

Quantifying cutthroat trout (*Oncorhynchus clarki*) predation on sockeye salmon (*Oncorhynchus nerka*) fry using a bioenergetics approach

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Abstract: Although some sockeye salmon (*Oncorhynchus nerka*) enhancement programs achieve production goals in Alaskan lakes, others like the Margaret Lake project fall well below expected levels. We used bioenergetics model simulations, coupled with field sampling of predator diet and distribution, to quantify the intensity of cutthroat trout (*Oncorhynchus clarki*) predation on stocked sockeye salmon fry in Margaret Lake during 1993 and 1994. Model results indicated that, by September, cutthroat trout consumed an estimated 34–51 and 32–100% of the 200 000 and 100 000 sockeye salmon fry stocked in May 1993 and 1994, respectively. September hydroacoustic survey results estimated a 82–87% decline of fry in 1993 and 90–93% in 1994. Stomach fullness and evacuation estimates of total consumption were 59% of model estimates after the first fry release in 1994 and 120% of the model estimates after the second release. All approaches to estimating cutthroat trout predation on stocked fry suggested that piscivores played a substantial role in the decline of sockeye salmon fry in Margaret Lake. The ability to estimate consumption is valuable in isolating predator influence on food web dynamics, especially in manipulated systems.

Résumé : Bien que certains programmes d'amélioration des stocks de saumon rouge (*Oncorhynchus nerka*) atteignent leurs objectifs de production dans les lacs de l'Alaska, d'autres comme le projet du lac Margaret obtiennent une production bien en deçà des niveaux attendus. Grâce à des modélisations bioénergétiques, alliées à un échantillonnage sur le terrain pour déterminer le régime et la distribution des prédateurs, nous avons quantifié l'intensité de la prédation exercée par la truite fardée (*Oncorhynchus clarki*) sur les alevins de saumon rouge ensemencés dans le lac Margaret au cours de 1993 et 1994. Les résultats de la modélisation indiquent que, dès septembre, la truite fardée avait consommé entre 34 et 51 % et entre 32 et 100 % des 200 000 et 100 000 alevins de saumon rouge ensemencés en mai 1993 et en 1994, respectivement. Selon les résultats d'un relevé hydroacoustique effectué en septembre, il y a eu réduction estimative de 82 à 87 % des alevins en 1993 et de 90 à 93 % en 1994. Des estimations de la consommation totale obtenues grâce à une évaluation de la plénitude et de l'évacuation gastriques correspondaient à 59 % des estimations du modèle après le premier lâcher d'alevins en 1994 et à 120 % des estimations du modèle après le deuxième lâcher. Selon toutes les méthodes d'estimation de la prédation exercée par la truite fardée sur les alevins ensemencés, les piscivores jouaient un rôle substantiel dans la réduction du nombre d'alevins du saumon rouge dans le lac Margaret. La capacité d'estimer la consommation est utile pour isoler l'effet des prédateurs sur la dynamique du réseau trophique, en particulier dans les systèmes aménagés.

[Traduit par la Rédaction]

Introduction

For several decades, aquatic ecologists have been interested in factors that regulate the biomass and production of fishes in freshwater lakes. The extent to which bottom-up and top-

down forces interact to regulate biomass at each trophic level is important to fisheries resource managers interested in predicting the outcome of manipulating the nutrient levels, forage base, or top predators in lake systems to enhance a fishery. Sockeye salmon (*Oncorhynchus nerka*) enhancement programs are a good example of how the duality of food limitation and predator-prey interactions can produce variable results in studies designed to increase smolt biomass and adult salmon returns to commercial, sport, and subsistence fisheries. Koenings and Burkett (1987) developed a bottom-up model to predict sockeye salmon smolt and adult production based on the euphotic volume of the lake, the product of euphotic zone depth (1% incident light level), and the area of the lake. In Alaska, this model is combined with zooplankton production estimates to determine the number of sockeye salmon fry that can be supported in lakes targeted for enhancement.

Although some sockeye salmon enhancement programs

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have been successful in Alaska, others like the Margaret Lake project have failed to reach expected smolt production levels. Six years of hydroacoustic surveys indicated that only 5–34% of the stocked sockeye salmon fry survived 1 month after initial stocking in Margaret Lake. Poor adult sockeye salmon returns ranging from 75 to 350 fish between 1991 and 1994 support these low acoustic estimates of fry and smolt abundance (Bryant et al. 1995). Mortality due to handling and transportation of sockeye salmon fry from the hatchery to Margaret Lake was negligible (Cartwright and Beauchamp 1995). Previous Margaret Lake studies confirmed that the zooplankton forage base was sufficient to support 350 000 sockeye salmon fry, based on the euphotic volume model (DeCino 1992). We hypothesized that intense predation by resident piscivores could account for a rapid decline in sockeye salmon fry abundance. Several studies have shown that fish predators can significantly reduce juvenile sockeye salmon populations (Ruggerone and Rogers 1992; Beauchamp 1994; Beauchamp et al. 1995).

In Margaret Lake, we examined the diets of all potential predators including cutthroat trout (*Oncorhynchus clarki*), Dolly Varden (*Salvelinus malma*), coho salmon (*O. kisutch*) smolts, and kokanee (*O. nerka*) during 1990–1994. Of these, resident cutthroat trout was the only predator on sockeye salmon fry (Bryant and Frenette 1993; Frenette and Bryant 1994; Cartwright and Beauchamp 1995). The objective of this study was to quantify cutthroat trout predation on stocked juvenile sockeye salmon fry in Margaret Lake during 1993 and 1994.

Study site

Margaret Lake is located in southern Southeast Alaska about 48 km northwest of Ketchikan, Alaska. The 62-ha lake lies within a 30.6-km² drainage at 41 m in elevation with a maximum depth of 39 m and a mean depth of 10.9 m. The lake is dimictic, stained, and oligotrophic with seasonally variable Secchi depth transparencies of 2.5–8.5 m. Mean summer epilimnetic temperatures range from 15 to 18°C. Resident fishes include cutthroat trout, Dolly Varden, threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), and kokanee (resident sockeye salmon). Anadromous species include steelhead trout (*O. mykiss*), coho salmon, pink salmon (*O. gorbuscha*), stocked sockeye salmon, and Pacific lamprey (*Lamprolaima tridentata*).

Methods

Piscivore diet and distribution sampling

The stomach samples of piscivorous species were examined to identify potential sockeye salmon predators. Stomach samples were taken from all captured cutthroat trout, kokanee, and rainbow/steelhead trout (snout to fork length (FL) \geq 140 mm) in 1993 and 1994. The stomachs of all resident Dolly Varden (FL \geq 140 mm) and coho salmon smolts captured in May and June were examined for fish parts. Dolly Varden were periodically examined throughout the rest of the season.

Sampling of potential piscivore diet and distribution was stratified along dimensions of space, time, and body size. Spatial dimensions were divided between two lake habitats, shore slope and offshore, and depth of capture for predators within each habitat. Shore slope habitat was defined as the littoral area of the lake out to a water column depth of 0–5 m and within 0–2 m of the shore slope below the

5-m isobath. The offshore habitat or the pelagic area of the lake included depths from the surface to 30 m deep but \leq 2 m off the bottom, excluding the littoral area.

Temporal components of sampling were stratified by season and within a 24-h period. Three seasonal predation periods were defined in relation to the fry stocking date on May 19 in both years: prestock (April 1 – May 18), acute poststock (May 19 – June 20), and summer. Acute poststock and summer periods were further divided according to the number of stomach samples collected within periods of varying environmental conditions and prey availabilities (Tables 1 and 2). Within a 24-h period, four diel periods were delineated: day, dusk, night, and dawn.

Because the age structure of the cutthroat trout population in Margaret Lake was unknown, size categories were determined by length frequency histograms and the size at which cutthroat trout became piscivorous in other lakes (Beauchamp et al. 1992, 1995). For diet analysis, we partitioned cutthroat trout into three size categories in 1993 (140–200, 200–250, and 250–350 mm) and four size categories in 1994 (140–200, 200–250, 250–300, and 300–400 mm).

Fish were captured in the shore slope area using fyke nets, large minnow traps, horizontal gill nets, and angling. Offshore capture methods included vertical gill nets, angling, large suspended minnow traps, and trolling simultaneously at depths of 0.5, 4.5, 8.5, 12.5, and 16.5 m with downriggers. The vertical gill net was 30 m deep and consisted of two 2.5-m-wide panels of 50- and 90-mm stretch mesh. The horizontal gill nets (2 × 40 m) consisted of four panels: one 16-m-wide panel with 20-mm stretch mesh and three 8-m-wide panels with 50-, 80-, and 100-mm stretch mesh. Large 3-mm-mesh cylindrical minnow traps (3.1 m³) were set individually and in sets of five: one every 5 m in both shore slope and offshore habitats. Fyke nets, covered with 3-mm-mesh nylon netting, were set in the littoral zone and a lead wing was attached to the shore. Gear sets coincided with changes in diel light regime. For example, nets were pulled and reset just before and just after crepuscular periods to obtain diet data for discrete diel periods.

Captured fish were enumerated by species, measured to the nearest millimetre (FL), and weighed to the nearest 0.1 g. A nondestructive gastric evacuation method was used to extract stomach contents (Foster 1977). Samples were individually preserved in a 16% buffered formalin–alcohol solution.

Diet analysis

Stomach samples from resident and sea-run Dolly Varden, kokanee, and coho salmon smolts were examined visually for fish parts. All cutthroat trout stomach samples were examined under a dissecting microscope. Fish prey were separated by species, insects grouped together, and miscellaneous prey such as fish eggs, plankton, mollusks, annelids, and the occasional amphibian and lamprey recorded as “other.” Each group was weighed to the nearest 0.01 g wet weight.

Temporal and spatial patterns of piscivory were incorporated into a weighted average diet composition for each predator size-class and for each predation period throughout the season. For each predator size-class, diet compositions (wet weight proportions of each prey category) were averaged across shore slope and offshore habitats and were summed over all diel periods for each predation period for input to the bioenergetics model (Tables 1 and 2). Weekly temperature profiles were taken at 1-m intervals over 0–30 m with a YSI model 57 thermistor. An average Secchi depth was also measured weekly.

Cutthroat trout and sockeye salmon fry abundance estimates

Abundance estimates of cutthroat trout were estimated with a multiple mark–recapture sampling design using Schnabel and Schumacher–Eschmeyer estimators (see Bryant and Frenette 1993 for detailed description of methods). In 1993, 200 000 (gravimetric method) 0.21-g sockeye salmon fry were released into Margaret Lake at noon on May 19 (B. Halloran, Southern Southeast Regional Aquaculture Association (SSRAA), 2721 Tongass Ave, Ketchikan,

Table 1. Cutthroat trout 1993 diet composition used in the bioenergetics model.

Size-class (mm)	Predation period	Dates	Model days	Sockeye salmon	Threespine stickleback	Cottids	Coho salmon	Insects	Cutthroat trout	Unidentified fish parts	Others	<i>N</i>
cal/g ^a				1251–1255	1000	1304	1377	1195	1377	1255	500	
140–200	Prestock	Apr. 1 – May 8	1–47	0.00	0.25	0.16	0.00	0.59	0.00	0.00	0.01	61
	Postacute	May 19–25	48–54	0.10	0.00	0.00	0.00	0.86	0.00	0.00	0.04	44
		May 26–30	55–59	0.45	0.09	0.00	0.24	0.20	0.00	0.00	0.01	43
		June 1–20	60–80	0.00	0.01	0.00	0.00	0.84	0.00	0.05	0.10	21
	Summer	June 21 – July 2	81–92	0.08	0.07	0.03	0.29	0.51	0.00	0.04	0.01	51
		July 3–28	93–118	0.00	0.00	0.00	0.07	0.91	0.00	0.00	0.02	18
		July 29 – Sept. 7	119–149	0.00	0.49	0.01	0.00	0.28	0.00	0.08	0.14	32
200–250	Prestock	Apr. 1 – May 8	1–47	0.00	0.13	0.00	0.00	0.21	0.00	0.66	0.00	20
	Postacute	May 19–25	48–54	0.74	0.00	0.00	0.00	0.15	0.00	0.94	0.10	47
		May 26–30	55–59	0.01	0.02	0.00	0.01	0.94	0.00	0.00	0.20	31
		June 1–20	60–80	0.06	0.35	0.00	0.03	0.39	0.17	0.00	0.00	24
	Summer	June 21 – July 2	81–92	0.00	0.46	0.01	0.33	0.14	0.00	0.00	0.06	33
		July 3–28	93–118	0.00	0.40	0.02	0.00	0.41	0.00	0.00	0.17	45
		July 29 – Sept. 7	119–149	0.00	0.63	0.12	0.00	0.29	0.00	0.02	0.39	49
250–350	Prestock	Apr. 1 – May 8	1–47	0.00	0.38	0.00	0.51	0.10	0.00	0.00	0.00	11
	Postacute	May 19–25	48–54	0.46	0.08	0.01	0.00	0.42	0.00	0.01	0.02	45
		May 26–30	55–59	0.09	0.06	0.00	0.00	0.64	0.00	0.00	0.22	14
		June 1–20	60–80	0.06	0.27	0.01	0.00	0.55	0.00	0.02	0.09	16
	Summer	June 21 – July 2	81–92	0.01	0.75	0.16	0.00	0.03	0.00	0.00	0.05	20
		July 3–28	93–118	0.00	0.38	0.00	0.16	0.56	0.00	0.00	0.06	24
		July 29 – Sept. 7	119–149	0.00	0.78	0.00	0.00	0.15	0.00	0.04	0.03	34

Note: April 1 is day 1 of the simulation.

^aEnergy density estimated from weight-dependent function in Beauchamp et al. (1989): cal/g = 150 + 1.851*W*.

Table 2. Cutthroat trout 1994 diet composition used in the bioenergetics model.

Size-class (mm)	Predation period	Dates	Model days	Sockeye salmon	Threespine stickleback	Cottids	Pink salmon	Insects	Sockeye salmon smolts	Unidentified fish parts	Others	<i>N</i>
140–200	Prestock	Apr. 1 – May 18	1–47	0.00	0.16	0.00	0.00	0.76	0.00	0.06	0.07	67
		May 19–22	48–51	0.09	0.00	0.00	0.00	0.56	0.06	0.24	0.05	111
	Postacute I	May 23–27	52–56	0.24	0.23	0.00	0.00	0.59	0.00	0.00	0.16	37
		May 28–31	57–60	0.40	0.00	0.00	0.00	0.55	0.00	0.00	0.05	41
		June 1–4	61–64	0.00	0.00	0.00	0.00	0.84	0.00	0.00	0.16	6
	Midsummer	June 5–20	65–80	0.23	0.00	0.00	0.00	0.68	0.00	0.01	0.07	52
		June 21 – July 16	81–106	0.06	0.01	0.00	0.00	0.78	0.00	0.02	0.13	34
	Late summer	July 17 – Aug. 16	107–137	0.00	0.33	0.00	0.00	0.60	0.00	0.00	0.07	15
		Aug. 17 – Sept. 10	138–162	0.00	0.35	0.00	0.00	0.24	0.00	0.34	0.06	12
	200–250	Prestock	Apr. 1 – May 18	1–47	0.00	0.05	0.00	0.01	0.90	0.00	0.00	0.04
May 19–22			48–51	0.14	0.21	0.00	0.00	0.48	0.09	0.03	0.02	102
Postacute I		May 23–27	52–56	0.01	0.01	0.00	0.00	0.79	0.00	0.00	0.18	35
		May 28–31	57–60	0.58	0.00	0.01	0.00	0.39	0.00	0.00	0.01	90
		June 1–4	61–64	0.00	0.05	0.00	0.00	0.95	0.00	0.00	0.00	15
Midsummer		June 5–20	65–80	0.08	0.05	0.00	0.00	0.76	0.05	0.01	0.05	89
		June 21 – July 16	81–106	0.19	0.01	0.01	0.00	0.68	0.00	0.00	0.02	30
Late summer		July 17 – Aug. 16	107–137	0.00	0.30	0.41	0.00	0.22	0.00	0.00	0.06	43
		Aug. 17 – Sept. 10	138–162	0.00	0.38	0.00	0.00	0.46	0.00	0.14	0.03	11
250–300		Prestock	Apr. 1 – May 18	1–47	0.00	0.02	0.00	0.06	0.90	0.00	0.01	0.01
	May 19–22		48–51	0.48	0.00	0.11	0.00	0.26	0.00	0.04	0.03	47
	Postacute I	May 23–27	52–56	0.34	0.05	0.00	0.00	0.48	0.05	0.01	0.07	25
		May 28–31	57–60	0.25	0.07	0.00	0.00	0.64	0.00	0.00	0.02	26
		June 1–4	61–64	0.00	0.09	0.00	0.00	0.78	0.00	0.01	0.13	6
	Midsummer	June 5–20	65–80	0.22	0.20	0.09	0.00	0.47	0.00	0.00	0.01	37
		June 21 – July 16	81–106	0.00	0.81	0.01	0.00	0.18	0.00	0.00	0.01	11
	Late summer	July 17 – Aug. 16	107–137	0.01	0.66	0.00	0.00	0.18	0.00	0.00	0.15	23
		Aug. 17 – Sept. 10	138–162	0.04	0.20	0.00	0.00	0.53	0.00	0.00	0.23	7
	300–400	Prestock	Apr. 1 – May 18	1–47	0.00	0.40	0.00	0.00	0.60	0.00	0.00	0.00
May 19–22			48–51	0.85	0.03	0.00	0.00	0.11	0.00	0.00	0.00	8
Postacute I		May 23–27	52–56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1
		May 28–31	57–60	0.03	0.22	0.00	0.00	0.74	0.00	0.00	0.01	3
		June 1–4	61–64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2
Midsummer		June 5–20	65–80	0.02	0.28	0.48	0.00	0.21	0.00	0.00	0.02	10
		June 21 – July 16	81–106	0.00	0.40	0.00	0.00	0.60	0.00	0.00	0.00	1
Late summer		July 17 – Aug. 16	107–137	0.00	0.40	0.00	0.00	0.60	0.00	0.00	0.00	4
		Aug. 17 – Sept. 10	138–162	0.00	0.40	0.00	0.00	0.60	0.00	0.00	0.00	1

Note: April 1 is day 1 of the simulation.

AK 99901, U.S.A., personal communication). In 1994, an estimated 50 000 0.3-g sockeye salmon fry were released in the lake at noon on May 19 (SSRAA, personal communication). An additional 50 000 0.3-g sockeye salmon fry were held in situ in a 227-m² net pen with 3-mm mesh and released at midnight on May 28 as 0.4-g fry.

The seasonal abundance of juvenile sockeye salmon was estimated by serial hydroacoustic surveys and midwater trawls (2-m² opening and 3-mm knotless mesh) conducted by the Alaska Department of Fish and Game (ADF&G) on June 23, July 24, and September 2 in 1993, on May 24, June 1, June 18, and September 2 in 1994, and on April 26 in 1995. The duration-in-beam method (Thorne 1988) was used to enumerate the number of fish targets collected with a 70-kHz Simrad EY-M scientific echo sounder and recorded in digital format from 10 randomly chosen transects selected for each survey. Species and age composition of acoustic targets were determined by sampling the pelagic area with midwater trawl gear.

Consumption model

The importance of predation versus other sources of mortality can only be evaluated explicitly by quantifying predation and comparing it with total mortality. The bioenergetics approach to modeling (Kitchell et al. 1977) is less labor intensive than the stomach fullness–evacuation approach (Elliott and Persson 1978) and offers fine-scale temporal resolution of piscivory not possible with the production-based method (Ney 1990).

We used the Wisconsin bioenergetics model 2 (Hewett and Johnson 1992) modified for cutthroat trout (Beauchamp et al. 1995) to estimate daily consumption rates (grams per day) by cutthroat trout for each prey type and for each specific predator size-class for the 1993 and 1994 seasons. April 1 of each year was designated as day 1 in the model runs, and May 10 (day 40) was defined as the spawning date in the adult cutthroat trout species file. Spawning weight loss was estimated at 8% (D.A. Beauchamp, unpublished data). Prey caloric densities (Table 1) were obtained from the literature (Cummins and Wuycheck 1971; Hewett and Johnson 1992; Beauchamp et al. 1995). Because prey caloric densities of prey can change over a season, we calculated salmonid prey caloric density as a function of weight (Beauchamp et al. 1989).

The bioenergetics model estimates average individual predator consumption (grams per day), given population-specific data on growth, diet composition (Tables 1 and 2), and thermal experience of the predator. We calculated a weighted mean thermal experience for cutthroat trout based on their vertical distribution and concurrent vertical temperature profiles (Table 3). Information on predator growth was derived from length and weight data collected during population estimates of cutthroat trout during April, June, and October (Frenette and Bryant 1994; Bryant et al. 1995) (Table 4).

Daily sockeye salmon fry consumption estimates (grams per day) for individual cutthroat trout were divided by the mean body mass of fry sampled from the lake at that time to estimate the number of fry consumed per individual cutthroat trout. Individual consumption was multiplied by size-structured population estimates ($\pm 95\%$ confidence interval (CI)) of cutthroat trout to estimate the total sockeye salmon fry biomass consumed by the entire cutthroat trout population during 1993 and 1994. The consumption estimate was then compared with hydroacoustic survey estimates of the number of sockeye salmon fry remaining in the lake throughout the season for each year.

To compare our model results with a more direct measurement of consumption, we calculated the daily ration of the mid-sized cutthroat trout (196–265 mm) using the stomach fullness–evacuation rate method (Elliott and Persson 1978) coupled with diet data collected over ecologically important feeding periods (day, dusk, night, and dawn). Data were pooled for three days immediately following the two fry releases: May 20–22 and May 28–30 in 1994. Mean stomach fullness with error bounds was calculated for these two periods. A fish evacuation rate (Elliott 1991) and an invertebrate evacuation rate (Elliott 1972) were calculated using temperatures taken May 22

and 29 and weighted by the average proportional weekly depth distribution of mid-sized cutthroat trout (Table 3). A final consumption estimate was weighted by the proportion of fish and insects in the diet during each 3-day period.

Sensitivity and error analyses

Sensitivity analysis of the internal parameters of the cutthroat trout model has been performed for similar salmonid models (Beauchamp et al. 1989; Ruggerone and Rogers 1992), so here, we will focus only on effects of error in our field inputs to the model. Error bounds (2 SE) were calculated as a percentage of the mean weights to estimate the 95% CI around the nominal weight values (Table 5). The average ratio of 95% CI/mean weight across all cutthroat trout size classes was 3.2% in 1993 and 5.5% in 1994. The model was rerun using these weight error bounds to calculate a range of consumption estimates (Table 5). Other field parameters were perturbed using only data from 1993. Prey caloric densities were changed $\pm 10\%$ from their nominal values. Temperature was changed $\pm 1^\circ\text{C}$ from nominal values to evaluate the sensitivity of our simulations to uncertainty in thermal experience.

To evaluate the collective effect of variation of several field values on the model consumptions estimates, an error analysis (Bartell et al. 1986) was performed on cutthroat trout consumption of sockeye salmon fry using 120 randomly generated values of growth, temperature, and diet composition (sockeye salmon and “other”) from the 1994 data between May 19 and 27. Because the editing capabilities of the Wisconsin bioenergetics model are cumbersome, we only performed the error analysis on the mid-sized cutthroat trout (196–220 mm), the size category with the largest number of diet samples and the highest abundance in the population estimates. Growth and temperature values were generated from a normal distribution. A binomial distribution was used to simulate random proportions of sockeye salmon fry and “other” prey around mean field values. The “other” diet category was assigned the insect caloric density value of 1195 cal/g (1 cal = 4.1868 J) because insects were the most dominant prey item in the diet of the trout in Margaret Lake.

Results

Stomach samples were taken from all captured cutthroat trout ($N = 694$ in 1993, $N = 1049$ in 1994) and kokanee (FL ≥ 140 mm; $N = 12$ in 1993, $N = 7$ in 1994) from April to mid-September in 1993 and 1994. Stomach samples were taken from resident Dolly Varden (FL ≥ 140 mm; $N = 110$ in 1993, $N = 55$ in 1994) during April–June of both years and periodically for the remainder of each year ($N = 28$ in 1993, $N = 61$ in 1994) after it became apparent that they did not consume sockeye salmon fry. In 1994, coho salmon smolts ($N = 17$) emigrating to the ocean in late May and early June and two sea-run Dolly Varden entering the lake in September were also sampled for diet composition. Cutthroat trout were the only piscivore examined that contained sockeye salmon fry in the stomach samples.

Predator and prey abundance

The estimated cutthroat trout population (FL > 140 mm) declined from 3000 (95% CI = 2600–3600) in October 1992 to 1600 (95% CI = 1300–2000) in October 1993 with an instantaneous daily mortality rate of -0.00177 . The cutthroat trout population continued to decline throughout 1994 with an instantaneous daily mortality rate of -0.00085 and a nominal number of 1200 fish (95% CI = 600–4000) by October 15, 1994.

Hydroacoustic estimates of sockeye salmon fry abundance

Table 3. Temperature (°C) model inputs for each cutthroat trout size class in 1993 and 1994.

Year	Model day	Small cutthroat trout, 10–200 mm	Medium cutthroat trout, 200–250 mm	Medium to large cutthroat trout, (250–300 mm)	Large cutthroat trout, 250–350 mm (300–400 mm)
1993	1	7.1	9.6		10.1
	48	7.1	9.6		10.1
	55	8.0	11.4		12.4
	64	9.2	13.5		15.0
	78	7.5	11.1		11.2
	85	8.4	11.1		11.1
	103	8.0	12.5		12.7
	115	8.0	13.3		12.7
	124	8.0	13.0		12.5
	142	8.0	13.7		13.0
	160	8.0	13.3		13.0
	168	8.0	12.7		12.4
	181	8.0	10.1		9.9
	190	8.0	10.1		9.9
	203	8.0	8.3		8.3
365	8.0	9.6		10.0	
1994	1	5.3	5.3	5.2	5.2
	38	7.9	8.0	7.7	7.7
	49	11.8	11.8	11.1	11.2
	52	11.0	10.6	10.0	10.3
	58	8.6	8.5	8.3	8.3
	64	8.1	8.0	7.8	7.9
	71	11.4	11.4	10.8	11.2
	78	12.5	12.2	12.1	12.0
	94	13.1	12.6	12.7	12.3
	101	12.1	11.6	11.8	11.4
	107	15.1	14.8	14.3	14.4
	115	16.7	16.3	15.8	15.7
	122	15.8	15.5	15.2	15.1
	128	16.3	14.9	16.1	15.0
	134	18.9	17.0	18.8	17.2
	141	18.1	16.3	17.8	16.9
	148	15.1	14.0	14.9	13.7
	155	13.9	13.1	13.7	12.8
	164	13.1	12.4	12.9	12.1
	171	10.9	10.7	10.9	10.7
365	5.3	5.3	5.2	5.3	

Note: April 1 is day 1 of the simulations. Model days represent the date the temperature profiles were taken. Temperatures describe a weighted average proportional to the weekly distribution of the cutthroat trout size-class in the water column. Size intervals in parentheses are 1994 only.

declined dramatically during the first month after stocking in both 1993 and 1994. In 1993, 34 800 (± 6200) fry out of 200 000 remained 1 month after stocking. Sockeye salmon fry mortality slowed considerably during the remainder of the growing season, and the acoustic estimate in September was 31 100 (± 5567) fry. Although 50% fewer fish were stocked in 1994, the estimated number of fry remaining 1 month after stocking ($32\,900 \pm 3000$) was similar to that of June 1993. However, the September 1994 estimate of 8600 fry (± 1100) indicated a substantial decline in fry numbers (8.5% survival) during the remainder of the growing season when compared

with 1993 (15.6% survival). The hydroacoustic survey conducted in April 1995 estimated that 5800 (± 1300) fry from the 1994 stocking cohort survived to age 1. The 68% over-winter survival rate is consistent with the standard survival assumption of 70% from fall fry to spring smolt developed for sockeye salmon in Southeast Alaska (T. Zadina, ADF&G, 2030 Sea Level Dr., Ketchikan, AK 99901, U.S.A., unpublished data).

Cutthroat trout experienced warmer temperatures on average in 1994 than in 1993 during the initial acute predation period which began on May 19 both years (Table 3).

Table 4. Average initial wet weights for each cutthroat trout length interval and cohort modeled in 1993 and 1994 and in the spring of 1995.

Year	Cohort	Model days	Length interval (mm)	Initial weight (g) (2 SE)
1993	J2	75–183	91–160	24.5 (2.1)
	J3	184–365	131–190	39.7 (3.4)
	J4	1–74	151–195	43.5 (1.2)
	J5	75–183	161–210	54.1 (1.5)
	J6	184–365	191–220	79.3 (2.2)
	A1	1–74	196–215	79.5 (2.1)
	A2	75–183	211–240	108.1 (8.1)
	A3	184–365	221–255	119.2 (8.9)
	A4	1–74	216–225	114.6 (5.2)
1994	J2	75–183	135–170	33.1 (2.7)
	J3	184–365	125–175	33.3 (2.7)
	J4	1–74	151–195	46.6 (1.8)
	J5	75–183	171–200	55.2 (2.1)
	J6	184–365	226–290	211.7 (15.8)
	A1	1–74	196–220	71.7 (3.2)
	A2	75–183	201–250	89.4 (4.0)
	A3	184–365	221–265	123.1 (5.5)
	A4	1–74	221–265	111.9 (8.4)
1995	J4	1–74	131–180	33.4 (2.7)
	J7	1–74	181–230	74.3 (2.8)
	A4	1–74	231–270	132.3 (5.9)
	A7	1–74	271–300	206.2 (15.5)
	A10	1–74	301–330	272.7 (23.3)
	A13	1–74	330–370	381.6 (52.2)

Note: April 1 is day 1 of the simulations. Cohort letter initials indicate whether juvenile (J) or adult (A) physiological parameters were used, and the number represents the cohort interval. The initial weight of the next cohort is the end weight of the preceding cohort. For example, the end weight of J3 is J4, the weight gained overwinter.

However, this thermal pattern was reversed by May 26, 1994, due to an intense and prolonged rainstorm. The storm caused the lake level to rise 2–3 m and remain in flood condition for 10 days, creating a dramatic decline in temperature and near-isothermic conditions during the acute predation period of the study in 1994. Although temperature regimes in 1993 were considerably different among cutthroat trout size-classes, all three groups occupied increasingly warmer temperatures between May 19 (model day 49) and June 3 (model day 64)

(Table 3). During the same period in 1994, thermal experience was similar among the four cutthroat trout size groups and dropped 2.0–2.3°C between May 22 and May 28 (Table 3).

Bioenergetics model estimates

For 1993 and 1994, bioenergetics model simulations estimated that roughly half the sockeye salmon fry stocked were consumed by cutthroat trout (Fig. 1). The nominal consumption estimate from the model was 82 800 fry in 1993 (Fig. 1A). Sockeye salmon fry consumption ranged from 67 800 to 101 000 fry based on 95% CI around cutthroat trout population estimates. In 1994, model simulations predicted that cutthroat trout consumed 51 400 fry (32 100 – 130 300, 95% CI) of the 100 000 fry released into the lake (Fig. 1B). In 1993, most predation occurred during the first 2 weeks after stocking whereas predation in 1994 proceeded at a more gradual rate throughout the summer (Fig. 1).

Although the two smaller cutthroat trout size groups consumed fewer grams of sockeye salmon per individual than the larger size groups, at the population level, they consumed as many or more sockeye salmon fry than the larger cutthroat trout in 1994 (Fig. 2). Insects dominated the diet of cutthroat trout during most of the growing season both years (Fig. 2; Tables 1 and 2). The increased proportion of threespine stickleback in the diet of all sizes of cutthroat trout during summer reflected the availability and vulnerability of newly emerging young-of-the-year in July.

Direct measurement of consumption

Using the stomach fullness–evacuation method (Elliott and Persson 1978), the mean (95% CI) total daily consumption estimate for 196- to 265-mm cutthroat trout was 1.98 g (1.23–2.72 g) per predator during May 20–22, 1994. When compared with the bioenergetics model estimate of consumption during the same time period, the direct measurement mean estimate was 59% of the nominal model estimate (3.36 g) with a range of 37–81% (Fig. 3). After the second release of sockeye salmon fry on May 27, 1994, the direct consumption estimate was 3.71 g (2.60–4.34 g) per predator during May 28–30, 1994 (Fig. 3). During this period, the direct estimate was 20% higher than the mean model estimate (2.98 g), but within the upper and lower 95% CI error bounds (Fig. 3).

Sensitivity analysis

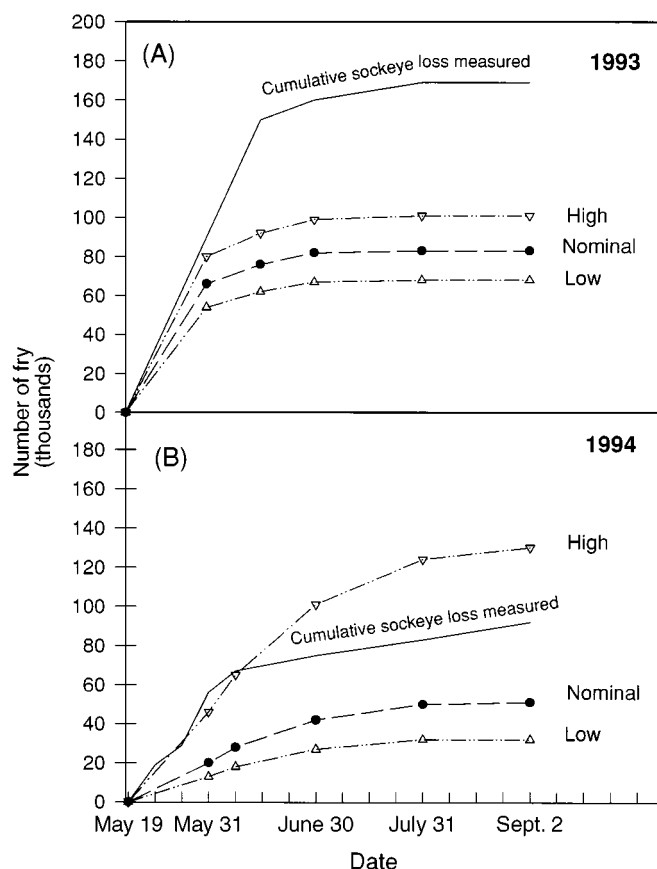
Individual parameter perturbations of 1993 field values for growth, caloric density, temperature, and cutthroat trout population estimates showed cutthroat trout consumption estimates of juvenile sockeye salmon to be most sensitive to changes in predator abundance estimates ($\pm 19\%$ of nominal value, Fig. 1) and least sensitive to changes in estimated growth (3.1–5.5%) between cutthroat trout size-classes (Table 5). In 1993, changes in cutthroat trout initial and end mean weights for each size-class and predation period produced an estimated range of 80 200 – 87 400 sockeye salmon fry consumed (Table 5). In 1994, model simulations encompassing the 95% CI around mean cutthroat trout growth resulted in consumption ranging between 46 150 and 54 300 fry. Changes in prey caloric densities had an inverse effect on fry consumption estimates; lowering prey caloric density increased the estimated number of fry consumed. In 1993, a

Table 5. Sensitivity analysis results of cutthroat trout consumption estimates of sockeye salmon fry in 1993.

Parameter	Amount parameter perturbed	Deviation from nominal value	% change in consumption	Consumption estimate
Cutthroat abundance	Lower 95% CI	19%	-18.0	67 853
	Upper 95% CI	19%	+22.0	101 047
Cutthroat weight (g)	-2 SE	-2595	-3.1	80 203
	+2 SE	+4569	+5.5	87 367
Prey caloric density (cal/g wet weight)	-10%	+9019	+10.9	91 817
	+10%	-8051	-10.8	74 747
Temperature (°C)	-1	5599	-7.8	77 199
	+1	5045	+6.8	87 843

Note: Nominal values of all other field input values and model parameters were used. The nominal consumption value was 82 798 sockeye salmon fry.

Fig. 1. Comparison of bioenergetics model estimates of cutthroat trout consumption (broken lines) with hydroacoustic measurement of stocked (age 0) sockeye salmon fry decline (solid line) for (A) 1993 and (B) 1994. The range of consumption estimates is based on 95% CI around cutthroat trout population estimates.



10% reduction in prey caloric densities resulted in a mean of 91 817 sockeye salmon fry consumed (Table 5). Conversely, a 10% increase in prey caloric densities resulted in a mean of 74 747 fry eaten in the 1993 growing season (Table 5). Raising and lowering the temperature by 1°C resulted in a 7.8% change in the number of sockeye salmon fry consumed. Higher temperatures increased consumption estimates to a

mean of 87 800 fry, and lower temperatures reduced consumption estimates to a mean of 77 200 fry (Table 5).

The error analysis of field values for growth, temperature, and diet for the 196- to 220-mm cutthroat trout ($N = 137$) generated a mean (95% CI) daily consumption of 2.44 g (2.22–2.66 g) of sockeye salmon fry per predator and a coefficient of variation of 52%. This translated into a mean daily consumption of 7.4 (6.7–8.1) 0.33-g sockeye salmon fry per predator during May 19–27, 1994.

Discussion

Results from the bioenergetics modeling of cutthroat trout consumption suggest that cutthroat trout predation is a significant contributor to the decline of sockeye salmon fry in Margaret Lake. Although half as many fry were stocked in 1994, consumption estimates and hydroacoustic estimates showed similar rates of sockeye salmon fry decline in both years. Cutthroat trout abundance estimates, stratified by size, produced large confidence intervals around mean abundance estimates. Population-level consumption estimates were sensitive to cutthroat trout abundance, and estimates of predation intensity accounted for 34–51% of the observed fry mortality in 1993 and 32–100% in 1994.

It appears that cutthroat trout in Margaret Lake are capable of sustaining a constant rate of predation even as the prey biomass declines until some low threshold is reached. Between 1990 and 1994, the number of fry stocked ranged from 100 000 to 518 000 (T. Zadina, ADF&G, 2030 Sea Level Dr., Ketchikan, AK 99901, U.S.A., unpublished data). The fall hydroacoustic surveys consistently showed that sockeye salmon fry were driven to low numbers (5000 – 75 000 fry, 2.5–16.7% of total number stocked). This suggests that cutthroat trout were efficient predators and exhibited a modified type II functional response to the introduction of stocked juvenile salmonids (Peterman and Gatto 1978). The functional response of the predators was not diminished when low numbers of fry were stocked in 1994. Because this broad range of stocking strategies did not improve sockeye salmon fry survival in Margaret Lake, stocking was discontinued after 1994.

We attempted to address several of the criticisms directed towards field inputs of previous bioenergetics model studies. Diet composition errors in this study are most likely minimal

Fig. 2. Seasonal 1994 patterns of individual daily consumption of major prey by size-class of cutthroat trout (top) and size-class population-level consumption of sockeye salmon fry (bottom). Predation stanza date codes: Pre, prestock, April 1 – May 18; Acute, acute poststock, May 19 – June 4; Jun, June 5–20; Sum, summer, June 21 – September 10.

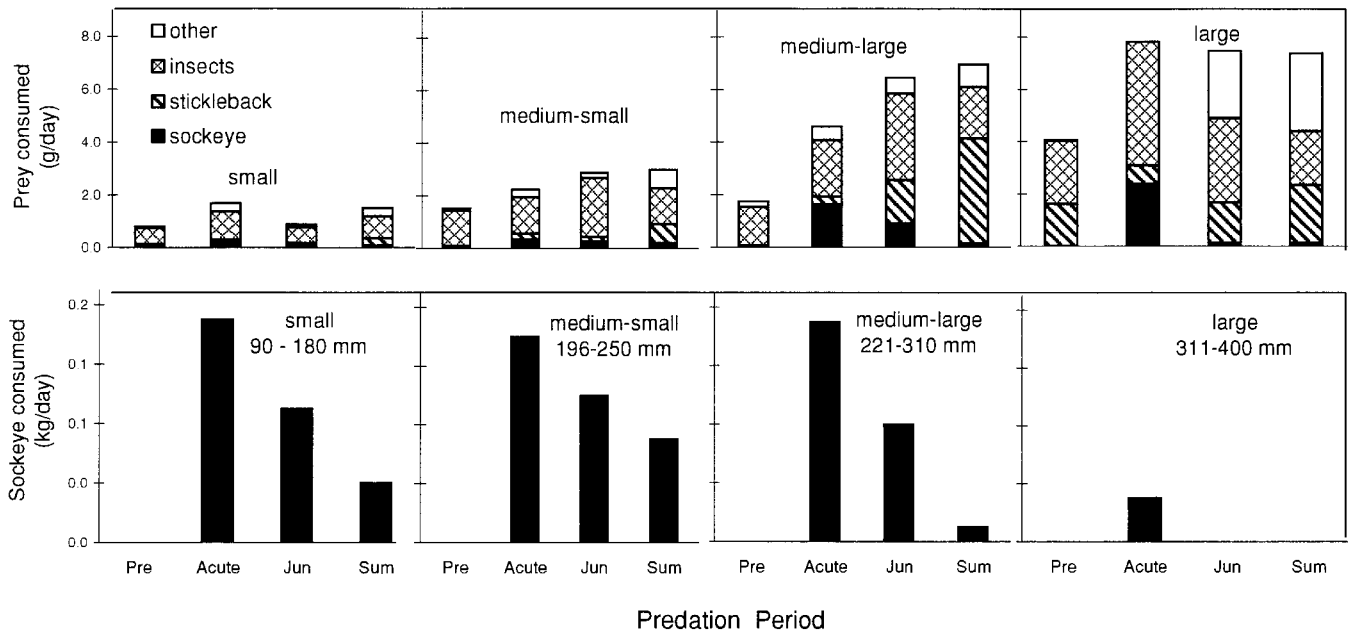
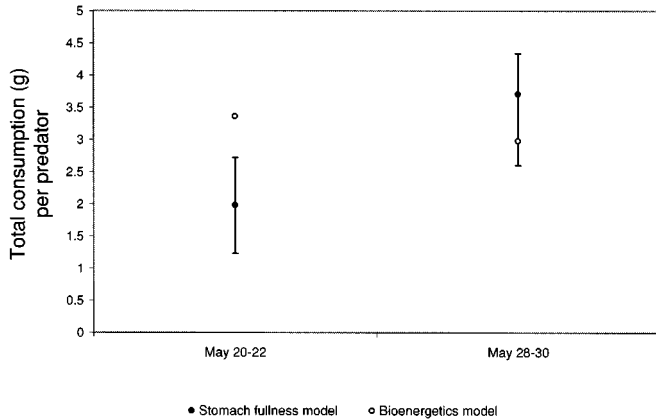


Fig. 3. Daily total consumption per predator estimated by the bioenergetics model and the stomach fullness–evacuation model for a 3-day period following the first fry release (May 20–22) and the second fry release (May 28–30) in 1994. The stomach fullness–evacuation model error bars were derived from the 95% CI around the mean stomach fullness values.



because stomach samples were collected on a fine-grained temporal and spatial scale. Temperature values were assigned according to the proportion of cutthroat trout distributed in the water column. Although this approach is not as accurate as telemetry studies of fish movement, it does include field data on distribution of the cutthroat trout not considered in the more common assumption of behavioral thermoregulation.

One criticism of the Wisconsin bioenergetics model is its inability to accurately represent energetic costs associated with activity (Boisclair and Leggett 1989; Hansen et al. 1993). Most studies reporting a wide variation in activity costs were conducted on juvenile planktivorous fish

(Boisclair and Leggett 1989; Post 1990; Madon and Culver 1993; Tang and Boisclair 1995), which have very different energetic demands than insectivorous and piscivorous adults. Germane to this study, the difference between activity costs measured in the Wisconsin model and by other methods appears to be less important for adult fish compared with more active juvenile fish (Post 1990), especially nonspawning adults (Rowan and Rasmussen 1996). In addition, sensitivity analysis of the Wisconsin model indicates only modest errors in consumption estimates associated with activity parameters (Bartell et al. 1986; Beauchamp et al. 1989).

Comparing bioenergetics model consumption estimates with estimates derived from an independent source is essential to the credibility of model outputs. Hydroacoustic abundance estimates of sockeye salmon fry throughout the season provided independent estimates of sockeye salmon fry abundance and mortality for comparison with model estimates of predation-induced mortality from cutthroat trout. Both the bioenergetics model and acoustic estimates showed a sharp reduction in fry numbers immediately after stocking and a more gradual decline of sockeye salmon fry in 1994 than in 1993 for the rest of the season. Consumption estimates from the bioenergetics model were also reasonably close to consumption estimates derived by the “direct” stomach fullness–evacuation method. Contradictory results in the comparison of model and direct measurement consumption estimates between the first (May 20–22) and second fry releases (May 28–30) may have been confounded by the dramatically fluctuating thermal experience of the predator during a heavy rainstorm after the second release of fry in 1994.

The density of cutthroat trout in Margaret Lake (16 fish/ha, FL \geq 175 mm) was similar to the average densities estimated in other Southeast Alaska lakes. The Sport Fish Division of

the ADF&G has estimated that cutthroat trout (FL \geq 180 mm) densities range 2–38 fish/ha for several Southeast Alaska lakes (see summary in Der Hovanisian and Marshall 1995). However, survival of stocked sockeye salmon fry in Margaret Lake was low compared with other stocked populations in the region. For example, after stocking 556 000 fry in Badger Lake on May 16, 1985, 65% of the fry survived to June 24 (Zadina and Haddix 1989) compared with 17% fry survival in Margaret Lake 1 month after stocking in 1993. The 2.5–16.7% range of fry to smolt survival in Margaret Lake is well below the 28–65% range for other Southeast Alaska lakes and on the lower end of a wide range reported for other Alaskan and Canadian lakes, 2.8–66% (Foerster 1968). Bradford (1995) placed sockeye salmon fry to smolt survival at 22% in northwestern lakes compared with 8% estimated for sockeye salmon fry stocked in 1994 in Margaret Lake.

Despite evidence in other lakes that piscivores are capable of compromising enhancement efforts, the Margaret Lake study is the only Alaskan lake where resident cutthroat trout densities and the associated predatory impact on stocked juvenile salmonids have been determined. The detrimental effects of resident trout on introduced sockeye salmon fry in Margaret Lake provide one example of the importance of predation in manipulated systems (Peterman and Gatto 1978). How piscivores affect juvenile sockeye salmon recruitment in other lakes may depend on a complex suite of physical (basin morphometry, water transparency, temperature, oxygen, etc.) and biological (density, distribution, and size structure of predators, availability of alternative prey, trophic state) conditions present in different lakes. Therefore, similar investigations in other lakes would provide valuable insights into the importance of piscivory across a range of different physical and biological conditions and may improve our ability to predict the relative importance of top-down or bottom-up control in different waters.

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