lake. Fish collected during the derby were pooled and treated as a single recapture effort and abundance estimates were calculated similar to kamloops.

Mortality was estimated for kamloops, bull trout, lake trout, and northern pikeminnow using numbers of fish in each age cohort. Numbers of fish per age class were converted to natural log and plotted against age (determined from scale and/or otolith readings). Instantaneous mortality (Z) was estimated from the slope of the descending limb (Appendix Table 1.9; Ricker 1975). Instantaneous mortality incorporates the effects of both natural mortality and harvest, although separate measurements of each could not be calculated. All kamloops, bull trout, lake trout, and northern pikeminnow sampled in Lake Pend Oreille were used to estimate mortality per species. To account for the potential differences in mortality due to the 'meta-population' structure of bull trout found in Lake Pend Oreille (B. Rieman, U.S. Forest Service, pers. comm.) a weighted mortality estimate was calculated for bull trout. Mortality was weighted (by tributary) for bull trout sampled in Granite Creek, Trestle Creek, East Fork of Lighting Creek, and the Clark Fork River (Appendix Table 1.9). Numbers of marked fish alive at the time of the recapture effort were calculated using daily survival rates

(Appendix Table 1.9). Survival was summed between the day each fish was tagged to the start of the recapture effort to provide a more accurate estimate of total marked fish alive at the start of the recapture effort.

Estimates of population abundance, length at age, and mortality for kamloops, bull trout, lake trout, and northern pikeminnow were used to determine the population structure of each species. Incremental growth (length and weight) by age cohort was calculated for kamloops, bull trout, lake trout, and northern pikeminnow by subtracting the growth (length or weight) between subsequent years (Appendix Table 1.9). Population abundance of each age cohort $\geq$ 406 mm of kamloops, bull trout, and lake trout was calculated using the instantaneous mortality to adjust $\hat{N}$ (Appendix Table 1.9). Standing crop for each age class of kamloops, bull trout, and lake trout $\geq$ 406 mm was calculated by multiplying the estimated number of individuals in each age class by the mean weight of an individual fish in that age class (Appendix Table 1.9). Total biomass of each predator $\geq$ 406 mm was calculated by summing the standing crop from each age cohort $\geq$ 406 mm (Appendix Table 1.9). Density estimates were calculated by dividing the area of kokanee habitat (22,564 ha) by $\hat{N}$ for kamloops, bull trout, and lake trout.

Scales were primarily used to age kamloops, bull trout, and northern pikeminnow, whereas otoliths were primarily used to age lake trout. Scales were collected from kamloops, bull trout, lake trout, and northern pikeminnow dorsally to the lateral line and posterior to the dorsal fin using techniques described by Nielsen and Johnson (1985). Using a blunt knife, scales were loosened by quickly and firmly scraping toward the head. Six to 12 scales were collected from each fish and sealed in a coin envelope labeled with the date, species, fork length, capture location, and general information about the visual condition of the fish: post spawn, hooking scars, healthy appearance, etc. Otoliths were collected from mortalities accrued during the sampling procedures by first removing the lower jaw from the fish, then cutting longitudinally into the skull across the insertion of the second gill arch, which aided in breaking the skull to expose the otoliths where they could be removed with forceps.

Scales were prepared by pressing 6 to 12 individual scales between two glass microscope slides then taping the sides together. Kamloops and bull trout otoliths were viewed without special preparations, whereas lake trout otoliths required additional preparation. Lake trout otoliths were stored for approximately 4 weeks in a 95% ethol alcohol and 5% glycerin solution. Immediately before viewing, otoliths were coated with a thin layer of clove oil, which lightly stained the surface of the otolith accentuating the annuli. Sandpaper (# 400) was used to lightly remove excessive calcium deposits from the surface of some otoliths. A representative sample of lake trout otoliths was sent to the Pacific Biological Station in Nanaimo British Columbia, Canada to confirm my aging.

Scales were viewed using a microfiche reader, whereas otoliths were viewed using a dissecting microscope equipped with an ocular micrometer. Areas of relatively slower growth signifying each winter season or the end of one year's growth (annuli) were counted to determine age. Aging techniques and backcalculating length at age measurements for scales are described by Nielsen and Johnson (1985) and for otoliths by Hu and Todd (1981). Distances were measured from the center of the focus of scales and otoliths along a consistent line to each annuli and to the anterior margin.

To confirm accurate aging of scales, otoliths were also aged from harvested fishes and angling mortalities. Scales and otoliths were read a minimum of twice, then a subsample of 10% was read again and compared to previous readings for precision.

I quantified annual growth increments (length at age) for all species (Appendix Table 1.9). I assumed a proportional relationship between total length of the fish and radius of the scale or otolith and used the following model to backcalculate length at age (Weisberg and Frie 1987):

$$L_i = L_c * A_d / S_c$$

where: L_i = length of fish at age 'i'

L_c = length of fish at capture

A_d = distance from focus to annuli at age 'i'

S_c = length from scale focus to scale margin.

Weight at length estimates were collected from random kamloops, bull trout, lake trout, and northern pikeminnow collected throughout the study. Fish were weighed by trained technicians at marinas around the lake on scales certified to read accurately to the nearest 30 g.

I determined catch per unit effort (CPUE) using angling effort throughout the project. Angling effort was pooled from anglers of various skills, and included efforts by anglers to target each species individually.

RESULTS

Kamloops

A total of 449 kamloops was tagged in Lake Pend Oreille, and 39 were recaptured between April, 1997 and October, 1998. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (November 1 –31, 1998) an estimated 331 marked kamloops were alive. There were 16 recaptures among the total 747 fish caught. The estimated abundance of kamloops on November 1, 1998 was 14,607 with a 95% confidence interval of [10,100**,** 26,381]. Estimated density per area, of kamloops was 0.64 kamloops/ ha, while estimated biomass per unit area was 2.2 kg/ha. Marked and recaptured fish were distributed throughout the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of kamloops was 186 days and ranged from 8 to 551 days. I found no relationship between distance moved and time between tagging and recapture. The catch rate for anglers pursuing kamloops was 34 hrs/ fish ≥ 406 mm (1997-1998; Appendix Table 1.2).

The average fork length of kamloops sampled in Lake Pend Oreille was 597 mm (Figure 1.2). Kamloops longer than 406 mm FL (431 mm total length) ranged from age 4.5 to 9 (n = 164; Appendix Table 1.6). The oldest fish sampled was 11 years, and the largest incremental growth was at age 4 (111 mm/year), whereas individual years (ages 1 to 11) averaged 87 mm growth/year and ranged from 49 to 111 mm. Kamloops exhibited the lowest annual mortality of all predator fishes examined. Total estimated instantaneous mortality was 0.289 or an annual survival rate of 74.9%. Based on this survival and age-length data, I estimate that age 4 kamloops were the most abundant age class ≥ 406 mm in Lake Pend Oreille (4,452;Table 1.2). I estimated fewer than 1,050 kamloops in Lake Pend Oreille were older than 8 years.

Table 1.1. Numbers of marked and recaptured kamloops, bull trout, and lake trout from Lake Pend Oreille, Idaho, 1997-1998. See Figure 1.1 for section locations.

Kamloops

	Section 1	Section 2	Section 3	unknown locations
Marked	55	110	242	42
Recaptured	0	5	8	26
Total	55	115	250	55

Bull Trout

	Section 1	Section 2	Section 3	unknown locations
Marked	33	32	191	93
Recaptured	3	4	7	29
Total	36	36	198	122

Lake trout

	Section 1	Section 2	Section 3	unknown locations
Marked	52	13	75	25
Recaptured	2	0	2	15
Total	54	13	77	184

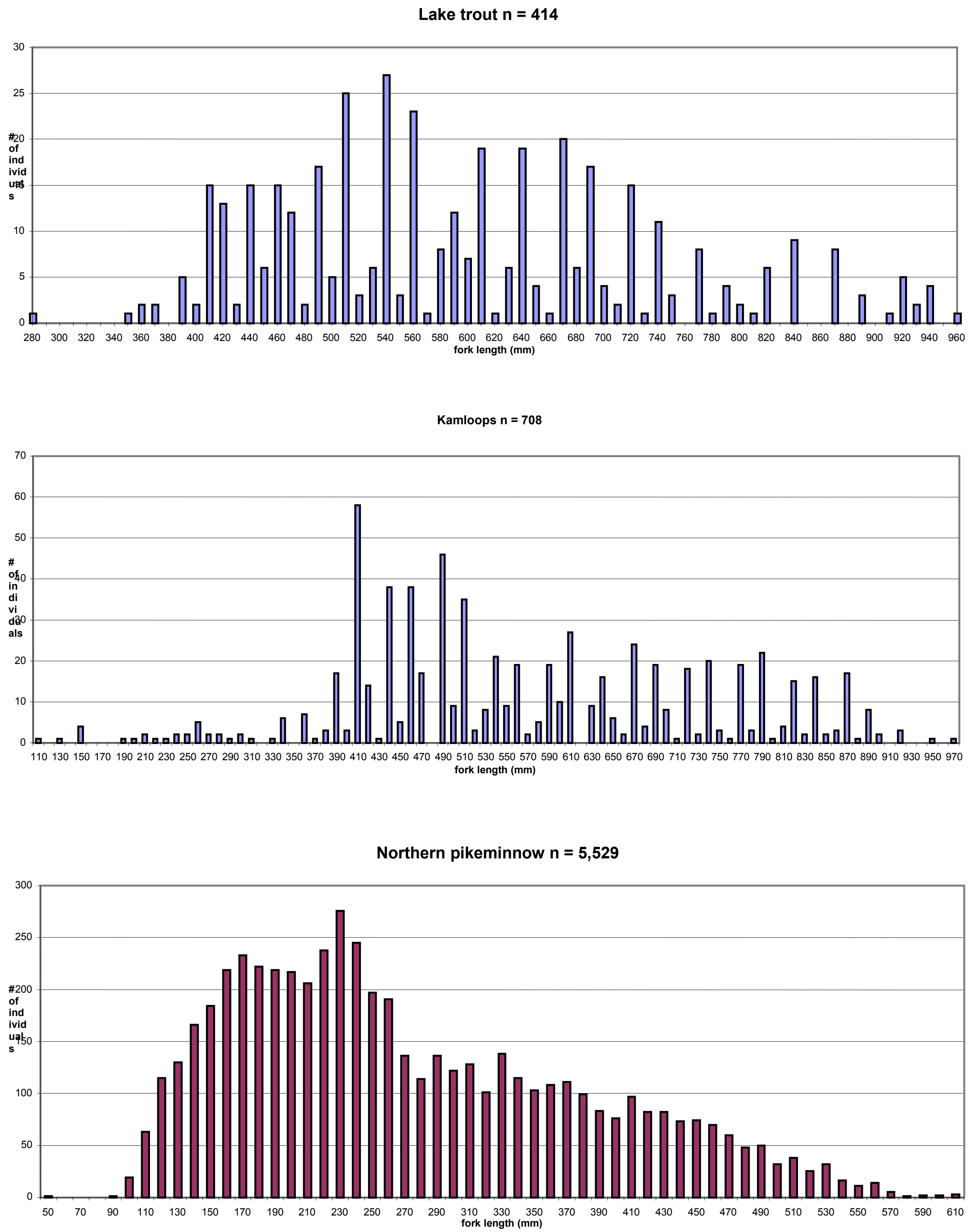

Figure 1.2. Length frequencies for lake trout, kamloops, and northern pikeminnow sampled in Lake Pend Oreille using all gears, 1997-1998.

Table 1.2. Estimated population abundance ($\hat{N}$) and mean length and weight for cohorts of kamloops, bull trout, and lake trout ($\geq$ 406 mm), and northern pikeminnow ($\geq$ 315 mm) including length and weight for each age cohort, Lake Pend Oreille, Idaho, 1997 - 1998. Population abundance was not estimated for northerm pikeminnow.

Kamloops

Age	Length (mm)	Mean weight (g)	$\hat{N}$
4.5*	406	2000	4452
5	495	2832	3335
6	593	3036	2498
7	676	3954	1871
8	735	6586	1401
9	816	8804	1050

Lake trout

Age	Length (mm)	Mean weight (g)	$\hat{N}$
6.75 *	406	934	849
7	427	1180	456
8	493	2235	246
9	564	2917	132
10	627	3808	71
11	700	4527	38

Bull trout

Age	Length (mm)	Mean weight (g)	$\hat{N}$
6	406	150	4347
7	475	540	2876
8	550	1050	1903
9	618	1583	1259
10	686	2222	833
11	754	2861	551
12	822	3500	365

Northern pikeminnow

Age	Length (mm)	Mean weight (g)
6	315	114
7	356	284
8	392	397
9	427	624
10	450	851
11	501	1078

* Adjusted based on predatory size.

Bull trout

A total of 349 bull trout was tagged in Lake Pend Oreille, and 43 were recaptured between April, 1997 and September, 1998. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (September 4 – November 4, 1998) an estimated 224 marked bull trout were alive. There were 14 recaptures among the total 808 fish caught. The estimated abundance of bull trout on September 4, 1998 was 12,134 with a 95% confidence interval of [8,252, 22,915]. Estimated density per area, of bull trout was 0.54 bull trout/ ha, while estimated biomass per unit area was 0.38 kg/ha. Marked and recaptured fish were distributed throughout the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of bull trout was 118 days and ranged from 3 to 387 days. I found no relationship between distance moved and time between tagging and recapture. Anglers pursuing kamloops caught bull trout ≥ 406 mm every 102 hrs; anglers pursuing lake trout caught bull trout ≥ 406 mm every 23 hours (1997-1998; Appendix Table 1.2).

The average fork length of bull trout sampled in Lake Pend Oreille was 524 mm (Figure 1.3). Bull trout longer than 406 mm FL (431 mm total length) ranged from ages 6 to age 11 (n = 14; Appendix Table 1.7). The oldest fish sampled was 13 years, and the largest incremental growth was at age 4 (85 mm/year); individual years (ages 1 to 12) averaged 68 mm growth/year and ranged from 49 to 85 mm.

Bull trout exhibited an annual mortality rate higher than kamloops and northern pikeminnow but lower than lake trout. Total estimated instantaneous mortality was 0.413 or an annual survival rate of 66.2%. Based on this survival and age-length data, I estimate that age 6 bull trout were the most abundant age class ≥ 406 mm in Lake Pend Oreille (4,347;Table 1.2). I estimated fewer than 3,008 bull trout in Lake Pend Oreille were older than 8 years.

Lake trout

A total of 165 lake trout was tagged in Lake Pend Oreille, and 19 were recaptured between April 1997 and April 1999. The majority of fish tagged and recaptured were collected by angling (Appendix Table 1.2). At the beginning of the recapture effort (April 24 – May 2, 1999) an estimated 65 marked lake trout were alive. There were 5 recaptures among the total 162 fish caught. The estimated abundance of lake trout on April 24, 1999 was 1,792 with a 95% confidence interval of [1,054, 5,982]. Estimated density per area of lake trout was 0.08 lake trout/ ha, while estimated biomass per unit area was 0.1 kg/ha. Marked and recaptured fish were distributed widely in the lake (Table 1.1). Movement of tagged fish varied from less than 1 km to over 30 km. The median number of days between initial tagging and recapture of lake trout was 297 days and ranged from 15 to 667 days. I found no relationship between distance moved and time between tagging and recapture. The catch rate for anglers pursuing lake trout was 14 hrs/ fish ≥ 406 mm (1997-1998; Appendix Table 1.2).

The average fork length of lake trout sampled in Lake Pend Oreille was 605 mm (Figure 1.2). Lake trout longer than 406 mm FL (442 mm total length) ranged from ages 6.75 to 11 ($n = 110$). The oldest fish sampled was 13 years, and the largest incremental growth was at age 10 (73 mm), whereas individual years (ages 1 to 10) averaged 64 mm growth/year and ranged from 47 to 73 mm.

Lake trout exhibited the highest annual mortality of all predator fishes examined. Total instantaneous mortality was 0.620 or an annual survival rate of 53.8%. Based on this survival and age-length data, I estimate that age 6 lake trout were the most abundant age class ≥ 406 mm in Lake Pend Oreille (849; Table 1.2). I estimated fewer than 110 lake trout in Lake Pend Oreille were older than 8 years.

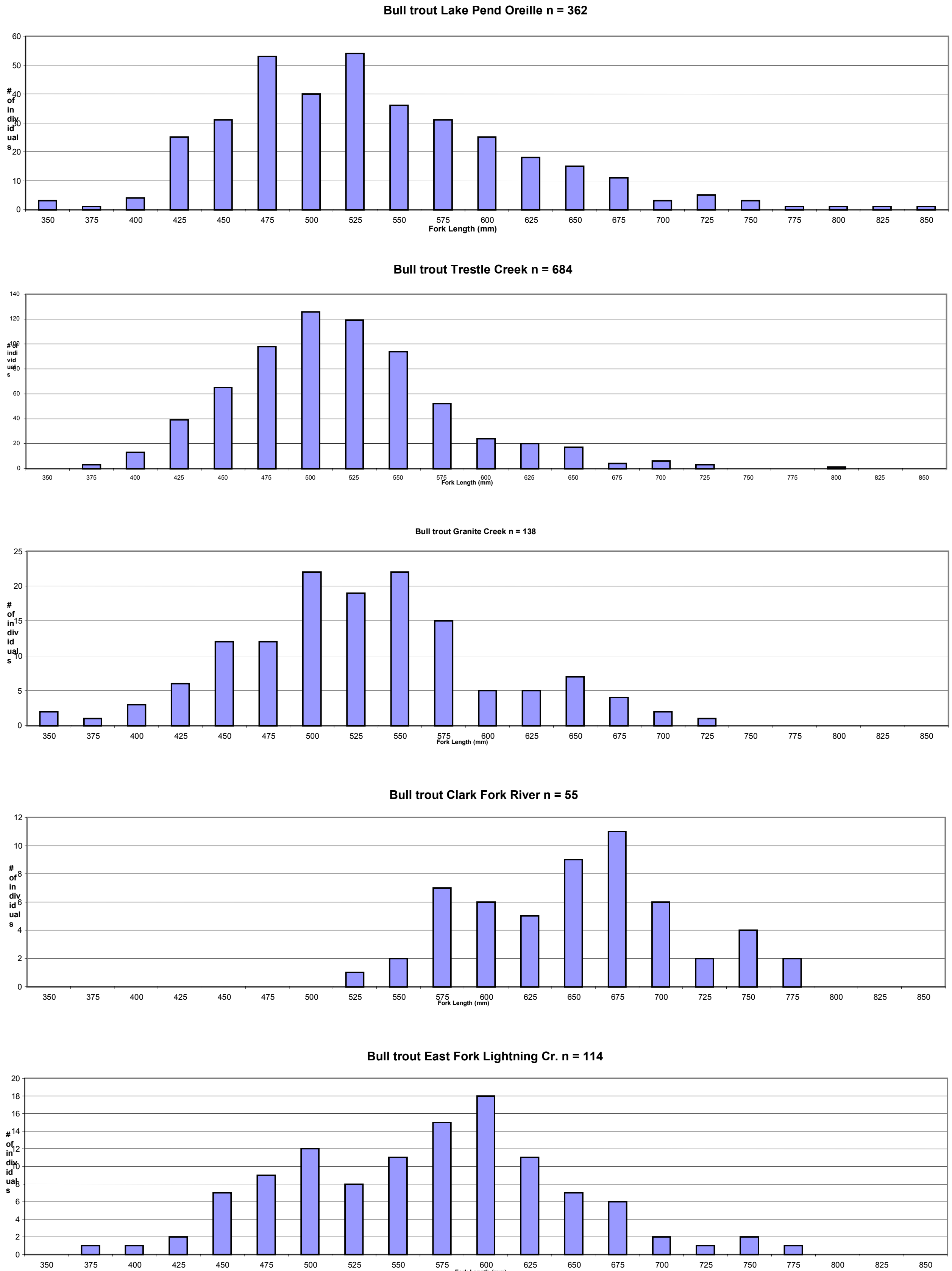

Figure 1.3. Length frequency of bull trout sampled in Lake Pend Oreille, Granite Creek, Trestle Creek, East Fork Lighting Creek, and Clark Fork River, Idaho using all gears, 1997-1998.

Northern pikeminnow

A total of 5,529 northern pikeminnow was sampled in Lake Pend Oreille between April 1997 and December 1998. The majority of fish were collected by angling. Population abundance was not estimated for northern pikeminnow because of a lack of willingness among anglers to release fish; however, relative to the abundance of other pelagic predator fishes caught by anglers for this project (kamloops, bull trout, and lake trout) northern pikeminnow were the least abundant (Appendix Table 1.2). Relative to the abundance of other littoral predator fishes collected by electrofishing (smallmouth bass *Micropterus dolomieu*, yellow perch *Perca flavescens*, pumpkinseed *Lepomis gibbosus*, bullhead *Ameiurus* spp., and sculpin *Cottus* spp.) northern pikeminnow were the most abundant (Appendix Table 1.3). The catch rate for anglers pursuing northern pikeminnow was 0.8 hrs/ fish (1997-1998; Appendix Table 1.2).

The average fork length of northern pikeminnow sampled in Lake Pend Oreille was 268 mm (Figure 1.2). Northern pikeminnow longer than 305 mm ranged from ages 6 to 12 (n = 227; Appendix Table 1.8). The oldest fish sampled was 13 years, and the largest incremental growth was observed at age 1 (66 mm). From ages 1 to 12, growth averaged 42 mm/year and ranged from 14 to 66 mm.

Northern pikeminnow exhibited an annual mortality similar to that of kamloops ($Z = 0.31$ and $S = 0.73$). Based on this survival and age-length data, I observed that fish < 305 were more abundant than fish ≥ 305 mm (Figure 1.2).

Other fishes

A total of 1,319 other fishes were sampled between April 1997 and December 1998 in Lake Pend Oreille. The majority of these were collected by electrofishing and gillnetting (Appendix Tables 1.3 and 1.4). Length frequencies for yellow perch, smallmouth bass, pumpkinseed, sculpin, bullhead, redside shiner *Richardsonius balteatus*, cutthroat trout *O. clarki*, and lake whitefish appear to be within expected ranges (Carlander 1969; Appendix Figures 1.1 to 1.2).

DISCUSSION

Low recapture rates demonstrate a difficulty with performing a mark-recapture study on a large system. Public education, weather conditions, and angler compliance proved to be the most important and challenging variables during this project. Return rates of marked fish throughout the project suggest the willingness of some anglers to participate and their potential to assist in making population estimates for trophy-sized sport fishes. Angler returns of tagged predatory fishes have been effectively used in Payette Lake (P. Janssen, Idaho Department of Fish and Game, pers. comm.) and Upper Priest Lake (J. Fredericks, Idaho Department of Fish and Game, pers. comm.) to estimate population abundance of lake trout.

Highly variable catch rates for lake trout throughout the year and negative angler attitudes toward releasing lake trout made tagging large numbers of lake trout difficult. Since 1995, IDFG personnel have encouraged lake trout harvest to reduce predation pressure on kokanee. My intention was to recapture 5% of the marked population (Ricker 1975). During the recapture effort used to estimate population abundance, I recaptured 5% of the marked kamloops (n = 16), 6% of the marked bull trout (n = 14), and 8% of the marked lake trout (n = 5). However, throughout the entire sampling period 39 kamloops, 42 bull trout, and 19 lake trout were recaptured. Mortality estimates used to calculate population estimates incorporated both natural mortality and mortality due to angling; estimates of annual mortality incorporate seasonal fluctuations due to angling.

In Lake Pend Oreille, anglers showed some preferences toward particular locations. However, I found no consistent trends in movements of pelagic predators. Distances traveled by marked fish between original capture and recapture showed that movements > 30 km are common.

The condition of tagged fish after recapture, including tagging scars, appeared good. Tagging wounds on kamloops healed the soonest but took longer to heal on lake trout and bull trout. I found no evidence that tagging reduced survival, no fish were found dead attributable to tagging. Angling mortalities were occasionally observed floating, volunteers were instructed to net and examine these fish for tags. To minimize potential tagging mortality, anglers were instructed not to tag fish which appeared injured or unhealthy, and were extensively trained to correctly handle fish. I assume that tagged fish behaved similarly and were recaptured proportionally to untagged fish.

Kamloops

Previous studies have recorded growth characteristics of kamloops > 431 mm total length, although mark and recapture techniques have never been used to estimate the abundance of kamloops > 431 mm total length in Lake Pend Oreille. Ellis and Bowler (1981) used total catch, survival and escapement estimates to model an approximate population of 8,252 kamloops > 431 mm total length in Lake Pend Oreille. No other known estimates exist for kamloops in Lake Pend Oreille.

I compared previous growth characteristics to my estimates of growth increments, age at first spawn, mortality, average weight and length, and CPUE for kamloops > 431 mm total length. Growth characteristics of kamloops collected in Lake Pend Oreille 1997-1998 indicated similar but slower growth than fish collected in 1972-1976 (Anderson 1978) and 1983-1984 (Pratt 1985). Kamloops in 1997-1998 had a slower growth and spawned at an earlier age than fish in 1972-1976 and 1983-1984 (Appendix Tables 1.5 and 1.6). Declining growth rates can result in changes to other life history traits, such as maturation and reproductive patterns (Sogard 1994). Other researchers used catch curves to estimate annual survival for kamloops > 431 mm similar to my techniques. Ellis and Bowler (1981) estimated annual survival for kamloops in Lake Pend Oreille at 40%, Pratt (1984) estimated annual survival between 52 and 69%, and my research (1997-1998) estimated survival at 75%. Creel surveys 1960 – 1983 estimated an average length of kamloops $\geq$ 406 mm for most years ranged from 587 to 693 mm (Hoelscher 1992; Figure 1.4), compared to an average 622 mm total length in my study. Average weight of kamloops in Lake Pend Oreille from 1960 - 1983 ranged from 3.6 to 5.4 kg/fish, whereas in my study average weight was 5.4 kg/fish (Figure 1.4). Catch rates from 1960 - 1983 for anglers targeting trophy kamloops (> 431 mm total length) ranged from 59 to 165 hours/fish, as compared to catch rate which averaged 34 hours/fish in my study (Figure 1.5).

Furthermore, an analysis of catch rates during fishing derbies 1997 - 1999 reported catch rates that ranged from 21 to 56 hours/fish (Idaho Department of Fish and Game, unpublished data). Despite these differences, catch rates of kamloops in 1997 - 1998 seemed to resemble those since the early 1960's. Successful local angling techniques coupled with strong catch and release ethics among most anglers are likely contributing to higher catch rates, lower mortality rates, and higher abundance in 1997-1998.

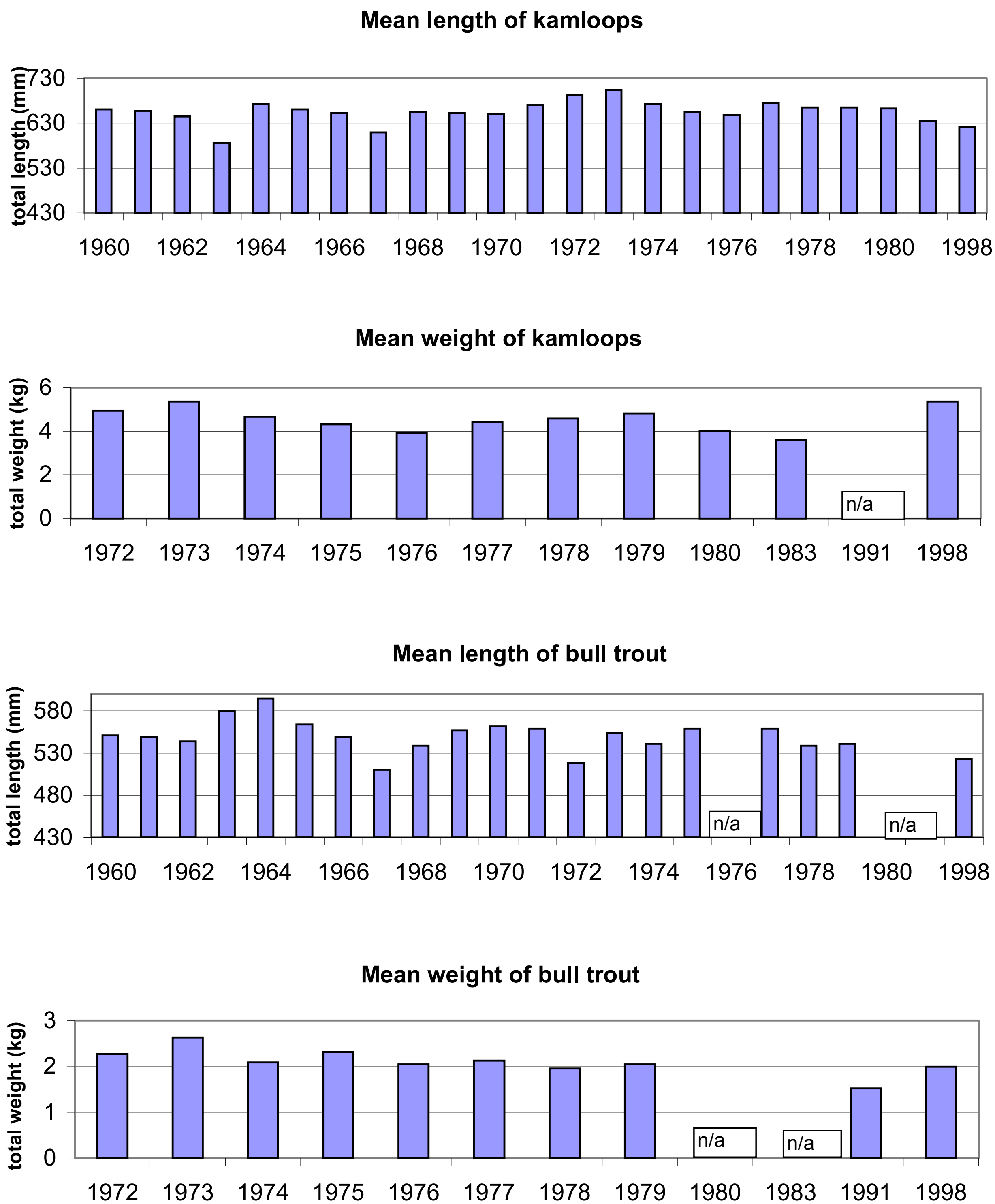

Figure 1.4. Mean length and weight of kamloops and bull trout (> 430 mm TL) in Lake Pend Oreille, Idaho. Data summarized from Hoelscher (1992). Data were not collected every year.

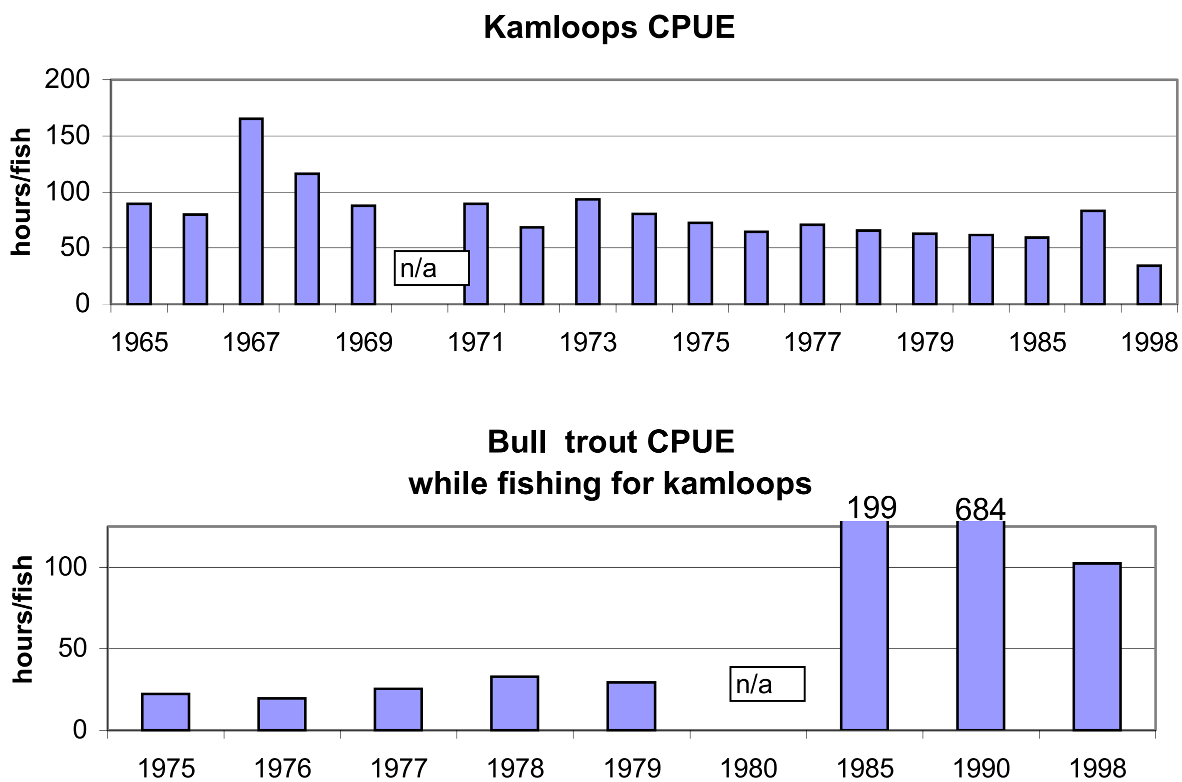

Figure 1.5. Catch Per Unit Effort (CPUE) for kamloops and bull trout (> 430 mm TL) while fishing for kamloops in Lake Pend Oreille 1965 to 1998. Data summarized from Hoelscher (1992).

I expected to see a smaller average length and weight of kamloops compared to earlier studies based on growth, age at spawn, and potential dilution of pure kamloops gene pool due to hybridization and lack of supplementation. Relying on anglers to record much of the data may have biased some of the results, reducing my ability to detect differences in the age and growth of kamloops from earlier studies. My annual mortality and length at age may have been variable due to inaccurate length records. Similar to Pratt's (1984) observations, anglers tended to release fish quickly to avoid stress, potentially resulting in inaccurate length records. Furthermore, continual changes in fishing techniques and technology may aid anglers in locating fish, thus introducing a bias in making comparisons with past years (Rand and Stewart 1998).

Bull trout

Previous studies have recorded growth characteristics of bull trout ≥ 406 mm fork length although mark and recapture techniques have never been used to estimate the abundance of bull trout ≥ 406 mm fork length in Lake Pend Oreille. Hoelscher (1992) used redd counts and average fish/redd to model an approximate escapement of 1,607 to 3,654 adult bull trout in Lake Pend Oreille, 1983 -1987. During this time, the age of first spawning for bull trout was between 4 and 6 years of age (Pratt 1984) similar to my results in 1997-1998.

I compared previous growth characteristics of bull trout to my estimates of growth increments, age at first spawn, mortality, average weight and length, and CPUE for bull trout ≥ 406 mm fork length. I found that bull trout (1997-1998) had slower growth than bull trout in 1983-1984 (Appendix Table 1.7), but spawned at similar ages. Pratt (1984) estimated annual mortality between 47 and 82%; my estimated annual mortality was lower (34%). Creel surveys 1960 – 1983 estimated an average length and weight of bull trout ≥ 406 mm FL for most years, total length for fish ≥ 406 mm ranged from 510 to 594 mm, compared to my average of 523 mm (Figure 1.4). Mean weight (1960 - 1983)

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ranged from 1.5 to 2.6 kg/fish, similar to my calculation of mean weight (2.0 kg/fish; Figure 1.4). Catch rates (1960-1983) for anglers catching bull trout while targeting trophy kamloops ($\geq$ 406 mm FL) ranged from 19.4 to 684 hours/fish, compared to an average of 102.3 hours/fish in my study (Figure 1.5).

Pratt (1984) observed that anglers tended to release fish quickly to avoid stress, potentially resulting in inaccurate length records. Consequently, if this occurred during my study, my estimates of length at age and annual mortality could have been variable. However, my results indicated slightly higher survival, higher population abundance, and the presence of older fish in the population than those of Pratt (1984). Some of these changes are attributable to the no-harvest regulation in the lake and all tributaries since 1996 and a strong catch and release ethic among most anglers.

Lake trout

Previously recorded growth characteristics for lake trout on Lake Pend Oreille are limited because of a small percentage of lake trout in angler catches until recent years. Successful local angling techniques for lake trout in the last 9 years have drawn attention to this fishery, particularly for anglers seeking to harvest fish for consumption. Lake trout were first documented in creel surveys in 1991 when anglers caught 25. The percent of lake trout that were caught and harvested in 1991 was 68% compared to 73% in 1997-1998. Harvest rates on Lake Michigan, where lake trout are highly exploited and rely on supplementation to maintain a fishery, are as high as 71% (Stewart et al. 1983). Average length of lake trout caught in Lake Pend Oreille in 1991 was 654 mm, and the average weight was 3.21 kg. Average length of fish caught in 1997-1998 was 605 mm, and the average weight was 3.30 kg. Weight at age of lake trout (1997-1998) in Lake Pend Oreille is less than that in other systems in the northerwestern United States and southwestern Canada (Appendix Figure 1.3). Similar research was performed on lake trout in Flaming Gorge Reservoir, WY, where annual survival of lake trout averaged 65% (Yule and Luecke 1993) compared to my estimates of 38%. Time between recaptures also varied; Yule and Luecke (1993) reported an average of 42 months between original marking and recapture for lake trout 601 to 800 mm and 51 months for lake trout > 800 mm. My data indicated an average of 10 months between original marking and recapture for lake trout $\geq$ 406 mm, which likely contributed to the nearly double annual mortality rates in Lake Pend Oreille.

Although catch rates for lake trout (14 hours/fish) are higher than those for kamloops (34 hours/fish), the population estimate for lake trout is considerably lower (14,007 kamloops vs 1,792 lake trout). The reason for this I believe is that angling for lake trout is labor intensive and when fishing is slow most anglers will not continue fishing for lake trout, whereas kamloops fishing is relatively easy and anglers will often continue fishing for kamloops when catch rates are low. Another explanation is that areas which are easy for lake trout anglers to fish (gradual sloping bottoms with smaller substrate in less than 40 m of water) seem to hold more lake trout. These areas are uncommon in Lake Pend Oreille; therefore, they may concentrate fish making them more susceptible to anglers.

I suggest that angler attitude encouraging the harvest of lake trout is holding the population at a low level. The lack of older fish in the age distribution suggests that harvest may be reducing the population abundance of lake trout in Lake Pend Oreille.

Northern Pikeminnow

Growth characteristics of northern pikeminnow collected in 1997-1998 indicated similar but smaller growth increments to fish collected in Lake Pend Oreille and Cocolalla Lake, Idaho 1953, 1957, and 1958. Northern pikeminnow in 1997-1998 had a slower growth than fish in 1953, 1957, and 1958 (Jeppson and Platts 1959; Appendix Table 1.8).

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Appendix Table 1.1. Fish species cited by common name and abbreviation in text.

Kokanee	ONE	*Oncorhynchus nerka*
Kamloops	OMY	*Oncorhynchus mykiss*
Cutthroat trout	OCL	*Oncorhynchus clarki*
Bull trout	SCO	*Salvelinus confluentus*
Lake trout	SNA	*Salvelinus namaycush*
Mountain whitefish	PWI	*Prosopium williamsoni*
Lake whitefish	CCL	*Coregonus clupeaformis*
Peamouth	MCA	*Mylocheilus caurinus*
Largescale sucker	CMA	*Catastomus macrocheilus*
Redside shiner	RBA	*Richardsonius balteatus*
Bullhead	AME	*Ameiurus spp.*
Sculpin	COT	*Cottus spp*.
Pumpkinseed	LGI	*Lepomis gibbosus*
Yellow perch	PFL	*Perca flavescens*
Brown trout	STR	*Salmo trutta*
Black crappie	PNI	*Pomoxis nigromaculatus*
Tench	TTI	*Tinca tinca*
Smallmouth bass	MDO	*Micropterus dolemieu*
Northern pikeminnow	POR	*Ptychocheilus oregonensis*

Appendix Table 1.2. Hook and line sampling effort and incidental catch, 1997-1998, while pursuing kamloops,lake trout, and northern pikeminnow, and total effort. Species abbreviations listed in Appendix Table 1.1.

Hook and line effort total

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	978.5	35	5	8	25
1997	1725	41	28	20	32
Total	2703.5	76	33	28	57
cpue hrs/fish		35.6	81.9	96.6	47.4

Hook and line effort while pursuing kamloops

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	911.5	34	4	4	0
1997	1543	38	20	9	2
Total	2454.5	72	24	13	2
cpue hrs/fish		34.1	102.3	188.8	1227.3

Hook and line effort while pursuing lake trout

Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	45	0	1	4	0
1997	160	2	8	11	1
Total	205	2	9	15	1
cpue hrs/fish		102.5	22.8	13.7	205.0

Hook and line effort while pursuing n. pikeminnow

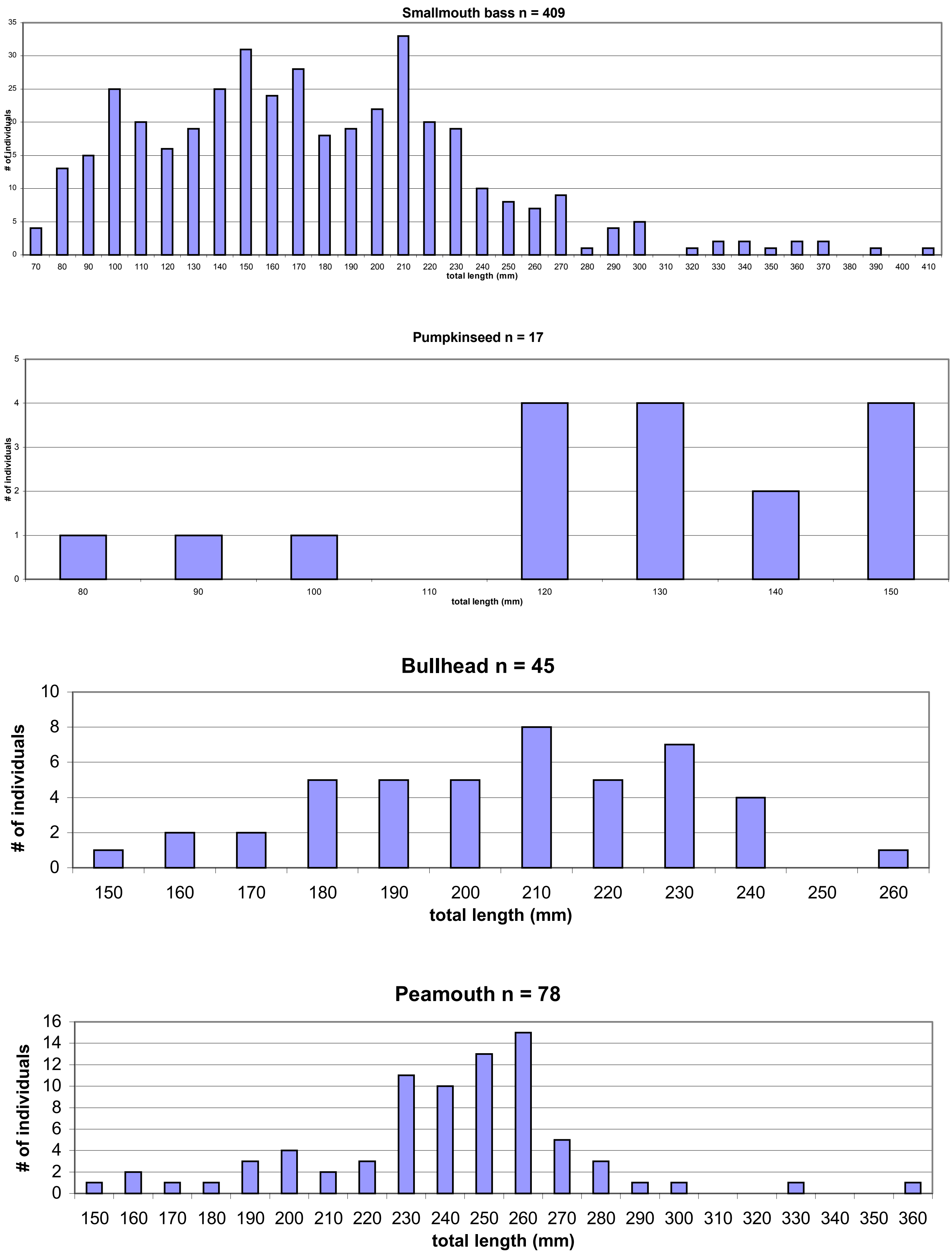
Year	Effort (hrs)	OMY	SCO	SNA	POR
1998	22	1	0	0	25
1997	22	1	0	0	29
Total	44	2	0	0	54
cpue hrs/fish		22	n/a	n/a	0.8

Appendix Table 1.3. Electrofishing catch and catch per unit effort (cpue) for 1997, 1998, and total, Lake Pend Oreille. Species abbreviations listed in Appendix Table 1.1.

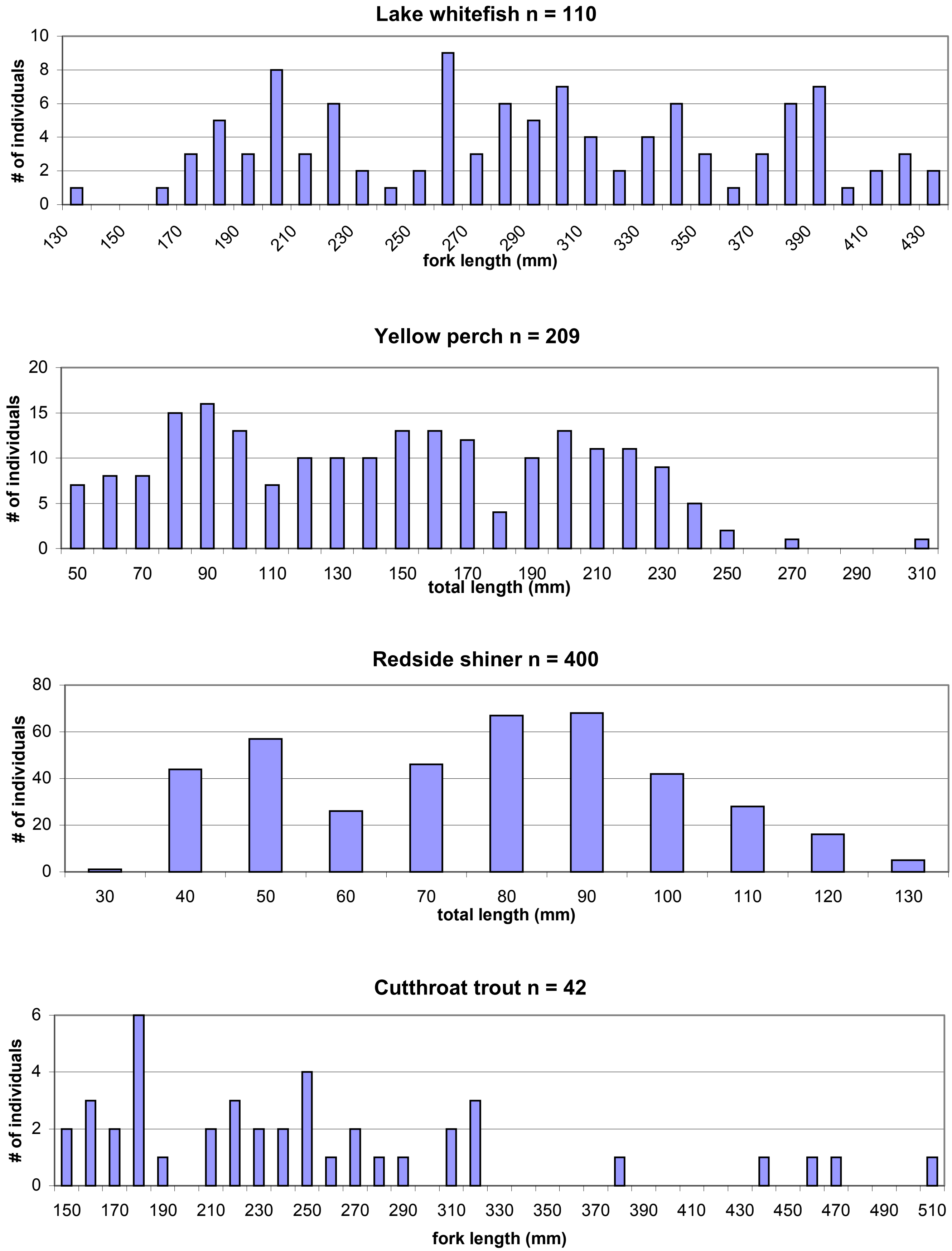
	1997		1998		Total	
Species	catch	cpue (hrs)	catch	cpue (hrs)	catch	cpue (hrs)
POR	671	0.01	2576	0.01	3247	0.01
MDO	28	0.24	410	0.07	438	0.08
PFL	8	0.84	209	0.15	217	0.17
CCL	25	0.27	38	0.80	63	0.59
OCL	11	0.61	49	0.62	60	0.62
AME	1	6.70	45	0.68	46	0.81
MSA	0	0.00	34	0.90	34	1.09
OMY	3	2.23	27	1.13	30	1.24
PWI	1	6.70	25	3.13	26	2.36
LGI	3	2.23	17	1.79	20	1.86
TTI	0	-	13	2.35	13	2.86
COT	0	-	8	3.81	8	4.65
STR	3	2.23	-	-	3	12.40
SCO	0	-	3	10.17	3	12.40
PNI	0	-	2	15.25	2	18.60
Total catch	754		3456		4210	
Total effort (hrs	6.7		30.5		37.2	

Appendix Table 1.4. Gillnet catch and catch per unit effort (cpue) for November 1-4,1998, Lake Pend Oreille, Idaho. Species abbreviations listed in Appendix Table 1.1.

		Species						
	Effort (hours)	SCO	SNA	ONE	CCL	POR	MCA	CMA
Total	2239	4	2	4	57	12	30	1
cpue (hrs/fish)	-	559.8	1119.5	559.8	39.3	186.6	74.6	2239.0



Appendix Figure 1.1. Length frequencies for all smallmouth bass, pumpkinseed, bullhead, and peamouth sampled in Lake Pend Oreille using all gears, 1997-1998.



Appendix Figure 1.2. Length frequencies for all lake whitefish, yellow perch, redside shiner, and cutthroat trout sampled in Lake Pend Oreille using all gears, 1997-1998.

Appendix Table 1.5. Age at first spawn for kamloops collected in Lake Pend Oreille from 1972-1976, 1983-1984 and 1997,1998. Sample sizes are in parentheses.

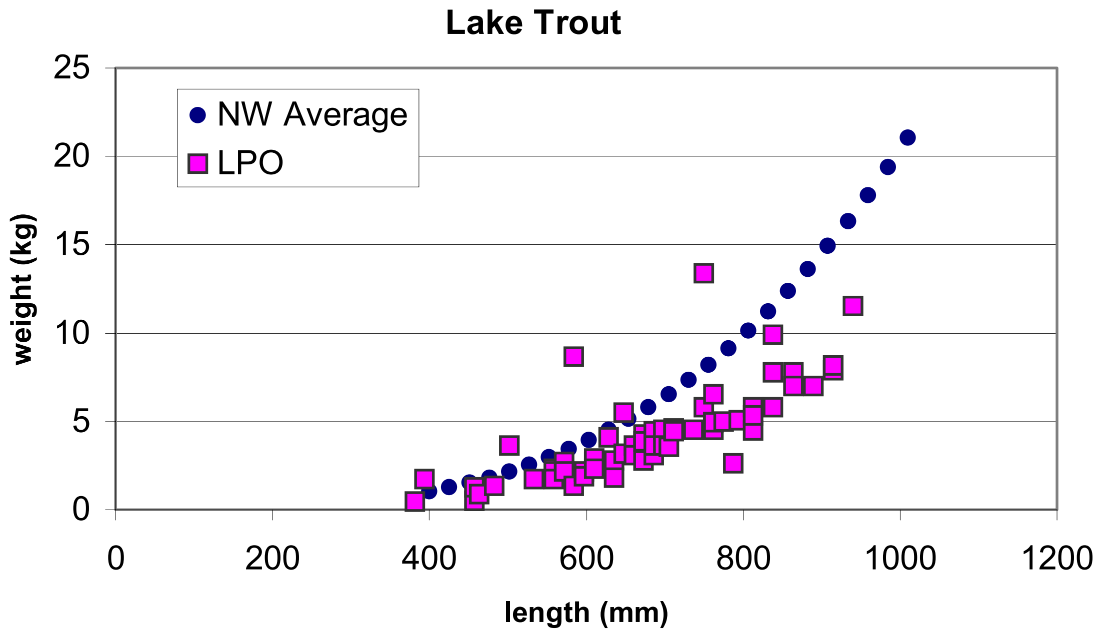
	Age					
Time period	3	4	5	6	7	8
1972-1976	-	1	18	61	20	-
(Anderson 1978)	-	(2)	(24)	(80)	(26)	-
1983-1984	5	19	22	37	17	-
(Pratt 1985)	(3)	(11)	(13)	(22)	(10)	-
1997-1998	-	4	32	26	33	5
	-	(2)	(18)	(15)	(19)	(3)

Appendix Table 1.6. Backcalculated mean length (mm) at age and increments of growth (△) for kamloops in Lake Pend Oreille, Idaho; 1972-1976 (Anderson 1976), 1983-1984, (Pratt 1985) and 1997,1998.

Time	Age										
Length at annulus	1	(△)	2	(△)	3	(△)	4	(△)	5	(△)	6
1972-1976 (Anderson 1978)	80	(63)	143	(146)	289	(145)	434	(191)	625	(154)	779
1983-1984 (Pratt 1985)	78	(83)	161	(128)	290	(156)	446	(116)	562	(101)	662
1997-1998	82	(103)	185	(104)	289	(95)	384	(111)	495	(98)	593

Appendix Table 1.7. Back calculated mean total length (mm) and increments of growth△) at age of bull trout from Lake Pend Oreille, Idaho, 1983 Pratt (1985) and 1997,1998.

		Age																
		1	(△)	2	(△)	3	(△)	4	(△)	5	(△)	6	(△)	7	(△)	8	(△)	9	(△)
Pratt (1985)	1983	91	(75)	166	(110)	276	(117)	393	(105)	498	(60)	558	(n/a)	n/a	(n/a)	n/a	(n/a)	n/a	(n/a)
	1997-1998	72	(49)	121	(54)	175	(71)	246	(85)	332	(70)	401	(74)	475	(74)	550	(n/a)	461	(n/a)



Appendix Figure 1.3. Comparison of weight at length between lake trout in Lake Pend Oreille, Idaho (squares), and the northwestern United States and Canada (circles; Carlander 1969).

Appendix Table 1.8. Estimated mean length (mm) at annulus formation of northern pikeminnow in Lake Pend Oreille, Idaho, for 1997 and 1998, and Lake Pend Oreille and Cocolalla lakes in 1953,1957, and 1958 (Jeppson and Platts1959).

	Age											
Years collected	1	2	3	4	5	6	7	8	9	10	11	12
1997-1998	56	122	178	230	277	315	356	392	427	450	501	515
1953, 1957-1958	89	152	203	267	305	356	381	406	432	483	-	-

Appendix Table 1.9. Equations used in Objective 1.

Estimator; context used	Equation
Instantaneous Mortality (Z); calculated from plot of age frequency	$\ln(n_a) = b + Za$ where: ln = natural log n_a = number of age a fish b = constant Z = instantaneous mortality a = age of cohort
Weighted Mortality (WM); calculated using mortality estimates from multiple locations	$WM = \Sigma n_l m_l / \Sigma n_l$ where: n_l = number of fish at location l m_l = mortality of fish at location l
Annual Survival (S); calculated from Z	$S = e^{-Z}$ where: e = base of the natural log (2.71828)
Daily survival (DS)	$DS = e^{-Z/365}$
Marked fish alive at start of recapture effort (M); using DS applied to days between initial tagging and recapture effort	$M = \sum_{j=1}^{\text{last day}} n_j d_{tr(j)} * DS$ where: n_j = number of fish tagged on day j $d_{tr(j)}$ = days between tagging and recapture of a fish tagged on day j
Population abundance estimate $\hat{N}_a$; for all age cohorts $\geq$ 406 mm	$\hat{N}_{age} = \hat{N}_{Initial} * e^{-Z(a-initial)}$; $\hat{N}_{Initial} = \hat{N}_{Total} / \sum_{i=0}^{\#\text{ of age classes - 1}} e^{-iZ}$ where: $\hat{N}_{Initial}$ = estimated abundance of the youngest age class
Standing Crop (SC_a); standing crop for each cohorts $\geq$ 406 mm	$SC = n_a * w_a$ where: w = mean weight of individual fish in age class i
Biomass (B);	$B_i = \Sigma_a SC_a$
Incremental growth (IG_a); annual growth of average fish in each cohort	$IG_a = L_a - L_{a-1}$ where: L_a = mean length of individual fish in age class i

Objective Two

FOOD HABITS

INTRODUCTION

The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). Kokanee, an important component of the Lake Pend Oreille food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981).

The type, quantity, and choices of prey are important components in understanding the trophic dynamics of predator/prey relationships (Popova 1978). Predatory salmonids in Lake Pend Oreille (kamloops, bull trout, and lake trout) rely heavily on kokanee (Anderson 1978; Pratt 1985; Rieman and Falter 1981). However, no one has assessed the impacts of each of these predators on the kokanee populations in Lake Pend Oreille. Understanding the dynamics of predation on kokanee is especially critical at this time because of the reduced population abundance of kokanee.

Objective 2. Identify food items in the stomachs of kamloops, bull trout, lake trout ≥ 406 mm and northern pikeminnow ≥ 100 mm from Lake Pend Oreille, Idaho.

METHODS

To quantify the importance of kokanee to selected predatory fishes in Lake Pend Oreille, stomach samples were collected from kamloops, bull trout, lake trout ≥ 406 mm, and northern pikeminnow ≥ 100 mm that were sampled mostly by angling throughout 1997 and 1998. Additionally, northern pikeminnow ≥ 100 mm were sampled by electrofishing along the lake shore in areas of known kokanee spawning and through the 'Summa Fun' Squawfish Derby May 23 through August 23, 1998 (Objective 1). The intensity of predation changes with seasonal and ecological conditions (Popova 1978; Garvey et al. 1998); therefore, I collected stomach samples throughout 1997 and 1998 to assess seasonal variability in the diets of selected predatory fishes. Samples were collected from both harvested fish and live fish. Stomach samples were collected from harvested fishes by extracting the entire stomach from the body and stripping the stomach's contents into a sampling bottle, whereas stomach samples were collected from live fishes using lavage techniques. Stomach samples also were taken from all incidental catches of kamloops, bull trout, and lake trout < 406 mm to describe the diets of smaller fishes not thought to be kokanee predators. Lavage techniques (Light et al. 1983; Yule and Luecke 1993) involved inserting a protected tube into a fish's mouth and down the esophagus, then pumping distilled water into the stomach causing the contents to be flushed back up through the mouth, where the contents were collected in a mesh screen to remove excess water and placed in a sampling bottle. All northern pikeminnow were sacrificed for stomach analysis, after determining that lavage techniques were not effective due to the elongated gut in these fish. All stomach samples were preserved in 10% formalin and labeled with species, location of catch, length of predator, and date.

I grouped northern pikeminnow into one of four categories because of the large number of samples. Stomach samples were placed in the following groups depending on the fish's total length: 100 to 149 mm, 150 to 304 mm, 305 to 459 mm, and $\geq$ 460 mm total length.

In the laboratory, trained technicians identified prey items from stomachs to the lowest practical taxonomic level, enumerated, and weighed them (blotted dry weight, mg). Prey of the same taxon were pooled together and weighed as a group. Diagnostic bones, including the opercle, dentary, cleithrum, and/or vertebrae, in addition to external morphological characteristics were used to identify fish. Representative samples of diagnostic bones were collected from common prey species. Fork, total, nape, and/or standard length of prey fish identified in stomach samples were recorded.

Numbers of kokanee consumed/individual kamloops, bull trout, lake trout, and northern pikeminnow were recorded and the average computed. Average length and range of sizes of kokanee consumed by predator fishes were compared to length at age estimates for kokanee (Idaho Department of Fish and Game, unpublished data) to identify age classes of kokanee consumed. Total length (TL) was measured on intact kokanee; however, if kokanee were not intact, I estimated their total length from standard (SL) or nape length (NL) measurements by a model similar to methods used by Madenjian et al. (1998) and Yule and Luecke (1993). I used the relationship TL = SL + 26.5 mm and TL = NL + 51.0 mm, derived from my own corresponding measurements of kokanee 63 to 226 mm, to convert from standard (SL) or nape length (NL) to total length.

RESULTS

Kamloops

I collected 180 stomachs from kamloops that ranged from 275 to 966 mm fork length between May 1997 and November 1998. Approximately 15% (n= 27) were empty. Kokanee were the principal food item of kamloops ≥ 406 mm throughout the year, comprising 76.81% by weight, while other fishes (20.87%), insects (1.66%) and opossum shrimp (0.66%) were of lesser importance. Kamloops < 406 mm fed primarily on insects (61.09%), opossum shrimp (35.4%), northern pikeminnow (3.35%), and redside shiners (0.16%; Table 2.1). An average of 0.63 kokanee (n = 136) were observed /stomach. Kokanee consumed by kamloops ranged from 63 to 226 mm total length and averaged 176 mm (n = 48; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 4.

Bull trout

I collected 11 stomachs from bull trout that ranged from 406 to 583 mm fork length between July 1997 and December 1998. Approximately 27% (n = 3) were empty. Kokanee were the principal food item of bull trout ≥ 406 mm throughout the year, comprising 65.6% by weight, while unidentified salmonid prey (15.75%), non-salmonid prey (5.96%), insects (< 0.01%), and unidentified fish and other material (12.68%) were of lesser importance. An average of 0.5 kokanee (n = 8) was observed/ stomach. The small number of stomachs analyzed precluded further analysis of prey consumed.

Table 2.1. Monthly prey consumption (%) by kamloops ≥ 406 mm fork length and total consumption by kamloops < 406 mm in Lake Pend Oreille, Idaho, 1997-1998. Fish were collected by electrofishing and angling.

Identifiable prey	January	February	March	April (n=7)	May (n=11)	June (n=9)	July (n=11)
Insecta	n/a	n/a	n/a	0.42	5.45	5.54	6.01
Opossum shrimp				0.32			
Larval fish							0.40
Kokanee				99.26	94.55	34.20	39.26
Rainbow trout							41.43
Lake trout							
Bull trout							
Whitefish spp.							
Peamouth							12.90
Redside shiner						60.26	
Northern pikeminnow							

Identifiable prey	August (n=11)	September (n=8)	October (n=17)	November (n=69)	December	Total Fish ≥ 406 mm (n = 142)	Total Fish < 406 mm (n=10)
Insecta	0.02	0.05	0.39	1.15	n/a	1.66	61.09
Opossum shrimp		0.03	0.13	2.13		0.66	35.40
Larval fish						0.01	
Kokanee	39.68	62.77	99.48	71.20		76.81	
Rainbow trout	26.20	36.69		14.41		11.41	
Lake trout				3.57		1.35	
Bull trout	29.65			7.54		5.27	
Whitefish spp.	4.45					0.36	
Peamouth						0.34	
Redside shiner		0.02				2.09	0.16
Northern pikeminnow		0.44				0.03	3.35

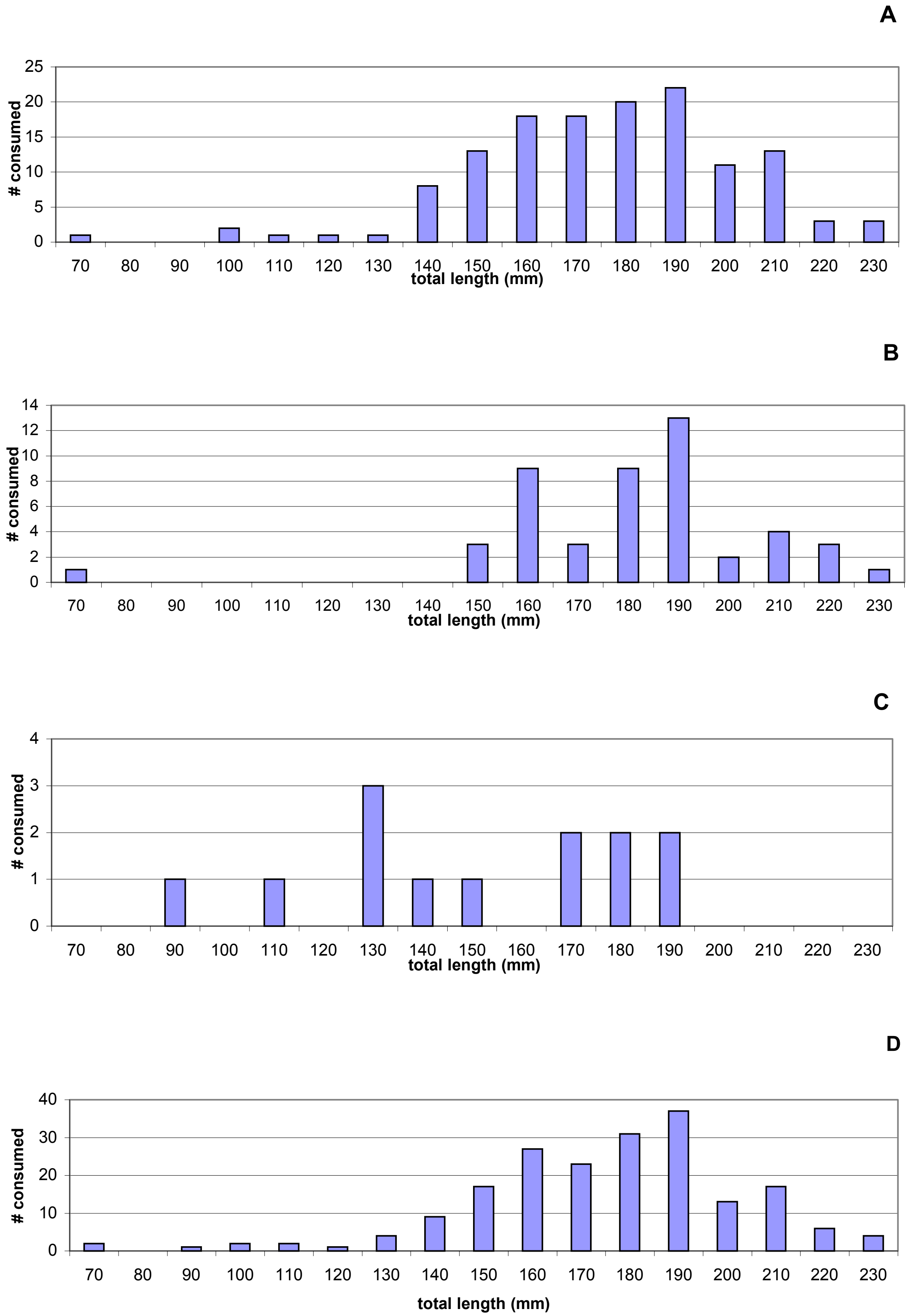


Figure 2.1. Number of kokanee consumed by various length classes of lake trout (A; n=135), kamloops (B; n=48), northern pikeminnow (C; n=13), and all predators (D; n=196) in Lake Pend Oreille, Idaho,1997-1998. Scale on axis are not equal.

Lake trout

I collected 242 stomachs from lake trout that ranged from 307 to 940 mm fork length between April 1997 and December 1998. Approximately 18% (n=42) were empty. Kokanee were the principal food item of lake trout ≥ 406 mm throughout the year, comprising 87.40% by weight, while other fish (12.35%), insects (0.21%), and opossum shrimp (0.04%) were of lesser importance. Lake trout < 406 mm (n = 5) fed exclusively on sculpin 68.4% and opossum shrimp 31.6%; (Table 2.2). An average of 0.88 kokanee (n =204) was observed/ stomach. Kokanee consumed by lake trout ranged from 70 to 225 mm total length and averaged 171 mm (n = 135; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 4.

Northern Pikeminnow

I collected 3,322 northern pikeminnow stomachs from fish that ranged from 100 to 610 mm fork length between June 1997 and December 1998. Approximately 21% (n=695) were empty. Northern pikeminnow consumed a variety of prey items. Insects were the principal food item of northern pikeminnow 100 to 150 mm (87.89%) and 150 to 305 mm (25.56%), while kokanee were the principal food item of northern pikeminnow larger than 305 mm (Tables 2.3 and 2.4). An average of 0.24 kokanee (n =250) was observed/ stomach of northern pikeminnow > 305 mm. Kokanee consumed by northern pikeminnow ranged from 84 mm to 185 mm total length and averaged 145 mm (n = 13; Figure 2.1). This size range of kokanee corresponded with length at age estimates for kokanee of ages 1 to 3.

Table 2.2. Monthly prey consumption (%) by lake trout ≥ 406 mm fork length and total consumption by lake trout < 406 mm fork length in Lake Pend Oreille, Idaho 1997-1998. Fish were collected by electrofishing and angling.

Identifiable prey	January (n=9)	February (n=8)	March	April (n=16)	May (n=20)	June (n=18)	July (n=34)
Insects		0.33	n/a	0.47	1.17		
Opossum shrimp				0.05			
Kokanee	58.71	75.16		79.90	91.46	86.86	91.16
Rainbow trout	17.27			3.63	7.37	8.42	8.84
Lake trout				14.46			
Bull trout							
Whitefish spp.	23.48						
Catostomidae				1.17		4.72	
Centrarchidae				0.32			
Cottidae							
Peamouth	0.53	24.51					
Northern pikeminnow							

Identifiable prey	August (n=20)	September (n=16)	October (n=5)	November (n=28)	December (n=21)	Total Fish ≥ 406 mm (n=195)	Total Fish < 406 mm (n=5)
Insects		0.01	0.04			0.21	
Opossum shrimp		0.13	0.44	0.14		0.04	31.60
Kokanee	85.90	99.85	99.52	82.51	87.54	87.40	
Rainbow trout				1.86	5.48	5.46	
Lake trout	0.09			0.30		0.62	
Bull trout				6.20	3.30	1.50	
Whitefish spp.	14.01				3.15	2.31	
Catostomidae						0.44	
Centrarchidae						0.01	
Cottidae							68.40
Peamouth				8.99		1.95	
Northern pikeminnow						0.05	

Table 2.3. Monthly prey consumption (%) by northern pikeminnow 100 to 150 mm and 150 to 305 mm in Lake Pend Oreille, Idaho. Fish were collected by electrofishing and angling. Sample sizes are in parentheses.

Northern pikeminnow 100-150mm

Identified prey	March (n=11)	June (n=150)	July (n=130)	August (n=110)	September (n=30)	October (n=82)	November (n=46)	Total (n=559)
Insecta	84.90	96.37	99.07	85.11	32.67	7.90	11.40	87.89
Decapoda		0.16				0.30		0.08
Opossum shrimp	14.67						19.39	0.95
Other crustacea		1.08		0.01	58.52	20.66		2.78
Mollusca		1.68	0.46	4.17	8.49	11.88	68.98	4.96
Unidentified salmonids						0.24		0.01
Cottidae						0.07		
Percidae				0.06				
Peamouth						50.12		2.27
Redside shiner				0.28	0.18	0.08		0.01
Northern pikeminnow					0.15	0.02		
Plant items	0.43	0.71	0.47	10.37		8.72	0.23	1.04

Northern pikeminnow 150-305 mm

Identifiable prey	May (n=220)	June (n=1,069)	August (n=250)	September (n=82)	October (n=71)	November (n=24)	Total (n=1,716)
Insecta	81.82	54.71	9.09	2.13	1.35	4.23	25.56
Decapoda	0.07	9.74	24.33	3.09	2.20		6.57
Opossum shrimp		0.08	0.04	25.77		1.14	4.50
Other crustacea	0.54	0.98	0.04		4.36		0.99
Mollusca	1.89	1.96	9.21	40.68	27.62	1.75	13.85
Larval fish				5.70			0.95
Kokanee		8.69	26.69		53.12		14.75
Rainbow trout							
Whitefish spp.		1.65	3.24	0.93		0.31	1.02
Cottidae	9.09	3.55	1.44				2.35
Percidae			4.01				0.67
Peamouth		1.45	2.71		8.59		2.12
Redside shiner	6.39	10.33	4.15	21.27	0.07	86.62	21.47
Northern pikeminnow		2.44	5.89				1.39
Plant items	0.20	4.42	9.18	0.42	2.69	5.95	3.81

Table 2.4. Monthly prey consumption (%) by northern pikeminnow 305 to 460 mm, and > 460 mm in Lake Pend Oreille, Idaho. Fish were collected by electrofishing and angling. Sample sizes are in parentheses.

Northern pikeminnow 305-460 mm

Identifiable prey	June (n=160)	July (n=47)	August (n=91)	September (n=8)	October (n=2)	November (n=4)	Total (n=312)
Insecta	24.78	8.73	1.21	0.03			8.73
Decapoda	11.13	2.59	32.07	20.67	100.00	77.86	23.36
Other crustacea	0.61					0.21	0.18
Mollusca	0.61		10.15	1.58			4.82
Kokanee	51.36	88.22	37.51	77.61			50.88
Rainbow trout		0.01	15.81				6.93
Bull trout	0.01						
Whitefish spp.							
Cottidae							
Peamouth	0.47			0.11			0.15
Redside shiner	0.03					21.70	0.27
Northern pikeminnow	10.18						2.97
Plant items	0.80	0.46	3.26			0.22	1.71

Northern pikeminnow > 460

Identifiable prey	April (n=1)	June (n=37)	July (n=2)	Total (n=40)
Insecta	100.00	99.00	12.00	12.00
Decapoda			3.00	3.00
Other crustacea		1.00		
Kokanee			41.00	41.00
Whitefish spp.				0.00
Plant items			44.00	44.00

Other fishes

I collected 782 stomachs from sculpin, bullhead, pumpkinseed, smallmouth bass, yellow perch, and cutthroat trout between June 1997 and December 1998. These fishes ranged in length from 50 to 508 mm. Approximately 30% (n= 237) were empty. No kokanee were identified in the stomachs of sculpin, bullhead, pumpkinseed, smallmouth bass, yellow perch, or cutthroat trout (Table 2.5). Insects were the principal food item for sculpin (72%), pumpkinseed (63%), and yellow perch (37%). Crustaceans were the principal food item for bullhead (34%). Opossum shrimp (62%) were the principal food item for cutthroat trout and redside shiners (40%) were the principal food item of smallmouth bass.

Table 2.5. Percent of prey items in the diet of selected predator fishes in Lake Pend Oreille, Idaho, 1997-1998. Sample sizes are in parentheses. Fish were sampled by electrofishing March through November 1997 and 1998.

Prey item	Sculpin spp. (n=5)	Bullhead spp. (n = 53)	Pumpkinseed (n = 12)	Smallmouth bass (n = 337)	Cutthroat trout (n= 14)	Yellow perch (n= 124)
Insecta	72.03	23.61	62.69	5.13	30.54	36.97
Decapoda		0.26				0.54
Opossum shrimp		8.60	0.59	0.01	62.17	10.18
Other crustacea	26.48	33.73	1.59	1.50	0.22	3.72
Mollusca		10.24	21.50	1.70		0.42
Larval fish			0.49	17.65		7.27
Unidentified fish			0.03		0.01	1.99
Unidentified salmonid						0.23
Kokanee						
Rainbow trout						
Lake trout						
Bull trout						
Whitefish spp.						
Unidentified non-salmonidae				17.07		3.82
Catostomida						
Centrarchidae						
Cottidae				0.92		
Ameiurus spp.						
Percidae						3.91
Unidentified cyprinidae						0.20
Peamouth				5.07		1.87
Redside shiner				39.81		
Northern pikeminnow				10.04		0.11
Plant items		0.39	0.12	0.14	0.28	0.96
Other food	1.48	17.97	1.57	0.95	0.01	5.43
Unidentified material		5.19	11.42	0.02	6.76	22.38

DISCUSSION

Predation is determined in part by spatial and temporal links to the food web influencing the predator's preference toward a particular food type and size of food and the availability of food (Popova 1978; Garvey et al. 1998). Food web interactions are difficult to assess because of multiple roles of individual fish species within an ecosystem and the potential for environmental conditions to change their ontogeny (Garvey et al. 1998). Kokanee are the preferred prey species for pelagic predator fishes throughout the year in Lake Pend Oreille although predator fishes could potentially prey on any of the 30 fishes found in Lake Pend Oreille (B. Harryman, Idaho Department of Fish and Game, pers. comm.). Kokanee numbers are presently at record low numbers; however, they are still the most commonly sampled pelagic prey fish in Lake Pend Oreille during IDFG's annual open water trawling surveys.

Some piscivorous salmonid fishes will not switch to alternative prey when their preferred prey declines and becomes more difficult to locate (Stewart and Ibarra 1991; Madenjian et al. 1998; Rand and Stewart 1998a; and Rand and Stewart 1998b). Although prey preference may not change, the size preference of a particular prey item may change depending on availability. This phenomenon could lead to a predator bottleneck resulting in a crash of the prey species, as observed with alewifes *Alosa pseudoharengus* in Lake Michigan (Rand and Stewart 1998a). Rand and Stewart (1998b) hypothesized that as the abundance of prey declined, the condition of predators may also decline. Although current data suggest that predatory fishes will consume prey relative to their own size (Garvey et al. 1998; Madenjian et al. 1998; Yule and Luecke 1993), I did not observe a preference of larger fish to consume larger prey in Lake Pend Oreille. I did observe all sizes of predatory fishes to consume a range of kokanee lengths focusing on smaller individuals, similar to the findings of Rieman and Myers (1991).

A number of characteristics may make kokanee, despite their current low numbers, highly susceptible to consumption by large predatory fishes. Kokanee exhibit schooling behavior while kamloops, bull trout, and lake trout in Lake Pend Oreille are pelagic feeders covering large areas in search of prey. Therefore, a decrease in prey abundance may not result in decreasing predation rates until prey densities are severely reduced (Eby et al. 1995; Rieman and Myers 1991). Prey distribution plays a significant role in the distribution of predators in some systems (Goyke and Brandt 1993). In recent years, anglers targeting kamloops between 30 m and the surface commonly catch lake trout and bull trout, possibly indicating that predatory fishes which prefer kokanee need to cover more area to find kokanee because of their low abundance (Idaho Department of Fish and Game, unpublished data).

Kamloops

Previous studies in Lake Pend Oreille have recorded similar diet composition of kamloops to what I found. In 1976, kamloops > 431 mm total length (n = 250) preferentially foraged on ages 2 and 3 kokanee (180 to 230 mm; Bowler et al. 1978). In 1976, the mean length of kokanee consumed by kamloops (n = 70) was 180 mm; in 1980, mean length was 100 mm, and in 1990, 58% of the kamloops (n = 12) contained kokanee that averaged 161 mm (age 2; Paragamian et al. 1991). In 1990, an average of 2.4 kokanee/stomach was found for those kamloops having consumed kokanee. In 1997-1998, 30% of the kamloops sampled (n = 180) contained kokanee with an average length of 176 mm (age 1 to 4 kokanee) with 3.2 kokanee/kamloops stomach for fish that consumed kokanee. Similar to my results, in 1976 the diets of kamloops < 431mm total length (406 mm FL) contained mostly terrestrial and aquatic invertebrates and opossum shrimp while only two of the stomachs contained fish remains (Bowler et al. 1978). The length at age for kokanee in Lake Pend Oreille has changed little since they became established in the late 1930’s (M. Maiolie, Idaho Department of Fish and Game, pers. comm.)

The percent of empty kamloops stomachs collected throughout the year was relatively low compared to those from other systems. In Lake Pend Oreille during 1997-1998, 15% of the kamloops stomachs were empty (n = 172; Table 2.6), in Lake Ontario 34% of the adfluvial steelhead stomachs were empty (n =644; Rand and Stewart 1998b), and in Lake Superior, 17% of the steelhead stomachs were empty (n=126; Conner et al. 1993).

Bull trout

Bull trout were listed under the U.S, Endangered Species Act as a threatened species in June 1998, resulting in a complete closure of the fishery making it illegal to harvest bull trout. Therefore, the capture of bull trout for this research was limited to those fish captured in the bycatch of anglers targeting other species.

Previous studies have recorded diet composition of bull trout in Lake Pend Oreille. In 1990, 37% of the bull trout sampled (n = 16) had consumed kokanee (Paragamian et al. 1991); bull trout with kokanee contained an average of 1.8 kokanee/stomach. In 1997-1998, 38% of the bull trout contained kokanee with 0.5 kokanee/stomach for those having consumed kokanee. Although both sample sizes are small, the similarity of diet composition adds credence to my proportional diet breakdown.

I compared the diets of bull trout in Lake Pend Oreille to the diets of bull trout in ‘similar systems’. Similar systems were those with stocks of adfluvial bull trout and where kokanee were the dominant available food base: Flathead Lake, MT, USA, 1979-1981 (Leathe and Graham 1982), Lake Billy Chinook, OR, USA, 1983-1984 (Ratcliff et al. 1996), Arrow Reservoir, BC, Canada, 1989-1997 (D. Sebastian, British Columbia Fisheries, pers. comm.), Libby Reservoir, MT, USA, 1983-1987 (Chisholm et al. 1989), and Priest Lake, ID, USA, 1975 (Rieman et al. 1979). Kokanee comprised the majority of the diet of bull trout in all five systems except Flathead Lake (Figure 2.2).

Lake trout

The dietary items of lake trout in Lake Pend Oreille were similar to those of lake trout in 'similar systems'. Kokanee were the single most dominant food item found in lake trout from Flathead Lake, MT (20%) and Flaming Gorge Reservoir, WY (52%). Similar research on Flaming Gorge Reservoir, WY (Yule and Luecke 1993) found that lake trout > 600 mm (n = 303) consumed kokanee that ranged in length from 50 to 425 mm. In Lake Pend Oreille, lake trout ≥ 406 mm (n = 195) consumed 87.4% kokanee which ranged in length from 70 to 225 mm. Rieman and Myers (1991) also observed that lake trout selected kokanee 150 to 200 mm in other kokanee lakes in Idaho. I speculate that differences in the length of kokanee consumed in Flaming Gorge Reservoir and Lake Pend Oreille is explained by different length frequencies of lake trout and kokanee in the two systems.

The percent of empty lake trout stomachs collected throughout the year from Lake Pend Oreille in 1997-1998 was less than those in Lake Ontario. In Lake Pend Oreille, 18% of the lake trout stomachs were empty (n =206; Table 2.6), compared to Lake Ontario where 40% were empty (n= 1,059; Rand and Stewart 1998b).

Northern pikeminnow

Anglers have speculated that northern pikeminnow consume large quantities of salmonids (mostly kokanee) in Lake Pend Oreille. Research on Cascade Reservoir (Casey 1962), Priest Lake (Bjornn 1961), and Lower Granite Reservoir (Naughton 1998) found that northern pikeminnow consume mostly crustaceans and insects and to a lesser extent salmonid fishes. Northern pikeminnow are, in general, opportunistic feeders (Scott and Crossman 1973) and feed on a wide range of dietary items in Lake Pend Oreille. My results indicated that diet varied between length groups; however, in general, insects were the most commonly consumed prey item, and only those fish > 305 mm regularly consumed kokanee.

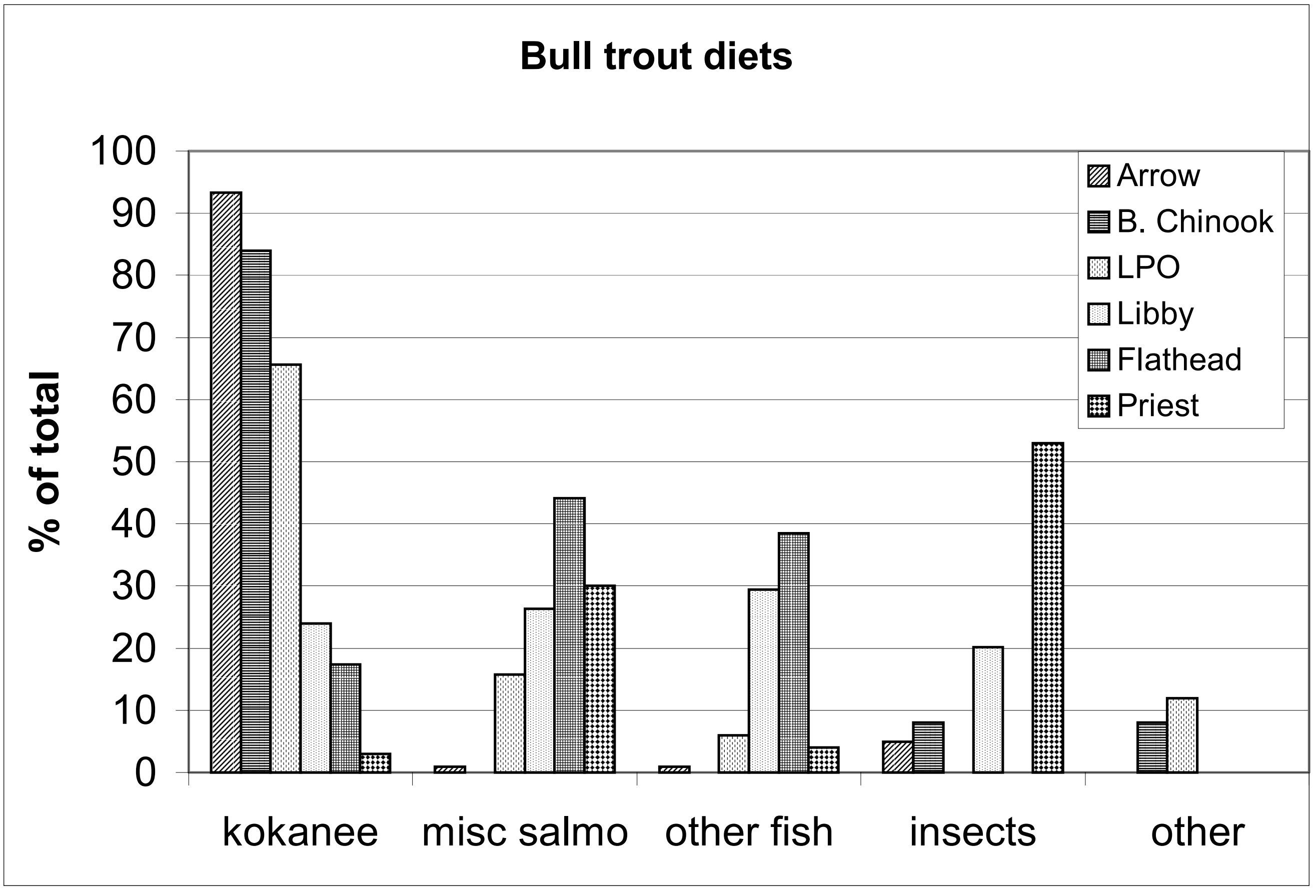


Figure 2.2. Diets of adfluvial bull trout in similar systems displaying percent kokanee, miscellaneous salmonids, other fish, insects, and other food items in diet. Flathead Lake, MT, USA ,1979-1981 (Leathe and Graham 1982), Lake Billy Chinook, OR, USA, 1983-1984 (Ratcliff et al. 1996), Arrow Reservoir, BC, Canada, 1989-1997 (D. Sebastian, British Columbia Fisheries, pers. comm.), Libby Reservoir, MT, USA 1983-1987 (Chisholm et al. 1989), and Priest Lake ID, USA, 1975 (Rieman et al. 1979)

Table 2.6. Number of full, empty and percent empty stomachs from sampled kamloops, lake trout and northern pikeminnow Lake Pend Oreille, Idaho 1997-1998. Blank spaces indicate no available data.

Kamloops

Month	Full	Empty	% empty	Total
Jan				
Feb				
Mar				
Apr	11	2	15.4	13
May	7	1	12.5	8
Jun	6	5	45.5	11
Jul	4	1	20.0	5
Aug	16	1	5.9	17
Sep	6	0	0.0	6
Oct	23	8	25.8	31
Nov	65	16	19.8	81
Dec				

Lake trout

Month	Full	Empty	% empty	Total
Jan	2	0	0.0	2
Feb				
Mar	3	0	0.0	3
Apr	18	0	0.0	18
May	20	3	13.4	23
Jun	34	0	0.0	34
Jul	24	1	4.0	25
Aug	25	1	3.8	26
Sep	12	2	14.3	14
Oct	4	1	20.0	5
Nov	28	10	26.3	38
Dec	18	0	0.0	18

Northern pikeminnow

Month	Full	Empty	% empty	Total
Jan				
Feb				
Mar				
Apr				
May				
Jun	993	579	36.8	1572
Jul	332	220	39.9	552
Aug	259	130	33.4	389
Sep	137	79	36.6	216
Oct	213	96	31.1	309
Nov	111	192	63.4	303
Dec				

The percent of empty northern pikeminnow stomachs collected throughout the year in Lake Pend Oreille was lower than in other systems. In Lake Pend Oreille, I found 21% of the stomachs were empty (n=3,341), whereas in Cascade Reservoir (n=132; Casey 1962) and the lower Columbia River (Thompson 1958) 60% and 63% were empty, respectively.

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Objective Three

PREDATORY IMPACT

INTRODUCTION

Kokanee populations in Lake Pend Oreille have declined over the last 30 years. The kokanee harvest is presently at 20% of its historic level because of population declines, supporting a recreational fishery of less than 200,000 fish annually (Maiolie and Elam 1993; Paragamian et al. 1991). Record low numbers of kokanee in the last 5 years have concerned managers, prompting research to quantify effects of predatory fishes on kokanee. In Lake Pend Oreille, kokanee, an important component of the food web, have provided both a prey base, enhancing the growth of predatory fishes, and a fishery for over 60 years (Wydoski and Bennett 1981).

Predation rates have been estimated by laboratory experiments, field observations, and bioenergetic modeling (Eby et al. 1995). Bioenergetic modeling is a valuable tool used to examine predator-prey relationships, including predator demand and prey abundance, incorporating effects of spatial, temporal and biological variation (Brandt and Mason 1994). Bioenergetic modeling may be the most accurate and economical means to estimate annual consumption needs for cohorts or entire populations of certain fish predators (Stewart et al. 1983; Ney 1993; Chipps and Bennett 2000; Madon and Culver 1993). Using measured survival rates of predators and their absolute abundance, spatial and temporal food habit data, and estimates of thermal experience, consumption of kokanee can be calculated using the bioenergetics approach (Beauchamp et al. 1989, 1995).

Evaluating total consumption by the dominant kokanee predators in Lake Pend Oreille and identifying which cohorts pose the highest predation impacts on kokanee will help managers decide whether predator abundance is excessive. Then managers can determine what balance between predators and prey will allow the kokanee population to increase while continuing to provide a trophy fishery for predators.

Objective 3. Estimate kokanee consumed by kamloops, bull trout, and lake trout $\geq$ 406 mm and relative consumption by kamloops, bull trout, lake trout and northern pikeminnow in Lake Pend Oreille, Idaho.

METHODS

The computer model Fish Bioenergetics 3.0 (Hanson et al. 1997) was used to estimate total annual consumption of kokanee by kamloops, bull trout and lake trout $\geq$ 406 mm fork length which are believed to be the dominant kokanee predators in Lake Pend Oreille (Anderson 1978; Pratt 1985; Rieman and Falter 1981). Additionally, a relative comparison of consumption was estimated for kamloops, bull trout, lake trout, and northern pikeminnow annually/1,000 fish. Consumption was estimated by fitting a known growth curve. Metabolism, swimming speed, egestion, and excretion parameters for kamloops, bull trout, and lake trout were obtained from the model; lake trout were used as a surrogate for bull trout and steelhead for kamloops (Hanson et al. 1997). Parameters used in the model and estimated from Lake Pend Oreille fish predators included population estimates of each predatory cohort, mortality estimates, weight at age estimates, temperatures available to fish throughout the year, and dietary composition.

Specific modeling used by Fish Bioenergetics 3.0 is described in detail in Hanson et al. (1997; Appendix Table 3.1) and summarized here:

$C = C_{max} * p * f(T)$

Where: C = specific consumption rate

C_{max} = maximum specific feeding rate

p = proportion of maximum consumption

$f(T)$ = temperature dependence function

T = water temperature (°C)

$C_{max} = CA * W^{CB}$

Where: W = fish mass

CA = intercept of the allometric mass function

CB = slope of the allometric mass function.

Annual consumption rates of kokanee by individual age cohorts of kamloops, bull trout, and lake trout $\geq$ 406 mm were estimated in terms of grams of kokanee consumed, and 95% confidence intervals were calculated using the population estimates (Objective 1). Numeric losses were converted from grams of kokanee consumed, using the mean weight of age 2 kokanee (1998; 37 g/kokanee) from population estimates made the same year by IDFG. The mean length of age 2 kokanee corresponded with the size of kokanee most commonly consumed by predator fishes (Objective 2). Total consumption estimates for each cohort of kamloops, bull trout, and lake trout $\geq$ 406 mm were related to kokanee production and yield. Production is defined as biomass added to the population, and yield refers to the total biomass lost from the population (Ricker 1975). Kokanee production and yield estimates were obtained from IDFG 1998 estimates of kokanee population abundance and kokanee growth based on hydroacoustic sampling (M. Maiolie, Idaho Department of Fish and Game, unpublished data).

I interpreted P-values for simulations from kamloops, bull trout, lake trout, and northern pikeminnow as presented in the literature (Hanson et al. 1997).

I evaluated the sensitivity of the model to each of the species specific variables over a

12 month period by varying each parameter by +/-10% while keeping all other variables fixed and comparing results to those using the average values. Variables used to evaluate sensitivity of the model included mortality, percent kokanee in diet, temperature, and energy density of kokanee.

Kamloops

Consumption rates in 1998 were estimated for kamloops with the bioenergetic model using steelhead as a surrogate (Hanson et al. 1997). I based model simulations of consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from kamloops in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year for ages 4 to 9 kamloops. Monthly averages of diet were used for simulations of all cohorts. Kokanee consumption by age 4 kamloops began on day 100 to compensate for the estimated time necessary for age 4 kamloops to attain predatory length of 406 mm (4.5 years). Diet composition for months when no stomach samples were collected (December – March) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 2,742 joules/g wet weight (wt) for *Chironomids* to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1). Energy content for each prey item was assumed

Table 3.1. Energy values for various prey items found in kamloops, bull trout, lake trout, and northern pikeminnow in Lake Pend Oreille, 1997-1998.

	Energy values (joules/g wet wt.)	Citation
Insects		
Chironomidae	2,742	Cummins and Wuycheck (1971)
Ephemeroptera	see below	used mean value for aquatic invertebrates
Hymenoptera (ants)	see below	used mean value for terrestrial invertebrates
Average aquatic invertebrates	3,178	Cummins and Wuycheck (1971)
Average terrestrial invertebrates	7,887	Cummins and Wuycheck (1971)
Salmonid fishes		
Kokanee	5,221	Beauchamp et al. (1989)
Rainbow trout	5,764	Hanson et al. (1997)
Lake trout	5,776	Stewart et al. (1983)
Bull trout	5,776	Stewart et al. (1983)
Whitefish	5,989	Rottiers and Tucker (1982)
Average salmonids excluding kokanee	5,826	average from above
Catostomid fishes		
Largescale sucker	7,524	Used general value for Cyprinidae from Cummins and Wuycheck (1971)
Cyprinid fishes		
Peamouth, Northern pikeminnow, and Redside shiner	6,703	Petersen and Ward (1999)
Centrarcid fishes		
Yellow perch	4,186	Hanson et al. (1997)
Other		
Opossum shrimp	3,474	Hanson et al. (1997)
Sculpin	5,439	Cummins and Wuycheck (1971)
Decapods	4,506	Cummins and Wuycheck (1971)
Mollusca	2,010	Cummins and Wuycheck (1971)
Plant food	2,558	Cummins and Wuycheck (1971)

constant throughout the year. I assumed kamloops inhabited their preferred temperatures (13° C; Scott and Crossman 1973) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profile data collected by IDFG personnel at 1 m depth intervals between the surface and 60 m to determine monthly temperatures available to fish (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were assumed similar to those for steelhead in the model (Hanson et al. 1997).

Bull trout

Consumption rates in 1998 were estimated for bull trout with the bioenergetic model using lake trout as a surrogate similar to methods used by Beauchamp (University of Washington, pers. comm.). I based model simulations of prey consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from bull trout in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year. Results from the diet analysis (Objective 2) were pooled, and the average annual aggregate of dietary items was compared to diets of bull trout in similar systems (Objective 2) and the relative abundance of fishes captured during the gillnet effort (Objective 1). A weighted mean of dietary items was then used in the model for bull trout consumption (ages 6 to 12): kokanee (74.0%), whitefish (13.85%), peamouth (7.29%), northern pikeminnow (2.92%), bull trout (0.97%), lake trout (0.49%), insects (0.24%), and opossum shrimp (0.24%).

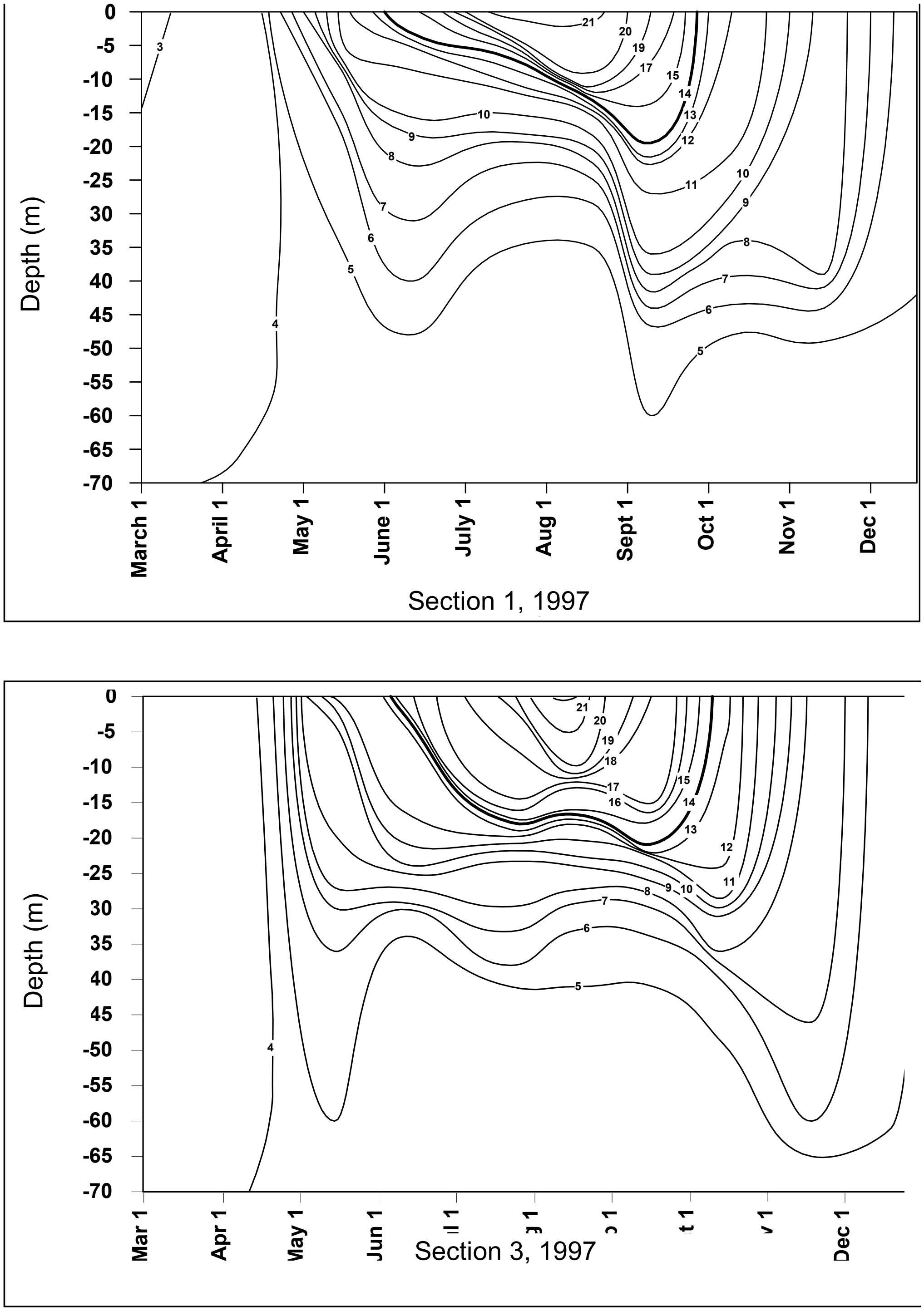

Figure 3.1. Isopleths of water temperatures (^{o}C) from sections 1 and 3 Lake Pend Oreille, Idaho, 1997 (see Figure 1.1).

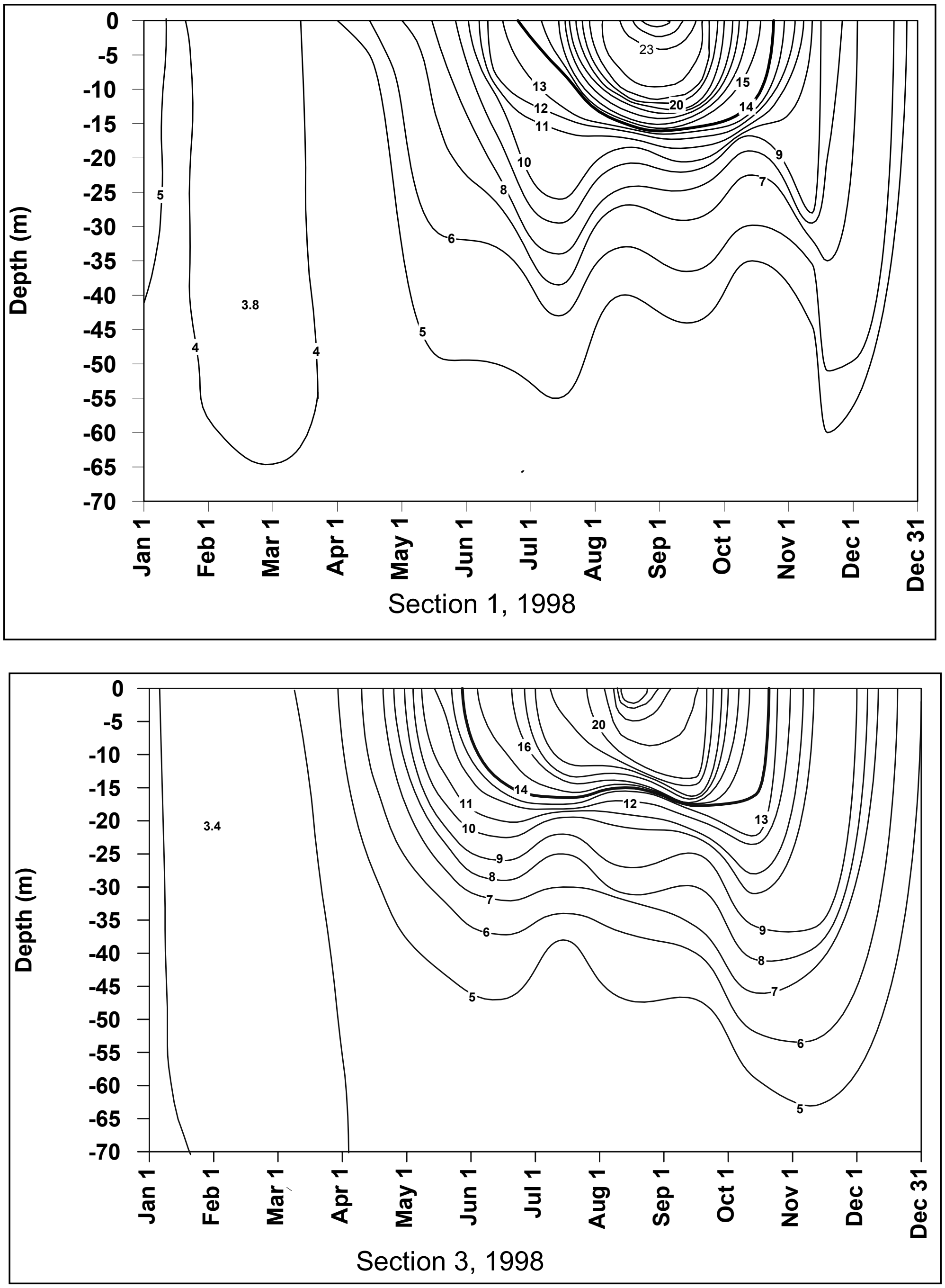

Figure 3.2. Isopleths of water temperatures (°C) from sections 1 and 3 Lake Pend Oreille, Idaho, 1998 (see Figure 1.1).

Energy values of prey items ranged from 3,178 joules/g wet wt (mean for aquatic insects) to 6,703 joules/g wet wt for peamouth and northern pikeminnow (Table 3.1), and energy content for each prey item was assumed constant throughout the year. I assumed bull trout inhabited their preferred temperatures (12 - 13 °C; Scott and Crossman 1973; D. Beauchamp, University of Washington, pers. comm.) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were those used for lake trout in the model.

Lake trout

Consumption rates in 1998 were estimated for lake trout with the bioenergetic model (Hanson et al. 1997). I based model simulations of prey consumption on estimates of population abundance, mortality, and growth (Objective 1), diet (Objective 2), and thermal history from lake trout in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations began on January 1 (simulation day 1) and ended December 31 the same year for lake trout ages 6 to 11. Monthly averages of diet were used for simulations of all cohorts. Kokanee consumption by age 6 lake trout began on day 255 to compensate for the estimated time necessary for age 6 lake trout to attain predatory length of 406 mm (6.75 years). Diet composition for months when no stomach samples were collected (March) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 3,178 joules/g wet wt (mean for aquatic insects) to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1), and energy content for each prey item was assumed constant throughout the year. I assumed lake trout inhabited their preferred temperatures (10 °C; Scott and Crossman 1973) when available similar to Brandt and Kirsch (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were those used for lake trout in the model.

Northern Pikeminnow

Consumption rates in 1998 were estimated for northern pikeminnow with the parameters defined by Petersen and Ward (1999) for the bioenergetic model. I based model simulations of consumption on estimates of mortality and growth (Objective 1), diet (Objective 2), and thermal history from northern pikeminnow in Lake Pend Oreille. Energy used for gamete production, migration, and spawning was not considered. Consumption simulations generally began on January 1 (simulation day 1) and ended December 31 the same year. Monthly averages of diet were used for simulations of all cohorts. Diet composition for months when no stomach samples were collected (December-February) was calculated by averaging the dietary items from the surrounding months. Energy values of prey items ranged from 2,558 joules/g wet wt for 'plant items' to 7,887 joules/g wet wt for terrestrial invertebrates (Table 3.1), and energy content for each prey item was assumed constant throughout the year.

I assumed northern pikeminnow inhabited their preferred temperatures (21.5 °C; Petersen and Ward 1999) when available similar to Brandt and Kirsh (1993) and temperatures nearest that at other times. I used temperature profiles collected monthly by IDFG personnel (Figures 3.1 and 3.2). Consumption rates, metabolism, swimming speed, egestion, and excretion parameters were estimated by Petersen and Ward (1999) for Fish Bioenergetics 3.0.

RESULTS

Bioenergetic modeling indicated that in Lake Pend Oreille kamloops, bull trout, and lake trout collectively consumed more than 153.5 metric tons-mt (65%) of the 235.2 mt of kokanee produced (e.g. biomass gained/yr) 95% CI: [105.4 mt**,** 286.3 mt] in 1998 accounting for 73% of the kokanee biomass lost. Kamloops constitute 82% of the pelagic predator biomass and consumed 53% of the annual kokanee production, whereas bull trout (14%) consumed 10%, and lake trout (4%) consumed 2%.

Kamloops

Bioenergetic modeling predicted kamloops ≥ 406 mm (ages 4 to 9) consumed 196.0 mt of prey in 1998. Kamloops consumed nearly 126.3 mt of kokanee followed by 'other-salmonids' (41.7 mt), cyprinids (21.7 mt), insects (4.7 mt) and opossum shrimp (2.1 mt). P-values for all cohort simulations ranged between 0.27 and 0.43 (Table 3.2). Monthly prey consumption by all cohorts ranged from 6.7 mt (February) to 23.8 mt (August). Kamloops ages 7 to 9 (> 676 mm) consumed 102.6 mt of prey, whereas kamloops ages 4-5 (384 to 592 mm) consumed 65.5 mt. Kamloops age 6 (593 to 675 mm) consumed 28.2 mt, considerably less than age 7 (37.3 mt).

Age 4 kamloops (384 to 494 mm fork length) consumed the highest quantity of prey (37.6 mt) kokanee (21.4 mt),'other-salmonids' (7.5 mt), and other items (Figure 3.3). Monthly prey consumption for age 4 kamloops ranged from 1.2 mt (March) to 4.6 mt (October). Estimated food consumed by other cohorts decreased proportionally (Appendix Table 3.2), although biomass of kokanee consumed did not. Kokanee consumption by kamloops ≥ 406 mm ranged from 18.4 mt (age 5) to 24.6 mt (age 7).

Table 3.2. P-values recorded from bioenergetic modeling of piscivorous cohorts for kamloops, bull trout, lake trout and northern pikeminnow from Lake Pend Oreille, Idaho, 1997-1998.

Kamloops

Age	P-value
4	0.32
5	0.27
6	0.32
7	0.43
8	0.42
9	0.40

Lake trout

Age	P-value
7	0.45
8	0.66
9	0.50
10	0.53
11	0.48
12	0.48

Bull trout

Age	P-value
6	0.46
7	0.39
8	0.35
9	0.34
10	0.32
11	0.31
12	0.29

Northern pikeminnow

Age	P-value
6	0.31
7	0.23
8	0.24
9	0.22
10	0.27
11	0.26

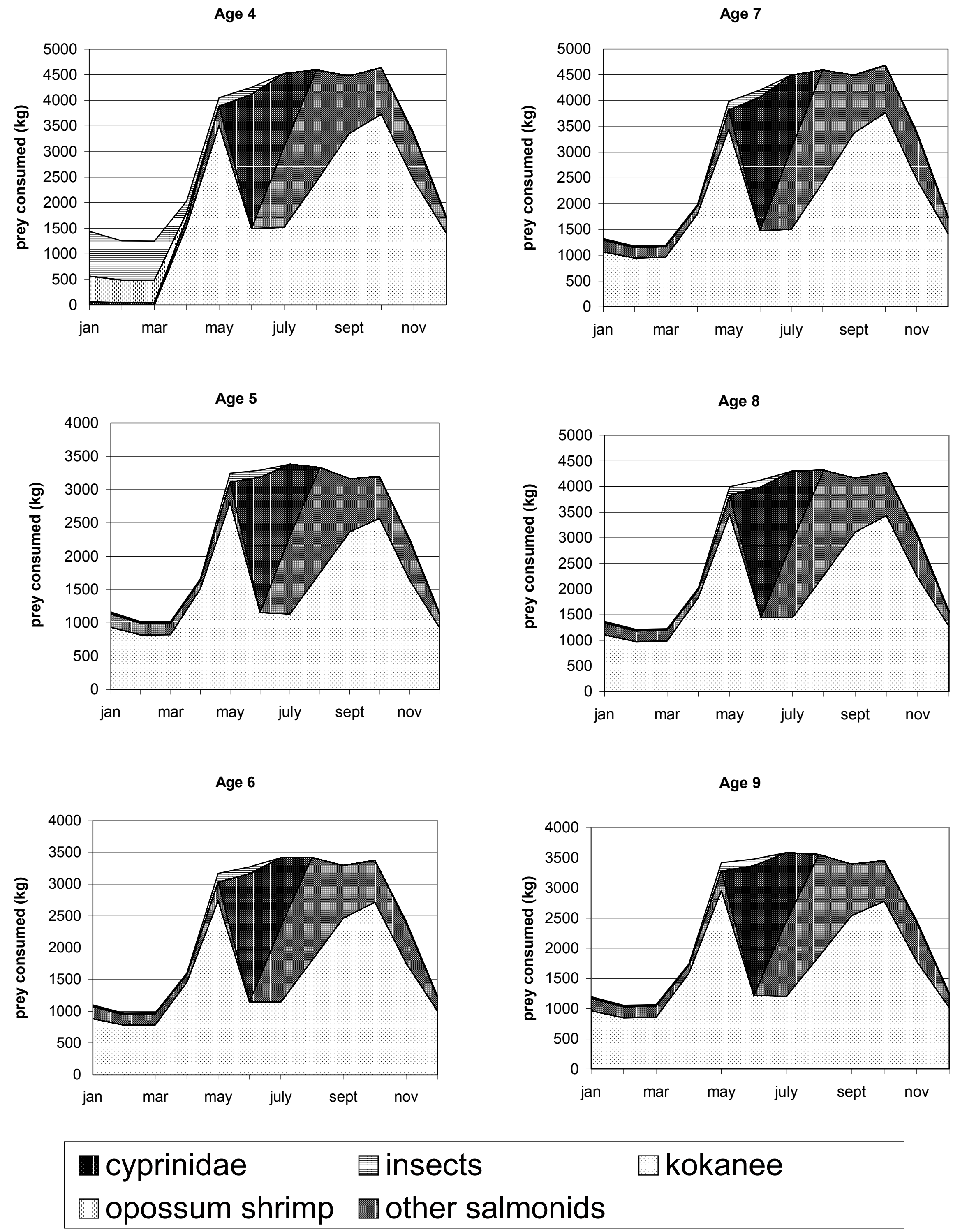

Figure 3.3. Estimated consumption (kg) of prey items by kamloops ages 4 to 9 in Lake Pend Oreille, Idaho, 1998.

Modeling predicted kamloops ≥ 406 mm consumed more kokanee biomass than bull trout and lake trout > 406 mm and northern pikeminnow ≥ 315 mm for 1,000 fish in 1998. Kamloops ≥ 406 mm in Lake Pend Oreille consumed an estimated 126.3 mt of kokanee (3,412,465 kokanee) in 1998 95% CI: [87.3 mt, 228.0 mt]. Kamloops 406 to 592 mm

consumed similar biomass of kokanee as kamloops 593 to 864 mm (93.7 mt vs 102.6 mt). Age 7 kamloops consumed more kokanee in October (3.8 mt) than any other cohort throughout the year.

My sensitivity analysis for kamloops indicated that a 10% increase of kokanee in diet resulted in a 14.0% change in kokanee consumption, fewer effects were seen for changes in temperature (11.9%), mortality (-9.9%), and energy value of kokanee (-6.0 %). A 10% decrease resulted in proportionally similar changes.

Bull trout

Bioenergetic modeling predicted bull trout ≥ 406 mm (age 6 to 12) consumed 30.4 mt of prey in 1998. Bull trout consumed nearly 22.5 mt of kokanee followed by whitefishes (4.2 mt), peamouth (2.2 mt), northern pikeminnow (1.0 mt), bull trout (0.3 mt), lake trout (0.2 mt), catostomids (0.1 mt), and insects (0.1 mt). P-values for all cohort simulations ranged between 0.29 and 0.46 (Table 3.2). Monthly prey consumption by all cohorts ranged from 1.1 mt (February) to 4.0 mt (October). Bull trout ages 6 and 7 (406-549 mm) consumed 9.1 mt of prey, whereas bull trout age 8 (550 to 617 mm) consumed 4.0 mt. Bull trout ages 9 to 12 (618 to 889 mm) consumed 9.4 mt. Estimated food consumed by other cohorts decreased proportionally (Figure 3.4).

Age 7 bull trout (475 to 549 mm) consumed the highest quantity of prey (6.4 mt): kokanee (4.7 mt), whitefishes (1.0 mt), and other items (Appendix Table 3.3). Monthly prey consumption for age 7 bull trout ranged from 0.2 (February) mt to 1.0 mt (October).

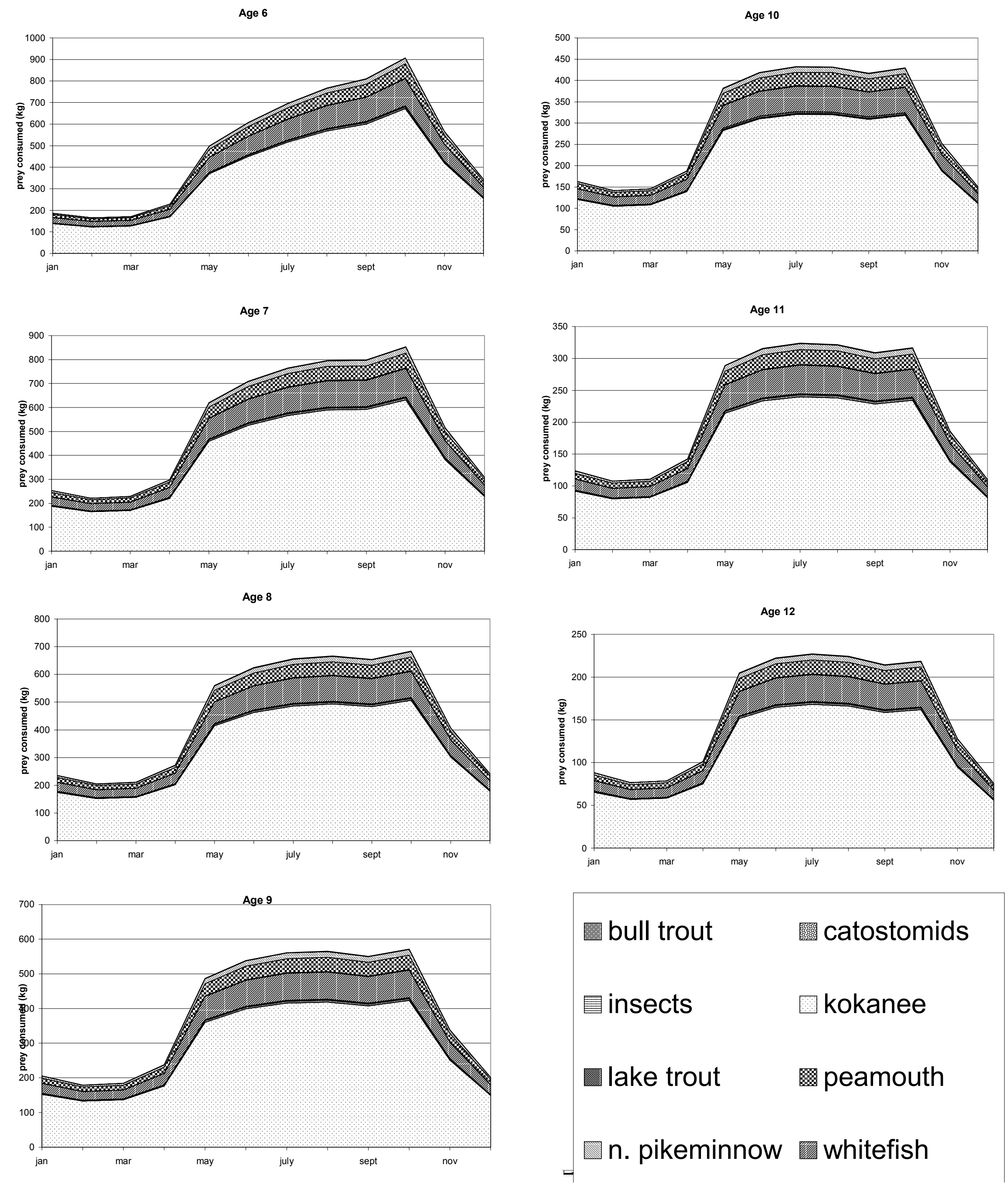

Figure 3.4 Estimated consumption (kg) of prey items by bull trout ages 6 to 12 in Lake Pend Oreille, Idaho, 1998.

Modeling predicted bull trout ≥ 406 mm consumed more kokanee biomass than lake trout ≥ 406 mm and northern pikeminnow ≥ 315 mm, for 1,000 fish in 1998. Bull trout ≥ 406 mm in Lake Pend Oreille consumed an estimated 22.5 mt of kokanee (608,825 kokanee) in 1998 95% CI: [15.3 mt, 42.5 mt]. Bull trout 406 to 549 mm consumed similar biomass of kokanee as bull trout 618 to 889 mm (9.1 mt vs 9.4 mt). Age 7 bull trout consumed more kokanee in October (0.63 mt) than any other cohort throughout the year.

My sensitivity analysis indicated a 10% decrease in mortality resulted in a 15.8% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (-11.3%), temperature (-0.5%), and energy value for kokanee (7.8%). A 10% increase in mortality resulted in a –13.6% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (11.6%), temperature (3.7%), and energy value of kokanee
(-6.7%).

Lake trout

Bioenergetic modeling predicted lake trout ≥ 406 mm (age 6 to 11) consumed 6.8 mt of prey in 1998. Lake trout consumed nearly 4.7 mt of kokanee followed by cottids (0.9 mt), unidentified salmonids (0.5 mt), peamouth (0.1 mt), catostomids (0.03 mt), insects (0.01 mt), opossum shrimp (0.4 mt), and centrarchids (0.002 mt). P-values for all cohort simulations ranged between 0.45 and 0.66 (Table 3.2). Monthly prey consumption for all cohorts ranged from 0.4 mt (February) to 0.8 mt (May). Lake trout age 6-7 (363-492 mm) consumed 4.1 mt of prey, whereas lake trout age 8 (493 to 563 mm) consumed 1.2 mt. Lake trout ages 9 to 11 (564 to 700 mm) consumed 1.3 mt. Estimated food consumed by other cohorts decreased proportionally (Figure 3.5).

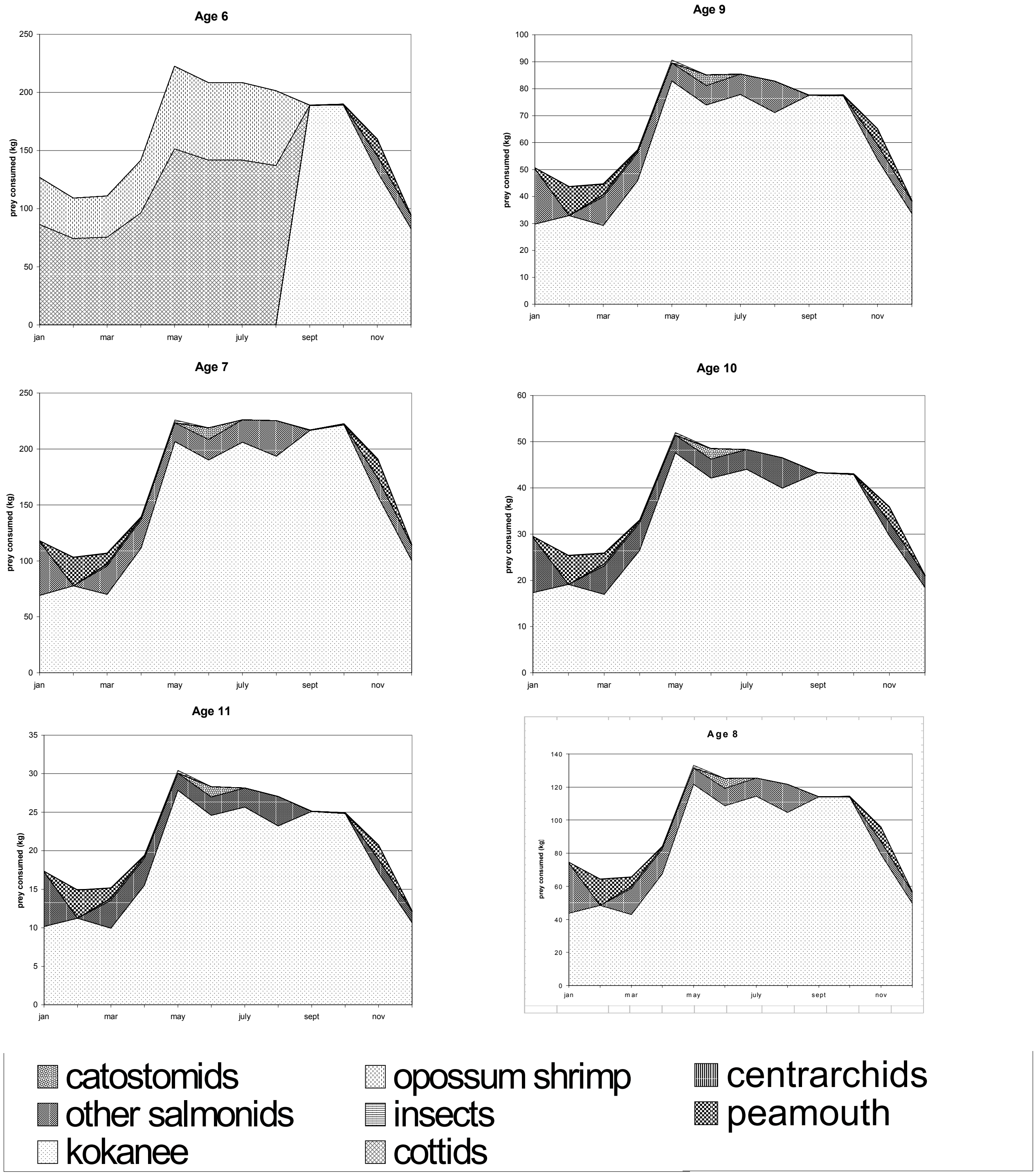

Figure 3.5. Estimated consumption (kg) of prey items by lake trout ages 6 to11 in Lake Pend Oreille, Idaho, 1998.

Age 7 lake trout (427 to 492 mm) consumed the highest quantity of prey (2.1 mt): kokanee (1.8 mt), unidentified salmonids (0.22 mt), and other items (Appendix Table 3.4). Monthly prey consumption by age 7 lake trout ranged from 0.1 mt (February) to 0.23 mt (July).

Modeling predicted lake trout $\geq$ 406 mm consumed less kokanee biomass than kamloops and bull trout $\geq$ 406 mm and more than northern pikeminnow $\geq$ 315 mm for 1,000 fish in 1998. Lake trout $\geq$ 406 mm in Lake Pend Oreille consumed an estimated 4.7 mt of kokanee (127,642 kokanee) in 1998 95% CI: [2.8 mt, 15.8 mt]. Lake trout 406-492 mm consumed more kokanee than the collective total of lake trout $\geq$ 493 mm (2.4 mt vs 2.3 mt). Age 7 lake trout consumed more kokanee in October (0.2 mt) than any other cohort throughout the year.

My sensitivity analysis indicated a 10% decrease in mortality resulted in a 23.0% change in total annual consumption of kokanee, fewer effects were seen for changes in diet (-10.0%), temperature (-4.0%), and energy content (9.5%). A 10% increase in mortality resulted in a –17.7% change in total annual consumption of kokanee; fewer effects were seen for changes in diet (8.1%), temperature (4.5%), and energy content (-7.9%).

Northern Pikeminnow (Relative Predation)

Bioenergetic modeling predicted northern pikeminnow $\geq$ 315 mm (ages 6 to 11) consumed 1.2 mt of prey/1,000 fish in 1998. Northern pikeminnow consumed nearly 0.47 mt of kokanee followed by decapods (0.34 mt), plants (0.14 mt), insects (0.14 mt), rainbow trout (0.03 mt), redside shiner (0.02 mt), molluscs (0.02 mt), northern pikeminnow (0.01 mt), and other crustaceans, peamouth, bull trout, whitefish, and cottids (< 0.001 mt). P-values for all cohort simulations ranged between 0.22 and 0.31 (Table 3.2). Monthly prey consumption/ 1,000 individuals ranged from 0.001 mt (March) to 0.24 mt (October). Age 6 northern pikeminnow (315 to 355 mm total length) consumed the highest quantity of prey (0.22 mt), consuming decapods (0.1 mt), kokanee (0.09 mt), and other items (Figure 3.6).

Monthly prey consumption for age 6 northern pikeminnow ranged from 0.002 mt (March) to 0.05 mt (October). Estimated food consumed by other cohorts decreased proportionally (Appendix Table 3.5). Kokanee consumption by northern pikeminnow ranged from 0.90 mt (age 8) to 0.06 (age 11)/1,000 individuals in 1998. Modeling predicted northern pikeminnow ≥ 315 mm consumed fewer kokanee (0.47 mt) for 1,000 fish in 1998 than kamloops (8.6 mt), bull trout (1.8 mt), and lake trout (2.6 mt) ≥ 406 mm. Northern pikeminnow ≥ 315 mm in Lake Pend Oreille consumed 12,683 kokanee in 1998/1,000 fish. Northern pikeminnow 315 to 426 mm (TL) consumed similar biomass of kokanee as northern pikeminnow 427 to 514 mm (0.26 mt vs 0.20 mt). Age 8 northern pikeminnow consumed more kokanee in July (0.024 mt) than any other cohort throughout the year.

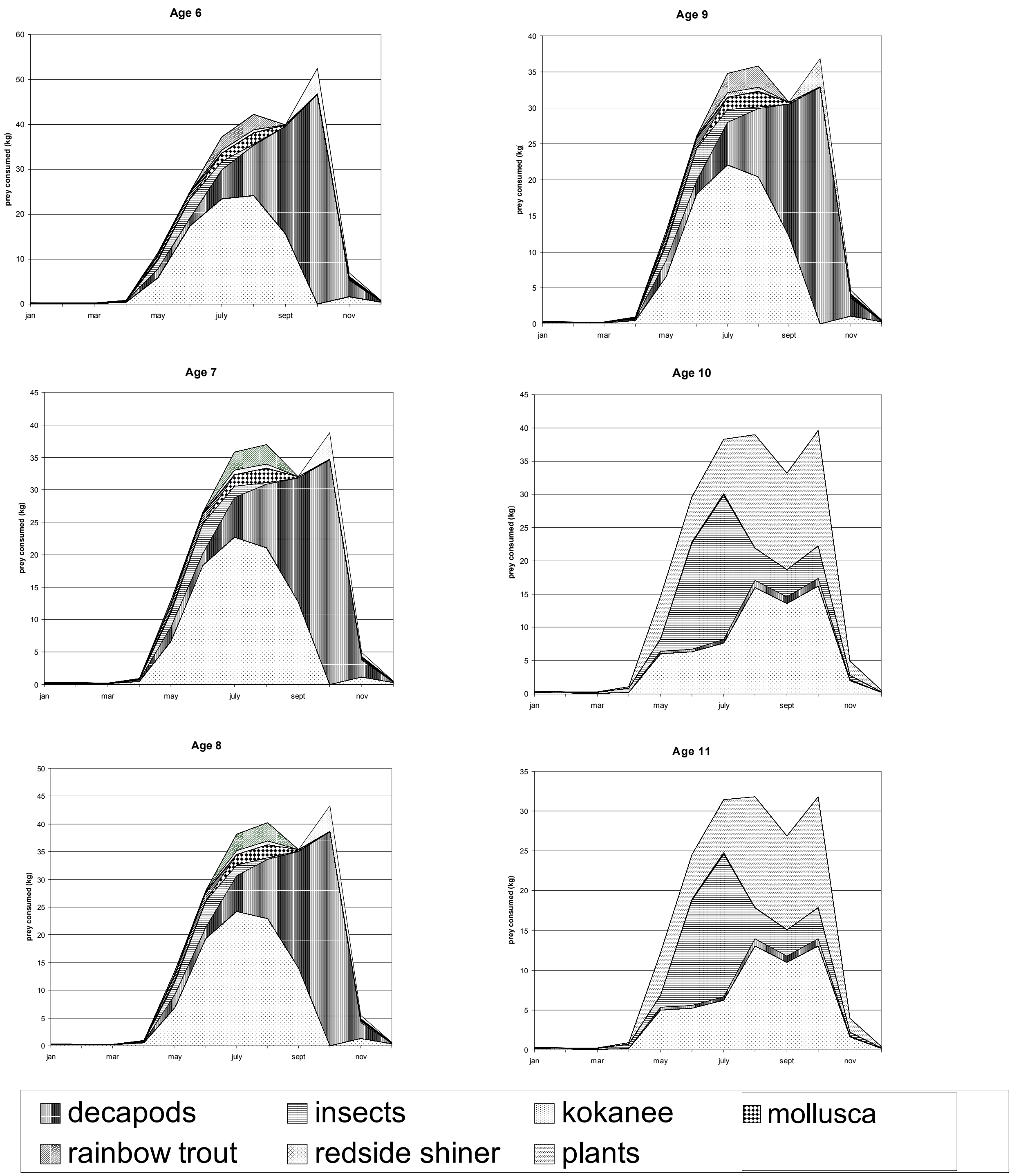

Figure 3.6. Estimated consumption (kg) of prey items by northern pikeminnow ages 6 to 11 based on 1,000 fish annually in Lake Pend Oreille, Idaho, 1998.

DISCUSSION

I feel the application of bioenergetic modeling to predict predator consumption based on species specific parameters estimated from Lake Pend Oreille (population estimates, diets, growth, mortality, and available temperatures) provided an accurate assessment of predator/prey dynamics. Numerous other investigators have used this model to estimate prey consumption for bull trout (Beauchamp et al. 1995); coho, chinook, steelhead, lake trout and brown trout (Rand and Stewart 1998); lake trout (Eby et al. 1995; Stewart et al. 1983;Yule and Luecke 1993); chinook and lake trout (Goyke and Brandt 1993); coho, chinook, and lake trout (Stewart and Ibarra 1991); and walleye (Lyons and Magnuson 1987).

Kokanee consumption by salmonid predators and northern pikeminnow is generally highest in October and lowest during the winter, similar to consumption by piscivorous-sized steelhead in Lakes Ontario and Michigan (Rand et al. 1993). I hypothesize that consumption varies seasonally primarily because of water temperatures. In Lake Pend Oreille, October is generally when the thermocline breaks down (Idaho Department of Fish and Game, unpublished) and temperatures preferred by most salmonids are distributed throughout the lake apparently providing higher foraging efficiency.

Younger piscivorous cohorts of predatory fishes (kamloops ages 4 to 7; bull trout ages 6 to 8; lake trout ages 6 to 7; and northern pikeminnow ages 6 to 8) consume more kokanee/yr than the cumulative total of their older cohorts, similar to trends observed for lake trout in Lake Champlain, Vermont (LaBar 1993). I hypothesize that younger cohorts collectively consume more prey because population biomass and growth are highest for younger piscivorous cohorts.

Kamloops (82% of the predator biomass) consumed 53% of the 1998 kokanee production compared to that for bull trout (14% of the predator biomass), which consumed 10% of the kokanee production. Lake trout comprised 4% of the predator biomass and consumed 2% of the kokanee production. Biomass estimates were not made for northern pikeminnow because population abundance was not estimated. Although northern pikeminnow ≥ 315 mm regularly consumed kokanee (24% of the annual diet; Objective 2), they constituted a small proportion of the population relative to fish < 315 mm (Figure 1.2). Predator fishes totaled 2.68 kg/ha (1.26 predators/ha), whereas kokanee (age 1 to 4) totaled 11.34 kg/ha (222 prey/ha). I estimated total biomass/ha of kamloops, bull trout, and lake trout ≥ 406 mm was approximately 24% that of kokanee, providing Y:C ratios of 4.23. Using total weight of prey species (Y) and total weight of predator species (C) Swingle (1950) made predictions about the 'balanced' state of predators relative to prey. He suggested that Y:C ratios between 1 and 3 are 'desirable' and ratios between 1 and 5 are balanced; however, if ratios are < 5 other factors must be examined in addition to the Y:C ratios in order to differentiate between balanced and unbalanced populations.

An alternative indicator of fluctuating prey abundance is to examine changes in size of prey consumed. For example, shifts to smaller prey by predatory salmonids have been used as an indicator of declining prey abundance (Stewart and Ibarra 1991). Previous research on Lake Pend Oreille has shown only minor differences in sizes of prey consumed among years of high and low kokanee abundances (Objective 2). Additionally, Rieman and Myers (1991) observed that kokanee predators in other Idaho lakes prefer smaller kokanee, although they are capable of consuming prey up to 50% of their length. Furthermore, Juanes (1994) concluded that predatory fishes will consistently select smaller prey when given a choice. The growth of predators also has been used as an indicator of prey abundances (Kitchell and Crowder 1986). Growth rates of kamloops and bull trout have declined over the last 20 years (Pratt 1985; Hoelscher 1992) probably as a result of reduced kokanee numbers. However, Eby et al. (1995) and Mittelbach and Osenberg (1994) concluded that growth rates are a poor indicator of prey abundance.

My estimates of kokanee consumption in Lake Pend Oreille were high according to other authors (Stewart et al. 1981; Rand and Stewart 1998; Rieman and Myers 1991). I estimated that 65% of the kokanee production and 73% of the yield was consumed by predatory salmonids in 1998. Assuming similar consumption to 1998, kokanee predation by salmonid predators ranged from 51% to 79% of production and 43% to 73% of yield from 1996-1999 (M. Maiolie, Idaho Department of Fish and Game, pers. comm.). In Lake Michigan, predator-prey interactions were thought to destabilize when bioenergetic modeling estimated 20-33% of the prey base was consumed by fish predators (Stewart et al. 1981), and the pelagic prey base was unable to recover when consumption exceeded 50% of the annual production (Rand and Stewart 1998). Rieman and Myers (1991) used bioenergetic modeling to predict kokanee/predator consumption ratios on different systems in Idaho, suggesting that consumption exceeding 50% of the annual production would pose a high risk of collapsing a kokanee population. They further speculated that biomass of predators should be between 2 and 10% of the prey biomass. My estimates identify the predator biomass as 24% of the prey biomass in Lake Pend Oreille (1998). Popova (1978) estimated that in any given ecosystem predaceous fishes comprise approximately 30% of the total fish production and generally consume the same amount. These indications from other investigators suggest that predator/prey ratios in Lake Pend Oreille are high and close to exceeding a level that would allow a sustaining kokanee population.

My sensitivity analysis predicted effects of mortality, temperature, diet, and energy density of prey on consumption among species. Estimating consumption by kamloops was influenced most by diet and least by energy value of prey, whereas bull trout and lake trout consumption was influenced most by mortality and least by water temperature. I believe the influence of sensitive parameters was minimal, however, the range of influence appeared to be correlated to population abundance. P-values ranged from 0.22 to 0.66. Hanson et al. (1997) suggests that P-values less than the theoretical maximum consumption rate (P-value = 1) may indicate that prey is limited because predators need to forage more frequently to obtain the observed growth rates.

I collected and analyzed the most extensive dietary analysis performed to date on Lake Pend Oreille fishes. Results from this analysis corroborate my bioenergetics modeling. Although previous dietary studies have been limited, general dietary items and their relative importance were similar to mine (Objective 2). To strengthen my diet analysis for bull trout, I compared my results to diets of bull trout in similar systems. My results were similar to those of comparable systems that sampled more fish, thus I feel confident using my diet analysis from Lake Pend Oreille bull trout. Every effort was made to accurately identify prey items; however, in some cases consumed fish were only able to be identified as 'unidentified salmonids' (Objective 2). Many of these 'unidentified salmonids' were likely kokanee, which if incorporated into the kokanee component of the diet would have increased the estimated total annual consumption of kokanee.

Dietary items used in this analysis may have been affected by sampling, as most samples were collected by angling. Studies in other systems have shown higher percentages of particular food items in angler caught fish than those collected by other methods (Eby et al. 1995). However, in Lake Pend Oreille percentages of dietary items in the various predators were similar to those from other systems or previous Lake Pend Oreille studies (Objective 2). Relying on angler participation to collect stomach samples limited or precluded collecting samples during extended periods of poor weather or fishing closures (December-March). Using months prior to and following these periods to estimate prey consumed during the winter season, I believe, provided the most representative results. Yule and Luecke (1993) calculated seasonal aggregate percentages for dietary items of lake trout similarly in Flaming Gorge Reservoir, WY. Prey consumption during the winter is greatly reduced as a result of low metabolic activity, and errors associated with my estimation methods would be minor. My sensitivity analysis predicted that varying diet +/- 10% can influence consumption estimates by -11% to 14% for all species of fish predators examined.

Another possible source of error in the consumption estimates could come from water temperatures. I assumed that fish would select their preferred temperatures when available (thermal regulation) similar to Brandt and Kirsch (1993). Water temperatures used by fishes are thought to be dictated by available temperature, preferred temperature, and acclimation to changing conditions (Stewart et al. 1983). I believe that profiles recorded by IDFG represented the most accurate water temperature data available. Estimating exact thermal habitat used by pelagic fishes was not feasible, although my sensitivity analysis predicted that varying water temperature +/- 10% can influence consumption estimates by -10% to 12% for all species of fish predators examined.

I explored several techniques to determine the most accurate estimate of mortality, including the use of length frequency, age frequency, and population estimates. Based on observed growth and age structure of each predator population, I concluded that length or age frequency provided the best estimates of mortality. Comparing my mortality estimates to those previously recorded in Lake Pend Oreille provided similar results. My sensitivity analysis predicted that varying mortality +/- 10% can influence consumption estimates by
-17% to 23% for all species of fish predators examined, although this range of influence appears to be directly correlated to the population abundance.

My estimates of predator abundance could have influenced estimates of consumption. My estimates of predatory salmonids in Lake Pend Oreille are the only known estimates for Lake Pend Oreille. Several factors could have influenced my population estimates of each predatory fish examined. Population estimates may not have included all recaptured fish due to tag loss or failure of anglers to report recaptures, thereby overestimating abundance estimates. Conversely, hooking mortality would have underestimated abundance estimates. More precise population estimates could be calculated for lake trout by increasing numbers of marked and recaptured fish.

I acknowledge that energy densities of prey vary throughout a year, thus influencing estimates of consumption. No information regarding these changes was available for prey items found in Lake Pend Oreille, therefore, I assumed that energy densities were constant throughout the year. My sensitivity analysis predicted that varying the energy density of prey (kokanee) +/- 10% can influence consumption estimates by -8% to 10% for all species of fish predators examined.

Another factor that can influence the assessment of predators on prey is the abundance estimates of prey. Hydroacoustic and trawling surveys are performed annually on Lake Pend Oreille following strict protocols and provide the best indication of year to year changes. Both methods show similar downward trends in kokanee abundance, however, neither survey was designed to show seasonal changes in prey abundance. Trawling estimates tend to underestimate prey abundances, which if used would show higher consumption rates at low prey abundances similar to observations by Brandt et al. (1991). Kokanee production and yield estimates used in this study were based on hydroacoustic estimates.

MANAGEMENT IMPLICATIONS

Salmonid predators are a depensatory mortality agent (Stewart et al. 1981), directly affecting the abundance, distribution, and age or size structure of prey (Crowder et al. 1994). As weak year classes of kokanee appear, they are subject to increasingly high predation pressure. Low recruitment by particular cohorts, coupled with stochastic increases in mortality may result in precipitous kokanee declines. One potential management response would be to encourage rapid and high exploitation of predatory salmonids and to carefully monitor the results to better manage in the future (Stewart et al. 1981).

Because of the current deleteriously low abundance of the kokanee population in Lake Pend Oreille, weak upcoming spawning classes, and the possibility of stochastic events (such as flooding), strong management actions are supported. Although predation may not be the catalyst for the kokanee declines, predatory fishes may limit the opportunity for kokanee to reach recovery goals. My consumption estimates have identified specific cohorts of each examined predator that are the most damaging to kokanee. The opportunity for management efforts in Lake Pend Oreille to remove kokanee predators is limited. Bull trout are a threatened species, and the daily harvest limit in 1999 (4 fish) for lake trout was rarely caught (anecdotal evidence 1997-1998), leaving the greatest opportunity for predator removal on kamloops. Kamloops are presently managed as a trophy fishery (2 fish over 20 inches, daily limit). My research indicates age 4 kamloops (409 to 520 mm total length) consume a substantial amount of kokanee (21.4 mt). Under existing management regulations in 1999, kamloops must be a minimum of 508 mm (total length) to harvest. Therefore, the most predacious cohort would not be affected by current angling regulations. Furthermore, my sensitivity analysis for kamloops indicated that annual consumption was most influenced by abundance of kamloops $\geq$ 406 mm. Therefore, I would recommend a management regulation to allow the harvest of all kamloops especially those age 4 and older. Based on my results, management recommendations currently proposed by IDFG for the year 2000 include opening the kamloop harvest for 6 fish daily, any size. Additionally, IDFG is now encouraging anglers to harvest legal kamloops that previously might have been released. Angler surveys during recent fishing derbies show an increased harvest of kamloops compared to past derbies (Idaho Department of Fish and Game, unpublished). Ironically, management recommendations in 1981 also stressed the need to keep the abundance of kamloops at a minimum until kokanee numbers increased (Ellis and Bowler 1981). The kokanee harvest is currently set at a 25 fish daily limit. Management recommendations proposed by IDFG for the year 2000 have also included closing the kokanee fishery. Both reductions in kokanee harvest and increased harvest of salmonid predators have the potential to increase kokanee abundance. Salmonid predators in Lake Pend Oreille are currently removing a substantial portion of kokanee production from the lake. Considering the current low kokanee abundance and level of consumption by predator fishes, fish predators could prevent the kokanee population from increasing or at worst push it to lower levels.

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Appendix Table 3.1. Parameter models used in Fish Bioenergetics 3.0 (Hanson et al. 1997).

Consumption = metabolism + wastes + growth

metabolism = respiration + active metabolism + specific dynamic action
wastes = egestion + excretion
growth = somatic growth + gonad production

Metabolism equations

Respiration = $RA * W^{RB} * f(T) * ACTIVITY$

where:

RA	intercept of the allometric mass function
W	fish mass
RB	slope of the allometric mass function
f(T)	temperature dependence function (Stewart et al. 1983)
ACT	activity multiplier (Kitchell et al. 1977)

Specific dynamic action = $SDA * (C - F)$

where:

SDA	specific dynamic action
C	specific consumption rate
F	specific egestion rate

Waste equations

Equation set 1 (Kitchell et al. 1977)

Egestion = $FA * C$

where:

FA	constant proportion of consumption
C	consumption

Excretion = $UA * (C - F)$

where:

UA	constant proportion of consumption
C	consumption
F	Egestion

Equation set 2 (Elliott 1976)

Egestion = $FA * T^{FB} * e^{(FG*p)} * C$

where:

FA	constant proportion of consumption
T^{FB}	ceofficient of water temperature dependence of egestion
$e^{(FG*p)}$	coefficient for feeding level dependence (P-value) of egestion
C	consumption

Equation set 3 (Stewart et al. 1983)

Egestion = $PF * C$

where:

PF	(PE - 0.1)/0.9) * (1 - PFF) + PFF
PE	$FA * T^{FB} * e^{FG*p}$
PFF	sum of (PREY (n) * DIET (n)) for n=1 to number of prey
C	Consumption

Excretion = $UA * T^{UB} * e^{(UG*p)} * (C - F)$

where:

UA	defined in equation set 1
T^{UB}	defined in equation set 1
$e^{(UG*P)}$	defined in equation set 2

Growth

Estimated on a site specific level as defined in Objective 3.

Appendix Table 3.2. Estimated consumption (metric tons-mt) of prey items by kamloops (ages 4 to 9) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
4	384-494	kokanee	21.40	21.4
		other salmonids	7.50	28.9
		cyprinidae	4.20	33.1
		opossum shrimp	1.60	34.7
		insects	3.00	37.7
5	495-592	kokanee	18.40	18.4
		other salmonids	5.90	24.3
		cyprinidae	3.13	27.4
		opossum shrimp	0.10	27.5
		insects	0.32	27.8
6	593-675	kokanee	18.70	18.7
		other salmonids	6.10	24.8
		cyprinidae	3.10	27.9
		opossum shrimp	0.09	28.0
		insects	0.30	28.3
7	676-734	kokanee	24.60	24.6
		other salmonids	8.10	32.7
		cyprinidae	4.00	36.7
		opossum shrimp	0.11	36.8
		insects	0.36	37.2
8	735-815	kokanee	23.60	23.6
		other salmonids	7.70	31.3
		cyprinidae	3.90	35.2
		opossum shrimp	0.10	35.3
		insects	0.40	35.7
9	816-865	kokanee	19.60	19.6
		other salmonids	6.30	25.9
		cyprinidae	3.30	29.2
		opossum shrimp	0.10	29.3
		insects	0.27	29.6
	Total		196.28	

Appendix Table 3.3. Estimated consumption (metric tons-mt) of prey items by bull trout (ages 6 to 12) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
6	401-474	kokanee	4.400	4.40
		bull trout	0.058	4.46
		lake trout	0.029	4.49
		whitefish	0.824	5.31
		catostomid	0.014	5.33
		peamouth	0.434	5.76
		n. pikeminnow	0.174	5.93
		insects	0.014	5.95
7	475-549	kokanee	4.710	4.71
		bull trout	0.062	4.77
		lake trout	0.031	4.80
		whitefish	0.882	5.69
		catostomid	0.015	5.70
		peamouth	0.464	6.16
		n. pikeminnow	0.186	6.35
		insects	0.015	6.37
8	550-617	kokanee	4.010	4.01
		bull trout	0.053	4.06
		lake trout	0.026	4.09
		whitefish	0.751	4.84
		catostomid	0.013	4.85
		peamouth	0.395	5.25
		n. pikeminnow	0.158	5.41
		insects	0.013	5.42
9	618-685	kokanee	3.421	3.42
		bull trout	0.045	3.47
		lake trout	0.022	3.49
		whitefish	0.640	4.13
		catostomid	0.011	4.14
		peamouth	0.337	4.48
		n. pikeminnow	0.135	4.61
		insects	0.011	4.62
10	686-753	kokanee	2.629	2.63
		bull trout	0.018	2.65
		lake trout	0.034	2.68
		whitefish	0.492	3.17
		catostomid	0.009	3.18
		peamouth	0.259	3.44
		n. pikeminnow	0.104	3.55
		insects	0.009	3.55
11	754-821	kokanee	1.967	1.97
		bull trout	0.026	1.99
		lake trout	0.013	2.01
		whitefish	0.368	2.37
		catostomid	0.006	2.38
		peamouth	0.194	2.57
		n. pikeminnow	0.078	2.65
		insects	0.006	2.66
12	822-889	kokanee	1.378	1.38
		bull trout	0.018	1.40
		lake trout	0.009	1.41
		whitefish	0.258	1.66
		catostomid	0.004	1.67
		peamouth	0.137	1.80
		n. pikeminnow	0.054	1.86
		insects	0.005	1.86
	Total		30.428	

Appendix Table 3.4. Estimated consumption (metric tons-mt) of prey items by lake trout (ages 6 to11) in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey items	Quantity of prey (mt)	Cumulative prey (mt)
6	363-426	kokanee	0.5900	0.59
		other salmonids	0.2500	0.84
		catostomids	0.0000	0.84
		centrarchids	0.0000	0.84
		peamouth	0.0100	0.86
		cottids	0.9040	1.76
		opossum shrimp	0.4300	2.19
		insects	0.0010	2.19
7	427-492	kokanee	1.8200	1.82
		other salmonids	0.2100	2.04
		catostomids	0.0130	2.05
		centrarchids	0.0010	2.05
		peamouth	0.0050	2.06
		opossum shrimp	0.0020	2.06
		insects	0.0040	2.06
8	493-563	kokanee	1.0100	1.01
		other salmonids	0.0300	1.13
		catostomids	0.0100	1.14
		centrarchids	0.0050	1.15
		peamouth	0.0300	1.18
		opossum shrimp	0.0010	1.18
		insects	0.0020	1.18
9	564-626	kokanee	0.6900	0.69
		other salmonids	0.0900	0.77
		catostomids	0.0050	0.78
		centrarchids	0.0004	0.78
		peamouth	0.0200	0.80
		opossum shrimp	0.0010	0.80
		insects	0.0020	0.80
10	627-699	kokanee	0.3900	0.39
		other salmonids	0.0500	0.44
		catostomids	0.0030	0.44
		centrarchids	0.0002	0.44
		peamouth	0.0010	0.44
		opossum shrimp	0.0003	0.44
		insects	0.0010	0.44
11	700-773	kokanee	0.2300	0.23
		other salmonids	0.0300	0.25
		catostomids	0.0020	0.26
		centrarchids	0.0001	0.26
		peamouth	0.0070	0.26
		opossum shrimp	0.0002	0.26
		insects	0.0010	0.26
	Total		6.8522	

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Appendix Table 3.5. Estimated consumption (kg) of prey items by northern pikeminnow (ages 6 to 11)/1,000 fish in Lake Pend Oreille, Idaho, 1998.

Cohort (years)	Range (length)	Prey item	Quantity of prey (kg)	Cumulative prey (kg)
6	315-355	kokanee	89.3216	89.32
		bull trout	0.0038	89.33
		whitefish	0.0011	89.33
		cottidae	0.0005	89.33
		decapoda	96.1982	185.53
		insects	8.7316	194.26
		molluscs	5.3635	199.62
		n. pikeminnow	2.1996	201.82
		other crustacea	0.1965	202.02
		peamouth	0.1472	202.16
		plant food	1.8532	204.02
		rainbow trout	7.1118	211.13
		redside shiner	6.5114	217.64
7	356-391	kokanee	83.8639	83.86
		bull trout	0.0037	83.87
		whitefish	0.0011	83.87
		cottidae	0.0005	83.87
		decapoda	76.8831	160.75
		insects	9.1038	169.86
		molluscs	4.9199	174.78
		n. pikeminnow	2.3661	177.14
		other crustacea	0.1891	177.33
		peamouth	0.1478	177.48
		plant food	1.7366	179.22
		rainbow trout	6.5673	185.78
		redside shiner	4.7438	190.53
8	392-426	kokanee	89.9639	89.96
		bull trout	0.0040	89.97
		whitefish	0.0012	89.97
		cottidae	0.0006	89.97
		decapoda	84.6144	174.58
		insects	9.6046	184.19
		molluscs	5.2948	189.48
		n. pikeminnow	2.4862	191.97
		other crustacea	0.2018	192.17
		peamouth	0.1570	192.33
		plant food	1.8616	194.19
		rainbow trout	7.0575	201.25
		redside shiner	5.2953	206.54
9	427-449	kokanee	81.5935	81.59
		bull trout	0.0036	81.60
		whitefish	0.0011	81.60
		cottidae	0.0005	81.60
		decapoda	73.6046	155.20
		insects	8.9403	164.14
		molluscs	4.7707	168.91
		n. pikeminnow	2.3328	171.25
		other crustacea	0.1846	171.43
		peamouth	0.1450	171.58
		plant food	1.6868	173.26
		rainbow trout	6.3682	179.63
		redside shiner	4.4874	184.12
10	450-500	kokanee	68.6209	68.62
		whitefish	0.0002	68.62
		decapoda	4.6878	73.31
		insects	54.9533	128.26
		other crustaceans	0.3612	128.62
		plant food	73.2543	201.88
11	501-515	kokanee	55.8957	55.90
		whitefish	0.0001	55.90
		decapoda	3.8184	59.71
		insects	45.1199	104.83
		other crustaceans	0.2979	105.13
		plant food	59.6699	164.80
	Total		1165.5085	