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[Article]

Effects of Introduced Fishes on Wild Juvenile Coho Salmon in Three Shallow Pacific Northwest Lakes

SCOTT A. BONAR*

Arizona Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey,
104 Biological Sciences East, University of Arizona, Tucson, Arizona 85721, USA

BRUCE D. BOLDING, MARC DIVENS, AND WILLIAM MEYER

Inland Fisheries Research, Washington Department of Fish and Wildlife,
600 Capitol Way North, Olympia, Washington 98501-1091, USA

Abstract.—Declines in Pacific salmon *Oncorhynchus* spp. have been blamed on hydropower, overfishing, ocean conditions, and land use practices; however, less is known about the impacts of introduced fish. Most of the hundreds of lakes and ponds in the Pacific Northwest contain introduced fishes, and many of these water bodies are also important for salmon production, especially of coho salmon *O. kisutch*. Over 2 years, we examined the predation impacts of 10 common introduced fishes (brown bullhead *Ameiurus nebulosus*, black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, golden shiner *Notemigonus crysoleucas*, green sunfish *L. cyanellus*, largemouth bass *Micropterus salmoides*, pumpkinseed *L. gibbosus*, rainbow trout *O. mykiss*, warmouth *L. gulosus*, and yellow perch *Perca flavescens*) and two native fishes (cutthroat trout *O. clarkii* and prickly sculpin *Cottus asper*) on wild juvenile coho salmon in three shallow Pacific Northwest lakes, all located in different watersheds. Of these species, largemouth bass were responsible for an average of 98% of the predation on coho salmon in all lakes, but the total impact to each run varied among lakes and years. Very few coho salmon were eaten by black crappies, brown bullheads, cutthroat trout, prickly sculpin, or yellow perch, whereas other species were not observed to eat coho salmon. Juvenile coho salmon growth in all lakes was higher than in nearby streams. Therefore, food competition between coho salmon and introduced fishes in lakes was probably not limiting coho salmon populations. Largemouth bass are widespread and are present in 85% of lowland warmwater public-access lakes in Washington ($n = 421$), 84% of those in Oregon ($n = 179$), and 74% of those in the eight northwesternmost counties in California ($n = 19$). Future research would help to identify the impact of largemouth bass predation across the region and prioritize lakes where impacts are most severe. Nevertheless, attempts to transplant or increase largemouth bass numbers in lakes important to coho salmon would be counterproductive to coho salmon enhancement efforts.

Pacific salmon *Oncorhynchus* spp. are integral to the aquatic ecosystems, the economy, and the Native American and European cultures of the Pacific Northwest. Five species of Pacific salmon have declined in abundance, especially along the southern half of their native range in California, Oregon, and Washington. These declines have been drastic, and many salmon stocks are now protected under the U.S. Endangered Species Act.

Salmon declines have been blamed on a combination of overharvest, habitat destruction, presence of dams, climate change, and interactions with hatchery fish (National Research Council 1996; Finney et al. 2000, 2002; Kareiva et al. 2000). While numerous studies have examined the effects of these factors, few have examined the role of introduced fishes in the decline of salmon stocks. During the late 19th and early 20th centuries, European settlers and the U.S. Fish Commission stocked lakes and rivers in the western United States en masse with nonnative fishes, including centrarchids, ictalurids, percids, and salmonids (Lampman 1946; Wydoski and Whitney 1979). The introductions and subsequent movement of these fishes were widespread, and virtually all lowland lakes and many river systems in the Pacific Northwest region of the United States now contain some introduced fishes. Few were stocked into lakes on the Pacific Coast of Canada; however, there is increasing interest by angling groups to introduce many nonnative species. Although popular with anglers (Zook 1999), introduced fishes have contributed to declines of native fishes in many regions of the American West (Minckley and Deacon 1991; Gunckel et al. 2002).

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* Corresponding author: sbonar@ag.arizona.edu

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TABLE 1.—Descriptions of study lakes in western Washington. Fish species are brown bullhead (BBH) *Ameiurus nebulosus*, black crappie (BC) *Pomoxis nigromaculatus*, chum salmon (CH) *Oncorhynchus keta*, cutthroat trout (CT) *O. clarkii*, coho salmon (CO), golden shiner (GDS) *Notemigonus crysoleucas*, green sunfish (GS) *Lepomis cyanellus*, largemouth bass (LMB) *Micropterus salmoides*, prickly sculpin (PKS) *Cottus asper*, pumpkinseed (PS) *L. gibbosus*, rainbow trout (RB) or steelhead *O. mykiss*, warmouth (WM) *L. gulosus*, yellow perch (YP) *Perca flavescens*, and bluegill (BG) *L. macrochirus*. Population estimate is number of LMB larger than 150 mm TL. The abbreviation CL stands for confidence limit.

					LMB			
Lake	Size (ha)	Watershed	Fish species	Elevation (m)	Population estimate	Lower 95% CL	Upper 95% CL	Density (fish/ha)
Symington	24	Big Beef Creek	BBH, BG, CO, YP, LMB, RB, CT, GS, PS, WM	120	338	218	549	14.08
Long	127	Salmonberry and Curley creeks	YP, BC, BG, LMB, CT, CO, CH, GDS, PKS, BBH	36	922	705	1,205	7.26
Wildcat	44	Wildcat Creek	CO, PKS, CT, RB, LMB	116	438	361	533	9.95

Most studies of interactions among introduced fishes and Pacific salmon have been conducted in large, deep lakes, reservoirs, or large river systems (Poe et al. 1991; Tabor et al. 1993; Fayram and Sibley 2000; Nowak et al. 2004). However, the most common introduced fishes found in the freshwaters of the Pacific Northwest evolved in warm, shallow waters of the eastern United States and prefer the littoral areas of lakes and ponds. Few of these species develop large populations in deep, cold lakes or reservoirs, or in fast-flowing Pacific Northwest streams. Shallow, off-channel sites such as ponds, sloughs, marshes, and the littoral zones of lakes provide more suitable habitat for these species. These areas are also important for salmon and reportedly contribute 15–62% of the total production of juvenile salmon in various watersheds (Bustard 1983; Brown and Hartman 1988; Beechie et al. 1994). In western Washington State alone, over 450 lakes and ponds are accessible to anadromous salmon, providing rearing habitat and migration corridors for their journey to the sea (Washington Department of Fish and Wildlife, unpublished data). The vast majority of these lakes and ponds are small and shallow, yet almost no information is available regarding the impacts of introduced fishes on the numerous small salmon runs that use the hundreds of shallow lakes throughout the Pacific Northwest.

The goals of our study were to (1) evaluate the degree to which the most common introduced fishes prey on juvenile salmon in three small, shallow western Washington lakes; (2) evaluate effects by season and predator size-group; (3) calculate the number of juvenile salmon removed by predation in each lake; and (4) compare juvenile salmon growth among lakes and nearby streams to investigate the potential for food competition to limit juvenile salmon growth. We focused our study on coho salmon *O. kisutch* because of their long freshwater residence time as juveniles (usually >1 year) and their propensity to use lakes and other off-channel habitats for rearing.

Methods

Our study was conducted over a 2-year period in three shallow (<8 m deep), lowland (<125 m above mean sea level in elevation) western Washington lakes, all located in different watersheds (Table 1). We used a standard combination of gear types to sample the diets, population sizes, and growth of introduced and native fishes in each of the lakes once or twice per month throughout the year. Each sampling year started on the first of April and continued to the first of April the following year. During April 1998 to April 1999 (first year), we sampled each lake twice per month during the salmon smolt migration period and once per month during the rest of the year. From April 1999 to April 2000 (second year), we sampled each lake once per month throughout the year. Water temperatures were taken on each sampling date by use of a Scout II hydrolab. In both the littoral zone and the deepest portion of the lake, we took temperature readings every 0.5 m from the surface to the bottom. For sampling fish, each lake was divided into eight sections. Half of the sections were randomly chosen and sampled during the day and half were sampled at night to provide diel information on diet. By the end of each sampling trip, the entire lake was sampled. Fish were captured in the littoral zones by use of minnow traps and gill nets set for 2 h to minimize mortality; boat electrofishing was used to sample the entire shoreline of each section. Deeper areas of the lakes were sampled by use of vertical and horizontal gill nets, slat traps, and minnow traps. In deep areas in the summer, when no fish were captured, hydroacoustic surveys were used to confirm the absence of fish. Additionally, we snorkeled portions of Big Beef Creek approximately 1.6 km below and 0.8 km above Lake Symington in midsummer 1999 to identify the distribution of introduced predators in streams adjacent to the lake.

All captured fish were anesthetized, and total length (TL) was measured to the nearest millimeter. To develop relationships between length and weight, weights (g) were measured from the first 100 fish of each species. At the start of the study, all fish were either fin-clipped or tagged for population estimates, but after three sampling periods we tagged only largemouth bass with individually numbered anchor tags. The stomachs of up to 30 individuals of each age-cohort of each species were pumped during both day and night sampling by use of gastric lavage to obtain contents. Minimum size of the fish pumped was 75 mm TL. Contents were then stored in a 10% formalin solution buffered with borax and were transported to the laboratory, where they were separated into the following 11 groups: insects, zooplankton, or other non-crayfish invertebrates; crayfish; salmon fry; salmon smolts; unidentified salmonids; other fish; unidentified fish; amphibians; birds; rodents; and detritus, plants, or other materials. We captured hundreds of juvenile coho salmon in the three lakes. The only other salmon captured were eight juvenile chum salmon from Long Lake. Therefore, we assumed that all salmon in the gut contents were coho salmon. Digested fish material was identified to species based on diagnostic bones (Hansel et al. 1988) when present. Salmon fry and smolts represented two distinct length-groups in each lake. Regressions of cleithrum (shoulder), dentiary (lower jaw), or standard length to TL were used to identify salmon juveniles as either smolts or fry. The sorted stomach contents were blotted on absorbent paper and weighed on an analytical balance to the nearest 0.001 g.

Predation was evaluated with the Wisconsin bioenergetics model (Hanson 1997) to estimate the weight of coho salmon consumed by each predator group over a 1-year period. The Wisconsin bioenergetics model is an energy balance equation that relates consumption rate to growth, metabolism, water temperature, and excretion in an individual fish. Population and survival estimates are used to expand the consumption by an individual fish to the population as a whole. Using this model, we calculated the rate of coho salmon consumption for each introduced species.

Data needed for the model included the thermal experience of predators in each lake; introduced fish diet, growth, survival, gonad growth, population estimates, and energy density; and energy density of the prey. Water temperatures used were those measured at the depth of fish capture. We assumed that species captured by boat electrofishing were feeding at the water temperature measured at a depth of 1.0 m in the littoral zone. For those captured by other techniques, such as nets or traps, we used the temperature at the depth where the device was set. Diet was the proportion of each diet item by weight for each month. If less than 10 fish were caught in a particular month, adjacent months were combined to obtain a sample size that was greater than 10. Growth was estimated by examining the movement of cohorts throughout the year from length-frequency histograms and was confirmed by monitoring the change in length of tagged fish between sampling periods. Because the model calculates growth from changes in fish weight, length data were transformed into weight data based on the weight–length relationships developed for each species at each lake. Predator population and survival estimates were used to expand the rate of consumption of coho salmon by individual predators to the population as a whole. Survival was calculated by use of an age–length key and by regressing numbers of fish against age (Ricker 1975). Energy is expended for gonadal growth in fishes, and consumption is required to supply this energy. Average gonad growth of introduced predators and time of spawning were estimated from field observations and the literature (Timmons et al. 1980).

Population sizes of largemouth bass greater than 150 mm TL were obtained over six sampling events from April 7 to June 18, 1998, by use of a Schnabel mark–recapture estimate (Ricker 1975). Mark–recapture estimates assume that there is no mortality or recruitment during the sampling period. Therefore, we calculated population sizes before most spawning activity, because we did not want recruitment to seriously affect our estimates. Assumptions of the mark–recapture method also include the following: (1) the marked fish become randomly mixed with the unmarked fish, (2) tags are not lost, (3) tags are visible to surveyors, (4) there is no difference in mortality between tagged and untagged fish, and (5) tagged and untagged fish are equally vulnerable to capture. We returned tagged fish to the lake sections where they were captured and allowed at least 1 week before recapture to ensure the random mixing of tagged fish with untagged fish. The floy tags we used were highly visible to the surveyors, and at the beginning of the study we fin-clipped and floy-tagged each largemouth bass and examined each untagged, captured fish for evidence of fin clips and wounds under the dorsal area to ensure that tag loss was minimal. We carefully inserted anchor tags in the dorsal musculature to reduce wounding and associated mortality.

Largemouth bass recruitment is more stable from year to year in small, maritime-influenced, shallow western Washington lakes than in cold, inland reservoirs, where year-class strength can be affected severely by water drawdown, winter mortality of young, and wave action. Therefore, population estimates calculated in 1998 were used to approximate those in 1999.

Consumption rates were calculated by season and then summed to obtain the estimate for the entire year. We subdivided consumption rate by spring–early summer (the period of smolt migration), late summer−early fall, and late fall–early winter because growth rates and available food differed among these three periods. Model default values for predator energy density were used. Energy densities of prey species or closely related surrogate species were reported in the literature and provided by the model. We used the following prey energy densities, expressed as joules per gram of prey body mass: 3,000 J/g for invertebrates; 4,186 J/g for other fish; 4,000 J/g for amphibians; 5,765 J/g for coho salmon fry; 3,000 J/g for crayfish; 5,774 J/g for coho salmon smolts; 4,000 J/g for birds; and 4,000 J/g for rodents.

Consumption rates were calculated as the mass of coho salmon fry or smolts in grams per day per individual predator of each cohort. We separated fry and smolts in the diet by using a cutoff of 100 mm TL, which was determined through examination of length frequencies. The number of smolts consumed was calculated by dividing total weight of smolts eaten by the average smolt weight determined from a length–weight regression equation. To calculate the number of fry eaten, we first calculated the TL of fry on that particular sampling date. We then converted TL to weight by use of length–weight regressions and divided total grams of fry consumed by the weight of an individual fry on that date. We transformed the number of fry consumed into smolt equivalents by multiplying the fry number by 0.12, a survival rate from fry to smolt estimated for the Big Beef Creek watershed (D. Seiler, Washington Department of Fish and Wildlife, unpublished data.). Smolt equivalents (Rand et al. 1993; Ford et al. 2001; Bartron and Scribner 2004) are a common method of expressing fry number in a form that can be compared to smolt number. Adding the number of smolts consumed to the number of smolt equivalents consumed provided an estimate of the number of smolts eaten over 1 year.

We calculated three estimates (low, nominal, high) of the number of coho salmon eaten by each predator species for each lake during each year. The low and nominal estimates included only fish that could be positively identified as coho salmon in the diet and were based on the lower 95% confidence limit (CL) and the nominal estimate of the largemouth bass population estimate, respectively. The high estimate was based on the upper 95% CL of the largemouth bass population estimate and included both fishes that could positively be identified as coho salmon and unidentified salmonid fishes in the diet.

Comparison of the number of juvenile coho salmon eaten by largemouth bass with a measure of juvenile coho salmon abundance gave an approximation of the impact to the run. We obtained estimates of the juvenile coho salmon smolt outmigration in the Lake Symington (Big Beef Creek) and Wildcat Lake (Wildcat Creek) watersheds from traps managed by the Washington Department of Fish and Wildlife (unpublished data). Lake Symington was located midway between the headwaters of Big Beef Creek and its outlet to Puget Sound, and the trap was located near the outlet to Puget Sound, so only a portion of the entire run would have been exposed to largemouth bass predation in the lake. The trap measuring the number of coho salmon smolts produced above Wildcat Lake was in place on Wildcat Creek, immediately at the outlet of Wildcat Lake. Trapping data from the Salmonberry Creek watershed, which contained Long Lake, were unavailable. Habitat–smolt production relationships produced for Washington streams (Zillges 1977; Baranski 1989) were used to calculate potential smolt production in Salmonberry and Curley creeks, which entered and exited Long Lake, respectively. Available habitat was calculated from a combination of air photos and ground surveys based on standard methods (Zillges 1977; Baranski 1989) for estimating low-flow wetted perimeter. All smolts produced in

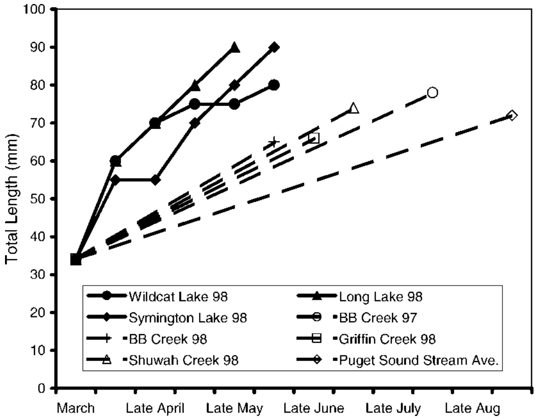

FIGURE 1.—Growth of coho salmon juveniles in Wildcat Lake, Lake Symington, and Long Lake, Washington, and in three Puget Sound streams (Big Beef [BB], Shuwah, and Griffin creeks). Coho salmon emerge from the gravel in nearby creeks in March at an average size of approximately 34 mm TL (Sandercock 1991).

Salmonberry Creek were exposed to competition or predation from introduced fishes; some smolts from Curley Creek may have been exposed to such competition or predation as well. Estimates of smolt production potential do not actually measure the number of juvenile salmon exiting a watershed but rather the potential of a watershed to produce salmon smolts, and thus they are prone to more error than trap counts are.

Results

Juvenile coho salmon rearing in all three lakes grew much faster than those in nearby streams draining into Puget Sound (Figure 1), suggesting that coho salmon populations were not food limited in the lakes. However, growth was recorded only in the spring because few juvenile coho salmon were found in the lakes during late summer.

Fish predation was a significant source of mortality for coho salmon juveniles. Over the 2-year study, 30,622 fish were sampled and the contents of 10,262 stomachs were pumped and analyzed. The percentage of coho salmon in the diet was highest for largemouth bass (Table 2). Other species primarily targeted insects and zooplankton. Some coho salmon were found in the diets of black crappies, brown bullheads, cutthroat trout, prickly sculpin, and yellow perch. Although in three instances salmon constituted 5–10% of the total stomach content weight for these fishes, this usually represented one coho salmon in the diet during the entire year for the species. We found no evidence that rainbow trout, bluegills, or pumpkinseeds fed on coho salmon.

Although some coho salmon were eaten by other species, the vast majority of total salmon were eaten by largemouth bass in all three lakes. Percentages of the total catch consisting of largemouth bass in each lake for each year were as follows: 81% in Wildcat Lake during 1998–1999; 88% in Wildcat Lake during 1999–2000; 35% in Lake Symington during 1998–1999; 42% in Lake Symington during 1999–2000; 27% in Long Lake during 1998–1999; and 35% in Long Lake during 1999–2000. Therefore, largemouth bass averaged 51% of the total numeric catch of fishes over all three lakes during both years. Among the three lakes, an average of 94% of the coho salmon found in diets each year were found in largemouth bass stomachs (Figure 2). When diet was standardized by catch (mean weight of salmon per individual fish of a given species × number of fish of that species in total catch), an average of 98% of the coho salmon prey from each lake were found in largemouth bass stomachs (Figure 2).

Our bioenergetics analyses concentrated on largemouth bass predation because the amount of coho salmon eaten by all other species was minimal. Lake Symington contained the smallest largemouth bass population, and Long Lake contained the largest population (Table 1). Density of largemouth bass was highest in Lake Symington but lowest in Long Lake. Most largemouth bass were captured in shallow areas of the littoral zones at average depths of approximately 1 m, and therefore experienced the thermal regime of this region (Figure 3). Annual survival of largemouth bass did not vary substantially between years in Long Lake or Lake Symington (Table 3). In Wildcat Lake, survival declined by about 26% between years. Examination of changes in modal size of largemouth bass cohorts and corroboration of size changes with data from tagged fish provided estimates of largemouth bass growth for the model (Figure 4). Largemouth bass growth was rapid compared to previously reported Washington State averages (Wydoski and Whitney 1979).

The bioenergetics analysis revealed that the largemouth bass populations in Lake Symington and Long Lake ate the most coho salmon smolt equivalents. The largemouth bass population in Wildcat Lake ate the fewest (Table 4). Largemouth bass predation varied by season ($F = 9.216$; $P < 0.025$; Table 5). Most predation occurred in spring, when coho salmon smolts were migrating through lakes to the sea or when coho salmon fry were

TABLE 2.—Percentage composition (by weight) of stomach contents in fishes captured from three western Washington lakes. Data were separated into two 1 year periods; April 1998–March 1999 and April 1999–March 2000.

Predator		Prey item									
Species	*N*	Inverte-brates (excluding crayfish)	Non-salmonid fish	Amphib-ians	Coho salmon	Crayfish	Uniden-tified fish	Uniden-tified salmonids	Birds	Rodents	Aquatic plants, detritus, and other
Wildcat Lake 1998–1999											
Coho salmon	15	99.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Prickly sculpin	162	89.62	2.72	0.00	4.64	0.00	0.19	0.00	0.00	0.00	2.84
Cutthroat trout	102	99.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.54
Largemouth bass	1,240	16.58	67.27	2.27	1.57	4.09	1.02	4.91	0.00	0.00	2.29
Rainbow trout[a]	121	86.77	5.79	0.00	0.00	0.00	1.82	3.36	0.00	0.00	2.27
Wildcat Lake 1999–2000											
Coho salmon	32	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prickly sculpin	82	99.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.44
Cutthroat trout	58	99.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52
Largemouth bass	971	25.29	57.77	8.76	5.96	1.01	0.97	0.01	0.00	0.01	0.24
Rainbow trout[a]	66	99.02	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.93
Long Lake 1998–1999											
Brown bullhead	227	95.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.09
Black crappie	210	88.61	5.29	0.00	2.31	0.00	0.45	0.03	0.00	0.00	3.31
Bluegill	329	97.53	0.26	0.00	0.00	0.00	0.03	0.00	0.00	0.00	2.18
Coho salmon	70	98.87	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Prickly sculpin	96	83.12	3.91	0.00	0.00	11.62	0.77	0.00	0.00	0.00	0.57
Cutthroat trout	332	96.58	3.14	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.24
Golden shiner	1	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Largemouth bass	1,008	6.34	74.62	2.75	3.09	6.67	1.43	1.42	1.23	0.26	2.18
Pumpkinseed	162	99.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.51
Rainbow trout[a]	12	89.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.22
Yellow perch	108	91.59	6.90	0.00	0.00	0.00	1.49	0.02	0.00	0.00	0.00
Long Lake 1999–2000											
Brown bullhead	115	79.38	2.32	0.00	9.34	0.00	0.00	0.00	0.00	0.00	8.95
Black crappie	136	69.90	27.49	0.00	0.00	0.00	2.05	0.00	0.00	0.00	0.56
Bluegill	372	95.68	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	4.24
Coho salmon	149	99.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23
Prickly sculpin	159	73.44	22.07	0.00	0.00	0.00	0.12	3.63	0.00	0.00	0.74
Cutthroat trout	333	86.63	12.38	0.29	0.00	0.00	0.07	0.00	0.00	0.00	0.64
Golden shiner	7	40.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	60.00
Largemouth bass	518	17.93	52.95	11.35	4.87	5.33	1.27	3.45	0.00	0.00	2.86
Pumpkinseed	130	98.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.05
Rainbow trout[a]	15	88.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.23
Yellow perch	447	89.39	6.39	0.15	0.00	0.00	0.04	0.00	0.00	0.00	4.03
Lake Symington 1998–1999											
Brown bullhead	186	90.01	2.22	0.00	0.00	0.00	0.26	0.00	0.00	0.00	7.51
Bluegill	48	99.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82
Coho salmon	55	99.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Cutthroat trout	136	95.38	2.07	0.00	0.11	0.00	0.35	0.00	0.00	0.00	2.09
Green sunfish	54	81.74	0.00	17.40	0.00	0.00	0.00	0.00	0.00	0.00	0.85
Largemouth bass	432	8.28	27.00	24.37	19.82	11.80	2.56	3.80	0.00	0.00	2.38
Pumpkinseed	212	93.46	0.28	0.41	0.00	0.00	0.05	0.00	0.00	0.00	5.79
Rainbow trout	12	99.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Yellow perch	165	92.29	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	7.07
Lake Symington 1999–2000											
Brown bullhead	191	96.41	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.18
Bluegill	26	77.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.12
Coho salmon	233	98.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.06
Cutthroat trout	58	88.30	4.94	0.00	6.31	0.00	0.00	0.00	0.00	0.00	0.45
Green sunfish	93	99.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66
Largemouth bass	281	18.39	25.01	19.72	12.59	9.12	0.42	6.93	0.00	0.00	7.82
Pumpkinseed	187	98.76	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	1.23
Rainbow trout	4	99.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66
Yellow perch	103	94.15	0.28	0.00	1.28	0.00	0.00	0.46	0.00	0.00	3.84

[a] Includes steelhead.

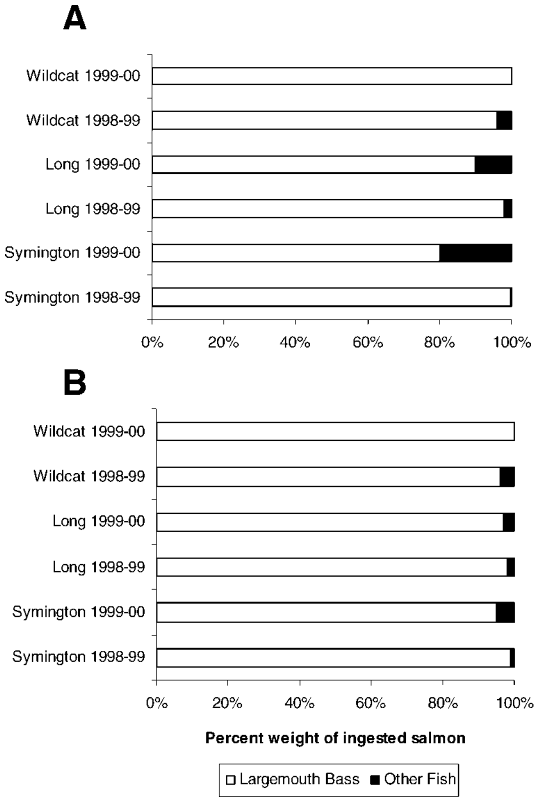

FIGURE 2.—Percent distribution of (A) the total weight of coho salmon in the diets of various predators and (B) the total weight of coho salmon in the diet, standardized by predator occurrence in the catch (mean number of coho salmon per individual of a given species × number of fish of that species in the total catch). Wildcat Lake 1999–2000 data were based on prey identified only as salmonids.

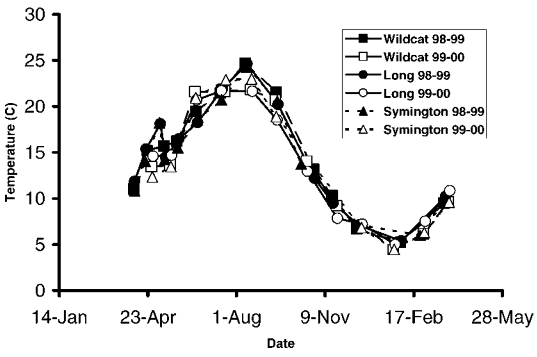

FIGURE 3.—Thermal regime experienced by largemouth bass in three western Washington lakes during April 1998–April 2000.

TABLE 3.—Survival of largemouth bass in three western Washington lakes. Numbers under the age columns are the numbers of captured fish from each age-group.

Lake	Year	Age 1	Age 2	Age 3	Annual survival rate (*S*)
Wildcat	1998–1999	802	233	213	0.52
	1999–2000	1,061	114	71	0.26
Long	1998–1999	894	147	312	0.59
	1999–2000	266	116	79	0.54
Symington	1998–1999	188	129	31	0.41
	1999–2000	235	12	25	0.33

moving from creeks into lakes. We captured few coho salmon in any of the lakes in summer or early fall (Figure 5). Consequently, predation was usually low at those times.

No coho salmon were found in the diets of age-0 largemouth bass. For age-1 and older largemouth

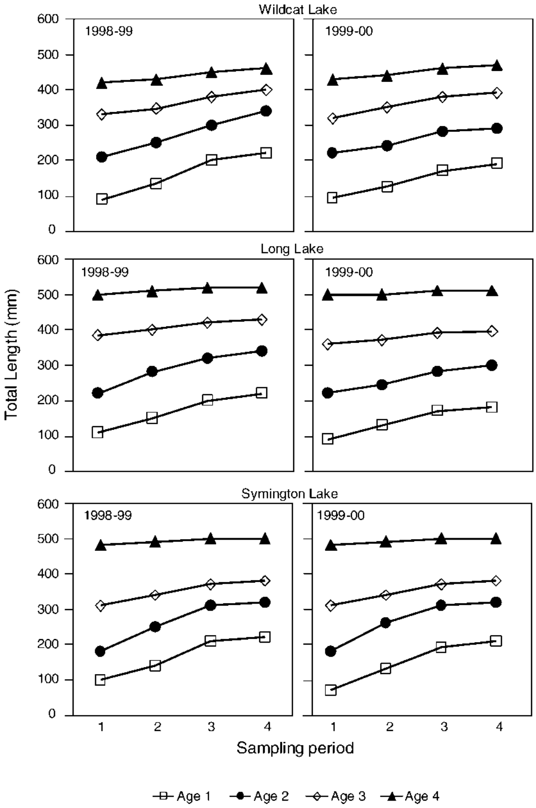

FIGURE 4.—Modal total length of largemouth bass age-classes at sampling periods 1 (April 7–9, 1998; April 27–29, 1999), 2 (July 14–17, 1998; July 15–20, 1999), 3 (October 13–28, 1998; Lake Symington: September 15, 1999; Wildcat and Long lakes: October 19–20, 1999), and 4 (March 23–25, 1998; March 28–30, 1999). Age-4 largemouth bass include age-4 and older fish.

TABLE 4.—Number of coho salmon smolt equivalents eaten by largemouth bass in three western Washington study lakes. The low and nominal estimates included only fish that could be positively identified as coho salmon in the diet and were based on the lower 95% confidence limit (CL) and the nominal estimate of the largemouth bass population estimate, respectively. The high estimate was based on the upper 95% CL of the largemouth bass population estimate and included prey that could be positively identified as coho salmon as well as unidentified salmonid fishes. Smolt abundance for Lake Symington was the number of coho salmon smolts that passed through the Big Beef Creek trap in 1998 and 1999, respectively. Smolt abundance for Wildcat Lake was measured by a trap at the lake outlet in 1998 and 1999, respectively. Smolt abundance for Long Lake was the range of smolt production potential for Salmonberry Creek only (low number) and for Salmonberry and Curley creeks combined (high number).

Lake	Year	Number of smolt equivalents consumed			Smolt abundance
		Low	Nominal	High	
Symington	1998–1999	1,131	1,754	3,311	22,222–20,967
Symington	1999–2000	603	908	2,356	
Long	1998–1999	1,082	1,414	2,108	3,478–8,404
Long	1999–2000	2,090	2,728	4,632	
Wildcat	1998–1999	73	88	461	30–55
Wildcat	1999–2000	0	0	109	

bass, we found no evidence that a particular size-group or age-class was responsible for more predation on coho salmon than the others. The total number of smolt equivalents eaten did not differ by largemouth bass age-class ($F = 0.747$; $P > 0.25$); grams of smolt equivalents eaten per gram of largemouth bass also did not differ among various age-classes ($F = 0.660$; $P > 0.25$).

Almost all of the predation by largemouth bass on coho salmon was likely confined to the lakes. During the midsummer-1999 snorkel surveys of Big Beef Creek (adjacent to the Lake Symington), we saw only a few age-0 largemouth bass, part of the cohort that did not eat any coho salmon. Additionally, even though it was mid-July, the water temperature in Big Beef Creek was considerably lower than that of the lake and was well below the optimal feeding temperature of largemouth bass.

TABLE 5.—Daily coho salmon consumption (number of fish) for three largemouth bass populations during three seasons as estimated by the Wisconsin bioenergetics model. Spring–early summer was defined as April 1–mid-July (14–20 July depending on lake and year). Late summer–early fall was defined as mid-July–late October (13–28 October). Late fall–winter was defined as late October–March 31. In Lake Symington during 1999, the late fall–winter season began on September 15.

Lake	Year	Spring–early summer	Late summer–early fall	Late fall–winter
Symington	1998–1999	16.047	0.522	0.036
Symington	1999–2000	7.505	0.000	0.773
Long	1998–1999	11.252	0.913	0.747
Long	1999–2000	7.217	5.443	8.858
Wildcat	1998–1999	0.838	0.000	0.000
Wildcat	1999–2000	0.000	0.000	0.000

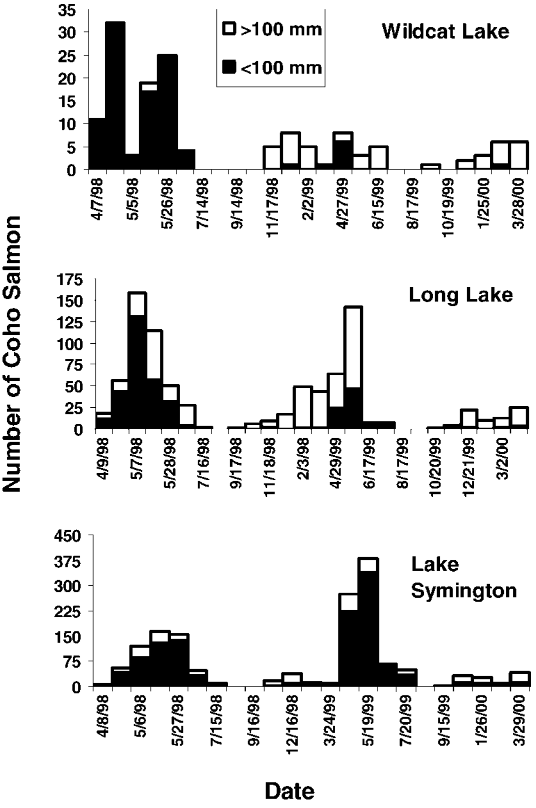

FIGURE 5.—Number of coho salmon captured three western Washington lakes from April 1998 to March 2000. Effort was similar for all surveys. Coho salmon catch per unit effort was underestimated for the spring of 1998 in Lake Symington. Not all electrofished coho salmon were brought onto the boat for counting and weighing.

Juvenile coho salmon out-migrations were largest in the Big Beef Creek watershed and lowest at the outlet of Wildcat Lake (Table 4). The amount of coho salmon smolt production eaten by largemouth bass also varied considerably among watersheds, from about 5% to over twice the number exiting the system. Lake Symington contained the smallest largemouth bass population (Table 1) and was located in the watershed that produced the largest number of coho salmon smolts of the three systems studied. Furthermore, Lake Symington was located midway in the Big Beef Creek watershed, and a substantial proportion of the smolts passing through the Big Beef Creek trap were produced below the lake and were never exposed to the largemouth bass predation in Lake Symington. Not surprisingly, the amount of smolt equivalents eaten by largemouth bass in Lake Symington expressed as a percentage of the number exiting the Big Beef Creek trap was lowest in this system.

Long Lake contained the largest population of largemouth bass and was fed by Salmonberry Creek and drained by Curley Creek. The number of consumed smolt equivalents expressed as a percentage of the juvenile coho salmon production potential in the watershed was much greater in Long Lake than in Lake Symington (Table 4). Wildcat Lake supported the smallest run of smolts because a screen was present at the outlet of the lake to prevent stocked trout from leaving the system. Even though the screen was in place, a few coho salmon were able to pass around the screen, and both fry and smolts were found above the barrier. The small smolt run exiting the lake was severely impacted by largemouth bass predation (Table 4). For example, in 1998–1999 the number of juvenile coho salmon smolts passing over the trap at the lake outlet was only half the number of smolt equivalents eaten by largemouth bass. Because the screen partially blocked salmon migration into and upstream of the lake, it was removed in 1999.

Discussion

Juvenile coho salmon growth was higher in the lakes than in several nearby streams and was higher than an average for south Puget Sound streams (Rounsefell and Kelez 1938; Kahler et al. 2001; Figure 1). This suggests that juvenile coho salmon were not growth limited in the lakes we studied and that food competition with introduced fishes, although possible, was probably unimportant in contributing to mortality of juvenile coho salmon. This is consistent with data from other authors (Swales and Levings 1989; Irvine and Johnston 1992; Bryant et al. 1996; Quinn and Peterson 1996), who found that coho salmon rearing in lakes grew faster than those in nearby streams.

We studied the effects of the most widely distributed introduced fishes in Washington's shallow lakes (Zook 1978; Fletcher 1982, 1983; Washington Department of Fish and Wildlife 2003). Of these fishes, largemouth bass were the most important predators of coho salmon. Predation on coho salmon was important in all systems studied. The percentage impact to the run was smallest in Lake Symington; however, only a portion of the run that encountered the Big Beef Creek trap also passed through the lake. Lake Symington was located midway in the watershed; therefore, if we assume that only half the coho salmon production occurred upstream of the lake, then 10–20% (rather than 5–10%) of the coho salmon exposed to predation would have been removed by largemouth bass.

Future research to prioritize where largemouth bass predation is most severe would allow for the maintenance of valuable, non-threatening largemouth bass populations for anglers while identifying those populations whose control would have a substantial beneficial effect on coho salmon runs. Predation impacts to coho salmon in our three lakes seemed greater when a small run passed through a lake with a large littoral zone supporting many largemouth bass than when a large run passed through a small lake.

No specific largemouth bass size-group (age 1 and older) was responsible for more coho salmon predation than other size-groups. Although rapidly growing largemouth bass juveniles typically require higher food rations, coho salmon were a small component of their diet. Because consumption of coho salmon was sporadic, there were no discernable differences in coho salmon predation among largemouth bass size-classes, even though smaller individuals may have eaten more food per gram of body weight overall.

The results of our study of three shallow lakes were different from the results of studies of some large Pacific Northwest rivers and deep lakes, where largemouth bass and smallmouth bass *M. dolomieu* were less important predators of juvenile salmon. Northern pikeminnow *Ptychocheilus oregonensis*, a native species, were the most important predators in John Day Reservoir on the Columbia River and were responsible for 78% of the total loss of juvenile salmonids (Poe et al. 1991). In large (8,966 ha), deep (85 m) Lake Washington,

Washington, smallmouth bass did not have a large impact on populations of sockeye salmon *O. nerka* (Fayram and Sibley 2000), in contrast to the significant effects of native cutthroat trout (Nowak et al. 2004). However, our results agree with those of others who have studied the impacts of black basses in shallow systems. Impacts of smallmouth bass in the Hanford Reach of the Columbia River were greater, presumably because of greater habitat overlap among juvenile salmonids and smallmouth bass (Tabor et al. 1993). In the shallow Tenmile Lake system of Oregon, Reimers (1989) found a dramatic time association between the introduction of largemouth bass (1971) and reduced levels of coho salmon for the next 15 years. He further stated that natural production of wild coho salmon smolts was limited to the tributary streams because of high levels of predation in the lakes. Smallmouth bass introductions have been shown to drastically alter littoral zone native fish communities in central Ontario (Vander Zanden et al. 1999; MacRae and Jackson 2001), and removal of smallmouth bass from a New York lake resulted in a significant increase in the abundance of five species of native fishes (B. C. Weidel, Cornell University, unpublished). In years past, piscicide application was regularly used to clear small- and medium-sized western Washington lakes of introduced warmwater predators and competitors so that stocked trout fry, many of similar size to coho salmon juveniles, could survive. Decreased piscicide use in Pacific Northwest lakes, especially in western Washington, has made it difficult to clear the lakes of introduced fishes, and survival of trout fry stocked into these systems is usually too low to support a viable fishery (Bradbury 1986). Currently, most trout fisheries in western Washington are maintained by stocking large, catchable trout (>150 mm) because mortality of smaller fry is too high to allow cost-effective stocking. In deeper systems, such as Columbia River reservoirs or Lake Washington, spatial separation of largemouth bass and salmon may be greater than in shallow lakes, allowing the salmon to avoid largemouth bass predation. In addition, the small amount of littoral zone available for establishment of largemouth bass in deep lakes or riverine systems may limit their populations.

Largemouth bass are widespread; the species is present in 85% of the lowland warmwater public-access lakes in Washington ($n = 421$), 84% of similar lakes in Oregon ($n = 179$), and 74% of such lakes in the eight northwesternmost counties in California ($n = 19$) (Washington Department of Fish and Wildlife 2003; Oregon Department of Fish and Wildlife 2003; California Department of Fish and Game 2003). Because hundreds of these lakes are accessible to anadromous salmonids and are often used as rearing areas and migration corridors, future examination of the effects of largemouth bass predation on juvenile salmon at a landscape scale could help identify the overall impacts of this introduced species.

Whether a decrease in predation on coho salmon juveniles in lakes would translate into larger adult populations is unclear at this time. Kareiva et al. (2000) estimated that modest reductions in first-year or estuarine mortality would reduce population declines in Chinook salmon *O. tshawytscha*. In addition, coho salmon smolt size is positively correlated with subsequent survival (Mathews and Ishida 1989; Holtby et al. 1990; Irvine and Johnston 1992), and coho salmon rearing in lakes are consistently larger than those in nearby streams. However, other important mortality factors, such as climate conditions affecting ocean survival, and the availability of summer low-flow habitat may dampen the benefits of attempting to improve lake survival by removing largemouth bass. Nevertheless, attempts to increase largemouth bass numbers in important coho salmon rearing sites or to transplant largemouth bass into vital coho salmon lakes would be counterproductive to coho salmon enhancement efforts.

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